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Complete Cross-Frequency Transfer of Tone Frequency Learning After Double Training

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A person's ability to discriminate fine differences in tone frequency is vital for everyday hearing such as listening to speech and music. This ability can be improved through training (i.e., tone frequency learning). Depending on stimulus configurations and training procedures, tone frequency learning can either transfer to new frequencies, which would suggest learning of a general task structure, or show significant frequency specificity, which would suggest either changes in neural representations of trained frequencies, or reweighting of frequency-specific neural responses. Here we tested the hypothesis that frequency specificity in tone frequency learning can be abolished with a double-training procedure. Specifically, participants practiced tone frequency discrimination at 1 or 6 kHz, presumably encoded by different temporal or place coding mechanisms, respectively. The stimuli were brief tone pips known to produce significant specificity. Tone frequency learning was indeed initially highly frequency specific (Experiment 1). However, with additional exposure to the other untrained frequency via an irrelevant temporal interval discrimination task, or even background play during a visual task, learning transferred completely (1-to-6 kHz or 6-to-1 kHz; Experiments 2–4). These results support general task structure learning, or concept learning in our term, in tone frequency learning despite initial frequency specificity. They also suggest strategies to design efficient auditory training in practical settings.

Keywords: perceptual learning, tone frequency discrimination, specificity, transfer, double training

Humans can learn to better discern fine differences of sensory stimuli through practice, a process called perceptual learning. Like other forms of learning, perceptual learning would be most useful if it transfers from the trained condition to untrained new conditions. However, perceptual learning is frequently observed to be specific, which would limit its practical usefulness. Indeed, one major goal of perceptual learning research is to find efficient training strategies to reduce specificity and promote learning transfer. On the other hand, the specificity or transfer of perceptual learning has been a fascinating topic in sensory research because it may inform how different brain mechanisms are involved in learning and brain plasticity. Various theories have been proposed in the past decades to explain the mechanisms underlying perceptual learning, and these theories are to a large degree either motivated, or constrained, by the observed specificity and transfer.

Take perceptual learning of tone frequency discrimination, the topic of the current study, as an example. Tone frequency discrimination plays a critical role in everyday hearing tasks such as listening to speech or music. Training can improve a person's ability to tell the fine differences in tone frequencies, even producing "perfect pitch" as often seen in musicians. Results vary regarding whether tone frequency learning is specific to the trained frequency or not (e.g., Delhommeau, Micheyl, & Jouvent, 2005; Demany & Semal, 2002; Irvine, Martin, Klimkeit, & Smith, 2000; Wright & Fitzgerald, 2005), which appears to depend on the stimulus configurations and training protocols. For example, frequency discrimination learning with longer continuous tones tends to transfer to a new frequency, while learning with brief tone pips requires multiple sessions of training and tends to show more specificity (Wright & Zhang, 2009).

Different results of frequency specificity have led to different understandings of tone frequency learning mechanisms. For example, Delhommeau, Micheyl, and Jouvent (2005) reported that learning is mostly transferrable to new frequencies, so they concluded that a general task structure of tone frequency discrimina-

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tion is being learned. In contrast, Wright and Fitzgerald (2005) used pairs of brief tone pips as stimuli in multiple sessions of tone frequency training and found significant specificity of learning to the trained frequency. The frequency specificity may occur because training induces plasticity in early, "low-level" stages of cortical processing that are specific to the trained frequency. This possibility receives support from single-unit recordings in monkeys, in that learning of tone frequency discrimination is accompanied by enlarged representations of trained frequencies in the primary auditory cortex (Recanzone, Schreiner, & Merzenich, 1993). Alternatively, the frequency specificity may result from response reweighting by a central learning unit, so that frequency responses from most relevant neurons could be attended or readout (Irvine et al., 2000; Jones, Moore, Amitay, & Shub, 2013), an idea first proposed by Mollon and Danilova (1996) and formalized by Dosher and Lu (1998) on visual perceptual learning. An unified view is that multiple high- and low-level mechanisms are involved in tone frequency learning, which together determine the degree of specificity and transfer (Wright & Zhang, 2009).

We suggest that when tone frequency learning shows specificity, it does not necessarily mean that learning is not transferable to untrained frequencies. In other words, learning could be frequency unspecific, but the transfer is hindered by some nonlearning factors such as attention allocation (Irvine et al., 2000) or other unknown processes. As a result, high-level learning may not be able to fully functionally connect to neurons representing the untrained frequency to enable complete learning transfer. This possibility has been demonstrated in visual perceptual learning, in that initially specific learning often becomes completely transferrable to an untrained retinal location or orientation when the latter is activated via an irrelevant task in a double-training protocol (Xiao et al., 2008; Xiong, Zhang, & Yu, 2016; Zhang, Zhang et al., 2010), as well as in visuomotor learning (Yin, Bi, Yu, & Wei, 2016).

We thus hypothesize that the frequency specific component of tone frequency learning can also be rendered transferrable with a variation of the double-training protocol (Xiao et al., 2008; Xiong et al., 2016; Zhang, Zhang et al., 2010). As its name indicates, double training consists of two training tasks. The primary training task here is tone frequency discrimination. The secondary training task is an irrelevant one, which is either temporal interval discrimination at the untrained frequency, or even the presentation of the untrained frequency as a background sound during a visual task. The word "irrelevant" means that the secondary training alone would have no significant impact on the primary training task. Rather the purpose of the second training task is to activate sensory neurons responding to the untrained frequency, so that high-level frequency-unspecific tone frequency learning from the primary training task can now functionally connect to neural inputs representing the new frequency to enable complete learning transfer.

Experiment 1

In Experiment 1 we set out to replicate the frequency specificity in tone frequency discrimination learning reported by Wright and Fitzgerald (2005), using a very similar task to theirs, to establish baselines for double training effects presented in Experiments 2–4. The training and transfer effects were tested between tone frequencies of 1 kHz and 6 kHz. These frequencies are encoded by different temporal or place coding mechanisms in the peripheral auditory system, respectively, and are also represented independently in the auditory primary cortex (Aitkin, Merzenich, Irvine, Clarey, & Nelson, 1986; Imig, Ruggero, Kitzes, Javel, & Brugge, 1977; Johnson, 1980; Siebert, 1970). Therefore, if learning reflects permanent neuronal plasticity in these lower-level mechanisms, double training would not be expected to induce complete learning transfer between two frequencies.

Method

Participants. Thirty healthy college students (11 males and 19 females; mean age = 21.2 years, *SD* = 2.2 years) with normal hearing (pure-tone thresholds ≤20 dB HL across 0.5–6 kHz) participated in this experiment. These participants, as well as those in later experiments, had no previous experience with psychoacoustic experiments and no knowledge of the purpose of the study. The study was approved by the Peking University Institutional Review Board. Informed consent was obtained from each participant prior to data collection in this and later experiments.

Sample size. The sample size was decided on the basis of a previous frequency discrimination learning study that used similar stimuli (the All-Freq [900 trials] condition in Figure 2B of Wright, Sabin, Zhang, Marrone, & Fitzgerald, 2010). To achieve 80% power at $p = .05$, for an effect size of Cohen's $d = 1.22$ when comparing pre- and posttraining test thresholds, a sample size of eight would be required. In our study, learning and transfer involved similar pre- to posttest comparisons in all experiments. Hence, we used a sample size of 10 for each experiment, with potential dropout of participants considered.

Apparatus. Auditory stimuli were generated with Psychtoolbox 3.0 software (Pelli, 1997) installed on a 15-in. MacBook Pro Retina laptop computer. The stimuli were presented binaurally using Sennheiser HD-499 headphones (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany). The experiments were conducted in a sound-attenuating booth.

Stimuli and procedure. The stimuli consisted of two 15-ms tone pips separated by 100 ms. The tone frequency was either 1 or 6 kHz. Each tone was 86 dB SPL loud and contained a 5-ms raised cosine ramp at each end. In each trial (Figure 1a), a black dot was first presented on the center of the computer screen for 300 ms to indicate the beginning of the trial. Then a base interval, which contained two tone pips at a fixed base frequency, and a target interval, which contained the same tone pips at a higher target frequency, were presented subsequently in a random order. The two stimulus intervals were separated by 785 ms as in Wright, Sabin, Zhang, Marrone, and Fitzgerald (2010). Participants were required to press a left- or right-arrow key on the keyboard to indicate whether a higher frequency was perceived in the first or the second stimulus interval (two-interval forced-choice trials). A happy or sad cartoon face was shown at the end of the trial to indicate whether the response was correct or not.

The tone frequency discrimination thresholds were measured with a staircase procedure. In each staircase, the starting difference between the base and the target frequency (Δf, in percentage of the base frequency) was 50%, which decreased by a factor of two after every correct response until the first incorrect response. After that the Δf was varied by a factor of 1.414 following a three-down-one-up rule for a 79% correct rate. Each staircase ended after 60 trials. The threshold was calculated as the geometric mean of the

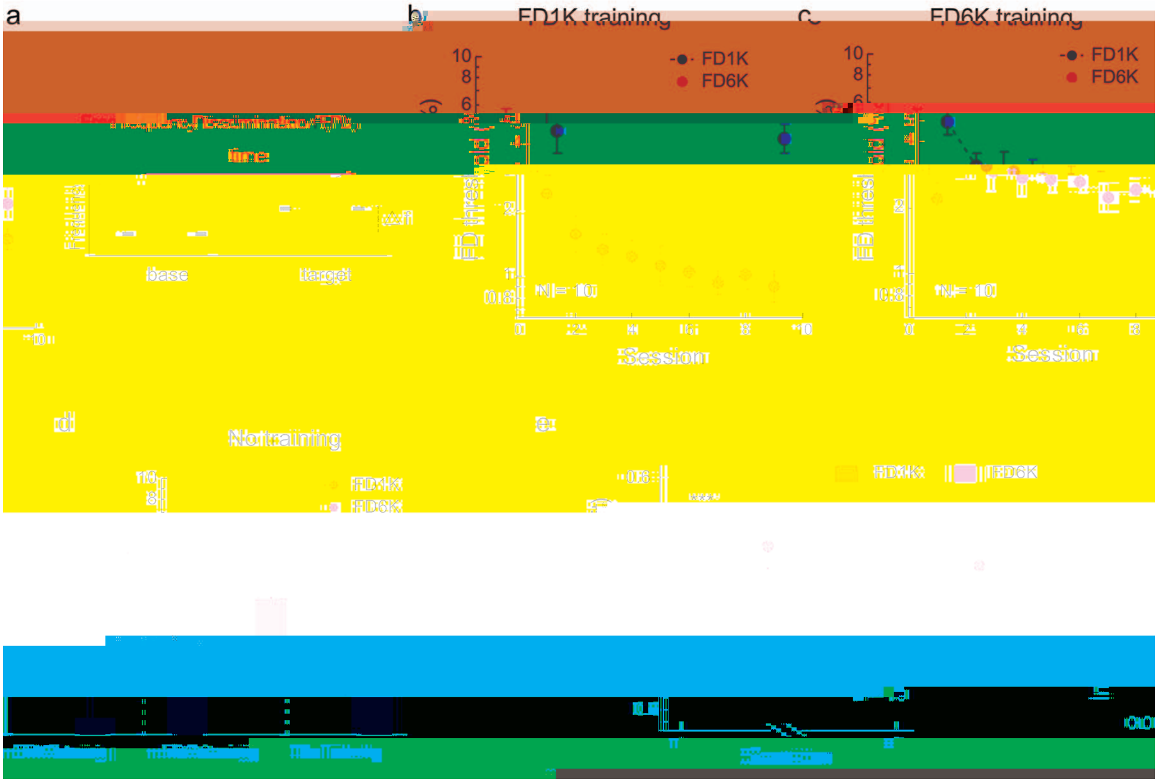

Figure 1. Frequency specificity in tone frequency discrimination learning. (a) An illustration of a frequency discrimination trial. Participants were required to report which interval contained the higher-frequency tone pips. (b) The mean frequency learning curve at 1 kHz and the pre- and posttest frequency thresholds at 6 kHz. (c) The mean frequency learning curve at 6 kHz and the pre- and posttest frequency thresholds at 1 kHz. (d) The pretest effects on frequency discrimination thresholds at 1 kHz and 6 kHz without training. (e) The improvements in frequency discrimination thresholds in log units at 1 and 6 kHz in FD1k, FD6k, and no-training groups. Error bars indicate ± 1 *SE*. FD: frequency discrimination. *** $p < .001$. See the online article for the color version of this figure.

last four reversals in a staircase run. The participants practiced 10 trials before starting the task.

Experimental design. Two groups of participants practiced frequency discrimination at 1 and 6 kHz, respectively. For these FD1k and FD6k training groups, each training experiment consisted of nine sessions, including a pretest session, seven training sessions, and a posttest session on separate days. The intersession gaps were no more than 2 days, and the experiments were completed within 9–14 days. Each pre- or posttest session consisted of 12 blocks of frequency discrimination trials, six for each base frequency (1 and 6 kHz). Each training session consisted of 12 blocks of trials on frequency discrimination at 1 kHz for the FD1k group or 6 kHz for the FD6k group, and lasted approximately 1 hr. As a control for the pretest effects, a third group only completed the pre- and posttests with no training. The gaps between the pretest and posttest sessions were 7–12 days, so that the length of the experiment was similar to those of the training groups.

Data processing and statistical analysis. Data were analyzed using the R software (R Core Team, 2015). In all experiments, the frequency discrimination thresholds were log-transformed to achieve normal distributions before statistical analysis (Shapiro-Wilk test: $p < .001$ at 1 kHz and $p < .001$at 6 kHz before log-transformation; $p = .67$ at 1 kHz and $p = .10$ at 6 kHz after log-transformation).

A linear mixed effects (LME) analysis was performed on data from Experiments 1–3 together to reduce Type-I errors. The analysis was performed using the lme function from the "nlme" package (Pinheiro & Bates, 2000). The model treated threshold as dependent variable, frequency (1 and 6 kHz), test (pre- and posttests), and group (no-training, FD1k, FD6k groups from Experiment 1; FD6k_TID1k, TID1k groups from Experiment 2, and FD1k_VR6k, VR6k groups from Experiments 3) as fixed effects. For each participant, we included random slopes for test and frequency and conducted model selection based on their significance. The significance of the random-effect components was evaluated by the likelihood ratio test, using the ANOVA program in the "nlme" package. The likelihood ratio test showed that the best fitting model had a random-effect structure that included random slopes of frequency. Post hoc analyses were then conducted on the best fitting model to test the learning and transfer effects under various frequency and group conditions. The post hoc analysis was conducted by the "emmeans" package (Piepho, 2004).

Results

Training at 1 kHz improved frequency discrimination thresholds in the FD1k training group by 0.42 ± 0.05 (mean ± 1 se) log units at 1 kHz and 0.04 ± 0.06 log units at 6 kHz (Figure 1b and 1e). Training at 6 kHz improved frequency discrimination thresholds in the FD6k training group by 0.32 ± 0.06 log units at 6 kHz and 0.14 ± 0.08 log units at 1 kHz (Figure 1c and 1e). The no-training group had their frequency discrimination thresholds improved by 0.11 ± 0.02 log units at 1 kHz and 0.09 ± 0.05 at 6 kHz (Figure 1d and 1e).

The LME analysis over Experiments 1–3 revealed significant main effects of test, $F(1, 190) = 120.99$, $p < .001$; and frequency, $F(1, 190) = 141.90$, $p < .001$; but not group, $F(6, 190) = 0.58$, $p = .75$. There were significant interactions between group and test, $F(6, 190) = 6.87$, $p < .001$; between group and frequency, $F(6, 190) = 3.19$, $p = .005$; and among group, test, and frequency, $F(6, 190) = 3.89$, $p = .001$.

In Experiment 1, post hoc analyses indicated that the frequency discrimination thresholds were significantly improved at 1 kHz ($t = 6.06$, $p < .001$, 95% confidence interval (CI) [0.29, 0.57], Cohen's $d = 1.92$), but not at 6 kHz ($t = 0.54$, $p = .59$, 95% CI [−0.10, 0.18], Cohen's $d = 0.17$; Figure 1b and 1e) in the FD1k training group. In the FD6k training group, the frequency discrimination thresholds were significantly improved at 6 kHz ($t = 4.60$, $p < .001$, 95% CI [0.18, 0.46], Cohen's $d = 1.45$), but not at 1 kHz ($t = 1.95$, $p = .053$, 95% CI [−0.002, 0.27], Cohen's $d = 0.62$; Figure 1c and 1e). There was no significant improvement at either frequency (1 kHz: $t = 1.59$, $p = .11$, 95% CI [−0.03, 0.25], Cohen's $d = 0.50$; 6 kHz: $t = 1.32$, $p = .19$, 95% CI [−0.04, 0.23], Cohen's $d = 0.42$; Figure 1d and 1e) in the no-training control group.

Discussion

Tone frequency learning at 1 and 6 kHz is specific to the trained frequency, in general agreement with previous results under similar conditions (Wright & Fitzgerald, 2005).

Experiment 2

Experiment 2 investigated whether tone frequency learning at 6 kHz could transfer to 1 kHz with double-training. In a double-training group, participants practiced tone frequency discrimination at 6 kHz, and received exposure to 1 kHz via performing a temporal-interval discrimination task, in alternating blocks of trials. To control for possible contributions of the exposure task, another group only practiced temporal-interval discrimination at 1 kHz between pre- and posttraining tests.

Method

Participants. Nineteen naïve and inexperienced healthy college students (seven males and 12 females; mean age = 22.8 years, $SD = 2.7$ years) with normal hearing participated in this experiment.

Stimuli and procedure. The auditory frequency discrimination task was identical to that at the same 6-kHz base frequency in Experiment 1. The temporal-interval discrimination task was also the same except that the target stimuli and base stimuli had the same frequency at 1 kHz, while the interpip duration of the target stimulus interval varied. The starting duration difference of the staircase between the base and the target (Δt) was 50 ms, which was half the base interval. The duration difference decreased by 10 ms before the first incorrect response, and was adaptively changed by 1 ms afterward following the three-down-one-up rule. Each staircase ended after 60 trials. The threshold was calculated as the geometric mean of the last four reversals in a staircase run.

Experimental design. The pre- and posttraining tests were identical to those in Experiment 1. In the double-training group (FD6k_TID1k group), each training session consisted of 12 staircases of frequency discrimination at 6 kHz and 12 staircases of temporal interval discrimination at 1 kHz in an alternating order, which lasted approximately 1.5 hr. In the control group (TID1k group), each training session only contained 12 staircases of temporal interval discrimination at 1 kHz and lasted approximately 1 hr. For both groups, the experiments were completed within 9–14 days, with intersession gaps of no more than 2 days.

Results

Double-training improved frequency discrimination thresholds by 0.46 ± 0.05 log units at the trained 6 kHz, and by 0.31 ± 0.06 log units at the untrained 1 kHz (Figure 2a and c). In the control group, temporal-interval-discrimination training at 1 kHz improved frequency discrimination thresholds at the same frequency by 0.08 ± 0.05 log units (Figure 2b and c).

Post hoc analyses of the previous LME outcomes (detailed in Experiment 1) revealed that double training improved frequency discrimination thresholds significantly at both the trained 6 kHz ($t = 6.28$, $p < .001$, 95% CI [0.32, 0.61], Cohen's $d = 2.09$) and the untrained 1 kHz ($t = 4.21$, $p < .001$, 95% CI [0.16, 0.46], Cohen's $d = 1.40$; Figure 2a and 2c), showing learning transfer from 6 to 1 kHz. To determine the extent of transfer, six participants further practiced frequency discrimination at 1 kHz for four sessions, which failed to produce additional improvement at 1 kHz (between Sessions 9 and 13; $t = 0.40$, $p = .71$, 95% CI [−0.13, 0.18], Cohen's $d = 0.16$, two-tailed paired t test, Figure 2a; Also indicated by the empty bar in Figure 2c), indicating that the learning transfer after double training was complete.

In contrast, there was no significant change in the frequency discrimination thresholds at 1 kHz in the control group ($t = 1.12$, $p = .27$, 95% CI [−0.05, 0.22], Cohen's $d = 0.35$; Figure 2b and 2c). These control data indicated that the exposure to 1 kHz frequency alone through temporal interval discrimination had no impact on tone frequency discrimination at the same frequency.

Discussion

When a double-training design is applied, frequency discrimination learning becomes completely transferrable from 6 to 1 kHz. The learning transfer is complete in the sense that subsequent frequency discrimination training at 1 kHz induces no further improvement. These results support our hypothesis that even with stimuli that can produce strong frequency specificity, tone frequency learning is essentially transferrable.

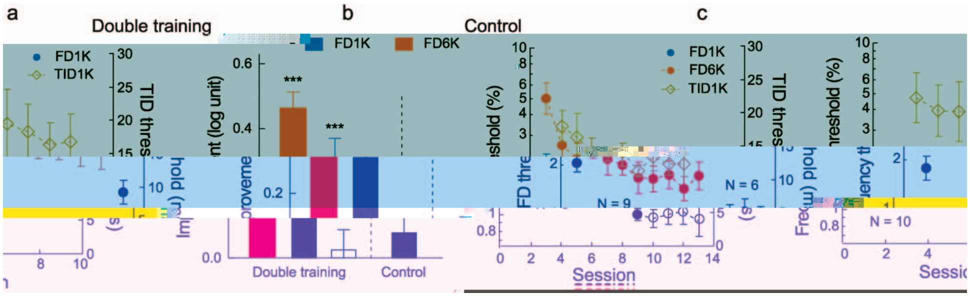

Figure 2. The transfer of frequency discrimination learning from 6 to 1 kHz with double training. (a) The double-training group practiced frequency discrimination at 6 kHz, as well as temporal interval discrimination at 1 kHz for 1 kHz exposure (Sessions 2–8). The learning transfer was tested at 1 kHz. After the posttest, six participants further practiced frequency discrimination at 1 kHz (Sessions 10–13). (b) The impact of temporal interval discrimination training alone on frequency discrimination thresholds at 1 kHz. (c) The improvements in frequency discrimination thresholds at 1 and 6 kHz in double training (FD6k_TID1k) and control (TID1k) groups. Error bars indicate ± 1 *SE*. FD = frequency discrimination; TID = temporal interval discrimination. *** $p < .001$. See the online article for the color version of this figure.

Experiment 3

Experiment 3 was parallel to Experiment 2, looking into transfer of tone frequency learning from 1 to 6 kHz with double training. Moreover, it investigated whether passive exposure to the untrained frequency could be equally effective to enable learning transfer. In the double-training group, participants practiced frequency discrimination training at 1 kHz, and received passive exposure to 6 kHz via background play in a visual recognition task. Again, the control group only practiced the visual task with 6-kHz tones played in the background between pre- and posttraining tests.

Method

Participants. Twenty naïve and inexperienced healthy college students (seven males and 13 females; mean age = 24.1 years, *SD* = 3.1 years) with normal hearing participated in this experiment.

Stimuli and procedure. The tone frequency discrimination task was identical to that at the same 1-kHz base frequency in Experiment 1. Visual recognition task with background tone play: The visual stimuli were randomly selected black English letters (24 × 24 pixels) presented on a white screen. A visual recognition trial contained a 300-ms fixation cross, a 300-ms blank, a four-letter string (200 ms per letter with 100-ms interletter gaps), a 900-ms blank, and a 200-ms target letter in a sequential order. Participants were asked to report whether the target letter was present in the earlier four-letter string and the response accuracy was measured. Between the onsets of the letter string and the target letter (a 2,000-ms period), the tone pips at 6 kHz were played at a randomly chosen onset time. These tone pips had the same temporal structure as of the frequency discrimination stimuli (i.e., two tone pips followed by another two with a 785-ms gap).

Experimental design. The pre- and posttests were identical to those in Experiment 1. In the double-training group (FD1k_VR6k group), each training session consisted of 12 staircases of frequency discrimination at 1 kHz and 12 blocks of visual recognition trials (60 trials per block) with background play of 6 kHz in alternating order, and lasted approximately 1.5 hr. In the control group (VR6k group), each training session only contained 12 blocks of visual recognition trials with 6 kHz background tone play, and lasted approximately 1 hr. For both groups, the experiments were completed within 9–14 days, with intersession gaps of no more than 2 days.

Results

Double training improved frequency discrimination thresholds by 0.42 ± 0.05 log units at the trained 1 kHz, and by 0.31 ± 0.05 log units at the untrained 6 kHz (Figure 3a and c). In the control group, the frequency discrimination thresholds at 6 kHz were improved by 0.11 ± 0.04 log units (Figure 3b and 3c).

Post hoc analyses of LME outcomes (see Experiment 1) revealed that double training improved frequency discrimination thresholds significantly at both the trained 1 kHz ($t = 6.02$, $p < .001$, 95% CI [0.28, 0.56], Cohen's $d = 1.90$) and the untrained 6 kHz ($t = 4.44$, $p < .001$, 95% CI [0.17, 0.45], Cohen's $d = 1.40$; Figure 3a and 3c). Seven participants further practiced frequency discrimination at 6 kHz for four sessions, which failed to produce additional improvement at 6 kHz (between Sessions 9 and 13; $t = 0.22$, $p = .83$, 95% CI [−0.27, 0.33], Cohen's $d = 0.08$, two-tailed paired *t* test; Figure 3a and 3c), indicating that the frequency discrimination improvement at 6 kHz had already maximized after double training, and that the learning transfer from 1 kHz was complete.

There was no significant change in the frequency discrimination thresholds at 6 kHz in the control group ($t = 1.63$, $p = .10$, 95% CI [−0.02, 0.25], Cohen's $d = 0.52$; Figure 3b and 3c). Hence the exposure to 6 kHz stimuli alone through background play produced no significant impact on frequency discrimination at 6 kHz.

Discussion

Consistent with Experiment 2, frequency discrimination learning becomes completely transferrable from 1 to 6 kHz with double-training after the participants receive passive exposure to the untrained frequency via background tone play. These results

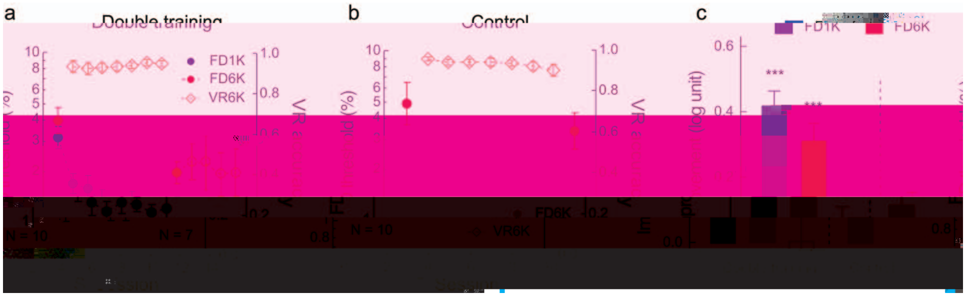

Figure 3. The transfer of frequency discrimination learning from 1 to 6 kHz enabled by double training. (a) The double-training group practiced frequency discrimination at 1 kHz, as well as receiving passive exposure to 6 kHz during a visual letter recognition task (Sessions 2–8). The learning transfer was posttested at 6 kHz. After the posttest, seven participants further practiced frequency discrimination at 6 kHz (Sessions 10–13). (b) Control condition: The impact of passive exposure to 6 kHz via background play alone on frequency discrimination thresholds at 6 kHz. (c) The improvements in frequency discrimination thresholds at 1 and 6 kHz in double training (FD1k_VR6k) and control (VR6k) groups. Error bars indicate ± 1 *SE*. FD = frequency discrimination; VR = visual letter recognition. *** $p < .001$. See the online article for the color version of this figure.

provide further support to our hypothesis that tone frequency learning is essentially transferrable.

Experiment 4

How does double training enable learning transfer? One possibility is that frequency training and exposure to the untrained frequency in the same training sessions would induce temporal coupling between 1 and 6 kHz tones to enable learning transfer. Such a possibility has been reported as task-irrelevant perceptual learning (Seitz & Watanabe, 2003). To test this possibility, a new sequential double training group first practiced the frequency discrimination task and then the temporal-interval task at an untrained frequency in two separate training phases. Because the sequential double training disallows temporal coupling, this possibility would be excluded if learning still transfers.

In addition, as we hypothesized earlier, the exposure to the untrained frequency in double training may prompt frequency learning to functionally connect to the untrained frequency inputs to enable learning transfer. If this is true, we can make two predictions: First, the facilitation may require frequency learning to be acquired either before or at the same time with the exposure to the transfer frequency. Second, learning may not transfer to a third frequency to which the participants receive no exposure. To check the first prediction, we had a second group of participants perform reverse double training. They first practiced the temporal-interval task and then the frequency discrimination task in two separate phases. To check the second prediction, both double training groups were tested at a third frequency (4 kHz) before and after training.

Method

Participants. Twenty naïve college students (six males and 14 females; mean age = 23.6 years, *SD* = 3.0 years) with normal hearing participated in this experiment.

Tasks. The tone frequency discrimination and temporal-interval discrimination tasks were identical to those in Experiments 2 in which simultaneous double training was performed.

Experimental design. Each training experiment consisted of a pretest session, a first training phase, a midtest session, a second training phase, and a posttest session on separate days. Each pre-, mid-, or posttest session consisted of 18 staircases of frequency discrimination, six for each base frequency (1, 4, and 6 kHz), and lasted approximately 1.5 hr. In the sequential double training group, frequency discrimination at 6 kHz was practiced in the first training phase for five sessions, and the exposure to 1 kHz via temporal interval discrimination was realized in the second training phase for four sessions. In the reverse double training group, the exposure to 1 kHz was realized in the first training phase, and frequency discrimination at 6 kHz was practiced in the second training phase. Each training session lasted approximately 1 hr. For both groups, the experiments were completed within 12–17 days, with intersession gaps of no more than 2 days.

Data analysis. An LME analysis was performed on threshold with test (pretest, midtest, and posttest), frequency (1, 4, and 6 kHz), and group (sequential double training group and reverse double training group) as the fixed effects (Pinheiro & Bates, 2000). For each participant, the LME model included random slopes of test and frequency, and the significance of the random components was evaluated by the likelihood ratio test. The likelihood ratio test showed that the best fitting model included random slopes of both test and frequency. Post hoc analyses were then conducted on the best fitting model with Bonferroni corrections to test the learning and transfer effects under various frequency and group conditions. The post hoc analysis was conducted by the "emmeans" package (Piepho, 2004).

Results

For the sequential double training group, the frequency discrimination practice at 6 kHz in the first training phase improved frequency thresholds by 0.11 ± 0.06 log units at 1 kHz, 0.12 ± 0.06 log units at 4 kHz, and 0.39 ± 0.06 log units at 6 kHz. After the exposure to 1 kHz in the second training phase through temporal interval discrimination, the frequency thresholds further improved by 0.20 ± 0.07 log units at 1 kHz, 0.05 ± 0.03 log units at 4 kHz, and −0.01 ± 0.03 log units at 6 kHz (Figure 4a and 4b).

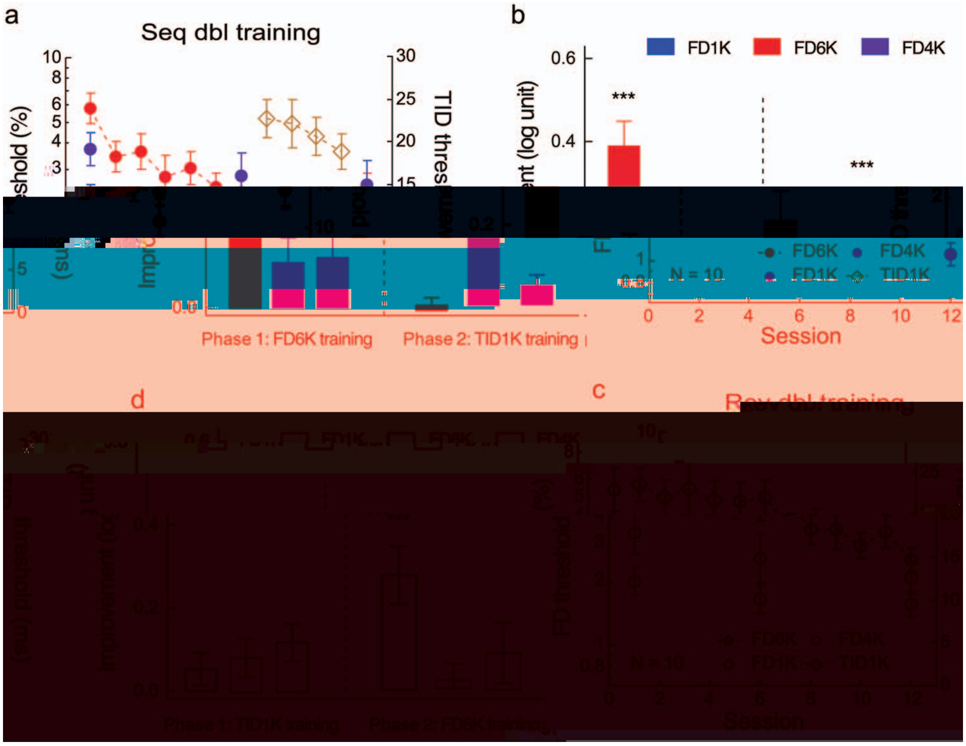

Figure 4. Sequential double training and reverse double training. (a) Sequential double training: Participants practiced frequency discrimination at 6 kHz in the first training phase and temporal interval discrimination at 1 kHz in the second training phase. Frequency discrimination thresholds at 6, 4, and 1 kHz were tested in pre-, mid-, and posttests. (b) The improvements of frequency discrimination thresholds at 6, 4, and 1 kHz after two phases of sequential double training. (c) Reverse double training: Participants practiced temporal interval discrimination at 1 kHz in the first training phase and frequency discrimination at 6 kHz in the second training phase. Frequency discrimination thresholds at 6, 4, and 1 kHz were tested in pre-, mid-, and posttests. (d) The improvements of frequency discrimination thresholds at 6, 4, and 1 kHz after two phases of reverse double training. Error bars indicate ± 1 *SE*. FD = frequency discrimination; TID = temporal interval discrimination. *** $p < .001$. See the online article for the color version of this figure.

For the reverse double-training group, initial exposure to 1 kHz with temporal interval discrimination improved frequency thresholds by 0.08 ± 0.05 log units at 1 kHz, 0.12 ± 0.05 log units at 4 kHz, and 0.05 ± 0.04 log units at 6 kHz. Frequency discrimination training at 6 kHz in the second training phase further improved the frequency thresholds by 0.02 ± 0.04 log units at 1 kHz, 0.09 ± 0.07 log units at 4 kHz, and 0.28 ± 0.07 log units at 6 kHz (Figure 4c and 4d).

The LME analysis conducted over the two double training groups showed significant main effects of test, $F(2, 144) = 43.06$, $p < .001$; and frequency, $F(2, 144) = 32.44$, $p < .001$; but not group, $F(1, 18) = 0.68$, $p = .42$. There were significant interactions between test and frequency, $F(2, 144) = 3.60$, $p = .008$; and among group, test, and frequency, $F(4, 144) = 6.96$, $p < .001$.

For the sequential double-training group, post hoc analysis indicated that the frequency discrimination practice at 6 kHz in the first training phase improved frequency thresholds at 6 kHz ($t = 6.94$, $p < .001$, 95% CI [0.26, 0.52], Cohen's $d = 2.19$), but not at 1 kHz ($t = 1.94$, $p = .16$, 95% CI [−0.02, 0.24], Cohen's $d = 0.61$) or 4 kHz ($t = 2.15$, $p = .10$, 95% CI [−0.01, 0.25], Cohen's $d = 0.68$). The exposure to 1 kHz in the second training phase further improved the frequency discrimination thresholds at 1 kHz ($t = 3.61$, $p = .001$, 95% CI [0.07, 0.34], Cohen's $d = 1.14$), but not at 4 kHz ($t = 0.82$, $p = 1.00$, 95% CI [−0.09, 0.18], Cohen's $d = 0.23$) or 6 kHz ($t = 0.21$, $p = 1.00$, 95% CI [−0.12, 0.15], Cohen's $d = 0.07$; Figure 4a and 4b).

For the reverse order double-training group, initial exposure to 1 kHz with temporal interval discrimination did not induce any significant change in frequency thresholds at 1 kHz ($t = 1.46$, $p = .44$, 95% CI [−0.05, 0.22], Cohen's $d = 0.46$), 4 kHz ($t = 2.14$, $p = .10$, 95% CI [−0.01, 0.25], Cohen's $d = 0.68$), or 6 kHz ($t = 0.94$, $p = 1.00$, 95% CI [−0.08, 0.19], Cohen's $d = 0.30$). The frequency discrimination training at 6 kHz in the second training phase improved the frequency thresholds at 6 kHz ($t = 4.91$, $p < .001$, 95% CI [0.14, 0.41], Cohen's $d = 1.55$), but not at 1 kHz ($t = 0.36$, $p = 1.00$, 95% CI [−0.11, 0.15], Cohen's $d = 0.11$) or 4 kHz ($t = 1.57$, $p = .36$, 95% CI [−0.04, 0.22], Cohen's $d = 0.50$; Figure 4c and 4d).

Discussion

Sequential double training enables complete cross-frequency learning transfer, indicating that the transfer is not a result of stimulus temporal coupling between the trained and exposed stimuli. The reverse double training fails to enable learning transfer, indicating that frequency discrimination needs to be learned either before or at the same time with the exposure to the untrained frequency. Moreover, double training only induces transfer to the exposed frequency, but not to a third frequency to which the participants receive no exposure. These results are consistent with the hypothesis that double training facilitates the functional connections of tone frequency learning to the exposed frequency.

General Discussion

In this study we demonstrate that perceptual learning of tone frequency discrimination, which is initially specific to the trained frequency (Figure 1), can transfer to a new frequency with double training. Learning becomes completely transferrable to a new frequency when the participants receive additional exposure to the new frequency through a temporal interval discrimination task, or even background tone play (Figures 2 and 3). It is only when the exposure occurs before frequency discrimination learning, or when the transfer effect is tested at another new frequency that the participants receive not exposure to, that the transfer is prevented (see Figure 4).

The frequently observed specificity in perceptual learning has often been interpreted as an indication of permanent neuronal plasticity in early, low-level stages of cortical processing. However, recent researches emphasize the decisive roles of high-level brain areas, which is supported not only by new neurophysiological and brain imaging results (Chowdhury & DeAngelis, 2008; Gu et al., 2011; Kahnt, Grueschow, Speck, & Haynes, 2011; Law & Gold, 2008), but also by psychophysical evidence for learning transfer, especially the removal of learning specificity with new training methods (Donovan, Szpiro, & Carrasco, 2015; Harris, Gliksberg, & Sagi, 2012; Xiao et al., 2008; Xie & Yu, 2019; Yin et al., 2016; Zhang, Zhang et al., 2010; Zhang, Xiao, Klein, Levi, & Yu, 2010). Tone frequency learning is special in the sense that whether and how much it is specific to the trained frequency depends on the stimulus configurations. For example, learning with longer continuous tones tends be mostly transferrable to a new frequency, but learning with brief tone pips tends to show more specificity (Wright & Zhang, 2009). Nevertheless, we demonstrate that even the strong specificity with brief tone pips can be completely removed with double training, in exactly the same manner as demonstrated in visual perceptual learning. Therefore, tone frequency learning, regardless of the training stimuli and the initially observed specificity, at its core is a high-level cognitive process.

It is unlikely that double training would induce plasticity in the primary auditory cortex at both the trained and transfer frequencies. Although our data cannot rule out low-level plasticity at the trained frequency (but see the last paragraph of the discussion), improved frequency discrimination at the transfer frequency has to rely on response reweighting through high-level processes. This is because the transfer frequency per se is not trained with frequency discrimination, and the control experiments show that training with a temporal interval discrimination task (the transfer frequency exposure task) alone has minimal impact on frequency discrimination at the same frequency. In the extreme case when the exposure to the transfer frequency is achieved through background tone play during a visual recognition task, plasticity at the transfer frequency is more unlikely.

Moreover, the reweighting function of responses at the transfer frequency may not be remapped from the trained frequency directly. The reweighting models assume that training improves readout of sensory inputs from a specific neural assemble that is only responsive to the trained stimulus, for the purpose of forming a stimulus-matched template (Dosher & Lu, 1998; Jones et al., 2013). In our study, the two testing frequencies are likely encoded by different peripheral mechanisms. That is, the superior discrimination performance at 1 kHz should be attributed to temporal coding mechanisms, while discrimination at 6 kHz can only rely on place coding ones (Johnson, 1980; Siebert, 1970). At the primary auditory cortex, the two frequencies are still separately represented in a tonotopic manner (Aitkin et al., 1986; Imig et al., 1977). Because the two frequencies are both physically and perceptually different, their templates, or the weighting functions of neuronal responses to two frequencies, must be different, which prevents direct remapping of response weighting functions. Some abstract rules of reweighting, as discussed below, have to be learned at high-level brain stages, and then applied to the transfer frequency.

We suggest that the participants are learning some statistical rules of reweighting frequency inputs, such as reassigning weights on the basis of standardized distributions of frequency responses. Therefore, learning in principle can transfer to other frequencies, regardless of the differences in physical appearances, sensitivities at threshold, and neural encoders of the tone stimuli. In other words, the participants are learning a conceptual representation of tone frequency, which is similar to a concept-learning account we proposed in visual perceptual learning (Wang et al., 2016). Such a conceptual representation is essentially the same as the "general task structure" of Delhommeau et al. (2005), in that participants acquire "knowledge about the general structure of the task, which may facilitate later transfer of the learning to new stimuli."

It is unclear why tone frequency learning with tone pips initially shows strong specificity. Our general view is that learning and specificity are two separate processes in perceptual learning (Xiao et al., 2008; Xiong et al., 2016; Zhang, Zhang et al., 2010). We suggest that learning is rule-based and conceptual, so that the reweighting rules can in principle be applied to new sensory inputs to enable transfer. However, whether learning can actually transfer depends on the functional connections between high-level learning and new sensory puts. Exposure to new sensory inputs in double training helps establish these functional connections to enable transfer. However, the absence of exposure to other new inputs would prevent such connection being established, which explains lack of transfer to 4 kHz in Figure 4a and 4b. Some brain evidence for the functional connections associated with learning and its specificity or transfer may come from an ERP study of ours (Zhang, Cong, Song, & Yu, 2013). The ERP results reveal that perceptual learning of visual Vernier discrimination is accompanied with significant occipital P1-N1 changes. However, the changes are only shown in the trained hemisphere of participants who show location specificity, and in both trained and transfer hemispheres of participants who show learning transfer. Because no training is performed in the transfer hemisphere, the related occipital P1-N1 changes likely indicate top-down modulation of low-level visual areas by high-level learning, or functional connections from high-level learning to Vernier inputs in the transfer hemisphere. Future imaging studies may provide more direct evidence for functional connections from high-level learning to sensory areas responding to untrained stimuli after double training.

Our findings may provide new insights into the seemingly conflicting results of changes in the primary auditory cortex with tone frequency learning. Tone frequency learning is first reported to be accompanied with enlarged representations of trained frequencies in the primary auditory cortex (Polley, Steinberg, & Merzenich, 2006; Recanzone et al., 1993). However, later evidence shows that the primary auditory cortex enlargement associated with tone frequency learning, which has been induced with pairing of tones with stimulation of the cholinergic nucleus basalis in rats, diminishes after training while learning persists (Reed et al., 2011). It is likely that the primary auditory cortex involves no long-term training-induced neural plasticity. Rather, it either mediates the perceptual learning process, or is top-down modulated during training by high-level perceptual learning. Therefore, the changes in the primary auditory cortex are temporary and will diminish after training is completed.

Context

The main idea in this study came from our previous research on visual perceptual learning. Visual perceptual learning mostly shows

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