Induction of auditory perceptual learning

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Performance on many perceptual tasks improves with practice even in adults, indicating that our sensory systems are not rigid but rather can be changed through experience. My co-workers and I have been investigating the factors that induce perceptual learning on auditory skills. We have evidence that two key requirements for perceptual improvement to occur across days are performance of the task to be learned and a sufficient amount of training per day. Beyond these core requirements, we also have documented that perceptual training can be made more efficient by not exceeding the required amount of daily training and by replacing a subset of the training trials with stimulus exposure alone. The elements of successful training regimens provide insights into perceptual-learning mechanisms. A greater knowledge of these mechanisms will lead to more effective training strategies to help restore perceptual skills in people with perceptual disorders as well as to enhance those skills in people with normal perception.

INTRODUCTION

Perceptual abilities improve with practice. This plasticity is of practical value because it provides an avenue for treating perceptual disorders as well as for enhancing normal perceptual skills. It is of scientific importance because it indicates that theories of perceptual processing must incorporate malleability.

My co-workers and I have been investigating the induction of perceptual learning in audition to gain a greater understanding of the kinetics and mechanisms of perceptual improvement. In these experiments we have focused on how a variety of multiple-day training regimens affect basic auditory skills in human adults. We chose to examine multiple-day as opposed to single-day regimens because improvement across days indicates that learning has moved to long-term memory (consolidated; McGaugh, 2000), performance across days is not necessarily predicted by performance within a day (Mednick *et al.*, 2002; Huyck and Wright, 2011), and the learning magnitude across days is typically greater than within a day. Our choice to evaluate learning on basic skills is based on the assumption that, at the physiological level, the general factors that trigger learning-related change are similar across a wide range of task and stimulus complexity. The particular neural circuits that are affected may differ, but the circumstances that lead them to change are largely the same. Though not described here, we have preliminary data

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suggesting that similar circumstances induce learning on both fine-grained auditory discrimination tasks and speech tasks, consistent with this assumption.

Here we summarize the results of these investigations, placed in the context of their implications for how best to elicit perceptual improvement. We suggest that effective and efficient perceptual training regimens include performance of the task to be learned and a sufficient, but not additional, number of training trials per day. We then show that a portion of the necessary daily training trials can be replaced with stimulus exposures without practice, providing a means to reduce the overall practice required to obtain improvement. We conclude with a brief discussion of what these training requirements suggest about learning mechanisms.

TASKS AND GENERAL PARADIGM

In all of the experiments featured in the following sections, the task was either frequency discrimination (Fig. 1A, left) or temporal-interval discrimination (Fig. 1A, right). In each two-presentation forced-choice trial a standard stimulus was presented in one randomly selected presentation and a signal stimulus in the other. The standard stimulus (filled horizontal bars) was the same for both tasks: two 15-ms, 1-kHz tones separated by a temporal interval of 100 ms. The signal stimulus (open horizontal bars) had a lower frequency than the standard in the frequency task and a longer temporal interval than the standard in the temporal-interval task. Discrimination thresholds were estimated using a three-down, one-up adaptive tracking procedure that yields the 79.4% correct point on the psychometric function (Levitt, 1971).

Each experiment consisted of a pre-training test, a training phase, and a post-training test. Trained listeners participated in all three segments. Controls participated only in the pre- and post-training tests, with no training in between. The time between the pre- and post-training tests was similar for the trained listeners and controls.

KEY TRAINING REQUIREMENTS

Practice on the task to be learned

One well-established requirement for learning on most perceptual tasks is practice on the task to be learned. The importance of active task performance is demonstrated primarily by two lines of evidence. First, learning resulting from performing one task rarely transfers to a different task even when both tasks are performed with the same standard stimulus. This lack of task transfer has been demonstrated repeatedly in the visual system. For just one example, observers who practiced either a local or a global visual orientation discrimination task with the same stimuli improved on the task on which they were trained, but did not transfer their learning to the other task (Ahissar and Hochstein, 1993). Figure 1 shows a similar outcome in the auditory domain. We trained two groups of adults 900 trials per day for 10-11 days on either a frequency-discrimination task or a temporal-interval discrimination task, using the same standard stimulus for both tasks (Fig. 1A), and then tested both groups on the

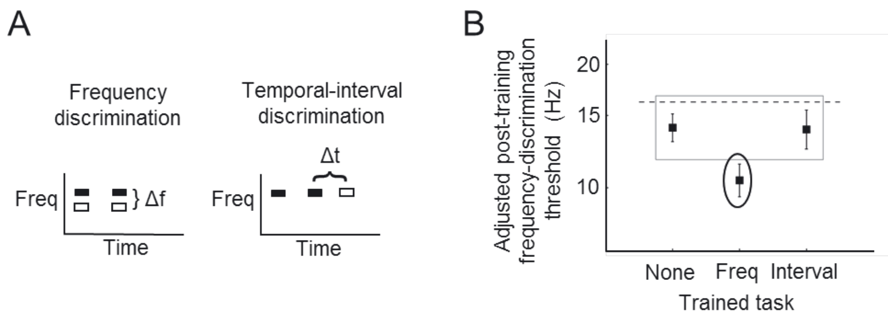

Fig. 1: Practice on the task to be learned. (A) Schematic diagrams of the frequency-discrimination (left) and temporal-interval discrimination (right) tasks. The standard stimulus was the same for both tasks (filled horizontal bars; two 15-ms 1-kHz tones separated by 100 ms), but the signal stimulus (open horizontal bars) had a lower frequency in the frequency task and a longer temporal interval in the temporal-interval task. The procedure was two-presentation forced-choice. (B) Mean post-training thresholds (filled squares; 79.4% correct detections) on the frequency-discrimination task following either no training (None), or 900 training trials per day for 10-11 days on frequency discrimination (Freq) or temporal-interval discrimination (Interval) (n = 6-10 per group). The post-training thresholds were adjusted to take into account individual differences in pre-training threshold (equation in Cohen, 1988). Also shown are the mean pre-training threshold across all listeners (dashed line), and the 95% confidence interval around the mean post-training threshold for the control group who participated in the pre- and post-training tests but received no training in between (None; gray box). Error bars indicate +/− 1 standard error of the mean. The post-training threshold that differed significantly from that of controls ($p < 0.05$) is marked (black circle). [Data from Wright and Sabin (2007) and Wright *et al.* (2010).]

frequency-discrimination task (Wright *et al.*, 2010). The frequency-trained group improved on the frequency task over the course of training and had lower frequency-discrimination thresholds at a post-training test than did the control group (Fig. 1B). In contrast, though the temporal-interval trained listeners improved on their trained task, their post-training thresholds on the frequency task did not differ from those of controls. Thus, learning did not transfer from temporal-interval discrimination to frequency discrimination. In another auditory case, learning did not transfer in either direction between the tasks of temporal-order discrimination and asynchrony detection at sound onset (Mossbridge *et al.*, 2006). If improvements were driven solely by stimulus exposure, learning should transfer between tasks. Second, cortical changes that have been observed to accompany perceptual learning either do not occur or are substantially reduced when the stimulus exposures are not linked with active performance of a task. For example, temporal resolution in primary auditory cortex improved in a group of rats trained to use an auditory temporal cue to locate food, but not in another group that were presented with the same sounds in a non-contingent manner (Bao *et al.*, 2004). Combining both lines of evidence, rats trained to perform one or another of two basic auditory tasks with the same stimuli showed behavioural improvement and corresponding cortical reorganization that was specific to the stimulus feature relevant to the task on which they were trained (Polley *et al.*, 2006).

Sufficient practice per day

Another apparent requirement for perceptual improvement across days is a sufficient, and sometimes substantial, amount of training per day. We observed this phenomenon on an auditory frequency-discrimination task, as shown in Fig. 2 (Wright and Sabin, 2007). We trained two groups of adults either 360 or 900 trials per day for 6 days on a frequency-discrimination task (Fig. 2A). The 900-trial-per-day group improved over the course of training and had lower frequency-discrimination thresholds at a post-training test than did the control group (Fig. 2B; data from Fig. 1B). In contrast, the 360-trial-per-day group showed no improvement on the frequency task over the course of training, and their post-training thresholds did not differ from those of controls. These conclusions held both when the total number of training days was held constant at 6 and when the total number of trials was held constant across the two groups. Thus, learning on this particular frequency-discrimination task required sufficient training per day. The need for sufficient training per day to yield learning across days has also been reported for a visual chevron-discrimination task (Aberg *et al.*, 2009) and a letter-enumeration task (Hauptmann and Karni, 2002).

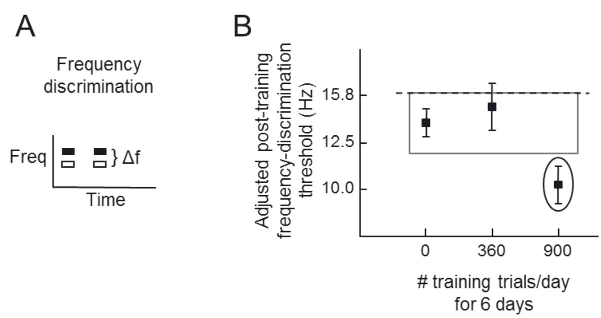

Fig. 2: Sufficient practice per day. (A) As in Fig. 1A. (B) Mean post-training thresholds on the frequency-discrimination task following 0 (no training), 360, or 900 training trials per day for 6 days on that task (n = 7-10 per group). Otherwise, as in Fig. 1B. [Data from Wright and Sabin (2007) and Wright *et al.* (2010).]

It is important to note that the sufficient amount of daily training required for learning can differ across tasks, and even across stimuli for the same task. We trained two groups of adults 360 trials per day for 6 days on either frequency discrimination or temporal-interval discrimination, using the same standard stimulus for both tasks (Wright and Sabin, 2007). The frequency-trained group did not improve on frequency discrimination, as illustrated in Fig. 2B (360 trials/day), but the temporal-interval trained group did improve on temporal-interval discrimination (not shown). However, sufficient daily training still seems necessary for learning on temporal-interval discrimination, because 50 training trials per day for 20 days yielded no improvement on that task (Rammsayer, 1994). Thus, the sufficient amount of daily training required for learning can differ across tasks, even when the standard stimulus is the same. Likewise, listeners who practiced ~360 training trials per day over multiple days on frequency discrimination improved on that task when the standard stimulus was a 300-ms, 1-kHz tone (Roth *et al.* 2003), but not when it was two brief 1-kHz tones separated by 100 ms (Fig. 2B). Thus, the sufficient amount of daily training required for learning can differ across stimuli, even when the task is the same.

Enough is enough

While perceptual learning across days appears to depend on sufficient training on each day, additional training beyond that amount can be superfluous. For example, we trained two groups of adults either 360 or 900 trials per day for 6 days on an auditory temporal-interval discrimination task (Wright and Sabin, 2007). Their learning curves essentially overlapped. Similar outcomes have been reported in investigations of learning on other tasks including auditory interaural-time-difference discrimination (Ortiz and Wright, 2010), visual chevron discrimination (Aberg *et al.*, 2009), and motor sequencing (Savion-Lemieux and Penhune, 2005). Thus, more daily training does not necessarily lead to greater improvement across days.

AN ALTERNATIVE ROUTE

Task practice plus additional stimulus exposure without practice

As described above, two core requirements for perceptual learning across days appear to be task performance and sufficient training trials per day. Here we show that these requirements can be met more efficiently through the combination of periods of practice and periods of additional stimulus exposure without practice (Wright *et al.*, 2010). This phenomenon is illustrated in Fig. 3, which shows thresholds on a frequency-discrimination task (Fig. 3A) at a post-training test for six different groups of adults (Fig. 3B): five groups who participated in different training regimens for 6-11 days, and a control group.

We trained two groups – Freq+Silence and All-Interval – using regimens that did not meet the requirements for learning established for this frequency-discrimination task. The Freq+Silence group practiced the frequency-discrimination task for 360 trials per day with the trials distributed in three bouts of 120 trials. The bouts were separated by ~6 minutes of silence during which the listeners completed a written symbol-to-number matching task. The post-training thresholds for this group were no better than those for controls, replicating the previous demonstration that 360 training trials per day are not sufficient to induce learning on this task (see Fig. 2B). The All-Interval group practiced 900 trials per day on a temporal-interval discrimination task using the same standard stimulus as in the frequency-discrimination task (Fig. 3A). As described above, this group did not transfer their learning from the temporal-interval to the frequency-discrimination task (data from Fig. 1B), demonstrating the need for performance of the task to be learned to induce improvement.

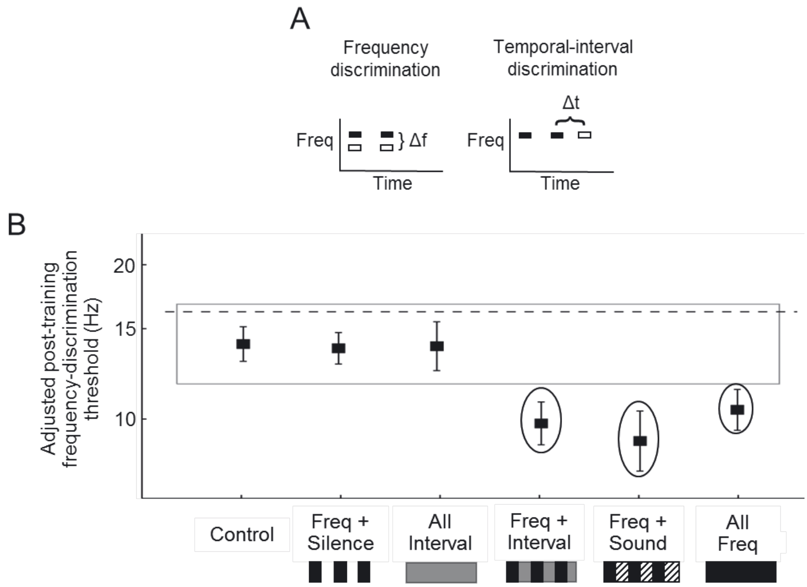

Fig. 3: Task practice plus additional stimulus exposure without practice. (A) As in Fig. 1A. (B) Mean post-training thresholds on the frequency-discrimination task following either no training (control), or one of five 6-11 day training regimens (n = 6-10 per group). See text for details. Otherwise, as in Fig. 1B. [Data from Wright and Sabin (2007) and Wright *et al.* (2010).]

We then combined variants of these two unsuccessful regimens to train two additional groups – Freq+Interval and Freq+Sound. Both combinations were successful. The Freq+Interval group practiced frequency discrimination for 360 trials per day and temporal-interval discrimination for 360 trials per day, alternating between the two tasks every 120 trials. The Freq+Sound group practiced frequency discrimination for 360 trials per day and also were exposed to, but did not perform, 360 trials per day of the temporal-interval discrimination task, alternating between the two tasks every 120 trials; the temporal-interval trials were presented in the background as the listeners completed a written symbol-to-number matching task. The post-training thresholds for these two groups were better than those for controls, and were similar to those for the All-Freq group (data from Fig. 1B) who practiced 900 trials per day on the frequency-discrimination task. Thus, though improvement on this task required task practice and sufficient daily training trials, task practice was not required throughout the entire training period. A portion of the practice trials could be replaced with additional stimulus exposures delivered either through performance of a different task or as background sounds.

In additional experiments we examined the influence of the temporal separation of the periods of task practice and additional stimulus exposure. Figure 4 shows the frequency-discrimination thresholds at a post-training test for four groups who participated in different 6-7 day training regimens and for a control group. One trained group practiced only frequency discrimination for 360 training trials per day (Short Freq). The other three trained groups practiced frequency discrimination followed by temporal-interval discrimination, each for 360 training trials per day, using the same standard stimulus for both tasks. The temporal separation between

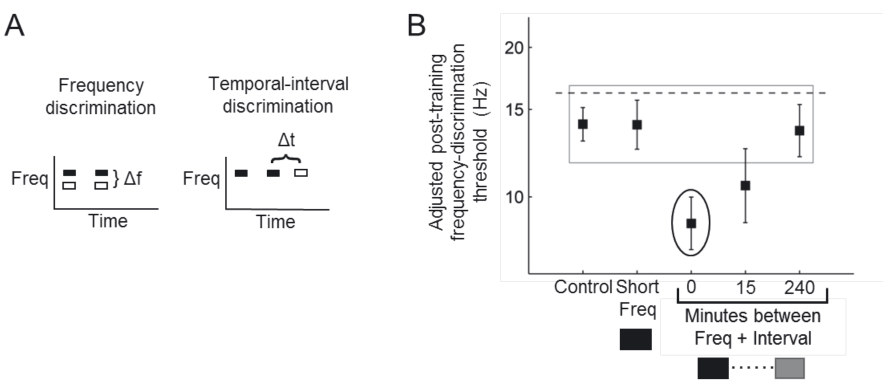

Fig. 4: Temporal separation between periods of task practice and periods of additional stimulus exposure. (A) As in Fig. 1A. (B) Mean post-training thresholds on the frequency-discrimination task following either no training (control), or one of four 6-7 day training regimens: 360 training trials per day on frequency discrimination alone (Short Freq), or 360 training trials per day on frequency discrimination and 360 on temporal-interval discrimination, using the same standard stimulus for both tasks, with the training trials on the two tasks separated by 0, 15, or 240 minutes (n = 8-10 per group). Otherwise, as in Fig. 1B. [Data from Wright and Sabin (2007) and Wright et al. (2010).]

the end of training on the frequency task and the beginning of training on the temporal-interval task was either 0, 15, or 240 minutes. Training on the frequency task alone yielded no improvement on that task, as described above (see Fig. 2B). Training on the temporal-interval task immediately after the frequency task did yield improvement on frequency discrimination, replicating the outcome obtained when the training alternated between these two tasks (see Fig. 3B). However, the effectiveness of the temporal-interval trials declined as the temporal separation between the two training periods increased to 15 minutes, and was gone when the periods were separated by 4 hours. Thus, the periods of task performance and of additional stimulus exposure need to occur within 15 minutes of each other.

We also examined the influence of the temporal order of the periods of task practice and additional stimulus exposure. We trained one group on the frequency task followed immediately by the temporal-interval task, as described above, and another group using the opposite order. Both groups improved on the frequency-discrimination task (data not shown). Thus, the temporal order of the two periods did not matter.

Finally, we examined the effect of stimulus differences between the practice and additional-stimulus-exposure periods. We trained two other groups on the frequency task followed immediately by the temporal-interval task, but varied the standard stimulus in the temporal-interval task. For one group, the temporal-interval standard had the same frequency as, but a different temporal-interval than, the frequency standard. This group improved on frequency discrimination. For the other group, the temporal-interval standard instead had the same interval as, but a different frequency than, the frequency standard. This group showed no improvement on the frequency task. Thus, the additional stimulus exposures had to share a key feature with the stimulus used during task practice, but the stimuli in the two periods did not need to be identical.

DISCUSSION

The elements of training regimens that yield perceptual improvement across days provide insights into perceptual-learning mechanisms, which, in turn, have implications for how to most effectively and efficiently train perceptual skills.

The need for task practice suggests that task performance provides an internal permissive signal that places the neural circuitry to be modified in a sensitized state. This permissive signal might arise from the attention required to perform the task or from rewards associated with performing the task, among other possibilities. The idea that top-down influences play a critical role in perceptual learning is well recognized (Ahissar and Hochstein, 2004; Seitz and Watanabe, 2005). The implication is that purely bottom-up exposure-based training regimens are unlikely to be successful.

Seemingly less appreciated is the apparent requirement for a sufficient amount, but no more, of practice per day. Most share the intuitive sense that training regimens should ‘provide enough training’, and accordingly design training plans that deliver the maximum amount of training allowed by time constraints. However, the observations that the actual number of daily training trials required for learning across days can be substantial, and that training beyond that amount can be superfluous, offer new insight into the learning process. The need for a sufficient amount of practice per day suggests that the neural circuitry to be modified must receive adequate stimulation to trigger consolidation (the transfer to long-term memory) (Wright *et al.*, 2010). That enough is enough suggests that consolidation may function as an all-or-none process (Wright and Sabin, 2007). By this view, the training (acquisition) and consolidation phases are functionally distinct. Additional support for this idea comes from reports in which the same intervening event (training on a non-target condition) disrupted learning on a target condition when presented during the acquisition stage, but not during the consolidation stage, of learning on that target condition (Banai *et al.*, 2010; Zach *et al.*, 2005). At a practical level, these observations suggest that training regimens could be made more effective and efficient by determining the amount of training that is necessary to generate improvement. Too little training will be ineffective, and too much inefficient.

Finally, the demonstration that the combination of task practice and additional stimulus exposure without practice can enhance perceptual improvement suggests that the influences of these two experiences on learning extend beyond the times in which they are elicited. The restriction of this temporal interaction to a period of minutes rather than hours implies that it is an aspect of the acquisition phase rather than the consolidation phase of learning. The lack of constraint on the presentation order of the two experiences raises the possibility that two different processes can create this beneficial interaction. The influence of task practice may extend into a following period of additional stimulus exposure, making those exposures function as if the task were still being performed, while a period of stimulus exposure may increase the effectiveness of subsequent task practice. It also appears that the neural circuitry engaged in the interaction is selective to stimulus features, not the whole stimulus, because, to be effective, the additional stimulus exposures needed to share a key feature with, but not necessarily be identical to, the stimulus used during task practice. Training regimens that take advantage of this interaction between task performance and additional stimulus exposures could reduce the amount of task practice necessary for learning on a given task by at least half. The saved practice trials could be replaced either with stimulus exposures without practice, to make the total regimen less work, or with training on a different task, to increase the regimen's overall impact.

In summary, we suggest that two key elements of successful multiple-day auditory perceptual training regimens are practice on the task to be learned, and a sufficient, and sometimes substantial, amount of training per day. Beyond these core requirements, perceptual training can be made more efficient by not exceeding the required amount of daily training and by replacing a subset of the training trials with stimulus exposure alone.

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