

## INVERTED-U FUNCTION RELATING CORTICAL PLASTICITY AND TASK DIFFICULTY

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**Abstract**—Many psychological and physiological studies with simple stimuli have suggested that perceptual learning specifically enhances the response of primary sensory cortex to task-relevant stimuli. The aim of this study was to determine whether auditory discrimination training on complex tasks enhances primary auditory cortex responses to a target sequence relative to non-target and novel sequences. We collected responses from more than 2000 sites in 31 rats trained on one of six discrimination tasks that differed primarily in the similarity of the target and distractor sequences. Unlike training with simple stimuli, long-term training with complex stimuli did not generate target-specific enhancement in any of the groups. Instead, cortical receptive field size decreased, latency decreased, and paired pulse depression decreased in rats trained on the tasks of intermediate difficulty, whereas tasks that were too easy or too difficult either did not alter or degraded cortical responses. These results suggest an inverted-U function relating neural plasticity and task difficulty. © 2012 IBRO. Published by Elsevier Ltd. All rights reserved.

**Key words:** task difficulty, sequence learning, cortical plasticity, auditory cortex, operant training.

Performance on visual, auditory, or somatosensory discrimination tasks improves with practice and is generally specific for the trained stimulus (Ball and Sekuler, 1982; Recanzone et al., 1992a; Ahissar and Hochstein, 1997; Fahle, 1997; Wright et al., 1997; Irvine et al., 2000; Karmarkar and Buonomano, 2003; van Wassenhove and Nagarajan, 2007). In many cases, the improved performance is correlated with expanded cortical maps, receptive field selectivity, or improved signal to noise ratio that is stimulus specific (Karni and Sagi, 1991; Recanzone et al., 1992b, 1993; Zohary et al., 1994; Elbert et al., 1995; Schoups et al., 2001; Fritz et al., 2003; Rutkowski and Weinberger, 2005; but see Brown et al., 2004; Ghose, 2004). Motivation is believed to regulate learning and plasticity (Bao et al., 2004; Blake et al., 2006), although previous experiments have shown that plasticity and learning effects in animal models and human individuals can be achieved using

passive exposure to stimuli (Dinse et al., 2003; Lotze et al., 2003; Frenkel et al., 2006; but see Recanzone et al., 1993; Bakin and Weinberger, 1996; Irvine et al., 2000; Bao et al., 2001). Cortical acetylcholine, which is released during operant training, modulates both learning and plasticity (Orsetti et al., 1996; Himmelheber et al., 2000). Repeatedly pairing simple tones with electrical stimulation of the cholinergic nucleus basalis (NB) results in receptive field, map, and temporal plasticity similar to that observed after operant training (Kilgard and Merzenich, 1998a,b; Bao et al., 2004). When a high tone, a low tone, and a noise burst separated by 100 ms (HLN) were paired with NB stimulation, the majority of primary auditory cortex (A1) neurons exhibited response facilitation that was specific to the paired sequence. The observations that exposure to complex stimuli can generate order- and interval-specific plasticity suggests these forms of plasticity could contribute to learning of natural stimuli (Kilgard and Merzenich, 1998b, 2002). Order- and interval-specific responses to behaviorally relevant vocalizations in birds, bats, monkeys, and ferrets further support this hypothesis (Fitzpatrick et al., 1993; Wang and Kadia, 2001; Gentner and Margoliash, 2003; Schnupp et al., 2006). However, it is not known whether cortical plasticity represents a general strategy for learning complex stimuli in mammals.

In this study, rats were trained to discriminate a target sequence from one or more distractor sequences (Fig. 1) to test the hypotheses that training (1) increases the response to the target stimulus relative to novel stimuli (as observed following operant training with simple stimuli) or (2) results in sequence-specific facilitation (as observed after the sequence was paired with NB stimulation).

### EXPERIMENTAL PROCEDURES

Rats were experimentally naive young adults (200–250 g) at the start of training or sound exposure. They were food deprived for ~12–14 h before training or exposure. Water was provided *ad libitum* at all times, and rats were maintained at 80–85% of their body weight. Each rat trained for two sessions a day for 1–1½ h per session, 5 days a week. Rats were housed individually at the Animal Facility at the University of Texas at Dallas and were maintained on a reverse 12-h light/dark cycle. Constant temperature and humidity were maintained in the rat colony room. Protocols and recording procedures conformed to the Ethical Treatment of Animals (NIH) and were approved by the Institutional Animal Care and Use Committee at the University of Texas at Dallas. Both the number of animals used and their suffering was minimized.

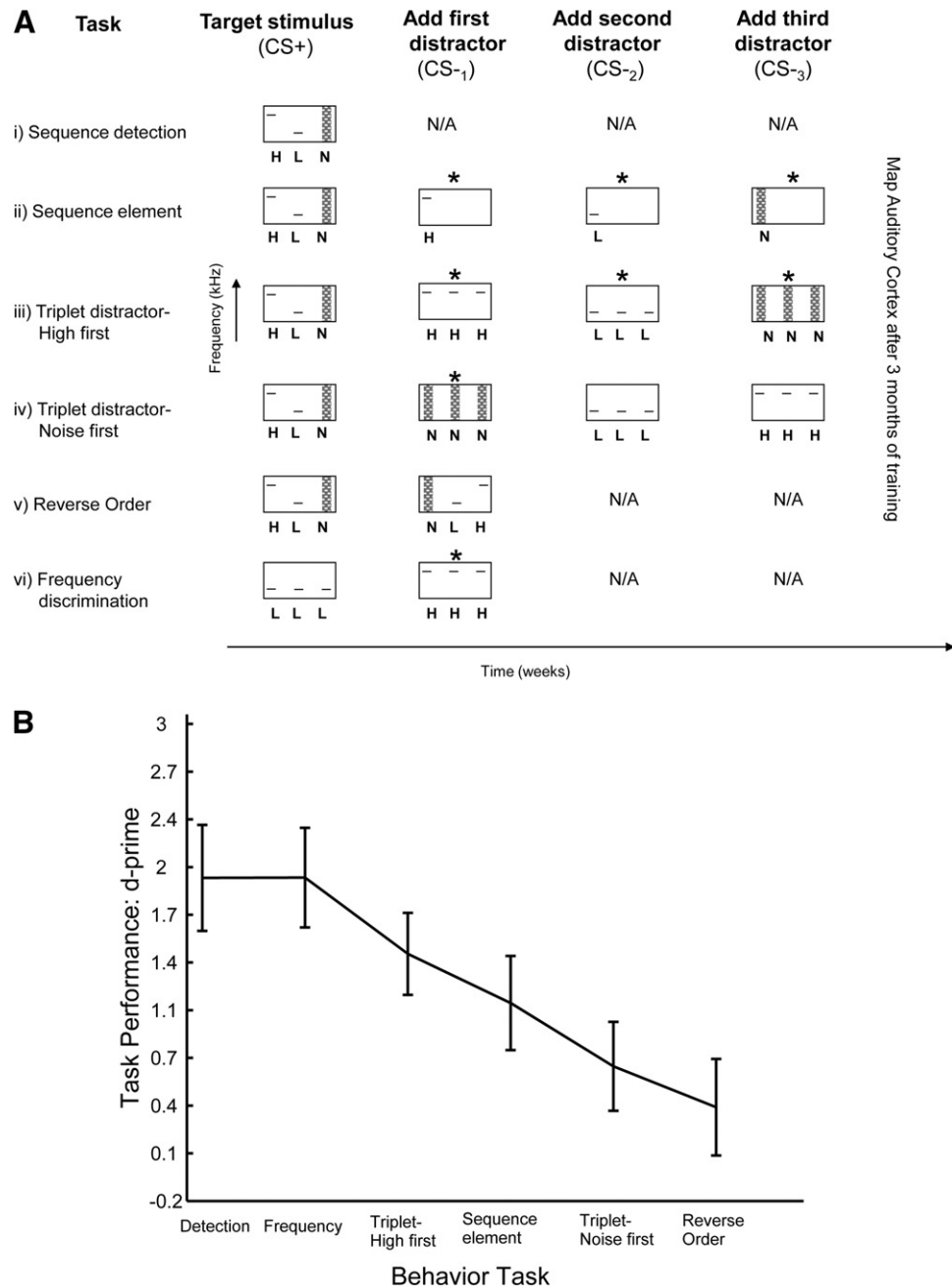
### Behavioral training

Thirty-one rats trained on go/no-go operant conditioning tasks for a period of ~3 months (Fig. 1). Rats were trained in an operant

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**Abbreviations:** A1, primary auditory cortex; CF, characteristic frequency; H, high tone; L, low tone; N, noise burst; NB, nucleus basalis; PPD, paired pulse depression; PSTH, post stimulus time histogram.



**Fig. 1.** Schematic of the go/no-go tasks and task performance. (a) Rats were required to lever press in response to the target sequence (CS+) and to withhold from pressing to 0, 1, or 3 distractor sounds (depending on the task). In all but the frequency discrimination task, the target sequence was a rapid HLN sequence (100 ms stimulus onset asynchrony). (i) Simple HLN detection task. No distractor sounds were presented. (ii) In the sequence element task, the distractors were the high tone, the low tone, and the noise burst elements presented individually. (iii, iv) In the two variants of the triplet distractor task, the three distractor sequences were the same (three high tones, three low tones, and three noise bursts), but the order the distractors were added during training was reversed. (v) In the reverse order task, the distractor was the target sequence played in reverse (NLH). (vi) For the frequency discrimination task, rats had to discriminate a target low tone sequence (LLL) from a distractor high tone sequence (HHH). An asterisk (\*) over a distractor sound indicates that rats were able to discriminate the sound from the target sound (d-prime above chance). After training, all rats were anesthetized and multi-unit responses were recorded from auditory cortex neurons. (b) Behavioral performance d-primes on the last day of training for each of the tasks (mean ± SEM).

cage (8" L×8" W×8" H) placed inside a sound-attenuated booth (19" L×10.5" W×20" H) in a closed room, and their behavior was monitored on a video monitor outside the room. A light source (house light) was affixed inside the booth and a second light source (cage light) was placed just above a lever inside the cage.

Lever press triggered the delivery of a sugar pellet from a dispenser into a receptacle placed inside the cage. Sound stimuli were delivered through a calibrated speaker (Motorola 40–1221, Radio Shack, Fort Worth, TX, USA) mounted outside the operant cage and ~10 cm away from the rat's left ear. Acoustic stimuli

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