

# Task Difficulty and Performance Induce Diverse Adaptive Patterns in Gain and Shape of Primary Auditory Cortical Receptive Fields

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DOI 10.1016/j.neuron.2008.12.027

## SUMMARY

Attention is essential for navigating complex acoustic scenes, when the listener seeks to extract a foreground source while suppressing background acoustic clutter. This study explored the neural correlates of this perceptual ability by measuring rapid changes of spectrotemporal receptive fields (STRFs) in primary auditory cortex during detection of a target tone embedded in noise. Compared with responses in the passive state, STRF gain decreased during task performance in most cells. By contrast, STRF shape changes were excitatory and specific, and were strongest in cells with best frequencies near the target tone. The net effect of these adaptations was to accentuate the representation of the target tone relative to the noise by enhancing responses of near-target cells to the tone during high-signal-to-noise ratio (SNR) tasks while suppressing responses of far-from-target cells to the masking noise in low-SNR tasks. These adaptive STRF changes were largest in high-performance sessions, confirming a close correlation with behavior.

## INTRODUCTION

Humans and animals commonly navigate noisy auditory scenes in which distracters abound and loud background sounds (acoustic maskers) obscure foreground (target) signals of interest. The mechanisms that give rise to the ability to discern and extract targeted auditory signals from noise are multifaceted, including simple adaptation to steady background noise, the perception of pitch that facilitates segregation of simultaneous speakers, and the localization and selective attention to one sound source among spatially distributed sound sources. One process that may underlie some of these abilities is real-time adaptive plasticity, in which the auditory system changes its filter properties in order to optimize its ability to discriminate foreground from background. We have previously described

a form of rapid cortical plasticity in which the spectrotemporal receptive fields (STRFs) in primary auditory cortex (A1) adapt during the task in a manner that maximizes the discrimination of the target (foreground) relative to reference (background) signals (Fritz et al., 2003). Different aspects of this process have been recently explored in a series of experiments in which animals were trained to discriminate tones or tone-complexes from broadband noise, or discriminate between two tones of different frequencies (Fritz et al., 2005, 2007b). In all these experiments, the pattern of STRF changes that emerged followed a simple model in which the acoustic features of the foreground were enhanced and those of the background suppressed, a hypothesis which we called a “contrast matched filter” (Fritz et al., 2007a). Such changes matched the signals’ spectra so as to enhance the STRF responsiveness to the target relative to the reference. For instance, when a target tone is discriminated from a broadband noise reference, an excitatory region at the frequency of the tone emerges in the STRFs, surrounded by a region of suppression; but when the target tone is discriminated from a different reference tone (Fritz et al., 2005), the enhanced target excitation now becomes contrasted with suppression at the frequency of the reference tone.

However, an important and currently unresolved question is whether the magnitude of these changes is influenced by task difficulty, or more specifically, by the perceptual difference between the target and reference signals that the animal must discriminate between. Furthermore, it is unknown how exactly the underlying receptive fields change under these circumstances, i.e., whether they simply exhibit a modulated gain, or alternatively, a change of shape such as via tuning or changing bandwidth. A handful of previous studies of visual processing have demonstrated that increased task difficulty generally enhances allocation of attention and the magnitude of its neural correlates in cortical responses (Boudreau et al., 2006; Spitzer et al., 1988; Spitzer and Richmond, 1991). These measurements, however, did not distinguish receptive field gain from shape changes, and how increased task difficulty affected them differentially.

We explored these issues using an auditory detection task in which a target tone was embedded in broadband noise of fixed amplitude, and task difficulty was modulated by varying the signal-to-noise ratio (SNR) of the target. As target SNR

decreased, distinguishing the target from the reference noise became more difficult, requiring more attention or effort, which, we predicted, could cause larger adaptive changes in the STRF. To explore this hypothesis, we trained ferrets to perform this task in a paradigm that was otherwise identical to one that used pure tone targets (Fritz et al., 2003). In such a paradigm, the reference broadband noise was one of a set of 30 specially designed spectrotemporally modulated broadband noisy sounds—called temporally orthogonal ripple combinations (TORCs)—that were used to measure the STRF of the cell while the animal performed the task (Klein et al., 2000). The target tone here was simply embedded in the last of a sequence of TORCs, with a variable SNR that ranged from +15 to -10 dB. This approach allowed us to measure the full STRF of the cell rather than just its firing rates in response to a stimulus within its receptive field. Such a broad view enabled assessment of a variety of adaptive gain and tuning changes that might otherwise be difficult to detect.

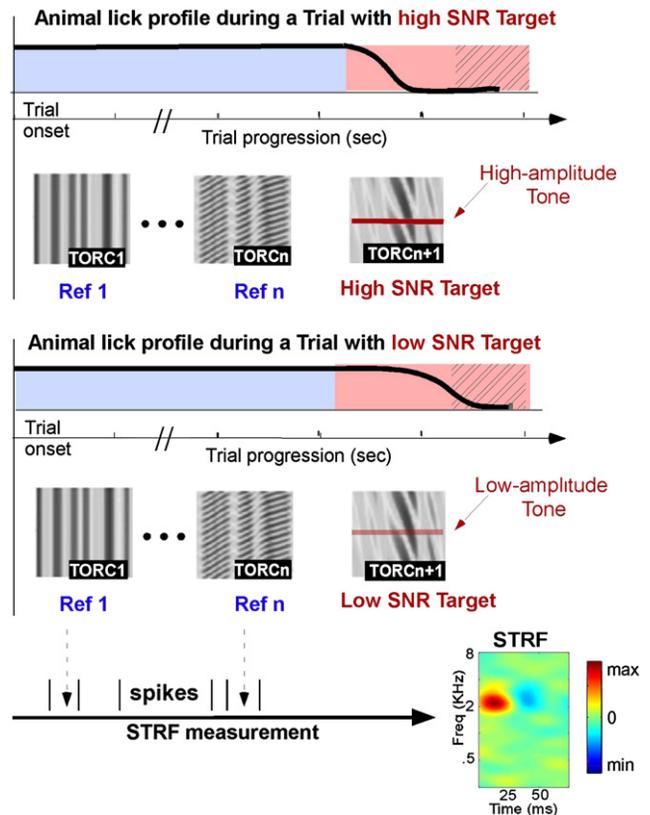
The key feature of the tone-in-noise task is that, unlike the case with pure-tone targets, the TORCs appeared not only as reference stimuli but also as maskers *in* the target stimulus, thus reducing the perceptual difference between target and reference signals. The animal presumably had to actively suppress the noise so as to enhance the detectability of the embedded target tone. We shall describe how rapid A1 plasticity in this task depended on three key factors: (1) task difficulty as reflected by the SNR of the target (i.e., high, medium, or low SNR); (2) cell's best frequency (BF) relative to the frequency of the target tone (i.e., near or far); and (3) attention level as reflected by task performance.

## RESULTS

### Behavioral Tasks and Results

Figure 1 illustrates the basic task, in which ferrets learned to lick a spout for liquid reward during a number (1–7) of reference sounds, but to refrain from licking during target sounds, using a conditioned avoidance paradigm (Fritz et al., 2003; Heffner and Heffner, 1995). The top and bottom panels illustrate the spectra of the noise (TORC) reference and target tone stimuli, respectively, in high- and low-SNR conditions. The noise added to the target was randomly chosen from the set of 30 possible spectrotemporally modulated and broadband TORCs, delivered at the same level as the reference TORCs. The target tone SNR was then adjusted by varying the level of the embedded tone. As indicated, ferrets recognized and responded more quickly to high-SNR than to low-SNR targets.

Figure 2A illustrates the typical average licking profile in one animal for a behavioral block of trials. The ferret consistently licked during the reference TORC stimuli (top panel), but decreased its licking when it recognized the target (bottom panel). This decrease in target licking occurred at different latencies and rates, reflecting the SNR of the target tone-in-noise. Thus, when the target tone was pure, the average lick rate dropped quickly after target recognition and approached zero in the poststimulus decision interval (1500–1800 ms) just prior to the shock interval (crosshatched interval of 1800–2200 ms). As the task became progressively more difficult at lower SNRs, lick rate decreased more gradually following target stimulus

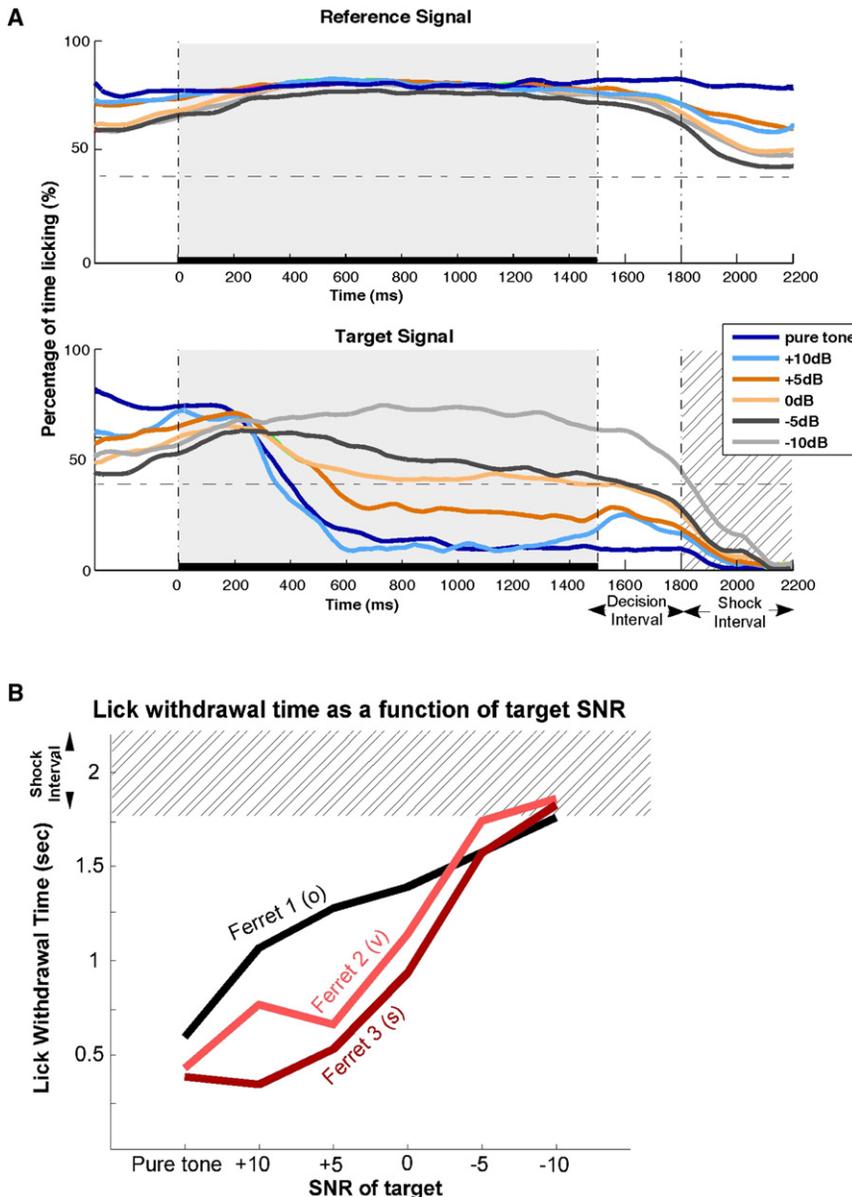


**Figure 1. Schematic of the Experimental Stimuli and Data Analysis**

A series of spectrotemporally modulated noise bursts (TORC1, TORC2, ...) served as reference sounds that ended with an embedded target tone whose level relative to the noise was adjusted in different tasks such that it fell within the range of high SNR ( $\geq 0$  dB), mid SNR ( $5 \text{ dB} \geq < 0$  dB), or low SNR ( $< -5$  dB). Animals licked water from a spout during the reference bursts (blue region), and were trained to withhold licking upon hearing the target tone (pink region). The response latency to the target was shorter in high-SNR (top panel) as compared with low-SNR tasks (bottom panel). STRF measurements were made only from responses during presentation of the reference TORCs, not from target responses.

onset and crossed into the shock interval at rates that were inversely proportional to the detectability of the tone. Licking during the shock interval constituted an error response, and therefore, reflected the decrement in performance of the animal at low SNRs.

In order to develop a quantitative behavioral index of task difficulty, we measured the average lick withdrawal time (LWT) of the animal, which we defined to be the time after target onset when the animal decreased its lick rate to half its average lick rate during the reference stimuli (i.e., down to 40% from 80% in Figure 2A). All three ferrets responded to pure tone targets quickly and suppressed licking with a minimum latency of ~200 ms, as shown by the inflection point in the bottom panel of Figure 2A. For the pure-tone detection task, the LWT was 350 ms from the onset of the target tone. However, when TORCs were added to the target and SNR decreased, ferrets' LWT increased, as shown in Figure 2B, for all three animals tested. This trend resembles the increasing reaction time at lower



**Figure 2. Detection of Tone in Noise in Different SNR Tasks**

(A) Lick rate during reference TORCs was relatively flat (top panel) and provided a baseline against which cessation of licking during target tone presentation was measured. Dashed horizontal line indicates the lick rate at half of this baseline. (Bottom panel) Lick rate began to drop at ~200 ms following onset of the tone. Lick rate decreased more rapidly in higher-SNR tasks, continued to diminish gradually during the tone (shaded interval of 1.5 s duration), and ceased rapidly after the onset of the shock period (300 ms after the end of the tone). (B) Response latency measured in three animals as the lick withdraw time (LWT) from onset of target tone to the point at which lick rate decreased by 50% of average lick rate during the reference period.

Specifically, average discrimination rate during hard blocks was 52.6% compared with 69.2% for the probe trials, whereas during easy blocks, average discrimination rate was 72.9% during easy blocks compared with 58.6% on the probe trials. Thus, performance on the probe trials (for the same SNR level, intermediate probes) varied ~10% depending on overall block difficulty or attentional load (from 58.6% to 69.2%).

**Physiological Results**

Neurophysiological recordings were conducted in A1 of two ferrets (#1 and #2 in Figure 2B) while they performed a tone detection task with target SNRs ranging from -9 to +15 dB. Patterns of receptive field plasticity (derived from a comparison of STRFs measured during the task condition to those measured during

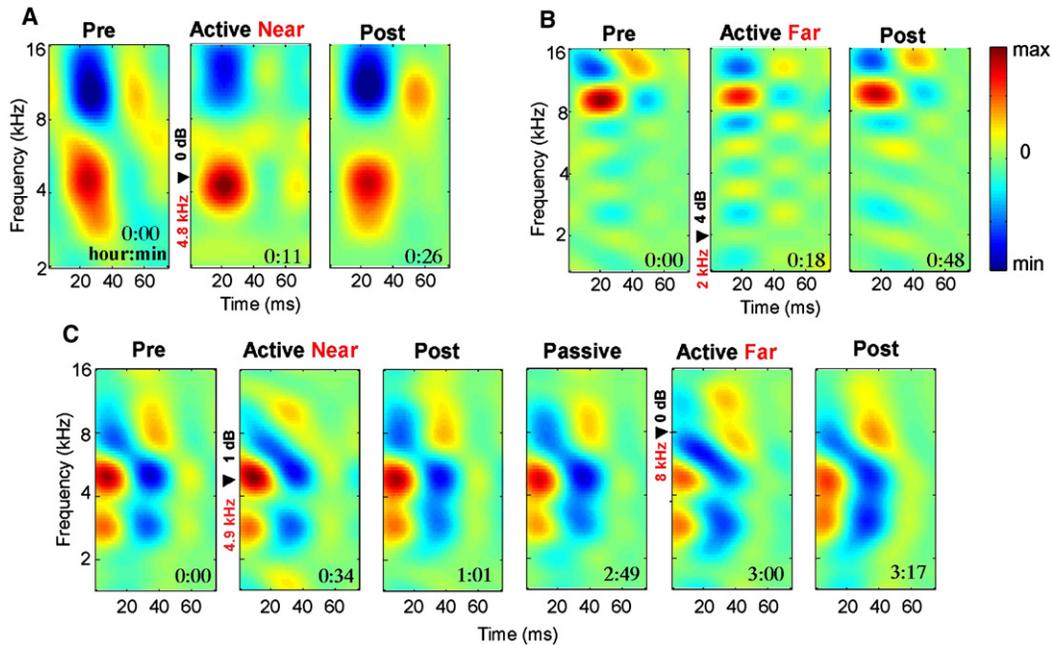
SNRs seen in detection of tone-in-noise with human subjects (Kemp, 1984).

To test the hypothesis that more attentional resources were devoted during difficult (low-SNR) tasks than those devoted during easy (high-SNR) tasks, we modified the task structure by randomly inserting probe trials (25%) of intermediate difficulty during a block of difficult or easy trials (75%). We reasoned that if detection levels of the rarer probes reflected the overall attentional level of the animal during the task that increased with task difficulty, then performance on the probe trials should be better during difficult tasks than during easy tasks (Boudreau et al., 2006; Spitzer et al., 1988). Behavioral experiments with four blocks of easy tasks (SNR = +10 dB) and four blocks of difficult tasks (SNR = -10 dB) tasks were carried out using intermediate probes of SNR = 0 dB. As predicted, probe discrimination rates differed considerably during easy and difficult tasks.

a passive sound presentation condition) were analyzed with respect to variations in two task parameters: (1) the frequency of the target tone relative to the BF of the recorded cells, and (2) task difficulty (i.e., target SNR). All STRF measurements were made from responses to the reference TORCs alone, not during any target presentations (as described in detail in Experimental Procedures and in Fritz et al., 2003).

Ferrets performed two or three tasks in a given recording session, but it was not always possible to maintain recordings from the same cell throughout multiple task conditions. Consequently, most of our STRF measurements are from single cells that were recorded during one task condition and also during its preceding passive state. In a given task, the target tone frequency and SNR were held constant throughout. Neurophysiological data were then pooled from all cells across different recording sessions.

### STRF changes in high SNR tasks



**Figure 3. STRF Changes in Three Units during High-SNR Tasks**

(A) STRF measured before, during, and after task performance. Target tone was set at 4.8 kHz, near the BF of the cell that was approximately at 4 kHz. During the task, the STRF sharpened its outlines considerably and became enhanced relative to the pretask STRF. The STRF reverted to its original shape after the task. The starting time of each STRF measurement (relative to the beginning of the series) was noted at the bottom right corner of each panel.

(B) STRF changed when the target tone (2 kHz) was placed far from the BF (9 kHz) of a cell. During the task, STRF became suppressed and partially recovered afterwards.

(C) STRF changes in a sequence of two tasks. In the first, the target tone was placed near the BF (4.9 kHz), causing the STRF to become enhanced. When the target tone was placed far from the BF (8 kHz), the STRF became suppressed during the task and partially recovered afterwards. All STRFs are shown relative to the same color scale.

For analysis, we subdivided the data into near and far cells according to the separation between the each cell's BF (defined in [Experimental Procedures](#)) and the target tone frequency. Cells were labeled as near the target if the unit's BF was within 0.6 octaves from the target tone and as far otherwise. Apart from giving a roughly balanced population of each type (112 versus 125), the precise choice of this dividing line was arbitrary, and none of the results described below depended critically on its exact position (See [Figure S4](#) in the [Supplemental Data](#), available online). Therefore, units designated as near were primarily driven by the target tone, but also partly by the simultaneously presented component of noise in their local spectral vicinity. In contrast, far neurons could be viewed as primarily encoding the reference TORC and the masking noise in the target signal. Data were also subdivided into three groups according to the difficulty of the tasks, as parameterized by the target SNR. The three nonoverlapping ranges were: high SNR ( $\geq 0$  dB), mid SNR ( $0 \text{ dB} > \text{SNR} \geq -5$  dB), and low SNR ( $< -5$  dB), with 93, 57, and 87 single units in each range, respectively.

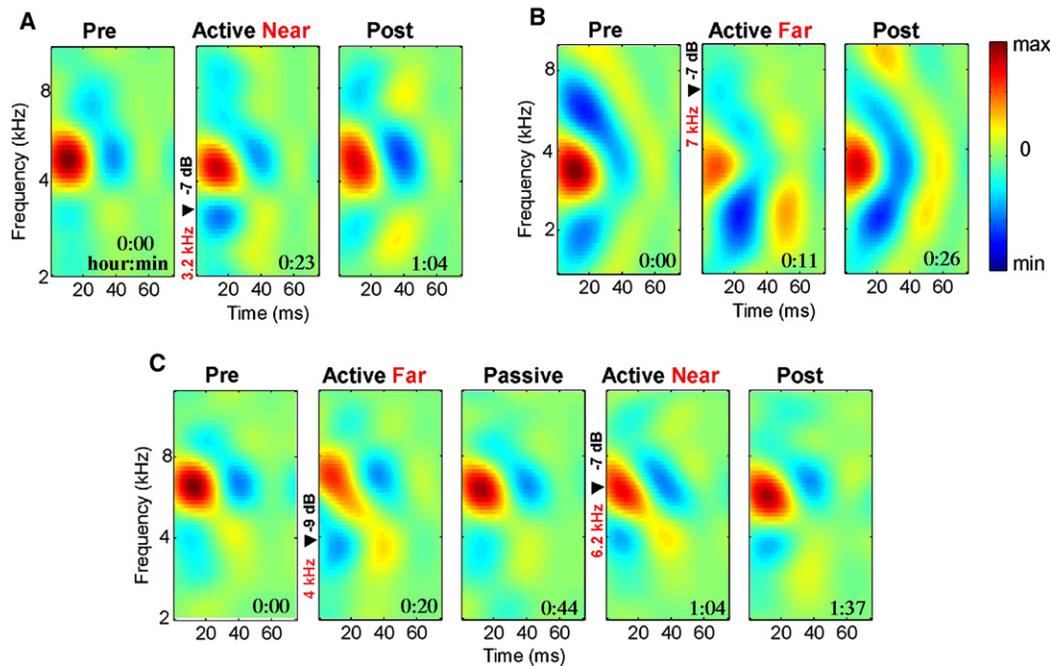
As in all our previous reports, all measured STRFs were normalized by their individual r.m.s. power (see [Experimental Procedures](#)). As a consequence, differences between the normalized STRFs reflected mostly changes in shape (as opposed to STRF gain). This issue is revisited later in this report

where we explore a model that explicitly distinguishes between the gain and shape changes.

#### Patterns of STRF Plasticity in Single Units

When an animal discriminates a pure target tone from a TORC reference or from a tone of a different frequency, the induced STRF plasticity in A1 neurons usually consists of an enhancement at the frequency of the target tone and a weaker suppression that reflects the broad spectrum of the reference signal ([Fritz et al., 2007b](#)). In the current experiments, the observed pattern of plasticity was roughly similar when the target tone level was high relative to the noise ( $\text{SNR} \geq 0$  dB) and the BF of the cell's STRF was near the target tone. An example of such STRF plasticity is shown in [Figure 3A](#), when a target tone (4.8 kHz) with a relatively high SNR of 0 dB was placed near the BF of the cell (4.3 kHz). During behavior, the unit's STRF sharpened and its excitatory region strengthened relative to the inhibitory sideband. Afterward, the STRF largely reverted back to its prebehavior shape. This kind of facilitatory change at target frequency during behavior is typical of results of the pure-tone detection experiments reported previously ([Fritz et al., 2003](#)). However, in sharp contrast, when the tone was placed far from a unit's BF, the STRF change became suppressive in high-SNR tasks. For example, the target tone (2 kHz) in [Figure 3B](#) (high SNR of

## STRF changes in low SNR tasks



**Figure 4. STRF Changes in Three Units during Low-SNR Tasks**

(A) STRF measured before, during, and after task performance. Target tone was set at 3.2 kHz, near the BF of the cell (4.7 kHz). During the task, the STRF became suppressed relative to the pretask STRF. The STRF partially recovered its original shape after the task.

(B) STRF changed when the target tone (7 kHz) was placed far from the BF (3 kHz) of a cell. During the task, STRF became strongly suppressed and recovered partially afterwards.

(C) STRF changes in a sequence of two tasks. In the first, target tone (4 kHz), the BF (6.3 kHz), and the STRF became suppressed. When the target tone was placed near the BF, suppression during the task was weaker than that during the first task and the STRF recovered afterwards. All plots are shown relative to the same color scale with red denoting increase and blue denoting decrease relative to the green baseline.

4 dB) was placed more than 2 octaves below the unit's BF (9 kHz). The excitatory region of the unit's STRF (near 9 kHz) became substantially suppressed relative to its prebehavioral levels. As has often been observed in examples in previous plasticity studies (Fritz et al., 2003), this change persisted after behavior was completed. Although we frequently observed persistent changes, there was no systematic trend in persistence versus the type of STRF plasticity.

This pattern of STRF changes is further illustrated by the sequence of two behavioral tasks shown in Figure 3C. Here the unit's prebehavioral STRF had two excitatory regions near 3 kHz and 5 kHz (the BF). When the high-SNR target was placed near the BF (4.9 kHz), the nearby region sharpened and became slightly enhanced during behavior, and then returned to its prebehavioral shape following the task. The task was then repeated but with a tone far from the BF (8 kHz). Consistent with the previous example, the excitatory region in the STRF was suppressed, a change that persisted afterwards.

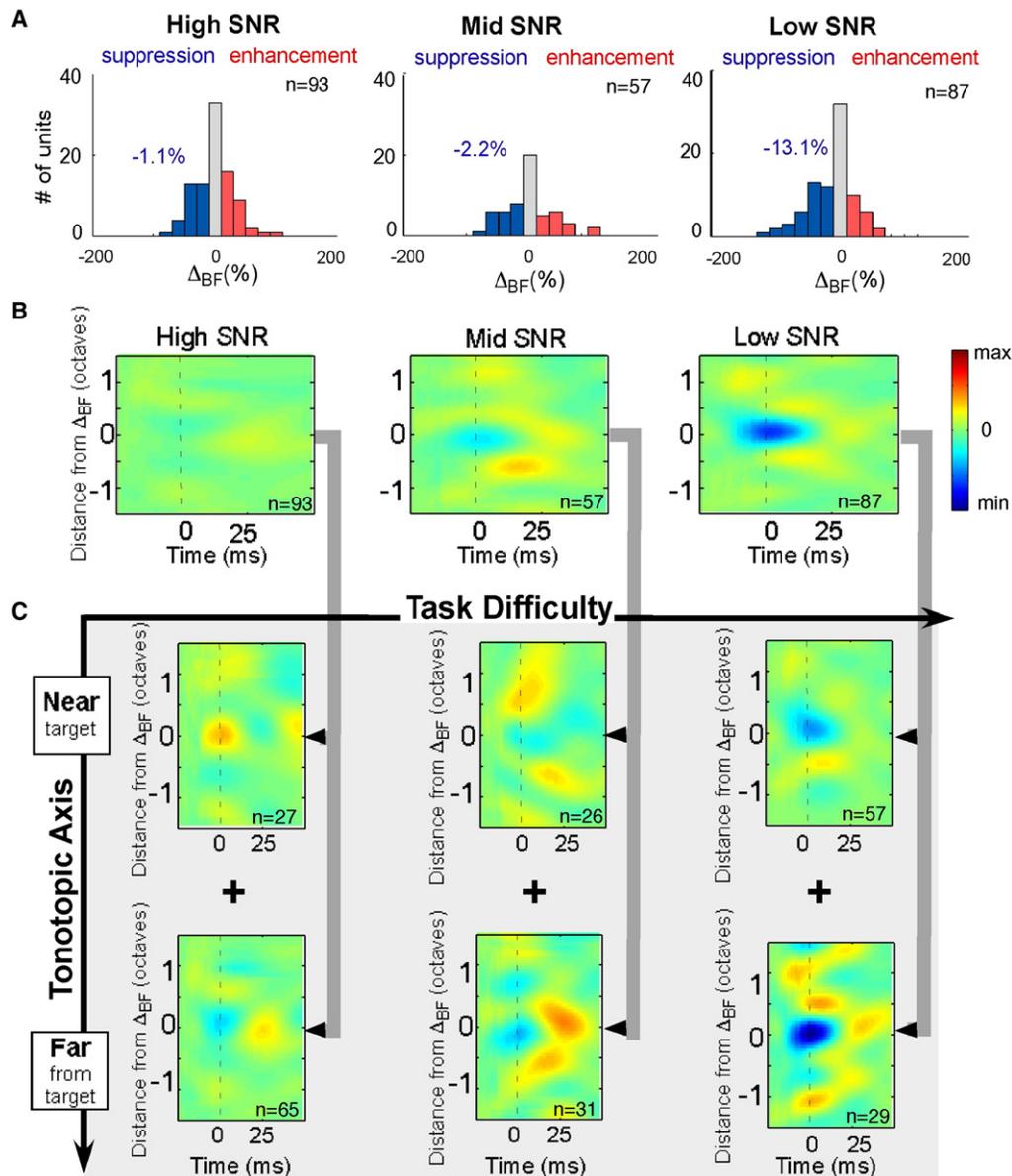
When the task was more difficult (low SNR), the plasticity pattern changed and STRFs on the whole became more depressed, especially far from the target. Three examples of such single-unit changes are depicted in Figure 4. In the first (Figure 4A), the target tone (3.2 kHz) was placed near the BF (4.7 kHz). During behavior, two changes were evident: the excit-

atory field was depressed and became more narrowly tuned around the BF, and a new inhibitory region appeared below the BF. Following behavior, the STRF partially recovered its broader excitatory field, which remained weak, however, relative to a strengthened postexcitatory inhibitory field. The example in Figure 4B illustrates the changes due to a low-SNR target tone placed far from the BF. Again, the STRF excitatory region weakened considerably during behavior, while the suppressive sideband below the BF strengthened. Note also the disappearance of inhibition above the BF near the frequency of the target tone (7 kHz) and the partial recovery of the original STRF after the behavior was completed.

Figure 4C illustrates these same changes in a sequence of two low-SNR tasks in which the tone was placed at two distances: first relatively far from, and then near, the BF (6.3 kHz). As in the previous two examples, the STRF excitatory field was suppressed in both cases and then mostly recovered postbehavior. Suppression, however, was stronger in the far than in the near condition (second versus fourth panels).

#### Population Patterns of STRF Plasticity

To obtain a global view of the receptive field plasticity in these tasks, and the factors that influenced the nature of this plasticity, we examined STRF changes in a population of 237 cells from two



**Figure 5. STRF Amplitude Changes as a Function of Target SNR**

(A) Histogram of STRF changes at BF ( $\Delta_{BF}$ ) in all cells tested during high-, mid-, and low-SNR tasks showing progressively deeper suppression with an average  $\Delta_{BF}$  of  $-1.1\%$ ,  $-2.2\%$ , and  $-13.1\%$  in high-, mid-, and low-SNR tasks, respectively.

(B) Average STRF differences ( $STRF_{diff}$ ) between the active and passive states. Net suppression increased with increasing task difficulty (lower SNRs). Note that the time axis here is not the same as in Figures 3 and 4, but instead is normalized relative to when the  $\Delta_{BF}$  occurred in each cell.

(C) STRF changes for each SNR divided into near and far groups. In all tasks, changes in the far cells were more suppressive than in near. Note that near cells showed an enhancement (positive  $\Delta_{BF}$ ) in the high-SNR task, which weakened with increasing task difficulty. All plots are shown relative to the same color scale.

animals. We defined an “amplitude” change ( $\Delta_{BF}$ ) in the STRF as the maximum difference between the “active” (during task) STRF and the “passive” (preceding the task) STRF measured within a spectrotemporal band  $\pm 0.2$  octaves and 0–25 ms around the BF (as discussed in more detail in Experimental Procedures). As explained earlier, each STRF was normalized with respect to its r.m.s. power. The results of the population analysis were relatively independent of the exact choice of parameters and manipulations of this spectrotemporal window and normalization.

#### Dependence on Task Difficulty

STRFs exhibited different overall patterns of change depending on task difficulty (i.e., target SNR), as shown in Figures 3 and 4. In Figure 5, we compile and contrast such STRF changes from all units measured in the different tasks. In Figure 5A, histograms of the  $\Delta_{BF}$  changes were subdivided into high-, mid-, and low-SNR conditions. Overall, suppression was greater in lower-SNR tasks, as evidenced by the increasingly leftward skewed histograms. Suppression was weak in high- and mid-SNR tasks,

and became significant (mean =  $-13.1\%$ ;  $p < 0.05$ ) only in the low-SNR tasks. Using ANOVA we found that  $\Delta_{BF}$  changes for high- and low-SNR conditions were significantly different ( $p < 0.05$ ). To present this trend in a more visually intuitive manner, we averaged the difference between active and passive STRFs ( $\text{STRF}_{\text{diff}}$ ) of all units within each SNR group after aligning them at the locations of their  $\Delta_{BF}$ s, as shown in the three panels of Figure 5B. As anticipated from the  $\Delta_{BF}$  histograms in Figure 5A, suppression gradually increased from low to high task difficulty (i.e., from high to low SNR) as indicated by the progressively darker blue region at the origin of each subpanel in Figure 5B.

The histograms and averages of Figures 5A and 5B include both near and far cells in each SNR condition. In Figure 5C we grouped the  $\Delta_{BF}$  changes according to target proximity in order to highlight the opposite effects that occur within each. Note that in the high-SNR tasks the net change across all cells was small and barely noticeable (Figure 5B, left panel). However, when we grouped the plasticity changes by near and far cells, it became apparent that near cells on average were enhanced (red) whereas far cells were suppressed (blue). This difference between near and far cells was also seen in the mid- and low-SNR groups, but this time relative to an overall progressively deeper (more blue) suppression. Figure S1 accumulates the data from all three SNR conditions to highlight the dependence of receptive field plasticity on the distance between the target tone and the BF of the STRF, regardless of task difficulty.

#### Dependence on Behavioral Performance

Fluctuating performance levels in a given task may reflect changes in the attentional and/or motivational state of the animal. To explore how performance correlated with STRF changes, we ranked the performance level for all experiments (as defined by the discrimination rate for behavioral sessions in individual physiology experiments; see Experimental Procedures) and then computed the average difference between active and passive STRFs for the experiments with best (top third) behavioral performance. Figure 6 displays the results from a total of 85 cells in the tone-in-noise detection task, sorted into three groups by SNR level.

The trend of increasing suppression for low SNRs (e.g., as in Figure 5) is repeated here, but with an important difference: STRF changes were amplified. For example, in Figure 6B, the STRF change in high-SNR tasks exhibited a strong net (excitatory) enhancement compared with its weaker counterpart in Figure 5B. By contrast, low SNR tasks induced a deeper suppression than seen earlier in Figure 5B.  $\Delta_{BF}$  changes for high- and low-SNR conditions here were more distinctly different as demonstrated by the divergence in their means ( $p < 0.01$ ). Therefore, the near and far cell populations within each of these three tasks (Figure 6C) displayed a divergence of enhancement and suppression similar to that of the entire neuronal population (Figure 5C), except that the changes were more pronounced.

To demonstrate further the crucial role of behavior in inducing these changes, we measured STRF changes in 93 units from three naive animals using exactly the same stimuli and analysis procedures as those used in the behavioral animals. We observed some minor, but no consistent, changes in the STRFs in the absence of behavior, as illustrated in Figure S2.

#### Task-Related Suppression of TORC Responses

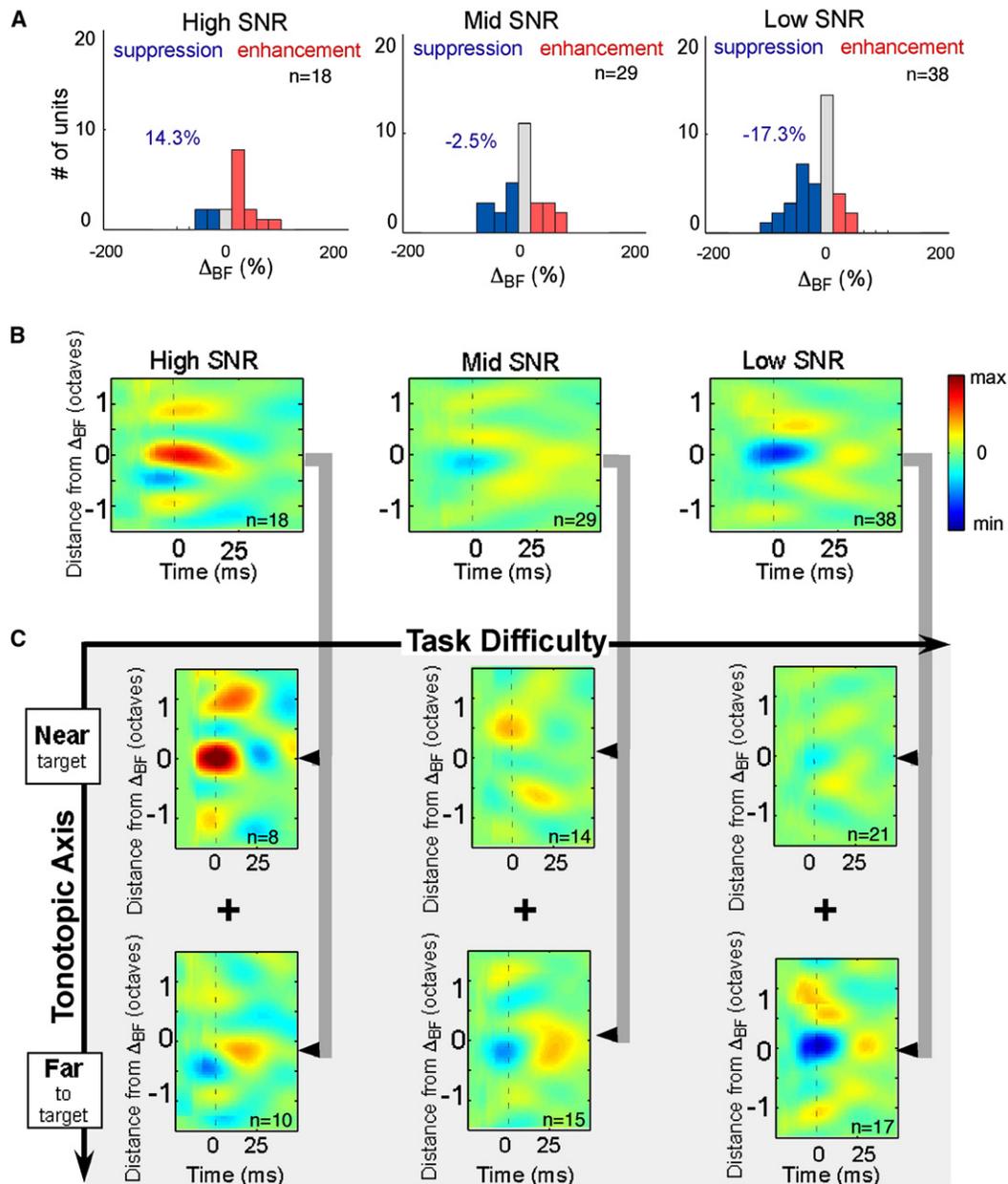
Our experimental technique and behavioral paradigm allowed us to measure the effect of STRF changes on the average peristimulus time histogram (PSTH) responses to the (reference) TORC stimuli since identical sets and sequences of TORCs were presented to all animals in all SNR tasks. Figure 7A contrasts the average TORC responses in the near and far cell populations (red and blue curves, respectively) during the two extreme tasks, the high- and low-SNR (left and right panels, respectively). This population of cells is the same group selected from sessions with best performance as shown in Figure 6. The normalized responses of these groups of cells during the passive epoch preceding the behavioral tasks are plotted in gray in each panel. Two obvious trends confirm earlier conclusions: (1) responses during behavior were more suppressed in far cells than in near cells, and (2) suppression strengthened with increasing task difficulty (lower SNRs). Thus, within a given level of task difficulty, far cells were more suppressed than near cells. Furthermore, increasing task difficulty from high- to low-SNR targets caused a uniform overall suppression of about one-third in the firing rate (as indicated by the dashed lines of Figure 7A).

#### Contributions of Gain and Shape Changes to STRF Plasticity

What are the relative contributions of gain and shape changes to rapid STRF plasticity? It is clear that changes in TORC responses described above were not due to a pure gain change because STRFs also exhibited substantial shape changes (e.g., the six examples in Figures 3 and 4), and because the results of Figures 5 and 6 were obtained despite the fact that STRFs were normalized to equalize their r.m.s. power (see Experimental Procedures).

As explained earlier, STRF power normalization, which we have used in previous publications (Fritz et al., 2003, 2005), does not completely differentiate between gain and shape changes. Thus, to assess more accurately the relative changes in gain and shape, we computed an alternative measure that explicitly and separately included both gain and shape changes. We defined the active (during) STRF ( $\mathbf{S}_a$ ) as the sum of a scaled passive (before-task) STRF ( $\mathbf{S}_b$ ) and a change in the shape of the STRF, i.e.:  $\mathbf{S}_a = g \cdot \mathbf{S}_b + \delta$ , where  $g$  is the gain that reflects the fraction of the STRF that maintained its original shape, and  $\delta$  is the remaining (orthogonal) shape change that could not be captured by scaling  $\mathbf{S}_b$  (this  $\delta$  was used to generate the plots in Figure 7C). To confirm that these results were robust with respect to measurement noise, we also computed shape changes using an alternative method developed by David et al. (2008) (described in more detail in Experimental Procedures and Supplemental Data), and replicated the same trends discussed below.

Figure 7B illustrates the distribution of the gain changes computed for the same cells in Figure 7A but broken into four groups: high versus low SNR and near versus far. To summarize these data: (1) in a majority of cells (>66% in high-SNR and near STRFs, and >80% in low-SNR and far cells), the gain was  $\leq 1$  (median of approximately 0.9 and 0.7, respectively), indicating an overall suppression of the gain during behavior. (2) Increasing task difficulty or distance from target caused an additional small depression of the gain in about 15% of all STRFs. This weak dependence of the gain on task difficulty, however, was not



**Figure 6. STRF Changes during Tasks with Best Performance**

All data were measured and presented exactly as in Figure 5, except in tasks with the best performance (see text). (A) Histogram of  $\Delta_{BF}$  changes in high-, mid-, and low-SNR tasks with average  $\Delta_{BF}$  of 14.3%, -2.5%, and -17.3% for high, mid, and low SNR, respectively. Changes in the high- and low-SNR cases are significant ( $p < 0.05$ ). (B) Average STRF<sub>diff</sub> between active and passive states. (C) STRF changes at each SNR divided into near and far groups. All plots are shown relative to the same color scale. All other details are as in Figure 5 panels.

confirmed when we pooled the results from all cells in this study, including all performance levels (see Figure S3A, where gain distributions remain relatively unchanged with SNR with medians of about 0.7). Finally, we replicated these trends in the gain distributions when using the alternative method of David et al. (2008) to take noise into account (see Figure S3B).

We next considered the contribution of the pure shape changes, which reflected STRF changes that remained after accounting for all gain effects. Figure 7C illustrates the average

$\delta$  for the same population of cells that were shown in Figures 7A and 7B. All panels employ the same color scale as Figure 6B. Unlike the suppressed gain, (1) the average shape change  $\delta$  was mostly positive and focused in the near cells during high-SNR tasks, and (2) shape changes followed the same trends seen above in Figures 5 and 6, both with respect to task difficulty (becoming more enhanced in high-SNR tasks) and with respect to distance from target tone (near STRFs are enhanced relative to far cells).

Finally, Figure 8 displays the average combined gain and shape (or net) changes induced during behavior in high- and low-SNR tasks, and in near and far cells. The pattern of changes looks similar to that due to shape in Figure 7C, except for a depression in all panels reflecting the overall suppression of the gain across all tasks and distances. To summarize, in high-SNR tasks, the target induces positive changes in nearby STRFs, thereby enhancing the representation of the target tone, similar to earlier findings with pure-tone targets (Fritz et al., 2003). Decreasing the target tone (low SNR) causes overall gain suppression, especially in far cells, thereby maintaining the enhanced representation of the target tone responses relative to those of the masking noise.

## DISCUSSION

When an animal performs an auditory task, its A1 receptive fields undergo rapid changes that reflect the stimuli and performance of the task (Fritz et al., 2003, 2007a). This study extends those findings by examining the effects of modulating the difficulty of a tone detection task by embedding it in noise at different SNRs. Behaviorally, increasing task difficulty has been shown to induce compensatory enhancement of attention (Boudreau et al., 2006; LaBerge et al., 1991; Lavie and Cox, 1997; Sade and Spitzer, 1998; Urbach and Spitzer, 1995; Yantis, 1996). Physiologically, this enhanced attention has been linked to increased responses to targets or more suppression of distracter responses (Chen et al., 2008). Either way, these changes enhance target representation and hence facilitate target detection.

We had hypothesized that attention-induced response modulation would serve to counter the detrimental effects of masking noise by maintaining the neural representation of the tone. Interpreted in this light, STRFs adapted differently across a wide swath of the tonotopic axis relative to the target tone. Cells tuned near the target tone frequency displayed an enhanced sensitivity at BF, while those tuned far from it became largely suppressed (Figures 5, 6, and 7). These effects were stronger in experiments when performance was best (Figures 6 and 7). While the analysis of STRF plasticity in the current study is centered on cell BF, the results are largely compatible with earlier studies of task-related plasticity in which analysis was centered on target frequency (Fritz et al., 2003, 2005, 2007b).

### Effects of Attention on Receptive Field Gain and Shape

In studies of visual cortex, attentional effects on neural responses have often been thought to reflect a change in both gain and shape of spatial (Connor et al., 1997; Luck et al., 1997) and feature (David et al., 2008; Maunsell and Treue, 2006) receptive fields. Our STRF measurements allowed us to separate these two factors and assess their relative contributions. By assuming that STRF changes were the superposition of a global gain change and an orthogonal shape change, the analysis revealed that engagement in the tasks resulted in a substantial (10%–30%) reduction in STRF gain during behavior (Figure 7B). This change was the same regardless of task difficulty, and occurred across most cells (near or far). However, the gain reduction was counterbalanced by an enhancement

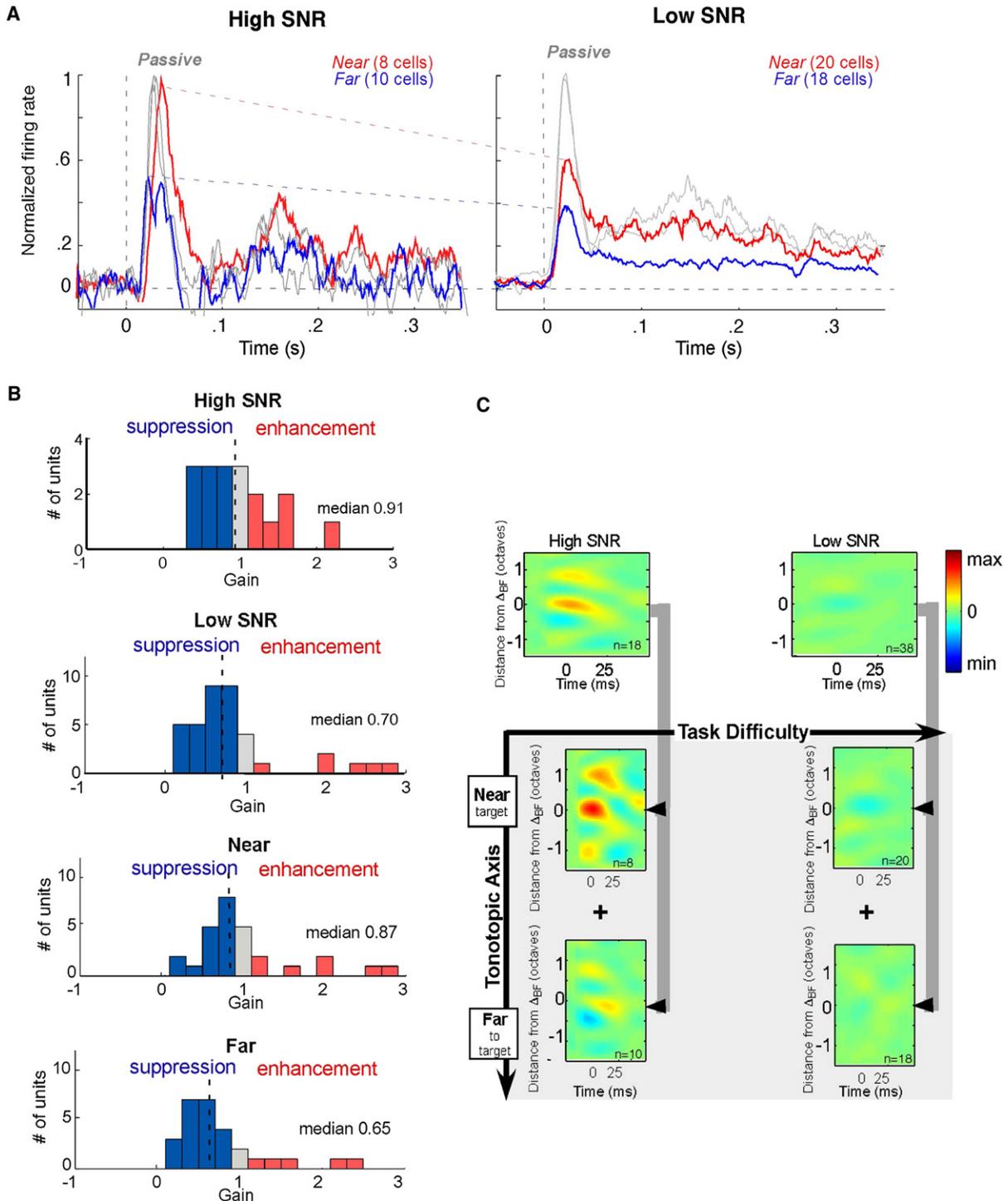
due to shape changes that was focused and largest in cells with BF near the target tone during high-SNR tasks (Figure 7C).

It is unclear to what extent this pattern of broad gain reduction and focused shape enhancement was dependent on the specifics of the tone-in-noise task. For example, it is possible that this gain suppression simply related to an increase in overall level of alertness when ferrets became engaged in any task (as suggested by G. H. Otazu and T.Z. Zador, 2006, Society for Neuroscience, abstract). Or, it could have been specific to our task design or valence (i.e., specific to a conditioned avoidance paradigm as opposed to the appetitive positive reinforcement paradigms more widely used in studies of attention). Finally, it is conceivable that our stimulus design—specifically, holding noise (TORC) levels constant through all SNR conditions (with only the level of the target tone varied)—was a reason for the relative constancy of the gain reduction regardless of task difficulty. We have not observed systematic changes in gain in previous studies that, unlike the present study, did not include broadband noise in the target. While definitive resolution to these issues will require further experiments that dissociate the contributions of the stimulus structure and the behavioral paradigm to these changes, we nevertheless offer a few conjectures below based on what we already know from the results of previous studies of attention-driven effects in the auditory and visual systems.

### Functional Significance of Rapid Plasticity

The diverse pattern of STRF changes described in this report is broadly consistent with the types of plasticity observed in previous studies in which ferrets detected a target tone or tones relative to a reference TORC noise (Fritz et al., 2003, 2007b), or discriminated a target tone relative to a reference tone of a different frequency (Fritz et al., 2005). In those experiments, target tones induced an enhanced sensitivity, whereas reference signals produced mild to strong suppression that reflected the reference spectral shape. We have interpreted such STRF transformations as a contrast matched filter that is driven by the spectral difference between target and reference signals that serves to amplify their differential neuronal responses and, thus, their perceptual distance and discriminability (Fritz et al., 2007b). In the current experiments, not only did the reference stimuli consist of broadband noise, but the target tone was also embedded in the same broadband noise. Hence the process of extracting the tone component of the target necessitated suppression of responses to this concurrent masking noise while simultaneously enhancing the sensitivity to the target tone.

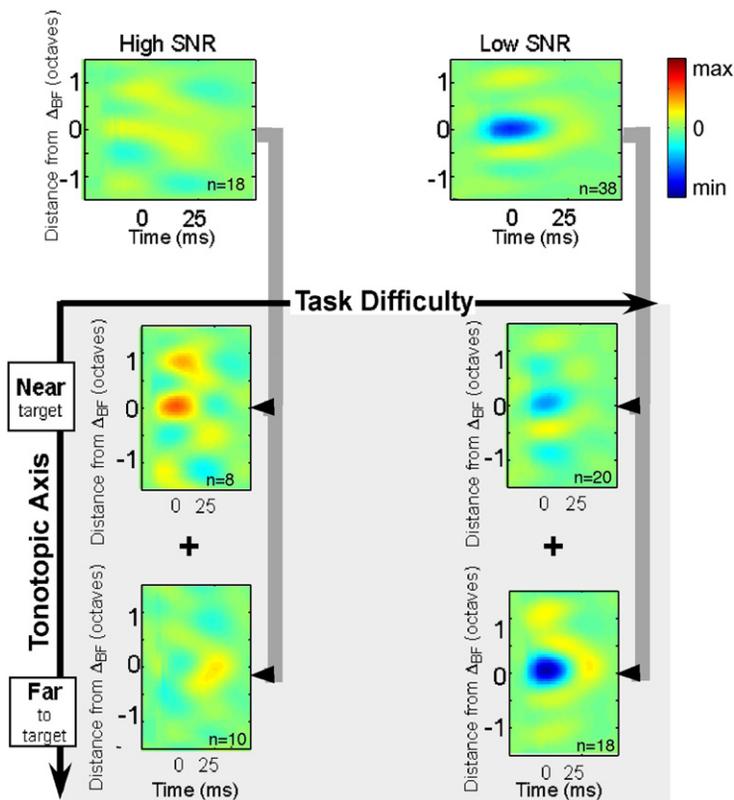
Such a differential pattern of plasticity in near and far cells is consistent with our previous findings that significant STRF plasticity occurred when the behaviorally relevant stimuli in the task (target and/or reference signals) were near the cell's BF (Fritz et al., 2007b). In the current experiments, the excitatory enhancements induced in the near cells stem from their proximity to the target tone, whereas the strong suppression in the far cells was due to the behaviorally relevant broadband masking noise that surrounded the target and drove the responses in those cells. Without this noise, we conjecture that changes in far cells would have been much smaller since the target tone was likely to be relatively far from the BFs of these cells (Fritz et al., 2003, 2005).



**Figure 7. Contributions of Gain and Shape Changes to TORC Responses and STRF Plasticity**

(A) Dependence of PSTH reference responses on task difficulty and BF separation from target tone. PSTH curves were computed from all cells selected for Figure 6 during the passive state (faint gray curves), and during the high-SNR and low-SNR tasks (left and right panels, respectively). In each panel, responses of near (red) and far (blue) cells are shown. All responses were normalized relative to their corresponding passive responses (after subtracting out the spontaneous activity). In general, far cells were more suppressed relative to the near cells. For both near and far cells, increasing task difficulty (from high to low SNR) caused comparable suppression of about 30%.

(B) Distribution of STRF gain changes during behavior relative to the prebehavioral state. These distributions depended weakly on task conditions and target distance from BF as shown in bottom and right panels. Specifically, these pure gain changes resulted in increased suppression of far STRFs (bottom panels) and of STRFs during low-SNR relative to high-SNR tasks (first and third distributions from the top).



**Figure 8. Average STRF<sub>diff</sub> between the Active and Passive States, Taking into Account the Superposition of Both Gain and Shape Changes**

All details of the averaging are as in previous plots (Figures 5, 6, and 7). The pattern of changes is analogous to that due to shape only (Figure 7C), except for an overall depression (blue) added to all panels. A net positive STRF change (red) is seen in the near cells during high-SNR tasks. By contrast, a net deep suppression is seen in far cells during low-SNR tasks. The two panels at the top display the dependence on task difficulty independent of distance from target. All panels are shown relative to the same color scale.

response. However, because of the limited frequency resolution of our STRFs, we also cannot rule out the possibility that some A1 neurons adaptively reshape their receptive fields to create narrow, highly selective, spectrally matched filters for the target tone frequency.

In interpreting the effect of behavior on the TORC responses (as shown in Figure 7A), it is important to consider the broadband nature of these stimuli, which precludes a simple correspondence with the underlying changes in the STRF shape or gain. For instance, consider the positive enhancement in the near STRFs of high-SNR tasks in Figure 6C. Such a change may not result in an increase in TORC responses of these cells (in Figure 7A) because the TORCs are broadband stimuli that overlap the entire STRF—both at its enhanced excitatory region and at any inhibitory sidebands. Nevertheless, it was evident that the overall suppressive trends in the STRFs were substantial enough to be reflected in the TORC responses during behavior. Furthermore, we found no such changes in TORC responses in naive animals listening to the same reference and target stimuli, confirming that the behavioral engagement of the animal was necessary for rapid plasticity in receptive field gain as well as shape.

#### Relation to Attention Effects on Visual Responses

Systematic STRF shape changes described in our experiments occur only when the animals are engaged in behavioral tasks requiring attention to target and reference stimuli, and do not reflect stimulus adaptation such as might be expected to occur during passive presentation of the same stimuli (Elhilali et al., 2007; Fritz et al., 2007b). We have used the term “rapid task-related plasticity” to describe these transformations because they are induced rapidly after the onset of the behavior (occurring within a few minutes, which is the earliest our methods allow us to measure them). Moreover, although rapid in onset, they often persist for minutes or hours following the conclusion of the task (Fritz et al., 2005). Despite these distinctive properties, the effects may be fundamentally similar to those transiently induced

#### Enhancement of Stimulus Representation

Ultimately, we can interpret STRF changes as task-related neural plasticity that serves to enhance the neural representation of target and reference stimuli so as to facilitate their behavioral discrimination. When an animal engages in a pure-tone or a high-SNR detection task, cells with BF near the target tone become sensitized, while far cells are weakly suppressed because of the broadband reference and masker noise (Fritz et al., 2003). As the tone level decreases (lower SNR), the near-target enhancement is replaced gradually by a net weak suppression of the STRFs. We conjecture that the suppression in cells with BFs far from the target is largely due to the broadband nature of the masker, i.e., suppression would have been confined to a narrower region of the spectrum if the masker had been a narrow band of noise surrounding the tone, or just a distracter reference tone (as in Fritz et al., 2005).

The fact that we observe larger changes aligned at the BF rather than at the target frequency (as observed in Fritz et al., 2003) suggest that, in the presence of masking noise in the target, plasticity mechanisms in A1 may not be able to facilitate responses to the exact frequency of the target tone. Instead, a slightly different, but compatible, view of plasticity may come into play in the tone-in-noise task, in which near cells that respond preferentially to the target would simply enhance their

(C) Contribution of STRF shape changes to plasticity was comparable in strength but almost completely positive and focused when the target tone was in a high SNR and near the BF of the cell. General trends remained the same as in Figures 5 and 6, indicating diminished shape changes in more difficult tasks (low SNR) and in far STRFs. All plots are shown relative to the same color scale for all panels in this figure.

by attentional demands in visual tasks. The contrast matched filter shares many properties with models proposed to describe the effects of attention in the visual system (Compte and Wang, 2006; Connor et al., 1997; David et al., 2008; Luck et al., 1997; Maunsell and Treue, 2006; Womelsdorf et al., 2008).

The different dynamics of the effects may simply reflect the varied design of the experiments rather than the basic underlying neural phenomenon. For instance, an important feature of our experiments is their block design, in which attention to a specific target (tone) is maintained throughout the task, thus allowing for sustained attentional effects to build up, which we conjecture may contribute to the strength of receptive field changes during behavior as well as to their postbehavioral persistence. There is also general agreement between our findings and the results of visual attention studies in which attention-induced response modulations have been interpreted as changes in receptive field shapes. For instance, in experiments manipulating selective spatial attention (Connor et al., 1997; Womelsdorf et al., 2008), receptive fields in the retinotopic vicinity of the focus of attention shifted and narrowed, while others far away remained unchanged. In our experiments, STRF shape changes were also largest in the tonotopic vicinity of the target tone (Figure 7C). However, further detailed comparison of these two sets of findings may be of limited value because of key differences in the behavioral paradigm and data analysis. First, we included masking stimuli (or effectively, distracters) in our tasks, which modulated task difficulty and probably caused the suppression in STRFs far from the target tone (see below). Second, we quantified STRF changes in terms of a pure gain and an orthogonal shape change, a parameterization that differs from the Gaussian fits of the visual receptive fields (Womelsdorf et al., 2008). Finally, during the tone-in-noise task, the strategy of the animal is unlikely to be to selectively attend to the frequency of the target tone. Instead, its strategy may be to discriminate between the target's narrowband structure and the broadband references (TORC).

Finally, there are close parallels between our results and those that examined the effects of task difficulty on the responsiveness of the visual cortex cells in monkey (Boudreau et al., 2006; Chen et al., 2008; Spitzer et al., 1988; Spitzer and Richmond, 1991). In one study, Boudreau et al. (2006) compared the activity of visual neurons during easy and difficult behavioral tasks in which targets and distracters were cued by their likelihood of occurrence. They observed that during difficult tasks, attending selectively to the likely stimulus (target) caused small increases in the responses near it, but substantial suppression of responses to the (unattended) distracter, results that are analogous to the net effects seen in our experiments (e.g., Figure 6). This pattern of attentional effects has been generally described as a center-surround pattern of "facilitation-suppression" that sharpens the sensory representation of competing stimuli by facilitating responses to the attended stimulus (foreground) and suppressing the rest (background) (Chen et al., 2008).

## Conclusion

This study investigated the effects of varying task difficulty on dynamic receptive field changes in auditory cortex. Manipulating task difficulty revealed a previously unreported dimension along

which plasticity occurs, suppressing the acoustic background while further enhancing the representation of the relevant auditory object. The magnitude of changes correlated with task performance, suggesting a direct relationship between the level of attention and magnitude of plasticity. These findings shed new light on the dynamics of plasticity in the brain and the mechanisms by which attention improves task performance.

## EXPERIMENTAL PROCEDURES

### Stimuli

Reference stimuli were randomly chosen from a set of 30 TORCs (Klein et al., 2000), broadband stimuli that spectrally span 5 octaves. Each of the 30 TORCs was a broadband noise with a dynamic spectral profile that is the superposition of the envelopes of six ripples. A single ripple has a sinusoidal spectral profile, with peaks equally spaced at 0 (flat) to 1.2 peaks-per-octave; the envelope drifted temporally up or down the logarithmic frequency axis at a constant velocity from 4 Hz up to 24 Hz (Depireux et al., 2001; Klein et al., 2000; Kowalski et al., 1996; Miller et al., 2002). Targets consisted of 1.5 s tones embedded in one of the set of 30 TORCs used as references. Target tone frequency was chosen based on the BF of one of the isolated units. The amplitude of the tone (and hence SNR) was set for a given experiment. However, across experiments tone amplitude ranged from  $-10$  dB to  $+15$  dB relative to the amplitude of the TORCs (Depireux et al., 2001; Klein et al., 2000). The ratio of the amplitude of the tone to that of TORCs is referred to as SNR of the target sound.

A trial consisted of a sequence of reference stimuli (ranging from 1–7 TORCs) followed by a target (except on catch trials in which seven reference stimuli were presented with no target). A target was equiprobable for every position (2–7) in the sequence (~20%).

During most of training and all active physiological measurements, the acoustic stimuli were 1.5 s in duration. In passive STRF measurements, TORC stimuli were longer (3 s), which allowed for more rapid receptive field measurements. During physiological recording from contralateral A1, the computer-generated stimuli were monaurally delivered through an inserted earphone (Etymotic) that was calibrated in situ at the beginning of each experiment. The amplitude of TORC stimuli was set at a value in the range between 60–75 dB (set for a given experiment) during physiological recording.

### Training Paradigm and Procedure

Three adult ferrets were trained on the tone-in-noise detection task using a conditioned avoidance procedure (Fritz et al., 2003; Heffner and Heffner, 1995). Ferrets licked water from a spout while listening to a sequence of reference stimuli until they heard a target sound consisting of a tone embedded in one of the reference stimuli. Length of reference and target stimuli was always the same, and for most training and all recording sessions stimulus length was 1.5 s. When presented with a target, the animals were trained to briefly stop licking, in order to avoid a mild shock.

We started behavioral training by initially training the ferrets on a pure-tone detection task (Fritz et al., 2003) until the animal reached criterion, defined as consistent performance on the detection task pure-tone targets for two sessions with  $>80\%$  hit rate accuracy and  $>80\%$  safe rate for a discrimination rate  $>0.65$ . Once the criterion for pure tone performance was reached, we started adding noise (a TORC) to the tone in the target sound, initially with high SNR. Once the animal reached the behavioral criterion for that SNR, we continued to decrease the SNR in subsequent sessions to as low as  $-10$  dB SNR (we found that the animals were at behavioral threshold and hence were not reliably able to reach behavioral criterion at levels below  $-10$  dB SNR).

The ferrets were trained daily (~60 trials/session) in a sound-attenuating chamber (IAC Isolation Booth). Initial training on pure tone detection in the free-running test box took about 4 weeks for each ferret to reach criterion. Subsequent training on the tone-in-noise detection task took an additional 4–6 weeks. Ferrets trained on the tone-in-noise task were further tested on the task with different SNRs ranging from  $-10$  dB SNR to  $+15$  dB SNR in 5 dB steps, with tone frequencies ranging from 125 Hz to 16000 Hz. We also

tested the ferrets on the pure-tone detection task as an extreme case of the tone-in-noise task with an infinite SNR. In each training session the target tone frequency was fixed and the animal was trained for four to six training blocks of 10 trials each. For each training block the target SNR was fixed, but was randomly varied between successive blocks.

During the physiological experiments, the animals performed from one to three separate task sessions, each consisting of about 40 trials. Within each task session, the target frequency and SNR were held constant, but were varied across successive task sessions.

### Surgery

To secure stability for electrophysiological recording, a stainless steel head-post was surgically implanted on the skull. During surgery, the ferrets were anaesthetized with a combination of Ketamine-Xylazine for induction, and isoflurane (1%–2%) for maintenance of deep anesthesia throughout the surgery. Using sterile procedures, the skull was surgically exposed and the head-post was mounted using bone cement, leaving clear access to A1 in both hemispheres. Antibiotics and postsurgery analgesics were administered as needed following surgery.

### Postsurgical Habituation and Training

After recovery from head-post implantation (2 weeks), the ferrets were habituated to head restraint in a customized Lucite horizontal holder over a period of 1–2 weeks, and then re-trained on the task for an additional 2 to 3 weeks while restrained in the holder (further details in Fritz et al., 2005). The task-naive control ferret received no behavioral training on the discrimination task, but like the other head-post implanted ferrets, also received gradual habituation to head restraint in the holder, before physiological recording commenced.

### Neurophysiological Recording

Experiments were conducted in a double-walled, sound-attenuation chamber (IAC). Small craniotomies (1–2 mm in diameter) were made over A1 prior to recording sessions that lasted 6–8 hr. We used single and multiple independently moveable electrodes (AlphaOmega). In our standard electrode configuration, there were up to four recording electrodes separated by ~500  $\mu\text{m}$  from their nearest neighbor. Single units (typically one to four neurons/electrode) were isolated using off-line spike sorting techniques with custom-designed MATLAB software. In each individual recording session, we slowly advanced electrodes until we had isolated cells on all separate electrodes. The range of BFs in a given experiment varied from 0.5–2.5 octaves. This allowed us to simultaneously test the effect of the target tone frequency on different cells whose BFs were at different spectral distances from the target tone. BF was defined as the frequency of the largest excitatory peak in the STRF.

Responses from each microelectrode were recorded and then stored, filtered, and spike-sorted off-line. Multiunit records were constructed by thresholding responses to obtain spikes by triggering at a level four SDs ( $4\sigma$ ) above baseline variation in the raw trace. Electrode location in A1 was based on the presence of distinctive A1 physiological characteristics such as latency and tuning (Bizley et al., 2005; Nelken et al., 2004; Shamma et al., 1993).

### STRF Analysis

STRFs were measured using reverse correlation (Klein et al., 2000). Response variance ( $\sigma$ ) was estimated using a bootstrap procedure (Depireux et al., 2001; Efron and Tibshirani, 1993) and an overall signal-to-noise ratio ( $\text{SNR}_{\text{STRF}}$ ) was computed for each STRF. STRFs with an  $\text{SNR}_{\text{STRF}} < 0.4$  were excluded from further analysis. Each STRF plot was therefore associated with a particular variance ( $\sigma$ ). Excitatory (positive) and inhibitory (negative) fluctuations from the mean of the STRF were deemed significant only if they exceeded a level of  $2\sigma$ . This analysis and criteria also applied in determining the significant changes between two STRFs, i.e., in the  $\text{STRF}_{\text{diff}}$ . Thus, a significant STRF change refers to a suppressive or facilitative region in the  $\text{STRF}_{\text{diff}}$  that exceeded the  $2\sigma$  criterion.

To measure the STRF with a reliable  $\text{SNR}_{\text{STRF}}$ , we collected neural responses to multiple repetitions of the set of stimuli used, with each repetition consisting of 30 TORCs. To measure the population effect of the task, we first computed the  $\text{STRF}_{\text{diff}}$  for each unit. We then located the maximum point of

each  $\text{STRF}_{\text{diff}}$  in a band  $\pm 0.2$  octaves around the BF of the cell and within the first 1–25 ms of the STRF. Each  $\text{STRF}_{\text{diff}}$  was then aligned at the local maximum points to measure the average effect across the population. To compare the population effects in behaving and naive animals (Figure S2), we accumulated the  $\text{STRF}_{\text{diff}}$  for units that showed significant changes in the spectrotemporal window defined above and divided the sum by the total number of units in that set of STRFs. To determine changes in the sharpness of tuning of the cell, we measured the bandwidth of the tuning of the cell. STRF bandwidth was defined as the width of excitatory area around the BF peak, measured at the frequencies where the amplitude decreased to 20% of the BF peak.

Gain and shape changes in STRFs were computed in two distinct ways to provide a counter check of the results. In the first method, we defined the active (during-behavior) STRF ( $\mathbf{S}_d$ ) as the sum of a scaled pretask passive STRF ( $\mathbf{S}_b$ ) and a task-dependent change in the shape of the STRF; i.e.:  $\mathbf{S}_d = g \cdot \mathbf{S}_b + \delta$ , where  $g$  is the gain that reflects the fraction of the STRF that maintained its original shape, and  $\delta$  is the remaining (orthogonal) portion of the STRF that could not be captured by scaling  $\mathbf{S}_b$ . We also assumed that our measurements of the  $\mathbf{S}_b$  and  $\mathbf{S}_d$  were contaminated by corresponding noise terms (e.g.,  $\mathbf{n}_b$  and  $\mathbf{n}_d$ , with  $\mathbf{S}_b = \mathbf{S}_b^\circ + \mathbf{n}_b$ ,  $\mathbf{S}_d = \mathbf{S}_d^\circ + \mathbf{n}_d$ , and  $\mathbf{S}_b^\circ$  and  $\mathbf{S}_d^\circ$  as the ideal STRFs). Taking the inner product with  $\mathbf{S}_b$  on both sides of the equation, and having (by orthogonality)  $\langle \delta, \mathbf{S}_b \rangle = 0$ , then gain =  $g = \langle \mathbf{S}_d, \mathbf{S}_b \rangle / (\sigma_b^2 - \sigma_{nb}^2)$  where  $\langle \cdot, \cdot \rangle$  is the inner product between the two STRFs, and  $\sigma_b^2$  is the power of the initial STRF (or  $\langle \mathbf{S}_b, \mathbf{S}_b \rangle$ ),  $\sigma_{nb}^2$  is the power in the noise of the initial STRF. Pure shape changes were therefore expressed as  $\delta = \mathbf{S}_d - g \cdot \mathbf{S}_b$ , and this  $\delta$  was used in generating Figure 7C.

The second method employed a gain fitting STRF model (David et al., 2008). The model measured the STRF from responses to TORCs presented in the passive prebehavioral, active behavioral, and passive postbehavioral epochs. This average STRF was then used to predict the response of the neuron to the TORCs, which was then compared to the actual neural responses observed during each of the three epochs. Predicted responses were then adjusted by a scalar gain so as to minimize the mean-square error separately for each of the three epochs, mentioned above. The ratio of the scalars computed during behavior and prebehavior was used as the gain shown in Figure S3B (which is analogous to those in Figure S3A and 7B using the previous method). This approach allowed an independent estimate of gain that reflected the response properties of the neurons and the variability of the responses between the three different epochs.

### SUPPLEMENTAL DATA

The supplemental data for this article include four Supplemental Figures and can be found at [http://www.neuron.org/supplemental/S0896-6273\(09\)00006-3](http://www.neuron.org/supplemental/S0896-6273(09)00006-3).

### ACKNOWLEDGMENTS

We thank Dr. Pingbo Yin for his assistance with implant surgeries and Dr. Nima Mesgarani for technical assistance with electronics and software design. The research was supported in part by NIH (R01-DC005779 and R01-DC007657).

Accepted: December 23, 2008

Published: February 11, 2009

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