

Chapter 51

Correlates of Auditory Attention and Task Performance in Primary Auditory and Prefrontal Cortex

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Abstract Auditory experience can reshape cortical maps and transform receptive field properties of neurons in the auditory cortex of the adult animal in a manner that depends on the behavioral context and the acoustic features of the stimuli. This has been shown in physiological and behavioral experiments, in which auditory cortical cells underwent rapid, context-dependent changes of their receptive field properties so as to sculpt the most effective shape for accomplishing the current auditory task. Here, we extend these findings to new behavioral paradigms (utilizing either positive or negative reinforcement) and explore the possible role of top-down signals from prefrontal cortex (PFC) in modulating plasticity in the primary auditory cortex. We also combine physiological experiments with microstimulation in PFC to test if it modulates cortical responses and receptive fields.

Keywords Auditory cortex • Prefrontal Cortex • Attention • Rapid plasticity

51.1 Introduction

Auditory experience can have profound global effects by reshaping cortical maps and significant local effects by transforming receptive field properties of neurons in the primary auditory cortex (A1) (King 2007; Weinberger 2007; Edeline 1999). The exact form of this remarkable plasticity is determined by the salience or task-relevance of the spectral and temporal characteristics of the acoustic stimuli, and may also reflect the behavioral state of the animal in relation to the dimensions of expectation, attention, motivation, motor response, and reward (Recanzone 2000; Kilgard et al. 2001a, b; Kilgard and Merzenich 2002; Knudsen 2007;

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Kacelnik et al. 2007; Rutkowski and Weinberger 2005). Consistent with findings in other neural systems (Nicollelis and Fanselow 2002; “Gilbert and Sigman 2007; Womelsdorf et al. 2008), auditory cortical cells undergo rapid, short-term, and context-dependent changes of their receptive fields and responses whenever an animal engages in a new auditory behavioral task that has different requirements and stimulus feature salience. In this kind of adaptive plasticity, top-down signals from higher cortical areas associated with engagement in behavioral repertoires may lead to changes in receptive fields that may enhance performance on the relevant sensory tasks (Fritz et al. 2001, 2004, 2007a; Li et al. 2004; see Sect. 51.1).

Cortical receptive fields are situated at the focal juncture of this process, depicted by the simplified and highly schematized model in Fig. 51.1a. During behavior in a trained animal, receptive fields adapt so as to enhance behavioral *performance*, monitored through external (reward or aversive) feedback signals. The auditory cortex receives behaviorally relevant acoustic stimuli (e.g., warning sounds associated with positive or negative reward, and safe sounds associated with positive reward), and generates corresponding *sensory representations* that are ultimately categorized and associated with meaning in the prefrontal cortex (PFC), resulting subsequently in the appropriate motor behavior. This sensory-motor mapping defines a specific *learnt task or behavioral context* (Blake et al. 2006). We hypothesize that this process conceptually involves a series of steps as follows: (a) When an animal engages in auditory behavior, a “behavioral gate” opens that allows specific A1 responses to pass on to higher cortical levels and the PFC (see Sect. 51.2); (b) PFC

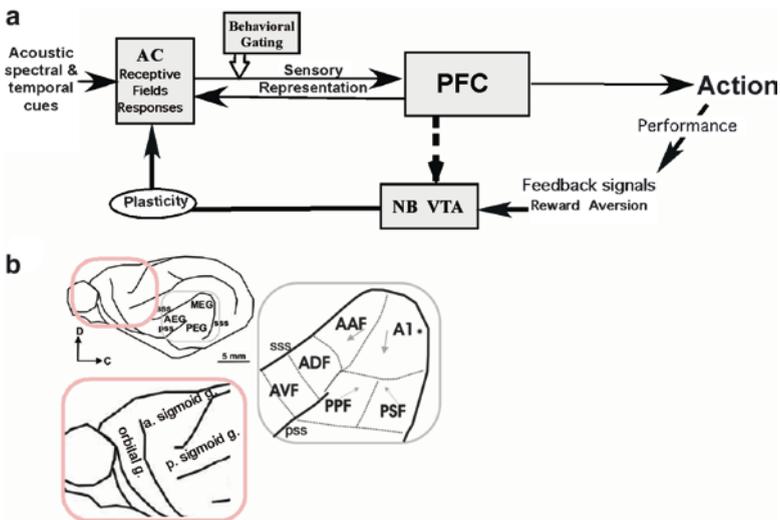


Fig. 51.1 Rapid plasticity during auditory behavior. (a) Schematic of cortical and subcortical interactions during auditory behavioral tasks. See text for details. (b) Layout of ferret auditory and prefrontal cortex. Recordings are focused in A1, anterior sigmoid gyrus, and dorsal-medial regions of orbital gyrus

responses categorize and encode the meaning of the sounds; (c) these responses [directly top-down or indirectly via nucleus basalis (NB)] induce plasticity in A1, but *only* when paired with the responses to the acoustic stimulus that induced them (see Sect. 51.3.2).

In this report, we shall explore this hypothesis by illustrating some results of combined physiological/behavioral experiments, in which we rapidly and comprehensively characterize cortical response properties in a given cell, e.g., tuning curves and spectrotemporal receptive fields (STRFs), while the animal engages in a series of auditory tasks, and compare these response measures across tasks or during passive listening. We shall illustrate responses during behavior in two cortical regions (Fig. 51.1b): A1, and PFC. We then explore the relationship between responses in these two areas. Our overarching scientific challenge is to explain how the rules and goals of behavioral tasks in combination with the salient acoustic cues dictate the form and extent of cortical plasticity.

51.2 Rapid Plasticity in A1 Receptive Fields

We hypothesize that receptive fields in A1 adapt during behavior so as to enhance processing of salient acoustic information that in turn optimizes behavioral outcomes (i.e. maximize positive reward and/or minimize negative consequences for the animal). This idea can be restated in terms of the various components of a task as follows (Fig. 51.1a): Adaptive changes reflect the nature of stimulus features relevant for performance (spectral, temporal, or spectrotemporal), task objectives (whether the sounds are *targets* or *references*, i.e., *foreground* or *background*), and rules of the task (aversive or appetitive rewards, and other task design constraints). Furthermore, while selective attention enhances plasticity to selective acoustic features, globally attending to a complex acoustic stimulus is sufficient to render all its features effective in inducing plasticity. Figure 51.2a illustrates these concepts in the context of several simple tasks that we have tested, highlighting in particular tone detection and tone discrimination. In all tasks, a trial consists of a random number of similar *reference* sounds (blue) followed by a *target* (red). In tone detection, the reference signals are TORC noise (especially designed spectro-temporally modulated broadband noise used to measure the STRFs; see right panel of Fig. 51.2a; Klein et al. 2006), followed by a target tone. In tone discrimination, the reference and target signals are tones of different frequencies; however, both targets and references have TORCs attached to them in order to measure the STRFs (Fig. 51.2a; Fritz et al. 2005a, b). All other tasks have similar structures. In the *aversive* (conditioned avoidance) version of these tasks, animals were trained to lick through the reference epoch, and to refrain from licking for a short period immediately following the target tone in order to avoid a mild shock (Fritz et al. 2003; Heffner and Heffner 1995). In the *appetitive* version of the task, the animals must avoid licking the spout during the reference stimuli, and only lick after they hear the target sound in order to receive a reward.

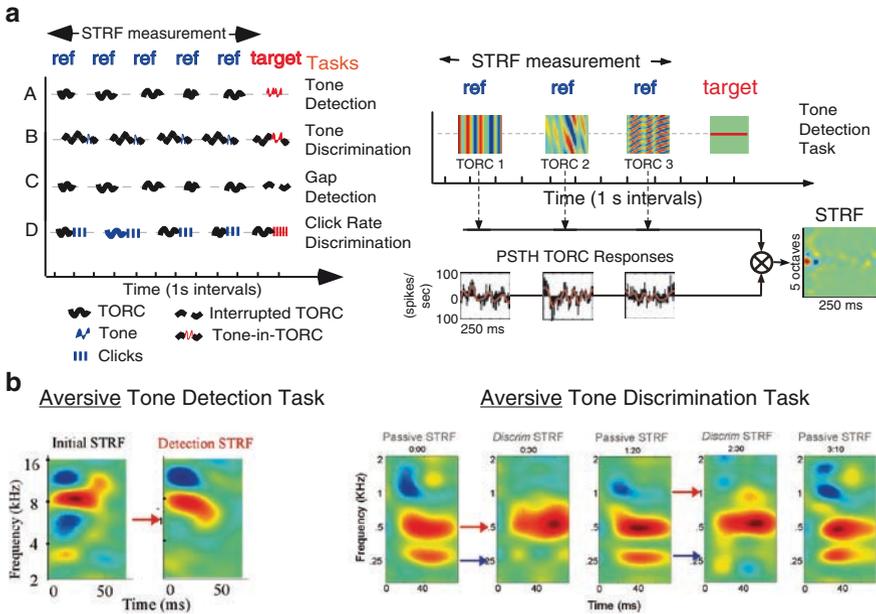


Fig. 51.2 Behavioral physiology and STRF adaptations. (a, left) Structure of behavioral tasks, illustrating a *reference* epoch (blue), followed by a *target* sound (red); (right) STRF measurements are performed *only* during the reference epoch using the responses to the TORCs, which are specially designed modulated noises. Therefore, target and reference tones and other cues are used to define the behavioral objectives of the task variants, while responses to the *same* TORCs are used to measure the STRFs under different behavioral states. (b) STRFs change when the animal engages in a task. Examples of single units in tone-detection task (left) and tone-discrimination (right) tasks. In these aversive tasks, target sounds induce facilitatory effects while reference tones induce suppression

51.2.1 STRF Plasticity in A1 During Aversive Tone Detection and Discrimination Tasks

STRFs measured before, during, and after performance of aversive tone detection and discrimination tasks exhibit characteristic changes that can be summarized as follows (Fig. 51.2b): Target tones (indicated by red arrows) induced enhanced sensitivity in the STRF at their frequency, whereas reference sounds (indicated by blue arrows) induced suppression. These changes are illustrated by the single-unit examples in Fig. 51.2b for the two-tone tasks. We have also found that two spectral factors increase the strength of these adaptations: high performance levels (Fritz et al. 2003; Atiani et al. 2009) and proximity of the target and reference tones to the center of the STRF being observed (Fritz et al. 2007a).

51.2.2 Contrasting Effects of Aversive and Appetitive Tasks

A separate group of ferrets were also trained on the behavioral “inverse” of the aversive (conditioned avoidance) tasks described above, namely on a positive reinforcement (or an appetitive go/no-go) paradigm in which they withheld licking during a (random) number of reference sounds (i.e., the TORCs), and licked only after onset of the target tone, as illustrated in Fig. 51.3a. These two behavioral paradigms form an excellent counterpoint to one another since the *rules and actions* are reversed while the stimuli and the sensory categories remain identical. The comparison of the neural responses in these two “inverse” behavioral paradigms

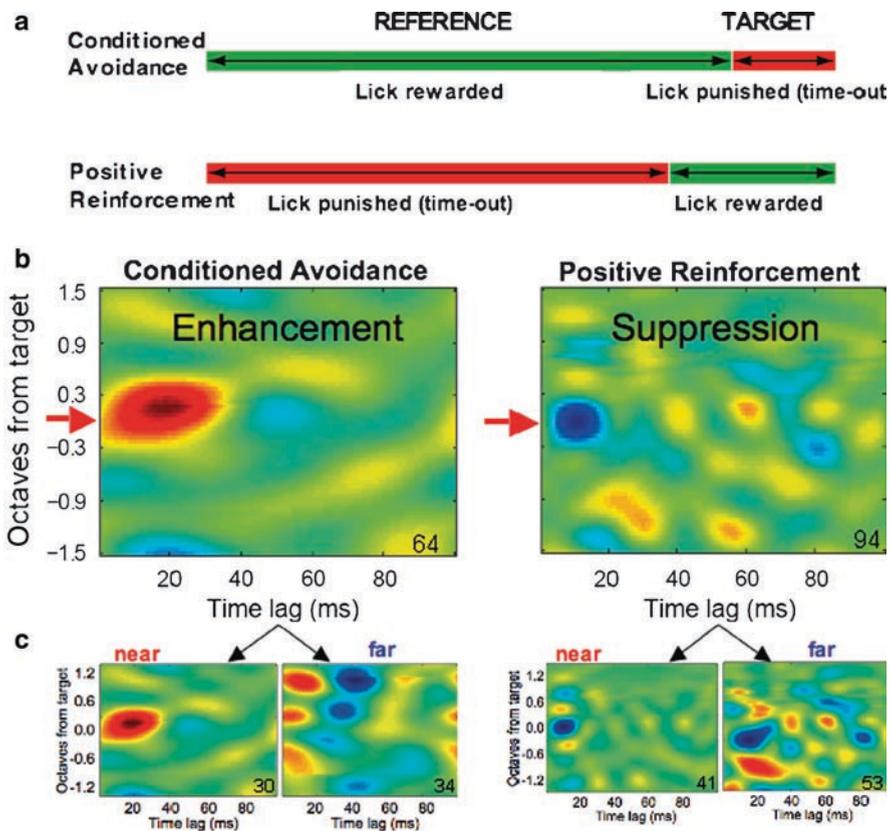


Fig. 51.3 Contrasting average STRF changes during aversive and appetitive tone-detection tasks. (a) Structure of the two behavioral tasks. (b) Changes from a population of cells reveal enhancement in *aversive* (left) and suppression in *appetitive* (right) conditions. The averaged changes are computed by aligning the STRF differences from all cells at the target frequency (red arrow), and then summing the results. (c) In both conditions, targets located *near* the STRF have the greatest impact on plasticity

allowed us to explore the effects of task rules on the responses in the PFC and potentially on the extent of adaptive changes in the primary auditory cortex.

Figure 51.3b contrasts the average plasticity in two populations of neurons in animals engaged in the two types of tone-detection experiments. All STRF changes during the appetitive tasks were measured in exactly the same way as in the aversive task (Fig. 51.2; Fritz et al. 2003). The neural results differed in an important respect. As illustrated above, STRFs in the conditioned avoidance task developed facilitation at the frequency of the target tone (red arrow), while exactly the opposite pattern emerged in the positive enhancement task. These results suggest that, in addition to salient target and reference features, motor and reward contingencies associated with the discrimination task play a central role in determining plasticity effects in A1. Intuitively, the results of Fig. 51.3b may be understandable if one interprets target enhancement as increased sensitivity. Such increased sensitivity in the aversive task would help the animal avoid the shock, but may also increase the “false alarm” rate (i.e. more frequent, but low cost, withdrawals during the reference epoch in aversive tasks). The opposite effect would occur during the appetitive task. Here, incorrectly detecting the target tone during the reference epoch would lead to a costly time-out, and hence could be avoided by *suppressing* target sensitivity. Another intuitively plausible “explanation” is that the sign of the target plasticity arises in relation to an inhibition of on-going behavior – in positive reinforcement, we are inhibiting restraint from licking, whereas in conditioned avoidance, we inhibit on-going licking, so one would expect the sensory-motor linkages to be opposite to one another, and also the plasticity to be opposite in sign.

51.3 Encoding of Task Rules and Stimuli in Prefrontal Cortex

If PFC responses are the source of top-down attentional influences that induce rapid A1 plasticity, then we predict that they should reflect some of its characteristic and distinctive properties such as being strongly contingent on the behavioral context, sensitive to the stimulus categories, dependent on task rules (aversive or appetitive), and would be modulated by task performance. Here, we summarize the basic properties of PFC responses during the same detection and discrimination tasks described above, and then extend the results to behaviors with multimodal (visual and auditory) stimuli.

51.3.1 *PFC Responses During Aversive (or Conditioned Avoidance) Tasks*

PFC responses in the ferret during task performance exhibit a wide range of properties that encode target onset and offset and other task events and contingencies. The most striking aspect of these responses is their near total dependence on the behavioral

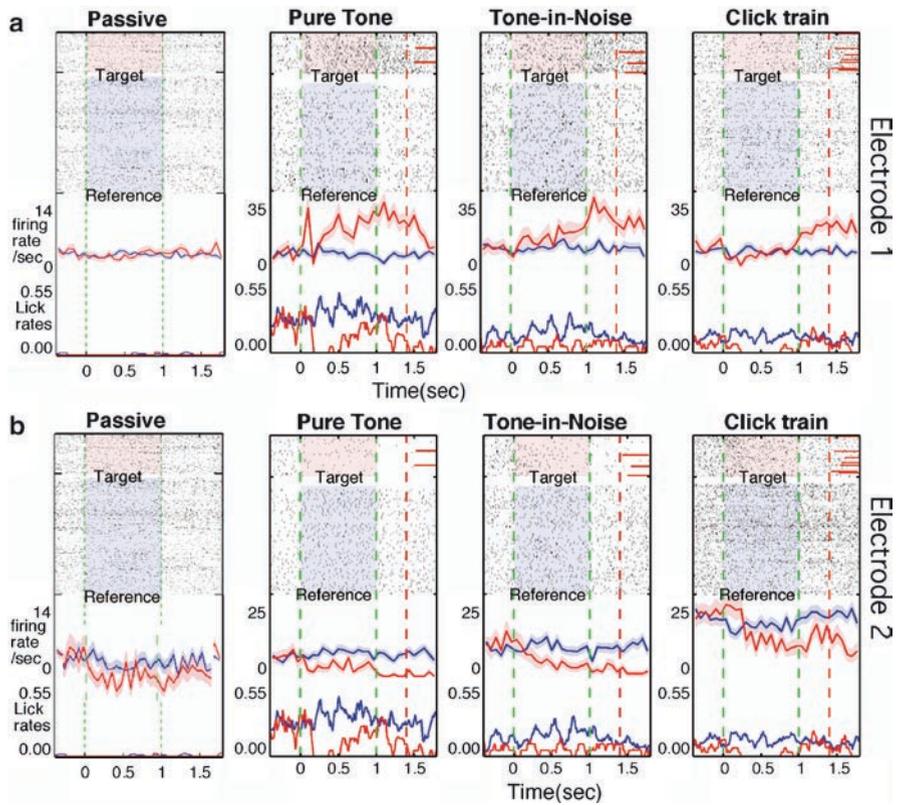


Fig. 51.4 PFC responses in two units recorded simultaneously during three aversive detection tasks. Only target response modulations (*red*) are strong, but *not* during passive state (first panel). (a) Response modulations in are all excitatory and roughly similar regardless of the nature of target sound, thus reflecting the meaning of the sound as a target. (b) Response modulations are all similar and suppressive in this cell, reflecting again only the meaning of the sound as a target

context. This is illustrated by typical responses shown in Fig. 51.4a, where initially the animal was in the passive state (leftmost panel), and then performed a series of tasks (each separated by a passive pretask stimulus presentation for each task condition): tone discrimination, tone pure tone detection, a tone-in-noise detection, and a click train detection. During the passive state, no significant responses were observed to the target (*red*) or reference (*blue*) sounds (first panel from the left). However, when the animal entered a behavioral context, performing the tone-detection task using exactly the same stimuli as in passive state, the identical target tone now induced vigorous excitatory responses. Reference TORCs, by contrast, did not show any change in responses. During the tone-in-noise task (third panel), responses were again strong only to the target (*red*). Finally, when the target was a click train (fourth panel), the target response buildup remained similar (*red*), demonstrating again that, in the PFC, the physical, acoustic parameters of the target

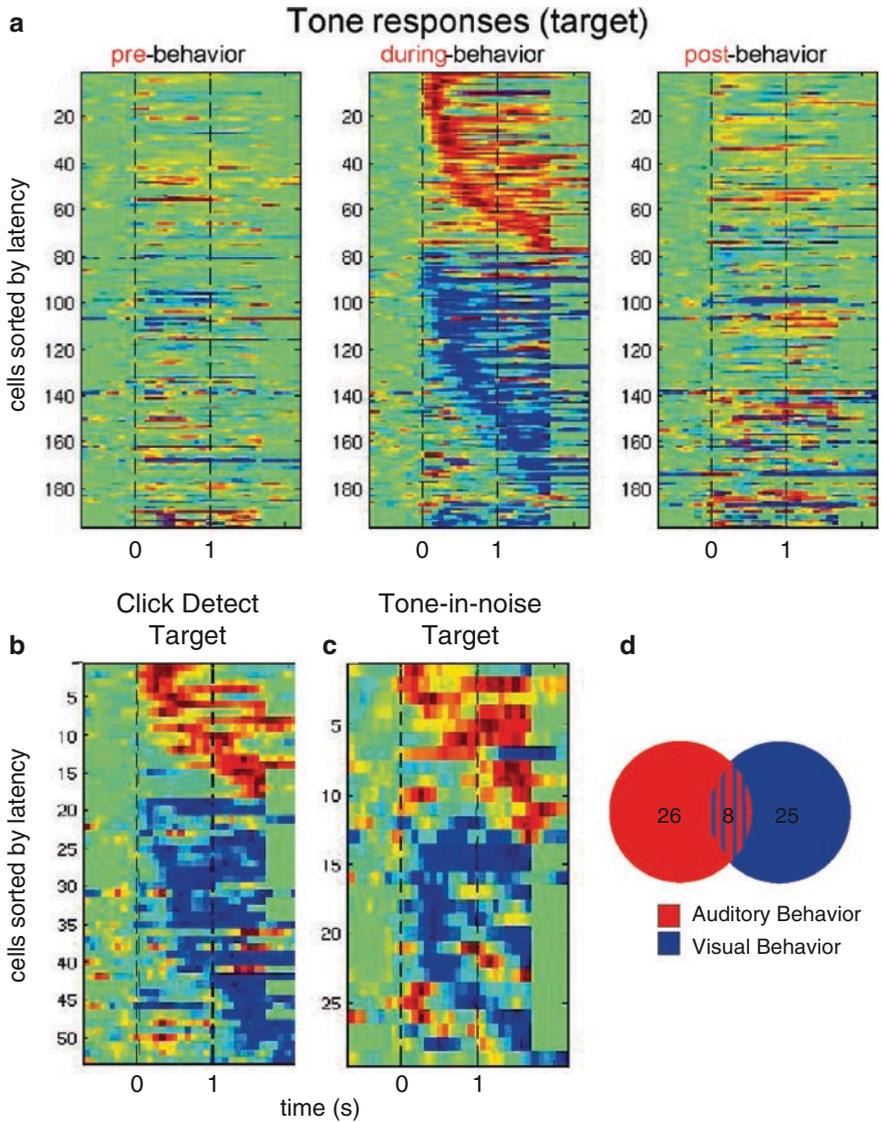


Fig. 51.6 PFC population and multimodal responses during aversive detection tasks. **(a)** PST responses from 200 cells organized according to their latency. Prebehavior passive responses are weak, compared to during the behavior. Persistent weaker responses remain postbehavior. Both excitatory and suppressive modulations of firing rates are found. **(b, c)** Similar responses are found with click train and tone-in-noise targets. **(d)** Cells are mostly segregated by modality (auditory and visual), although some overlap exists, thus demonstrating a class of PFC neurons that encode a task target independent of stimulus modality

characteristics common to most cells in PFC: (1) *Responses are context-dependent*, being the strongest *during* task performance, and barely measurable prior to that; (2) cells come in two flavors of *response polarity* to the target, in approximately equal proportions; (3) onset and latency of the peak response relative to onset of target tone are widely and uniformly distributed from about 30 ms to 2 s; (4) responses can be phasic or sustained in roughly equal proportions. Similar trends are seen in data from detection tasks with click trains (Fig. 51.6b) and tone-in-noise (Fig. 51.6c) targets.

51.3.2 PFC Responses During Appetitive Tasks

Basic response properties during appetitive tone-detection tasks were similar in the behavioral contingency, polarity, and latencies. One key difference was the abundance of strong responses to the reference (TORC) sounds. Target responses remained strong, and often of the same polarity in a given cell (enhanced or suppressed). A possible explanation for the stronger responses to reference sounds is their enhanced behavioral significance in the appetitive tasks. This is especially true of the first reference TORC since it was the cue to the animal that the trial has commenced and that they must cease licking (much like the target tone in the aversive tasks).

51.3.3 PFC Responses in Tasks with Visual Stimuli

Ferrets were also trained on a simple visual discrimination task, that paralleled the auditory detect task, using the conditioned avoidance paradigm. They learned to lick freely to a sustained (1 s) dim light – the safe visual stimulus, and refrain from licking after presentation of a bright flashing light (4–8 Hz for 1 s) – the warning, target visual stimulus. As was the case with auditory tasks, PFC responses were selective for the target stimuli, and showed a similar time course. Some PFC neurons responded only to visual targets, others only to auditory targets, and some responded to both visual and auditory targets (see Fig. 51.6d).

51.4 Relationship Between A1 and PFC Responses

We also explored aspects of the relationship between responses in A1 and prefrontal cortices by *simultaneously recording* and measuring the correlations in the activity between these two regions during behavior and also by *microstimulating PFC* neurons so as to induce plasticity in A1. Given the direct and substantial indirect connections between PFC and A1, it is plausible that their responses and local field potentials (LFPs) are dynamically coherent and functionally related, and that

microstimulation in PFC (in conjunction with paired acoustic stimuli) could induce forms of plasticity in A1 receptive fields that would be consistent with observed plasticity changes elicited during behavior. Examples of preliminary findings along those directions are shown below.

51.4.1 Analysis and Coherence of Local Field Potentials

Synchrony of neural activity between the PFC and A1 could be indicative of functional connections between them, and also of the distributed representation of attended stimuli (Barcelo et al. 2000; Fuster et al. 1985; Gazzaley et al. 2004; Womelsdorf et al. 2007). In order to understand cortical network activity on a large scale, we recorded LFPs simultaneously with single-unit recordings in A1 and PFC. LFPs were acquired from the single-unit electrodes by low-pass filtering the recording below 1 kHz; spikes were measured by band-pass filtering from 1 to 6 kHz.

51.4.1.1 Within PFC and A1 Correlations

Thus far, preliminary analysis of LFP spectrograms *within* PFC during task performance has revealed that (Fig. 51.7a, b): (a) *During* tone detection in the aversive task, the spectral power in two commonly studied LFP bands – β (10–30 Hz) and γ (50–80 Hz) – change systematically relative to the *passive* state. Namely, the β -band always *decreases*, whereas the γ -band *increases* during behavior (Fig. 51.7a). (b) Significant changes also occur in the *relative* power of

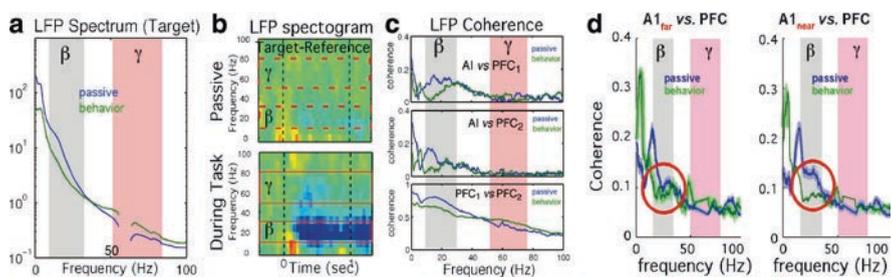


Fig. 51.7 LFP spectrograms and coherence. (a) Average LFP spectrum during target stimuli during passive and active states. The β - and γ -bands are indicated by the shaded ranges. Break in curve is the 60 Hz line filter. (b) Spectrogram of LFP's induced by target tone (relative to reference TORCs) highlighting dynamics of different bands of PFC activity during passive and aversive tone-detection task performance. β - and γ -bands are indicated by the dashed and solid red lines. (c) Coherence of LFPs between A1 and two locations in PFC (top two panels), compared to locations within PFC (bottom panel). (d) LFP coherence before and during behavior between PFC and two BF locations in A1 – near target tone (right) and far from it (left)

the target and reference responses in these two bands during different phases of the tasks. For example, the (power) spectrogram of the “target-reference” (Fig. 51.7b) shows modest changes during the *passive* state (top panel), but substantial changes during the *aversive* tone-detection task (lower panel), where the relative power in the β -band was severely depressed following onset of the target. The γ -band exhibited only a weaker decline (Fig. 51.7b).

51.4.1.2 Coherence Between PFC and A1

Another key objective of the experiments in this aim is to measure the coherence of activity *during* the task between simultaneously recorded signals in AC and PFC. Our preliminary data suggest changes in coherence during behavior between these two regions.

For example, in one of several simultaneous recordings, we contrasted the LFP coherence between A1 and PFC (top two panels of Fig. 51.7c) during target duration of the appetitive tone-contour discrimination task (green curve) and passive state (blue curve). This was further contrasted with coherence within the PFC (between the two PFC channels) in the same two states (bottom panel of Fig. 51.7c). Coherence in the β -band (gray shaded) between A1 and PFC decreased dramatically during the task, compared to the (relatively) smaller changes within the PFC. *Within* the PFC, and *within* A1 (not shown), behavior brought about a small decrease in the power of the β -band (gray shade Fig. 51.7c), and a small increase in γ -band (pink shade Fig. 51.7c), a pattern that is seen in all experiments. These coherence patterns, however, were location and task dependent. For instance, in another experiment using the *aversive tone-detection* task (Fig. 51.7d), we found the same substantial β -band coherence decrease *only* between PFC and BF locations in A1 with frequency tuning *near* to the target frequency (Fig. 51.7d: within red circle in right panel), and not in those *far* from the target (Fig. 51.7d: left panel). Full interpretation of these coherence patterns must await more data and further study, but they nevertheless suggest the *hypothesis* that interareal communication and synchrony patterns may become dramatically modulated in the β -band and γ -band during behavior.

51.4.2 Microstimulation in PFC Modulates Receptive Fields in A1

If the PFC is a significant source of the top-down signals responsible for adapting auditory cortical receptive fields and responses, then it might be possible to simulate its natural action during behavior with microstimulation that is paired with the appropriate stimuli. Figure 51.8 illustrates the results of one such preliminary experiment in a *naïve* animal, in which the *reference* stimuli consisted of random tones that covered a range of frequencies surrounding the BF and ending with a

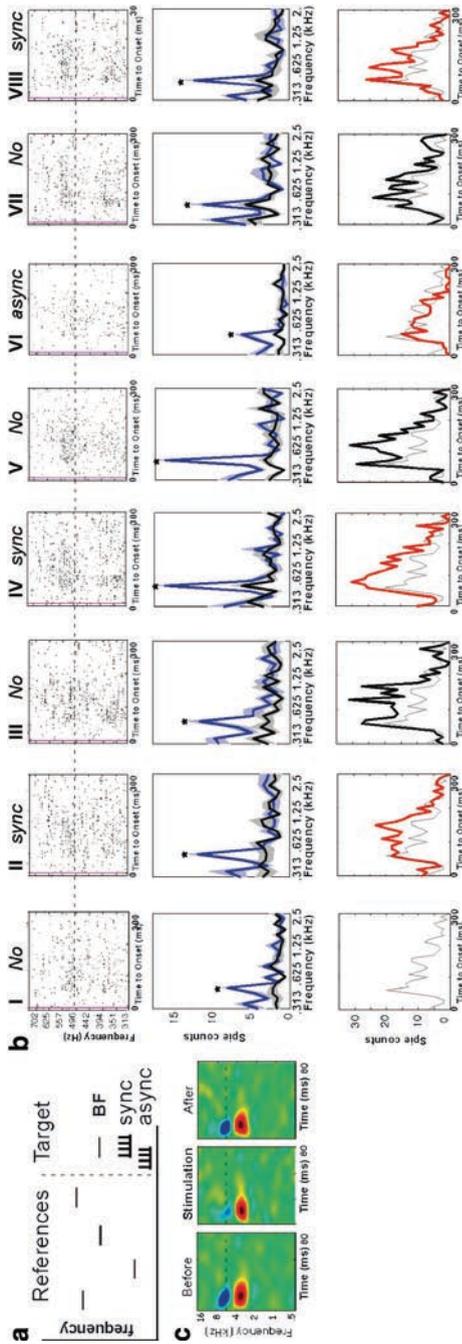


Fig. 51.8 PFC microstimulation alters AI receptive fields. (a) Stimuli and stimulation mode. (b) Changes in a cell's responses through a sequence of tests (*panel columns I–VIII*) alternating between no stimulation, and PFC *synchronous* or *asynchronous* stimulation. (Top) Response rasters; *dashed line* is at BF; (Mid) tuning curves (in *blue*) and spontaneous activity (in *black*) during the tests; (Bottom) PSTs at BF. Initial measurement in *panel I* (gray), during stimulation (red) and no stimulation (*black*). (c) STRF enhancement induced by PFC stimulation paired with the target tone (at *dashed line*) in a passive tone-detection paradigm

150 ms *target* tone set at BF (495 Hz). An electrode inserted in the PFC was used to deliver a series of current pulses that were paired (synchronously or asynchronously; Fig. 51.8a) with the *target* BF tone in alternating blocks of trials. Initially, the unit was tuned near 500 Hz as shown in panel I raster responses (top), tuning curve (middle), and PSTH histogram of the BF tone (bottom). *During* synchronous stimulation with the *target* BF tone (panels II), the unit became more responsive to the BF tone (*asterisk*), and the changes persisted during the following passive epoch (panels III). A second block of stimulation considerably enhanced the responses and tuning around the BF (panels IV), changes which persisted afterward (panels V). In the following block (panels VI), the stimulation pulses *asynchronously* preceded the BF tone by 75 ms. The result was a striking resetting of the cell's responses to its initial state (as in panels I). Subsequent passive measurements showed only a partial rebound (panels VII), but another synchronous stimulation session led to a reemergence of the enhanced tuning and BF responses (panels VIII). In Fig. 51.8c, we illustrate the results from a different animal under *passive* conditions, where we presented the stimuli of the tone-detection paradigm (P1) of TORCs and target tone to measure A1 STRFs simultaneous with microstimulation in PFC, paired with the target tone at 6 kHz. In this case, substantial enhancement occurred at the tone frequency *during* stimulation (dashed line) that altered its shape, only to return partially to its original shape afterward. In summary, PFC stimulation paired with tone stimuli can induce *rapid, reversible, or persistent frequency STRF* changes, mimicking those seen with behavior.

51.5 Summary and Discussion

In a series of experiments over the last few years, we have sought to elaborate the role of A1 in expressing rapid plasticity during behavior in various auditory tasks, and to delineate the limitations and requirements of the overall process illustrated in Fig. 51.1. For instance, we found that plasticity does not occur in a naïve *or* nonbehaving trained animal (Elhilali et al. 2007) as that effectively breaks the upper and lower loops of Fig. 51.1a, and with it, the feedback into the A1. Furthermore, we confirmed that enhancement of the acoustic spectral or temporal difference between warning and safe sounds was the key to shaping plasticity (Fritz et al. 2005a, 2005b, 2007a), that STRF changes were significant when salient features of the stimuli were *within* its receptive field boundaries, and were the largest when these features were near the center of the receptive field (Fritz et al. 2007a). We also explored in detail the contribution of task difficulty to the extent of plasticity, and the breakdown of STRF changes into pure gain and (orthogonal) shape changes (Atiani et al. 2009). Finally, we confirmed the hypothesis that “spectral” targets and references induce plasticity that mirrors their spectral structure in a manner consistent with a contrast filter (Fritz et al. 2007a). These findings have suggested new hypotheses that we are currently investigating especially concerning the

role of attention on STRF plasticity in A1 and the exact nature and function of the top-down signals from the PFC (Fritz et al. 2007b). For example, our current hypothesis is that attention plays a global role in these auditory tasks, that target (warning) and reference (safe) stimuli essentially “imprint” their appropriate spectrotemporal signature upon the STRFs during an active task, and that the PFC provides the necessary top-down feedback *during* behavior to initiate and maintain the adaptive processes that change the A1 STRFs. Finally, it should be stressed that in the highly schematized and simplified account of Fig. 51.1a, we have left out many other important factors in initiating, directing, and modulating rapid plasticity such as the neuromodulatory influences on the auditory cortex arising from subcortical structures including the amygdala, NB, ventral tegmental area, and locus coeruleus, the concurrent plasticity of the task itself (or of the sensory-motor map) in the auditory, motor, and premotor cortices (Li et al. 2000; Singh and Scott 2003; Stefan et al. 2004; Selezneva et al. 2006; Frost et al. 2003).

The scientific challenge we face now is to understand how this broadly distributed orchestration of multiple changes in the attentional network, dynamically modulates sensory processing in concert with achieving behavioral goals.

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