

# AUDITORY CORTICAL FUNCTION: INSIGHTS FROM CURRENT APPROACHES

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Over the last decade, an expanding array of innovative approaches has been used to explore the organization, processing, and behavioral/perceptual contributions of the auditory cortex in various animal models. Several investigators were invited to present an overview of current developments in the field of auditory cortical processing at the occasion of Acoustics 2012 Hong Kong, a joint meeting including the 163rd meeting of the Acoustical Society of America (ASA), the 8th meeting of the Acoustical Society of China (ASC), the 11th Western Pacific Acoustics Conference (WESPAC) and the Hong Kong Institute of Acoustics (HKIOA). In this article, a brief overview of five different aspects of these influential approaches represented at that meeting are presented to provide a mosaic of current progress in our understanding of auditory cortical function.

## **Synapses and receptive fields of the auditory cortex are plastic**

A major feature of adult mammalian primary auditory cortex (AI) is frequency tuning. Frequency tuning is reflected in synaptic and spiking receptive fields, and it is loosely related to the fact that the relative strengths of exci-

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tatory and inhibitory inputs are proportional across tone frequency; i.e., synaptic excitation and inhibition are essentially balanced in mature AI (Froemke *et al.*, 2007; Tan and Wehr, 2009; Tan *et al.*, 2004; Volkov and Galazjuk, 1991; Wehr and Zador, 2003; Zhang *et al.*, 2003). Excitatory and inhibitory balance is interpreted in the sense that they are usually co-tuned, i.e., sharing best frequencies (BFs) and having correlated response magnitudes across other frequencies (Fig. 1A). However, although the relative amplitudes of inhibitory responses scale with the size of excitatory responses for a given stimulus, the onset of inhibition is delayed by a few milliseconds (Wehr and Zador, 2003; Zhang *et al.*, 2003). As a consequence, there is a

brief window in which excitatory responses can sum together and generate action potentials.

Though we have begun to understand the synaptic inputs to single neurons, it remains unclear how changes to specific inputs must be coordinated within larger neural networks. Understanding how inputs are coordinated is critical, however, since changes in inputs ensure that a neuron’s excitability and functional feature selectivity are appropriately configured for both processing and perceiving the sensory environment.

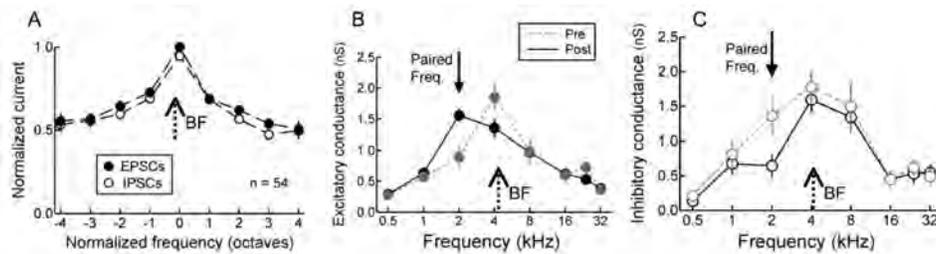


Fig. 1. (A) Average normalized frequency tuning of excitation and inhibition from voltage clamp recordings for pre-nucleus basalis pairing. Synaptic currents were normalized to the amplitude of the largest EPSC (excitatory postsynaptic conductance) and IPSC (inhibitory) across frequencies. The center frequency (0 octaves) was set to the best frequency (BF) of excitation. Filled symbols, excitation; open symbols, inhibition. Error bars=sem. (B) Example excitatory frequency tuning curves based on measurements of synaptic conductance for an AI cell. Excitatory conductance at the paired frequency (2 kHz) increased from  $0.9 \pm 0.2$  nS to  $1.6 \pm 0.1$  nS (77.8%,  $p < 0.006$ ). Mean tuning curves before (dashed) and 10 min after (solid) plasticity induction. Down arrow=frequency of the paired tone; up arrow=pre-induction BF. (C) Example inhibitory frequency tuning curves based on measurements of synaptic conductance for same cell as shown in (B). Inhibitory conductance at the paired frequency (2 kHz) decreased from  $1.4 \pm 0.3$  nS to  $0.6 \pm 0.2$  nS ( $-57.1\%$ ,  $p < 0.04$ ).

Recently, using whole-cell recordings of synaptic conductances, we found that long-lasting positive and negative changes to auditory cortical excitatory synapses were induced, if acoustic stimuli were paired with activation of the nucleus basalis cholinergic neuromodulatory system (Froemke *et al.*, 2007). Pairing of a sub-optimal stimulus inside the receptive field with release of acetylcholine for only a few minutes enhanced the excitatory response to the paired frequency (Fig. 1B), but decreased the excitatory activity at the former BF of the neurons. In addition, the inhibitory conductance of the neurons at the paired frequency was reduced temporarily (Fig. 1C), but recovered after several tens of minutes matching the new BF of the neuron (Froemke *et al.*, 2007).

We also found that nucleus basalis-enabled plasticity could be extended to shape intensity tuning. When synaptic tuning curves for sound level intensity were examined, we found that tone-evoked excitation monotonically increased as sound level grew louder. However, after pairing a quiet, low-intensity tone with nucleus basalis stimulation, responses to soft tones that were initially weak became stronger, and responses to louder tones were depressed (Carcea *et al.*, 2012). These synaptic modifications were precisely orchestrated across entire receptive fields, conserving mean excitation while reducing overall variance, which implied that each parameter of cortical synaptic receptive fields (frequency and intensity) could be modified independently of the other (Carcea *et al.*, 2012).

Computational analysis indicated that decreased variability should increase detection and recognition of near-threshold or previously imperceptible stimuli and this was confirmed psychophysically with nucleus basalis pairing in behaving animals. Pairing in anesthetized animals can lead to behavioral improvements after animals woke up. The effects of pairing lasted only a few hours unless pairing was performed daily for several (6+) days, after which the effects of pairing endured. Furthermore, pharmacological manipulations indicated that changes to auditory cortex were both necessary and sufficient for behavioral enhancement. Thus, direct modification of specific cortical inputs leads to wide-scale synaptic changes, which collectively support improved sensory perception and enhanced behavioral performance.

## Micro-organization and plasticity of the primary auditory cortex

The auditory cortex is a laminated structure that adaptively processes auditory information from the external environment. Prior studies have revealed that on large spatial scales the auditory cortex in mammals has a tonotopic arrangement based on frequency selectivity and a more patchy organization of other response properties (Read *et al.*, 2002). However, the precise nature of the transformation of sensory information at the level of auditory cortical networks and single cortical neurons is unknown. In the last few years, it has been possible to monitor large populations of neurons using new imaging technologies. In particular, *in vivo* two-photon calcium imaging techniques can be used to measure response properties and functional organization of cortical areas with single cell resolution.

When *in vivo*, 2-photon calcium techniques were applied to the supragranular layers of primary auditory cortex (A1) neurons in mouse, we found that the large scale tonotopic architecture of A1 breaks down at smaller scales (around 300 microns), and that nearby frequency and level tuning properties were quite heterogeneous (Fig. 2; Bandyopadhyay *et al.*, 2010, Rothschild *et al.*, 2010). Imaging with dyes of differing sensitivity for calcium enabled the observation of signals arising from two sources: (1) suprathreshold spiking responses, or (2) a combination of subthreshold inputs and suprathreshold spiking responses. The comparison of these signals revealed a pronounced difference in heterogeneity (Fig. 2). This suggested that the observed heterogeneity on small spatial scales is likely created by the diverse inputs to supragranular neurons (Bandyopadhyay *et al.*, 2010), which was recently observed by imaging sound driven  $Ca^{2+}$  signals in dendritic spines (Chen *et al.*, 2011). Thus each supragranular neuron may sample from a large frequency range of inputs.

There are multiple possible intra- and inter-laminar network topologies that can give rise to the observed heterogeneity. For example, intra-laminar connectivity within layer 2/3 could provide input from “distant” frequency channels. To reveal the inputs to A1 networks, current experiments have focused on stimulating single cells.

Supragranular cells have access to a large range of frequencies, and these inputs might provide a substrate for a

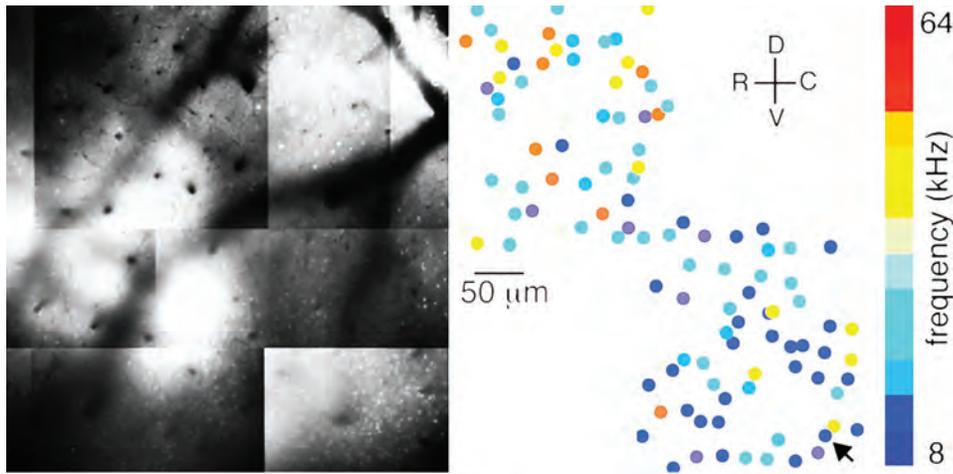


Fig. 2. Left: Montage shows low-magnification view of auditory cortex neurons loaded with  $\text{Ca}^{2+}$  dye. Black shadows are blood vessels. Right: two adjacent imaged fields in A1. The best frequency (BF) is indicated by color. Note the local variability of BFs. Adapted from Bandyopadhyay *et al.* (2010).

large degree of plasticity in individual neurons. A1 neurons can rapidly change their tuning depending on the demands of a behavioral task. Thus, the large sampling space of supragranular neurons might determine the repertoire for such rapid adaptive shifts in a neuron's selectivity. Higher-order cortical regions likely control the behavioral induced shifts. To elucidate this plasticity, we are currently using micro-stimulation of top-down projections to A1 to test the extent to which A1 neurons can rapidly change tuning their properties.

By monitoring behavior and recording the sound-evoked responses of large populations of A1 neurons, we will be able to examine how A1 circuits adjust depending on behavioral demands. In addition, by imaging single-cells and stimulating selected neurons to probe connectivity, we will be able to reverse-engineer A1 circuits. Ultimately, we hope to obtain a wiring diagram of A1 for different behavioral conditions, which will then contribute towards understanding how stimuli are detected and classified. Future improvements of optical techniques, which will allow imaging over longer time frames and at higher temporal rates, will allow us to gain a more detailed view of cortical processing and how it changes as learning occurs. Collectively, the results gained with the application of single-cell imaging techniques provide insight into how sensory information is represented and adaptively transformed in auditory cortex.

### Brain-state dependent modulation of auditory cortical neurons

Auditory cortex (AC) experiments are commonly performed in anesthetized animals thus prohibiting normal behavioral reactions. Even in recordings from unanesthetized animals, movements are generally constrained and animals are not fully able to behave adaptively in response to stimuli that predict discomfort or reward. To assess natural situations, a full spectrum of complex, sound-induced behaviors must be considered. However, sounds delivered under different behavioral conditions and, consequently, brain states may be processed and perceived differently. Indeed, response variability to the same sensory stimulus has been shown to depend on the state of the brain at the time the

stimulus is presented, such as under attentive versus inattentive conditions (e.g., Hubel *et al.*, 1959), or in conditions where animals could escape, or were prevented from escaping, during signals that predicted a threat (Seligman and Beagley, 1975).

When higher-order brain regions are activated, they may induce changes in behavior (Fritz *et al.*, 2010). Therefore, behavioral and brain-state shifts are expected to adaptively modify the responses of sensory neurons. We confirmed this phenomena in guinea pigs in which a behavioral shift was induced by suddenly changing the ambient illumination from light to dark—this maneuver shifted guinea pigs from a passive/stationary to an active/exploratory state. When the light was turned off, guinea pigs typically stood up from a sitting position and started walking. This behavioral shift did not require training and was evoked in >70% of the trials in non-sleeping animals (Ojima *et al.*, 2010).

We also examined the electrophysiological correlates of guinea pig behavior. When guinea pigs were sitting quietly, many neurons in the supragranular layers of cortical field A were silent, or their spontaneous firing was at very low rates. In infragranular layers, some neurons showed an intermediate-to-high rate of background discharges. When illumination changed from light to dark, which induced exploration activity, a fraction of the infragranular neurons showed dramatic changes in background discharge from high to low rates. The low firing rates typically continued for several minutes, and did not increase, even when the animal was transiently immobile during the dark condition (Ojima *et al.*, 2010).

We also assessed state-dependent processing differences for a variety of sounds, including a set of natural sounds as well as pure tones and band-passed noises. Preferred sounds vigorously generated discharges whether ambient light was either on or off. However, in the illumination-on condition, with animals sitting quietly, sounds evoked a burst of spikes, which often obscured stimulus-synchronized responses. By contrast, during the illumination-off condition, usually only a single burst of spikes was evoked. This resulted in much reduced interference between the evoked spikes and the low spontaneous background activity, and thus a better signal-to-

noise ratio, which allowed stimulus-related response periods to be more easily detectable (Ojima *et al.*, 2010).

The different brain states seem to be reflected in the degree of background activity of a restricted population of neurons. The discharge pattern evoked during different brain states may contribute differentially to the processing, and potentially the perception, of stimuli because of the varied signal-to-noise ratio. There are several possible converging pathways that can mediate changes in neuronal responses evoked by relevant sound stimuli (Fig. 3). In particular, neuromodulators may have long-lasting effects, since they are suitable for changes in background firing, and they contribute to plasticity, cognitive functions, and changes in brain states (e.g., Aston-Jones and Cohen, 2005).

Audition is not only related to sound identification, but is linked also to emotional effects and, in turn, to behavioral responses. Little is known about how emotional conditions are reflected in brain state-dependent perceptual changes. In the future, continuous and simultaneous monitoring of brain state, behavior, and neuronal discharges are required to interpret important basic questions in the auditory field: (1) how can ambient sounds be largely ignored and how does a particular sound attract one's attention; and (2), how can an acoustically identical sound be perceived as either attractive or aversive, depending on distinct internal and external conditions? Only by carefully evaluating sound-induced behavioral actions and emotional states will we be able to fully understand cortical sound processing and perceptual correlates.

### Rapid plasticity in auditory and prefrontal cortex during active listening

The brain is an extraordinarily adaptive and predictive machine: it adapts to present demands and predicts the future. The brain also undergoes tremendous plasticity in multiple diverse forms, from birth through adulthood. Neuronal plasticity is a fundamental property of neurons and neuronal circuits, because it facilitates adaptation to new environments, dynamically adjusts cortical sensory filters to improve processing of salient stimuli to optimize task performance, enables prediction of reward, and provides the basis for learning from experience. Depending upon the time scales and mechanisms involved in induction and persistence of receptive field (RF) plasticity, these changes may be described as ephemeral stimulus-driven adaptive plasticity, rapid attention-driven plasticity, or consolidated learn-

## Sources to drive or modulate AI neurons

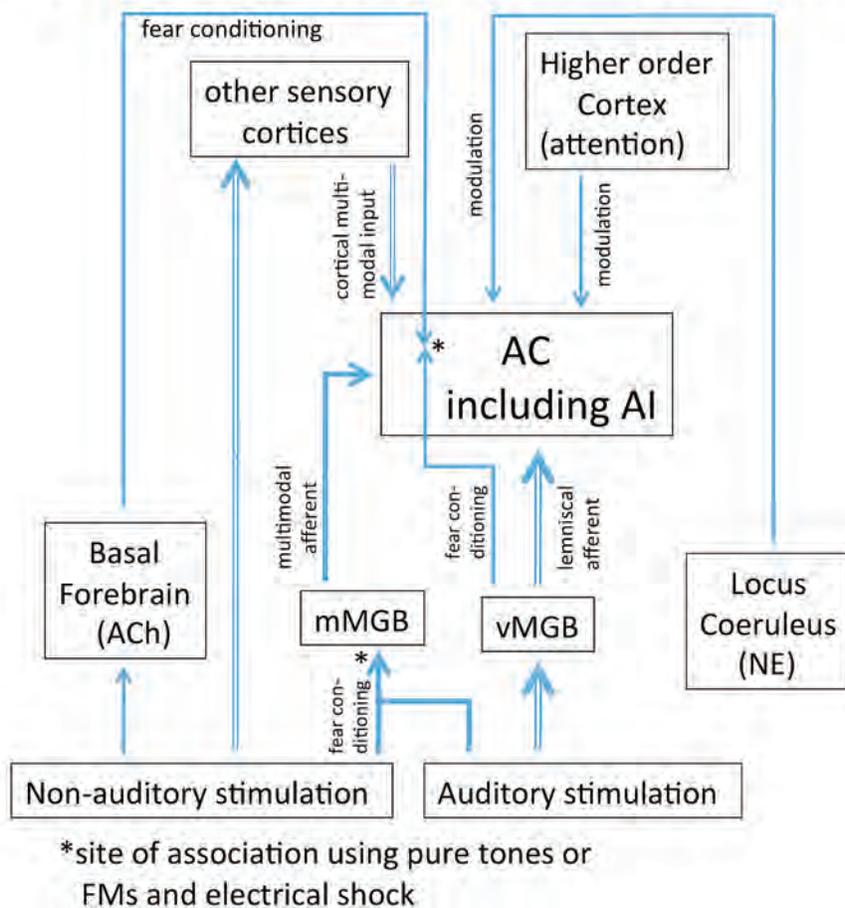


Fig. 3. Possible pathways to drive and modulate neurons in auditory cortex (AC) including the primary field (AI). These routes may explain changes in acoustic response properties, such as frequency selectivity, following fear conditioning, i.e., association of simple tones or complex frequency-modulated (FM) sounds with foot shock, direct and indirect effects of neuromodulatory substances, modulatory effects of non-auditory stimuli, and feedback modulation from higher brain regions. AC, auditory cortex; ACh, acetylcholine; AI, primary auditory field; NE, norepinephrine; vMGB and mMGB—ventral and medial nuclei of the medial geniculate body.

ing-induced plasticity. Though there are likely to be common molecular and synaptic mechanisms underlying all rapid RF transformations, there may also be some striking differences.

Rapid plasticity is generated so that the brain can adapt to the current environmental context and accentuate responses to the most salient cues in the present moment, to optimize processing of the most important stimuli. One of the major functions of rapid RF plasticity is contrast enhancement of the attended auditory object against the acoustic background. There are many ways of achieving this, not only by simple response enhancement at the task-relevant or conditioning stimulus tone frequency, but also by more complex changes in RF shape, gain, and neuronal activity and connectivity, depending upon stimulus features, task, and behavioral context. Hence, it is important to emphasize that in the adult brain, there are likely to be multiple forms of plasticity, each with its own characteristic context of sensory experience, or behavioral challenge, and its unique set of cellular mechanisms and sites of plasticity. One of the major

challenges for the field is to come up with a synthesis that explains the origins and mechanisms, roles, and interactions of the different kinds of plasticity.

We have studied the dynamic, RF transformations in the auditory cortex that accompany top-down attentional modulation of auditory processing. The dynamic changes reveal that the brain is able to make nimble, adaptive changes from one moment to the next as acoustic context and task demands change (Fritz *et al.*, 2005a,b; 2010). These transformations occur at the level of synapses, single neuron receptive fields, and also at the level of brain networks. They are related to issues such as rapid, “automatic” RF adaptive plasticity that is not driven by attention, possible common mechanisms of RF plasticity contributions of the broader attentional network to task-driven plasticity, and insights from human neuroimaging studies that may help to put the results of animal studies in perspective.

The essence of our approach is to record from single neurons in primary auditory cortex (A1) and frontal cortex, while the animal performs a variety of different auditory tasks (Fig. 4). Our goal is to quantify the nature and time-course of state-dependent, task-dependent adaptive plasticity in the auditory cortex on a cellular and network level. Our approach to quantification of RF changes is illustrated (Fig. 5) with examples of rapid RF changes during tone detect and two-tone discrimination tasks.

Overall, a distinct pattern of change was found in spectro-temporal RFs (STRFs), i.e., there was selective enhancement not only at a target tone frequency, but also by an equally selective depression at the reference tone frequency. When single-tone detection and frequency discrimination tasks were performed sequentially, neurons responded differentially to identical tones, reflecting distinct predictive values of

stimuli in the two behavioral contexts. Our findings show that A1 neuronal responses can swiftly change to reflect both sensory content and the changing behavioral meaning of incoming acoustic stimuli (Fritz *et al.*, 2005a).

Rapid auditory task-related plasticity is an ongoing process that occurs as the animal switches between different tasks and dynamically adapts auditory cortical STRFs in response to changing acoustic demands. Rapid plasticity modifies STRF shapes in a manner consistent with enhancing the behavioral performance of the animal. The specific form of the STRF change is dictated by the salient acoustic cues of the signals in the behavioral task, and is modulated by general influences reflecting the animal’s state of arousal, attention, motor preparation and reward expectation.

Top-down signals from frontal cortex are important in cognitive control of sensory processing. We compared activity in ferret frontal cortex and A1 during auditory and visual tasks requiring discrimination between classes of reference and target stimuli. Frontal cortex responses were behaviorally gated, selectively encoded the timing and invariant behavioral meaning of target stimuli, could be rapid in onset, and sometimes persisted for hours following behavior. These results indicated that attention led to rapid, selective, persistent, task-related changes in spectrotemporal receptive fields. This suggests that A1 and frontal cortex dynamically establish a functional connection during auditory behavior that shapes the flow of sensory information and maintains a persistent trace of recent task-relevant stimulus features (Fritz *et al.*, 2010).

### Acoustic motion processing in auditory cortex

Within extrastriate visual cortex of humans, monkeys and cats, individual cortical areas are specialized for spatial or

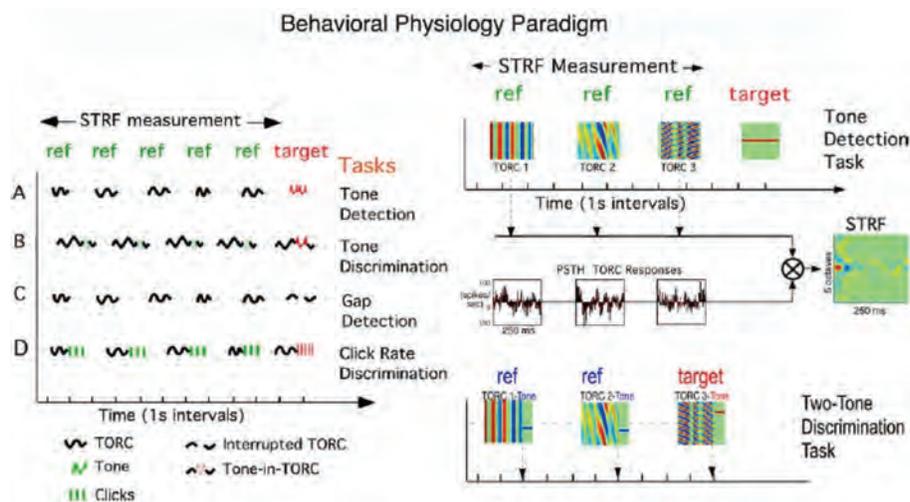


Fig. 4. Design of experimental stimulus presentations. Upper left: On a given trial during a behavioral session, a random number of temporal orthogonal ripple combinations (TORCs), i.e., 1–6 noisy reference signals, were followed by a ‘target’ tone. The panels at right illustrate spectrograms of three such TORCs and of the following tonal target. Responses to each TORC are collected in post-stimulus time histograms (PSTHs) at middle right that are cross-correlated with the TORC spectrograms to estimate the spatio-temporal reference field (STRF) above. Although the animal behaves in anticipation of the target, all spike measurements to derive the STRF are made during the presentation of the reference TORCs. Lower right: Similar design for a two-tone discrimination task in which the ferret is presented with a random number of TORC tone combinations (1–6 reference signals in which the reference tone is fixed in frequency) followed by a target TORC-tone combination (in which the tone component changes to a different frequency than that of the reference tone). The panels at left represent a schematic of various possible experimental paradigms, including (A) tone detection, (B) two-tone discrimination, (C) gap detection, and (D) click rate discrimination. All follow the same basic design. The reference signals are (or include) TORCs used to measure the STRF. The target varies from one experiment to another. (Reprinted with permission from Fritz *et al.* 2005b).

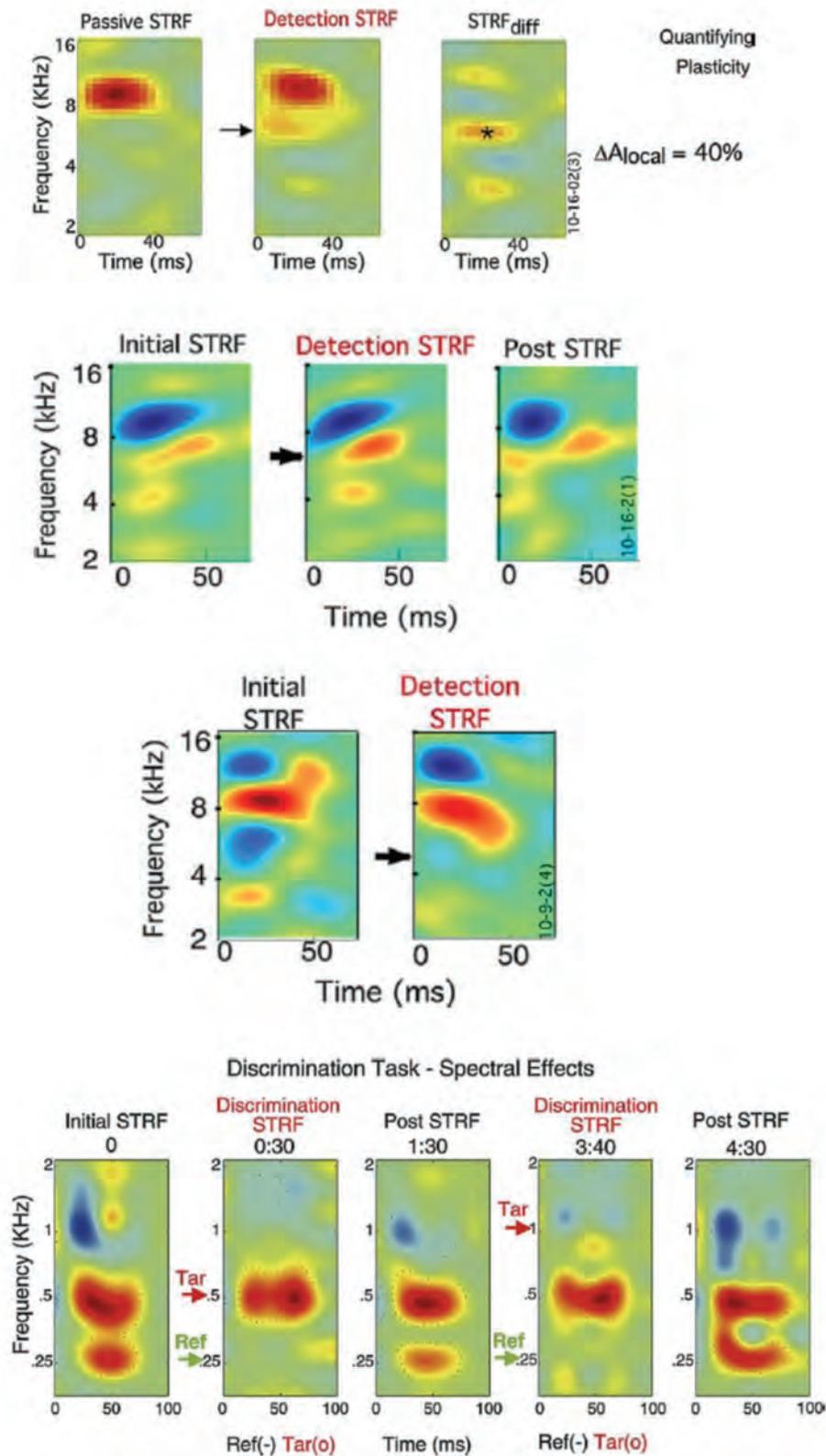
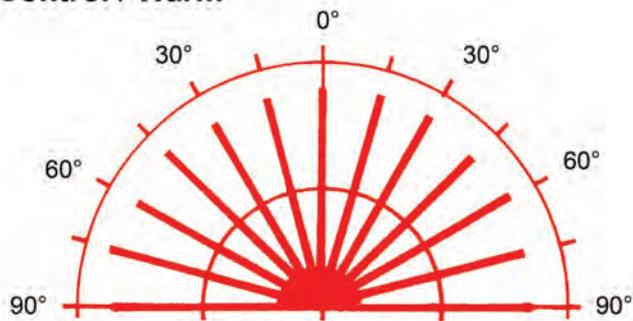
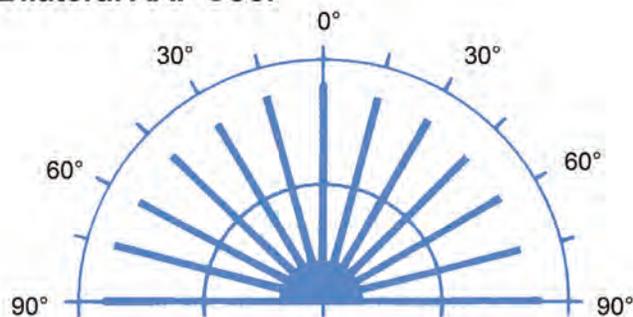


Fig. 5. (Top row) Comparison of a pre-behavior, normalized quiescent spatio temporal STRF (left panel) and behavioral reference field (STRF) (middle panel). Color scale: increased (red) to suppressed (blue) firing about the (green) mean; red and blue are statistically significant deviations from the mean. Top row--black arrow: frequency of the target tones during the detection task. The difference between the normalized quiescent and detection STRF is shown in the right panel (STRFdiff). Asterisk marks the location of maximal change. Second and third rows--facilitative STRF plasticity in AI. STRFs from two single-units in AI illustrate typical changes observed during performance of the tone-detection task. Second row--pre-behavior STRF (left panel). Localized enhancement of an excitatory region in the STRF at the target frequency during behavior (middle panel). The post-behavior quiescent STRF (right panel) reverted immediately to a RF very close to its original shape. Pre-behavior STRF (left panel). Local decrease (near elimination) of lower inhibitory sideband at the target frequency in the detection STRF (coincident maxima at target frequency). Fourth Row--three quiescent STRFs interleaved with two sequential two-tone discrimination tasks, all measured during recordings from the same neuron. The times at which STRFs were measured relative to the beginning of recording are shown on top of each panel. The arrows mark the reference (green) and target (red) frequencies used. Note the disappearance of the excitatory area in the near 250-Hz in the STRFs measured during the discrimination tasks. Reprinted with permission from Fritz et al. (2005b).

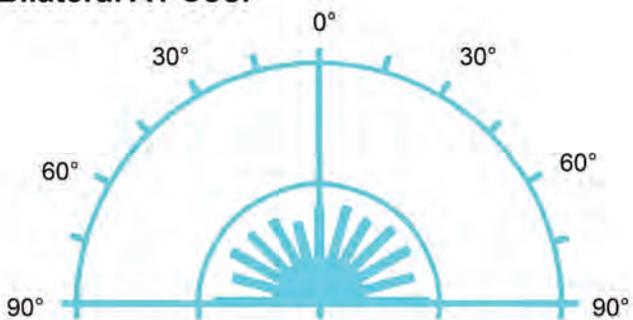
### A) Control / Warm



### B) Bilateral AAF Cool



### C) Bilateral A1 Cool



### D) Bilateral PAF Cool

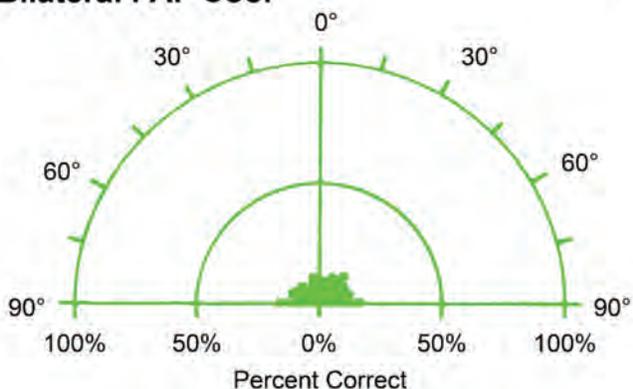


Fig. 6. Localization of a stationary acoustic target (mean performance from four cats) (A) prior to, and following, cooling deactivation (warm), (B) during bilateral cooling of the anterior auditory field (AAF), (C) during bilateral cooling of A1, and (D) during bilateral cooling of the posterior auditory field (PAF). The two concentric semicircles represent 50% and 100% response levels and the length of each bold line corresponds to the percentage of correct responses at each location tested. Stimulus was a 100-ms broadband noise burst presented at 20 dB(A) above background levels.

motion processing. Specifically, area MT (middle temporal visual area) or area V5 in the primate (posteromedial lateral suprasylvian area (PMLS) in the cat) is an area uniquely identified to be critical for the discrimination of visual motion (velocity, direction, etc.; see Born and Bradley, 2005). In the auditory system, the ability to discriminate the direction of a moving sound is also a critical survival feature, whether on the part of a predator or prey. Therefore, we have been investigating whether there is a locus in auditory cortex that is essential for the accurate discrimination of motion in the absence of involvement in static auditory target localization. If such a cortical area exists, it would strongly support the concept of an acoustic MT. However, it may also be the case that for an area to be involved in acoustic motion direction discrimination that it might be a prerequisite for it to also contribute to the localization of stationary acoustic targets.

In cat auditory cortex, four areas have been identified to be critical for accurately determining the spatial location of a static acoustic stimulus (Malhotra and Lomber, 2007; Malhotra *et al.*, 2008). These areas include primary auditory cortex (A1), the posterior auditory field (PAF), the dorsal zone of auditory cortex (area DZ), and the field of the anterior ectosylvian sulcus. Is there an auditory cortical area specialized for acoustic motion processing, or are areas involved in static spatial localization also critical for acoustic motion processing? Cats were trained to perform two tasks: a spatial localization task using a static stimulus and a task that required the animals to discriminate leftward from rightward apparent acoustic motion. Focal, reversible cooling deactivation was then used to bilaterally deactivate the anterior auditory field (AAF), A1, or PAF.

Both tasks were conducted in an acoustic orienting arena (Lomber *et al.*, 2007) and broad-band noise was delivered at 20 dB SPL above a background level of 58 dB SPL as a stimulus. To determine the contribution of the three cortical areas to the accurate spatial localization of a static sound source, the cats were first trained in a semicircular arena to identify the location of a 100-ms broad-band noise burst randomly emitted from one of 13 speakers placed at 15°-intervals across 180° of azimuth. Before and after each cortical deactivation, acoustic spatial localization accuracy and precision were excellent, with performance above 80% correct for all locations (Fig. 6A). During bilateral deactivation of AAF cortex, sound-localization performance was unimpaired (Fig. 6B). Bilateral deactivation of A1 resulted in a spatial-localization impairment throughout the entire field examined to between 40-50% correct across all tested positions (Fig. 6C). In contrast, bilateral deactivation of PAF profoundly impaired the ability of all the cats to accurately and precisely localize the acoustic stimulus (Fig. 6D) to levels just above chance (7.7%). These findings were in agreement with earlier studies (Malhotra and Lomber, 2007; Lomber and Malhotra, 2008; Malhotra *et al.*, 2008).

Next, acoustic-motion discrimination during bilateral deactivation of the same three areas (AAF, A1, and PAF) was examined in the same four cats used in the static acoustic target localization task. While each animal was fixating on a central LED, apparent motion of 90°/s was generated by

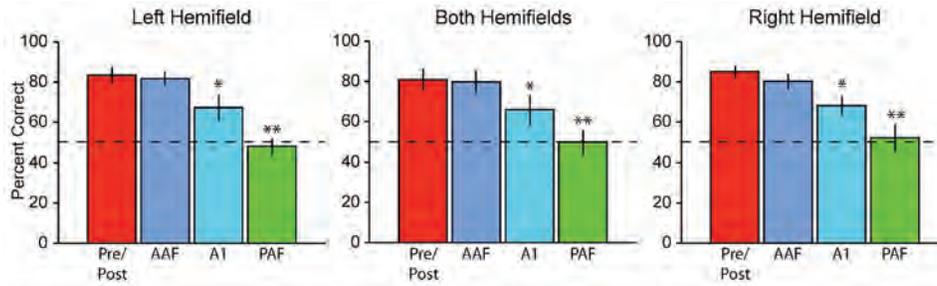


Fig. 7. Direction of acoustic-motion discrimination (mean performance from four cats) performance in the left hemifield, right hemifield, and positions that traverse the midline (both hemifields) prior to, and following, cooling deactivation (Pre/Post, red), during bilateral cooling of the anterior auditory field (AAF) (dark blue), during bilateral cooling of the primary auditory field (A1) (light blue), and during bilateral cooling of posterior auditory field (PAF) (green). Single asterisk indicates performance significantly different ( $p < 0.01$ ) from pre/post cooling levels, and double asterisks indicate performance significantly different ( $p < 0.01$ ) from both pre/post cooling levels and from bilateral A1 cooling deactivation performance. Dashed line=chance performance of 50% correct.

sequential noise bursts (78 dB SPL) emitted from five speakers across 60° of arc. The cat then made a correct response by approaching a left or right 30° LED to indicate leftward or rightward motion, respectively. Both rightward and leftward motion were examined in three different zones of the auditory field: positions confined to the left hemifield; positions that crossed the midline; and positions that were confined to the right hemifield (Fig. 7). Performance prior to, and following, cooling deactivation was in excess of 80% correct. During bilateral deactivation of AAF cortex, discrimination of acoustic-motion direction was unimpaired and not significantly different from control levels (Fig. 7). Bilateral deactivation (i.e., cooling) of A1 resulted in an acoustic-motion discrimination impairment throughout the entire field examined, with performance falling to ~65% correct ( $p < 0.01$ ; Fig. 7). In contrast, bilateral deactivation of PAF performance fell to chance levels during bilateral cooling of PAF. Therefore, as with the static-localization task, deficits were most profound during bilateral deactivation of PAF, moderate during bilateral deactivation of A1, and absent during bilateral AAF deactivation.

Overall, the results show that areas involved in acoustic-motion processing are also involved in static acoustic spatial localization. An area that is uniquely involved in acoustic-motion processing was not identified. These results suggest that spatial-localization functions may be a prerequisite for acoustic-motion processing in auditory cortex, and do not support the possibility of the existence of an auditory equivalent of the visual field MT. **AT**

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