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Focusing attention on sound

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Abstract

A new study finds that neurons in the ferret frontal cortex typically respond to sound only during trained auditory tasks and that these neurons depict the task-related meaning rather than the acoustical properties of stimuli.

Our auditory scene constantly changes as voices and other sounds come and go and as we move from one setting to another that may differ greatly in its acoustical properties. Our perception of the world therefore critically depends on the capacity of the brain to adapt rapidly to changes in incoming sounds¹ and to focus attention toward sounds of interest². This involves an interaction between top-down and bottom-up signals in the brain. Top-down signals are believed to endow sensory inputs with meaning and they allow attention to be directed toward particular stimulus features. The classic example of these top-down effects is provided by the relationship between prefrontal and sensory cortices (Fig. 1a). In this issue, Fritz and colleagues³ reveal more about this relationship, finding that neuronal activity in the frontal cortex of ferrets encodes the behavioral meaning of acoustic stimuli and that the coupling between these neurons and the region of auditory cortex that represents the target sounds changes during sound detection or discrimination tasks.

Rather than having fixed tuning properties, neurons in primary sensory cortices show task-dependent changes in their receptive fields during behavior. This has been most clearly demonstrated in a series of elegant studies carried out on the ferret primary auditory cortex (A1) that showed that the spectral filter properties of the neurons, their so-called spectrotemporal receptive fields, undergo rapid modifications when the ferrets are engaged in behavioral tasks that require them to pick out a particular target sound against a background of reference sounds^{2,4}. Such task-related plasticity is thought to enhance the capacity of the animals to hear the target stimuli and should therefore be correlated with behavioral performance⁴. Top-down influences on the auditory cortex are likely to trigger these effects, as spectrotemporal receptive field plasticity has been observed only when the ferrets carry out tasks requiring attention to the target and reference sounds and not during passive presentation of the same stimuli.

Fritz and colleagues³ adopted the same procedure to determine whether task-related plasticity is also a property of the frontal cortex, a likely source of any top-down influence. The ferrets were trained to lick a spout from which water was delivered during the presentation of several reference sounds, but had to stop licking once the target stimuli appeared to avoid receiving a mild electric shock. By comparing the activity of neurons in the frontal cortex when the ferrets made this categorical distinction between the stimuli and

during passive presentation of the same sounds, the authors found that most of the responses to the target sounds were behaviorally gated.

In a previous study of ferret A1, Fritz and colleagues^{2, 4} focused on how behavior modulates the gain and even the shape of the neurons' spectrotemporal receptive fields. In the frontal cortex, however, many of the neurons did not respond at all to the target sounds except during behavior (Fig. 1b), with approximately equal numbers showing an increase or a decrease in their firing rate. These responses had widely varying latencies, but they often built up rapidly after target onset. In some cases, responses to target stimuli that emerged during behavior disappeared immediately after the task was over, whereas other neurons produced more persistent responses.

Although responses in the frontal cortex were time locked to the onset and offset of the target sound in some cases (Fig. 1b), Fritz and colleagues³ found that these neurons depict the task-related meaning rather than the acoustical properties of the stimulus. Thus, responses to a tone frequency that served as a target sound in one task were lost when that same tone became a reference in a different task. Furthermore, some of the neurons that they recorded showed similar behavioral gating when the ferrets performed either an auditory or a visual task using the same procedure, suggesting a more general sensory role in encoding target importance.

The resemblance between these results and those reported previously in A1 implies a possible link between the two regions and that task-related changes in the activity of neurons in the frontal cortex might contribute to the real-time reshaping of the receptive field properties of auditory cortical neurons. To explore this possibility, Fritz and colleagues³ recorded local field potentials simultaneously from the two areas while ferrets carried out the tone-detection task. Coherence analysis revealed a behaviorally driven reduction in synchronous activity between the frontal cortex and A1 in the alpha- and beta-frequency range of the local field potential (10–20 Hz) (Fig. 1c). Notably, this was found to be specific for A1 neurons that were tuned to the frequency of the target tone. This finding does not by itself show that outputs from the frontal cortex are responsible for the task-dependent modulation of A1 neurons, but it does suggest that top-down attentional control can be directed in a frequency-specific fashion that reflects the tonotopic organization of A1.

Particular mention should be made of the animal model used in this study. Although previous work on the influence of prefrontal cortex on processing in sensory cortical areas has been dominated by research on primates^{5, 6}, ferrets provide another option for studying the effects of attention and learning on hearing. They can be trained on a variety of tasks and are now widely used in auditory neuroscience research. Nevertheless, it is not a straightforward matter to show that activity in frontal cortex reflects target recognition as opposed to motor planning in the behavioral procedure, which was chosen by Fritz and colleagues³ for its ease of use with ferrets. By correlating activity with task-related licking, the authors attempted to isolate any contributions resulting from motor behavior. However, there is no doubt that the use of an approach that dissociates sensory and motor effects, such as a delayed matching-to-sample procedure⁷, would be desirable, although it remains to be seen whether ferrets can be trained to perform such a task.

Another issue concerns our primitive understanding of frontal cortex in nonprimate species. Fritz and colleagues³ propose that the region they recorded from is likely to be homologous to primate prefrontal cortex and this is supported by recent anatomical data⁸. Several questions naturally follow from this. Foremost among these is whether the domain specificity hypothesis put forward previously⁹ to describe the functional organization of prefrontal cortex in both human and nonhuman primates also applies to ferrets. Do equivalent regions exist that are devoted to spatial working memory and to the processing of object features or object-related working memory¹⁰? Fritz and colleagues³ found that neurons responding during auditory and/or visual tasks were intermixed in ferret frontal cortex, suggesting a lack of modality specificity. Given how widespread multisensory convergence is, even in ferret auditory cortex¹¹, this is not surprising, but further work is obviously needed to characterize the inputs to different parts of the frontal cortex in this species.

The frontal cortex is not the only forebrain region thought to be involved in adjusting the cortical processing of sensory signals. Cholinergic inputs from the basal forebrain also seem to mediate attention and learning by modulating the responsiveness and tuning properties of cortical neurons in ways that enhance the representation of behaviorally relevant stimuli¹². Recent evidence points to the existence of a sensory cortex–prefrontal cortex–basal forebrain loop¹³ comprising neural components capable of integrating bottom-up sensory input with top-down attentional processing and inputs from the limbic system. Such a loop has the potential to respond to real-time changes in task demands by way of the prefrontal cortex and to induce changes in neuronal firing in auditory cortex by the action of the cholinergic inputs from the basal forebrain.

These circuits are also likely to provide the mechanism by which top-down inputs dictate how the response properties of A1 change in a task-specific fashion during perceptual learning¹⁴. In turn, their influences may be transmitted by way of the auditory cortex to lower parts of the auditory pathway, as suggested by the loss of learning-induced behavioral plasticity after the selective elimination of layer V pyramidal neurons that project to the inferior colliculus¹⁵. The study by Fritz and colleagues³ implies that prefrontal cortical neurons might create a flexible framework for focusing attention on behaviorally relevant sounds and provides an intriguing insight into the brain circuitry that allows the dynamic processing of sensory information.

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Figure 1.

Top-down relationship between frontal and auditory cortices.

(a) A tangential-flattened section of the ferret brain. A, anterior; D, dorsal. (b) An example of a neuron in the ferret frontal cortex that responded vigorously to a target tone during a task in which that stimulus had to be discriminated from several reference sounds; no response was elicited by the same stimulus sequence presented before behavior. PSTH, peristimulus time histogram. (c) When the ferret is engaged in these tasks, the coherence between local field potentials (LFP) recorded simultaneously in A1 and in the frontal cortex (FC) was strongly depressed.