Computational and neurophysiological principles underlying auditory perceptual decisions

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A fundamental scientific goal in auditory neuroscience is identifying what mechanisms allow the brain to transform an unlabeled mixture of auditory stimuli into distinct perceptual representations. This transformation is accomplished by a complex interaction of multiple neurocomputational processes, including Gestalt grouping mechanisms, categorization, attention, and perceptual decision-making. Despite a great deal of scientific energy devoted to understanding these principles of hearing, we still do not understand either how auditory perception arises from neural activity or the causal relationship between neural activity and auditory perception. Here, we review the contributions of cortical and subcortical regions to auditory perceptual decisions with an emphasis on those studies that simultaneously measure behavior and neural activity. We also put forth challenges to the field that must be faced if we are to further our understanding of the relationship between neural activity and auditory perception.

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Introduction

Hearing is fundamental to and spans our human existence. This remarkable capacity is associated with a number of computational cognitive processes that act both in parallel and serially, including (but not limited to): perceptual grouping, attention, categorization, and decision-making [1,2]. (1) Perceptual grouping is a form of featu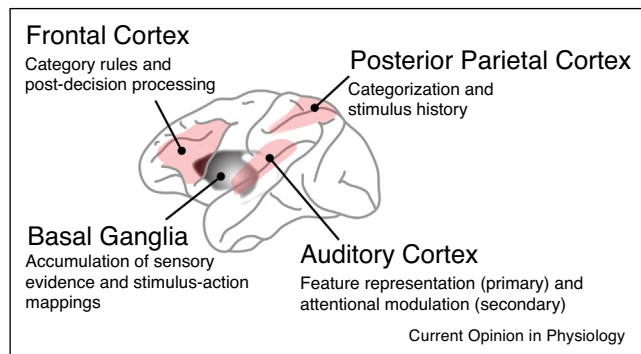re-based stimulus segmentation that determines whether acoustic events are grouped into a single sound or are segregated into distinct sounds. (2) Although attention is not always necessary, our awareness of a sound can be influenced by attention. (3) Categorization is a process in which sounds are classified and grouped based on their acoustic features and other types of information. (4) Auditory decision-making is a deliberative process that produces a categorical perceptual judgment. Did I hear the stimulus? From where and whom did it come? What does it tell me?

In this review, we focus on the neural and computational processes that underlie auditory perceptual decisions. We emphasize recent studies that combined neural recordings with controlled auditory behavior (Figure 1). We attempt to integrate new findings, integrate different sets of studies, pose challenges to the field as to how to best study auditory perceptual decisions, and define some key open questions that remain unresolved.

Selective attention as a neuronal mechanism for auditory scene analysis

Our environment is filled with acoustic stimuli that our brain transforms from low-level sensory representations into perceptual representations called 'auditory objects' (i.e. sounds) [3]. These objects are the foundational building blocks of our auditory-perceptual world and are the computational result of the brain's capacity to detect, extract, segregate, and group regularities in the acoustic environment, a process often referred to as 'auditory scene analysis'.

The mechanisms underlying auditory scene analysis have yet to be fully identified but may include bottom-up processes such as the detection of temporal coherence and neuronal adaptation [4–8]. In addition to these bottom-up processes, top-down processes, like attention, play a pivotal role in parsing the auditory scene. For example, Schwartz and David [9] recently trained ferrets to detect a target tone burst that was masked by 1 of 2 simultaneous continuous noise streams. The spectral bandwidth of one noise stream was centered over the best frequency of a recorded A1 neuron; the target tone burst was embedded in this noise stream. The other noise stream had a bandwidth that was outside of the neuron's tuning curve. When the ferrets attended to the noise stream that contained the target, the neural response to the noise stream was reduced without a concomitant change in the neural response to the target tone burst.

Figure 1

Frontal Cortex
Category rules and
post-decision processing

Posterior Parietal Cortex
Categorization and
stimulus history

Basal Ganglia
Accumulation of sensory
evidence and stimulus-action
mappings

Auditory Cortex
Feature representation (primary) and
attentional modulation (secondary)

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Summary of highlighted findings. A cartoon schematic of a non-human primate brain showing the outer cortical surface and the basal ganglia. Cortical areas discussed in this review are shaded in red. The basal ganglia (striatum) is shown in the black-grey gradient. We highlight the major findings discussed in this review. By no means is this an exhaustive list of the functions of each of these brain regions.

This attentional suppression effectively improved the neural discriminability of the target, leading to improvements in behavioral detection.

Attention can also enhance information processing by modulating the neural tuning properties that are relevant for solving an ongoing auditory task [10]. Various mechanisms, which are not mutually exclusive, may allow attention to enhance neural coding of relevant auditory information. For instance, attention may preferentially increase the responsivity of attended stimuli that are near the peak of a neuron's response profile [11]. Attention may also sculpt the neural response profiles. As a result of this sculpting, a neuron's response profile for a particular feature (e.g. frequency) becomes more selective [12]. At the population level, attention can generate sparser networks that have more positive pairwise noise correlations, which can support decision-making [11].

When and where does attention have its largest effect? The effect of attention on neural activity is most pronounced when subjects need to make fine discriminations and, more generally, when more attention is needed to successfully complete the task [9]. Further, the effects of attention on neural activity increase in deeper regions of the cortex: neural activity in non-primary auditory cortex is modulated more by attention than activity in primary auditory cortex [5,13]. At first blush, these principles are comparable to those seen in the visual system [14], suggesting that attention, under certain circumstances, can act comparably on both modalities. Though, the neural mechanisms underlying auditory attention have not been studied anywhere as much as those underlying visual attention.

The difference between attention's effects in the primary and non-primary auditory cortices is not just quantitative,

but it is also qualitative. For example, in O'Sullivan *et al.* [13], electrocorticographic activity was obtained in neurosurgical patients while they selectively attended to one speaker's voice in a two-speaker auditory scene. Not unexpectedly, O'Sullivan *et al.* found that neural activity in the primary auditory cortex was modulated by the acoustic features of both speakers. However, this neural modulation was relatively unaffected by the subjects' attentional state (i.e., which speaker the listener was attending). In contrast, in the non-primary auditory cortex, neurons responded selectively to the attended speaker, even when the acoustic features of the two speakers overlapped. This study also implies that attention, along with other non-attentional mechanisms, contributes to the generation of noise-invariant representations of auditory objects [15].

Emergence of category representations along the auditory pathway

Listeners can form categories based on several different principles. For example, categories can be 'hierarchical' in that a stimulus can simultaneously belong to several different categories, depending on the categorical rules. Although this notion of categorical hierarchy is well accepted, there is considerable disagreement about the relationship between specific brain regions and the categorical functions that they might subserve [16].

Inspired by computational models of visual categorization [17], Jiang *et al.* [18] trained human listeners to categorize morphed versions of two different monkey vocalizations. These listeners also underwent functional-imaging scans before and after training. Jiang *et al.* found that training increased the neural selectivity in the left auditory cortex – in particular, non-primary auditory cortex – to the features of monkey vocalizations. Interestingly, this improvement in neural selectivity correlated with the steepness of each listener's behavioral category boundary. The neural mechanism underlying this improvement may be a dynamic adjustment of each neuron's selectivity that reflected the ongoing task demands and the listener's trial-by-trial choices, similar to that seen with attention's effects on neural processing [10–12].

However, the Jiang *et al.* study did not identify a category representation in the auditory cortex but rather in the left inferior frontal gyrus [18]. These findings are consistent with a two-stage model in which auditory-category learning leads to sharper feature encoding in the auditory cortex and a frontal network that classifies these representations into categories [18]. Similarly, a recent ferret study explored the temporal dynamics of category selectivity in the auditory and frontal cortices [19]. The study found that category-like responses appear first in the frontal cortex and only later in the auditory cortex. The observation of category responses in the ferret auditory cortex but not in the Jiang *et al.* human study is not

necessarily in conflict. This difference may simply be due to the finer spatiotemporal resolution afforded to single-unit studies compared to the coarser resolution inherent in functional-imaging studies.

Contribution of the posterior parietal cortex to categorization and decision making

A traditionally 'non-auditory' area appears to be important for categorization and auditory decisions in rodents is the posterior parietal cortex [20,21]. In the visual system, the contributions of the parietal cortex to visual decisions are well documented [22], but less so for auditory decisions. Recent work by Zhong *et al.* [23] found that the inactivation of the mouse posterior parietal cortex — in particular, the parietal neurons that project to auditory cortex — impaired performance on the categorization of recently learned auditory stimuli as well as the re-categorization of well-learned stimuli. Parietal inactivation also affected how the mouse used stimulus history to bias its current choices. This latter finding is consistent with work by Akrami *et al.* [24], who identified a representation of stimulus history in the posterior parietal cortex. In fact, parietal inactivation improved performance: without a representation of stimulus history and the resulting idiosyncratic choice biases (that are unrelated to the actual task dynamics), the animals based their choices only on the current stimulus.

Contribution of the striatum to decision making

A contribution of striatal circuits to perception and decision-making is becoming increasingly apparent [25]. For example, the mouse anterior dorsal striatum appears to have a causal role in representing accumulated sensory evidence (i.e. the temporal integration of stimulus observations) needed for an auditory decision [26]. Several previous papers have identified brain regions with neural activity that reflects this accumulation process [20,22,25,27–29]. However, what is unique and important about Yartsev *et al.* is that a brain region was for the first time found that causally influences behavior throughout the entire accumulation process [26].

In contrast, the rodent posterior dorsal striatum does not appear to have a direct role in the decision process [30]. Dorsal-striatal neurons encode both actions and sound identity but not the animal's choices. Indeed, stimulation of this striatal region did not systematically shift the animals' choices. Instead, stimulation biased choices toward actions contralateral to the stimulation site. This finding, along with the observation that neural activity is not modulated by the subject's choices, suggests that the posterior dorsal striatum is more intimately involved in the sensorimotor mappings necessary for successful completion of the task. These sensorimotor mappings may contribute to the linkages between auditory stimuli and actions that are found in the auditory cortex [31].

Using response timing to understand the neural correlates of auditory decisions

Signals relating to auditory choice have been identified in a variety of brain structures: in early sensory regions [32–37], in relatively later cortical regions [20,21,38], and in subcortical regions [26]. A critical question is to understand the relationship between these different signals. That is, what is the contribution of different regions to choice and what does it mean that neurons in different regions are differentially selective to choice? Certainly, quantitative differences between different brain regions might reflect actual differences in feedforward hierarchical information processing [37]. However, it is also conceivable that choice selectivity might not reflect feedforward hierarchical information processing. Instead, it could reflect feedback from later regions to earlier regions [39–41].

One way to disambiguate these possibilities is to identify *when* choice selectivity (and other neuronal correlates of behavior) arise. One successful approach is to combine neural recordings and behavioral tasks with variants of sequential-sampling models, like the drift-diffusion model [22]. The advantage of such models is that they partition a subject's reaction times into a 'decision' time that reflects the time needed to make a perceptual decision and a 'non-decision' time that reflects sensory delay, motor preparation, and other post-decision processing.

Using this approach, we recently examined the role of the ventrolateral prefrontal cortex (vlPFC) [38] in auditory decision-making. We found that, as a current decision is being formed, vlPFC activity is not modulated by either the task or by the stimulus' features. However, a different story emerged *after* the time of the decision. In particular, we found vlPFC population activity was modulated by the sensory evidence, the monkeys' choices, and the trial outcome (i.e. whether the trial response was correct or incorrect). This suggests that post-decision information plays a role in evaluating the just-completed decision as well as biasing the next one. Consistent with this hypothesis, we found that vlPFC activity predicted the monkeys' subject-specific choice biases on the next trial. Moreover, this activity is causal: vlPFC microstimulation affected the subsequent choice but not the current one. This information may be relayed to the auditory cortex to facilitate its role in sensory prediction [42]. Such sequential effects on a subject's choices have also been recently identified in the rodent parietal cortex [24].

Open questions

Many fundamental questions remain about neural processing subserving auditory decision-making (Figure 2). The Yin *et al.* study [19] was an important first analysis of the differential contribution of feedforward and feedback information flow. However, it is critical to conduct simultaneous recordings in different cortical regions to more

Figure 2

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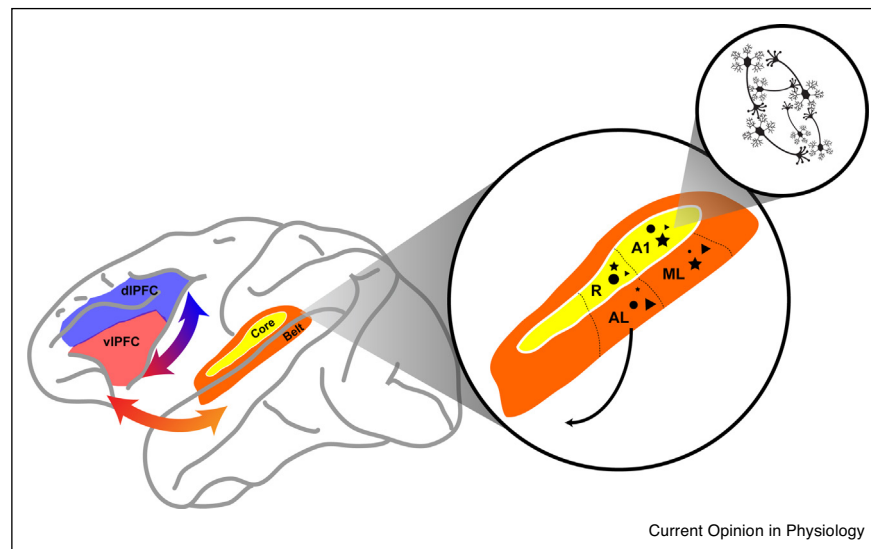
Open questions in auditory perceptual decisions. A cartoon schematic of a non-human primate brain illustrating some of the open questions that relate neurophysiological mechanisms with auditory decisions. The cortical fields in orange, yellow, and red represent those cortical regions that project to and are part of the ventral auditory pathway. The one in blue represents a cortical region in the dorsal auditory pathway. We do not show all of the regions in both pathways. The orange-red arrow signifies future experiments that probe the differential contribution of feedforward and feedback projections along the ventral auditory pathway (or any pathway that underlies auditory perception). The red-blue arrow signifies future experiments that probe how different auditory pathways (information processing streams) work together to create unified perceptual representations; here, for illustration purposes, we choose the ventral and dorsal pathways (which contains the dlPFC). In the larger cut-out, the circles, stars, and triangles represent future experiments that explore the notion that different tasks and/or stimuli may differentially involve different cortical regions: the larger/smaller the symbol, the more/less the region may contribute to auditory perceptual decisions. For example, in A1, the neural activity generated by the task (stimulus) represented by the star might contribute more to auditory decisions than the task (stimulus) represented by the circle, and even more than the task (stimulus) represented by the triangle. We show this for a few select regions but it applies to all cortical and subcortical regions. In the smaller cut-out, the network of neurons illustrates how future experiments need to further test how pairwise and higher-order correlations contribute to auditory decisions. A1: primary auditory cortex; R: auditory cortical field R; ML: the mediolateral belt region of the auditory cortex; AL: the anterolateral belt region of the auditory cortex; vlPFC: ventrolateral prefrontal cortex; dlPFC: dorsolateral prefrontal cortex.

rigorously understand how brain regions interact and contribute to information flow. Relatedly, the degree to which subcortical processes interact with decision-making and how these feedforward and feedback loops contribute to auditory decisions is an open question [43]. Second, at least in mice, the primary auditory cortex contributes to simple and more complex choices in different ways [44]. However, the degree to which different types of auditory judgements differentially engage brain regions downstream of primary auditory cortex has yet to be fully articulated. Third, although this review did not emphasize specific information-processing streams, the so-called ventral auditory pathway is known to contribute causally to auditory perceptual decisions [1,37]. Is this the only pathway that contributes to perceptual decisions? In the future, it will be important to identify the manner (if any) in which other pathways (e.g. the dorsal auditory pathway) interact with the ventral pathway to form a consistent and coherent representation of the auditory scene. Finally, future work should examine the contribution of pairwise correlations and potentially higher-order interactions of auditory neurons to auditory decisions [11].

Conflict of interest statement

Nothing declared.

Author contributions

TB, J-H L, and YEC wrote the paper.

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