Neural maps in insect versus vertebrate auditory systems

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The convergent evolution of hearing in insects and vertebrates raises the question about similarity of the central representation of sound in these distant animal groups. Topographic representations of spectral, spatial and temporal cues have been widely described in mammals, but evidence for such maps is scarce in insects. Recent data on insect sound encoding provides evidence for an early integration of sound parameters to form highly-specific representation that predict behavioral output. In mammals, new studies investigating neural representation of perceptual features in behaving animals allow asking similar questions. A comparative approach may help in understanding principles underlying the formation of perceptual categories and behavioral plasticity.

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Introduction

The sense of hearing has evolved separately many times in the animal kingdom, most prominently in several insect [1] and vertebrate groups [2]. With the ability to transduce and encode sound comes the need to represent and process auditory information at central stages. One such representation is a neural map: a topographic representation of stimulus features, usually of continuous parameters. These features can be physical attributes of the stimulus, but sometimes are better described by their perceptual meaning.

Why represent information in a topographical way? Which constraints or requirements favor the formation of maps in the auditory pathway? One way to answer such questions is to compare the representation of information about sound in animals that have independently acquired the sense of hearing. Insects are a natural choice here, because hearing has evolved many times separately [1]. However, all insects face some common constrains: their size and their often limited behavioral repertoire in response to sound stimuli. Thus, the present review will take some prominent examples from vertebrate audition, focusing mostly on mammalian model species, and compare these to central representation of sound in insects.

When describing a neural map, it is crucial to know which parameter is being mapped — this implies the question what is a *relevant* parameter. The best way to assess this is via behavioral experiments. To this end, insect model systems provide the advantage of highly stereotyped behavior in response to sound. The range of possible relevant parameters can be explored to a great extent without training, for example by measuring phonotaxis [3], aversive reactions [4] or duet singing in response to test stimuli [5]. Consecutive neural recordings can then be related to previously tested 'perceptual' features and compared to parameters more closely linked to the physical properties of the sound [6•,7]. Only the recent adaptation of techniques allowing to record many neurons simultaneously in freely behaving animals have enabled investigations in vertebrates to proceed along similar lines. In mammals, with their much larger and more plastic behavioral repertoire, it is often essential to compare neural coding and behavioral outcome on a trial to trial basis, relating it to a task that helps to define the relevant stimulus attributes.

The present review will first explore three basic types of sound features, ordered along the processing chain: (1) spectral content as an example of a peripherally generated map of the receptor surface, (2) sound direction as an example of a computational map, and (3) temporal features that are represented superimposed on the peripherally generated map. For all of these I will first introduce maps that have been reported in vertebrates and will then ask whether maps for similar features exist in insects and if not, what is the alternative form of representation. Finally, in a fourth, part I will discuss representation of perceptual categories at more central stages of both vertebrate and invertebrate auditory pathways.

Representation of the sensory periphery: tonotopy

In the mammalian ear, sound is decomposed into its spectral components. The magnitude of the activity of different hair cells along the cochlea encodes for the relative level (amplitude) of each frequency. The tonotopy is maintained for at least seven synapses into the central pathway up to the auditory cortex (e.g. [8]) and constitutes the most fundamental and widespread neural map in the auditory system (Figure 1). In insects, at least a basic peripheral frequency decomposition has evolved in most species with a tympanic ear: among others, it has

Figure 1
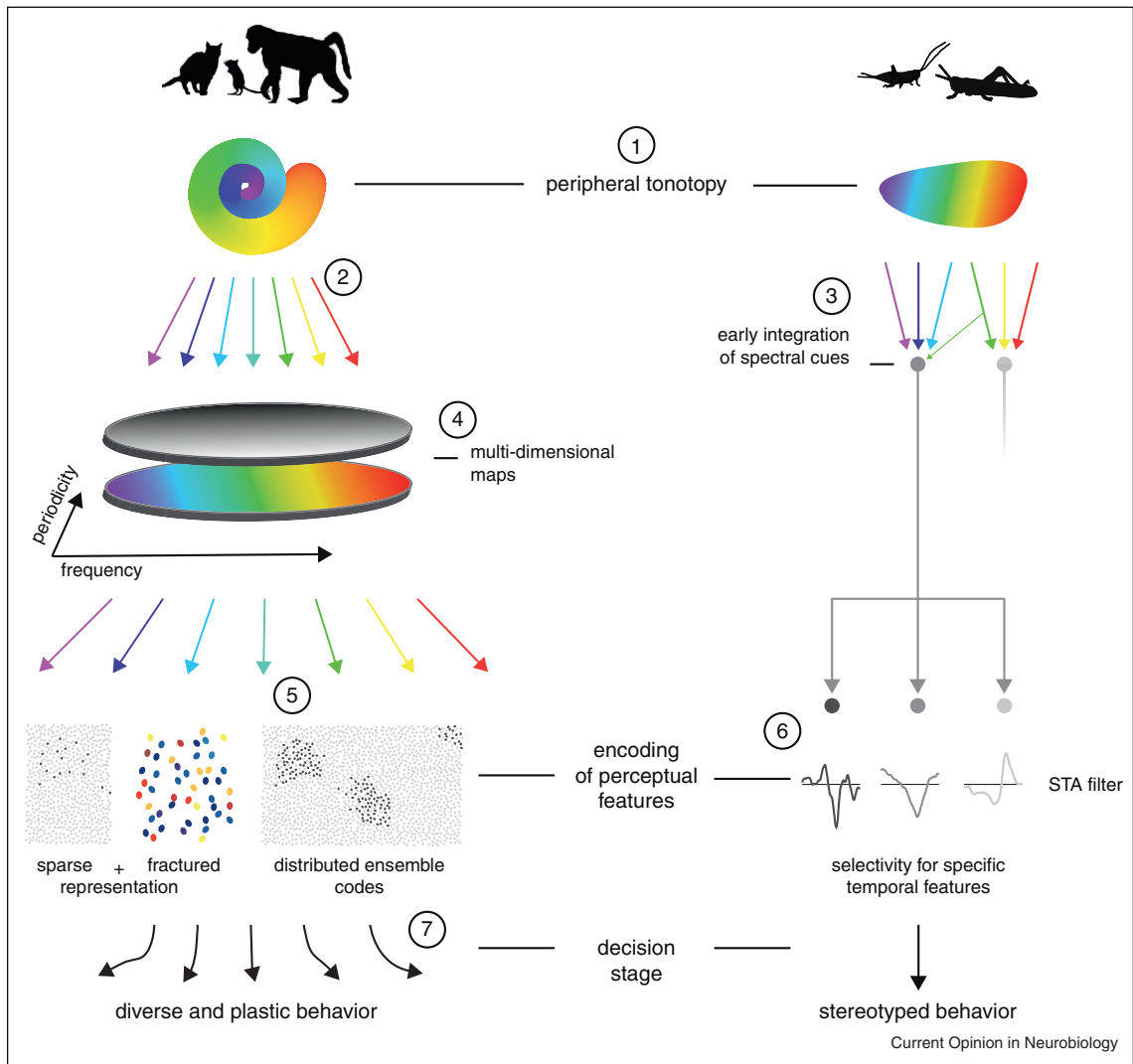
Representation of sound along the auditory pathways of insects and mammals. Both schematic pathways combine findings from several species and represent general principles rather than a specific animal model. (1) Sound is represented tonotopically at the ears of both insects and mammals with varying resolution. Colors represent preferred frequencies. (2) In mammals, this topographical representation is propagated to consecutive stages and sound representation diverges at each step. (3) In most insects, the number of neurons decreases from the receptor level to the next processing stage. Thus, frequency information is integrated at this stage already, combining different frequency channels and thereby shaping frequency responses, enabling streaming and highly non-linear interaction between the channels. (4) At more central stages in mammals, maps of temporal features (grey scale) are superimposed on the basic tonotopy (color scale), thereby creating multi-dimensional maps. (5) At the thalamo-cortical level, neural activity increasingly represents perceptual or categorical features. These are no longer represented in clear topographical maps but representation becomes sparse [57] and fractured [58,59], and distributed ensembles of neurons may code for stimulus categories [50]. (6) In insects, identified neurons only two synapses away from the peripheral receptors selectively code for behaviorally relevant temporal features, as indicated by the distinctive filters for each neuron type (STA — spike triggered average, re-plotted from [42••]). (7) Mammals display a much larger behavioral repertoire in response to sound than insects.

been found in crickets [9], grasshoppers [10] and cicadas [11]. Two recent studies [12,13••] were able to show that the same principles of hearing, namely impedance matching, a traveling wave and a tonotopic layout of the largest amplitude of the wave underlie the previously described tonotopy in the bushcricket ear [14]. Given this stunning example of convergent evolution in vertebrates and bushcrickets, the question arises whether convergent evolution also occurs for central tonotopic maps.

In bushcrickets, the central projections of the receptors show a tonotopic arrangement [15,16]. Overlaying of the projection with the input region of the next layer of neurons predicts their tuning [17]. However, in contrast to mammalian auditory pathways, almost all central auditory pathways in insects show strong neuronal convergence (Figure 1, #3). Even though different ascending neurons are tuned to different frequencies, their resolution seems to be much lower and neither the neurons nor