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Review Article

Subcortical pathways: Towards a better understanding of auditory disorders

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ABSTRACT

Hearing loss is a significant problem that affects at least 15% of the population. This percentage, however, is likely significantly higher because of a variety of auditory disorders that are not identifiable through traditional tests of peripheral hearing ability. In these disorders, individuals have difficulty understanding speech, particularly in noisy environments, even though the sounds are loud enough to hear. The underlying mechanisms leading to such deficits are not well understood. To enable the development of suitable treatments to alleviate or prevent such disorders, the affected processing pathways must be identified. Historically, mechanisms underlying speech processing have been thought to be a property of the auditory cortex and thus the study of auditory disorders has largely focused on cortical impairments and/or cognitive processes. As we review here, however, there is strong evidence to suggest that, in fact, deficits in subcortical pathways play a significant role in auditory disorders. In this review, we highlight the role of the auditory brainstem and midbrain in processing complex sounds and discuss how deficits in these regions may contribute to auditory dysfunction. We discuss current research with animal models of human hearing and then consider human studies that implicate impairments in subcortical processing that may contribute to auditory disorders.

Contents

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1. Introduction

The ability to process complex sounds effectively depends on neural networks that extract information from acoustic features that change over time. When acoustic feature extraction is impaired, a variety of disorders can occur that negatively affect individuals of all ages and from all walks of life. Recently, there has been growing concern regarding auditory disorders that manifest behaviorally even when audiometric thresholds are not impaired. While impairments in auditory cortex processing and/or cognitive processes are typically considered as underlying these types of disorders, there is strong evidence to suggest that, in fact, deficits in subcortical auditory processing play a significant role. The purpose of this review is to highlight the importance of the auditory brainstem and midbrain in the processing of complex sounds and to discuss how deficits in these auditory regions may contribute to hearing disorders. Understanding subcortical processing is critical in an attempt to develop suitable treatments targeted to alleviate or prevent central auditory processing disorders.

Auditory disorders are often identified when speech sounds are loud enough to hear but individuals nonetheless have difficulty understanding what is said, particularly in challenging acoustic environments (Moore, 2006). Research efforts into the neural causes of this type of impaired speech discrimination focus on gaining a better understanding of the segregation of complex sounds from multiple sources into auditory objects that form distinct perceptual "streams" (Bregman, 1990; Shamma and Micheyl, 2010). Deficits in auditory streaming may lead to problems in which listeners are unable to adequately recognize and understand attended speech while ignoring background noise and competing speech. Merging complex sounds into objects and subsequent streaming has long been thought to occur in higher-order brain regions, and the primary auditory cortex has served as a starting point for examining pathways that mediate the perception of speech. However, subcortical neural circuits are also essential for complex sound processing and are implicated in the grouping and segregation of acoustic features (Pressnitzer et al., 2008). These functions may be based on the extraction of shared acoustic features over time, ultimately resulting in the creation of auditory objects in the cortex. Currently, our understanding of how subcortical pathways contribute to complex sound processing is incomplete. The fact that several functions of auditory processing previously attributed to the cortex are now demonstrated in subcortical pathways (e.g., Pressnitzer et al., 2008; Slee and David, 2015) warrants a closer examination of these lower-level circuits.

The focus of this review is on subcortical lemniscal pathways implicated in complex sound processing and how dysfunction of these pathways may contribute to auditory disorders. We highlight current research with animal models of human hearing that include a range of species, conducted under various experimental conditions and states of arousal. These model systems permit the use of methodological tools that are currently unavailable for humans and provide insight into the potential neural mechanisms of auditory function. We first review brainstem circuits implicated in extracting spectral and temporal features of complex sounds and spatial information from multiple sound sources. We then consider how early auditory processing could contribute to neural selectivity for biologically relevant sounds in higher-order cortical networks, and discuss how descending inputs from the cortex might influence selective attention subcortically. We then attempt to bridge the gap between animal (mainly rodent) and human studies by considering how alterations in subcortical circuits could contribute to speech processing deficits associated with auditory disorders.

2. Salient features of complex sounds are extracted subcortically

Natural sounds including human speech, animal vocalizations, and other non-speech sounds contain salient features that can be identified from psychoacoustics: pitch, timbre, starts and stops, among others. Our perception of these sounds requires the neural extraction of acoustic features that are merged into acoustic objects at the level of the cortex (Nelken, 2004; Snyder and Elhilali, 2017). Studies from a variety of mammalian species indicate that much of the feature extraction observed in the cortex has already been performed at the level of the auditory midbrain by neurons in the inferior colliculus (IC) through the integration of multiple ascending pathways from the brainstem (Fig. 1). Distinct brainstem networks possess specializations that enable recoding of both identity and source information of complex sounds. These attributes, along with selective attention, are critical for understanding speech in acoustically challenging environments.

2.1. The brainstem uses fundamental frequency and harmonic cues to segregate complex sounds

The ability to recognize and understand concurrent complex sounds, for instance two people speaking simultaneously, is aided by detecting differences in perceived pitch among competing acoustic signals (Micheyl and Oxenham, 2010). Mechanisms by which pitch may be encoded involve synchronous neural activity evoked by periodicities of complex sounds. Periodicity information is conveyed by the activity of auditory nerve fibers that first contact neurons in the anteroventral cochlear nucleus (AVCN) (Frisina, 2001). Two populations of AVCN neurons, primary-like responders with spiking patterns similar to those of auditory nerve fibers and chopper neurons that respond to sound with regularly-spaced bouts of transient spiking (Pfeiffer, 1966), have been shown to faithfully represent pitch information (Rhode, 1994; Rhode and Greenberg, 1994). When these cell types are examined under ideal listening conditions, responses tuned to low sound frequencies are capable of entrainment to the stimulus fine structure, whereas responses tuned to higher frequencies represent temporal modulations of the sound envelope (Sayles and Winter 2007, 2008a). The combination of these encoding strategies enables AVCN neurons to extract information across the perceptual range of pitch frequencies. However, when the listening environment is contaminated by extraneous noise and reverberation, AVCN pitch processing is degraded (Sayles and Winter 2008b). These findings suggest that early brainstem networks are not fully capable of faithfully representing ongoing speech sounds in the acoustically challenging conditions that we often experience (Sayles et al., 2016).

Primary-like and chopper responders in the AVCN either directly or indirectly target the IC where they are integrated along with inhibitory inputs and multiple projections from other

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