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Review

The layering of auditory experiences in driving experience-dependent subcortical plasticity

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ABSTRACT

In this review article, we focus on recent studies of experiential influences on brainstem function. Using these studies as scaffolding, we then lay the initial groundwork for the *Layering Hypothesis*, which explicates how experiences combine to shape subcortical auditory function. Our hypothesis builds on the idea that the subcortical auditory system reflects the collective auditory experiences of an individual, including interactions with sound that occurred in the distant past. Our goal for this article is to begin to shift the field away from examining the effect of single experiences to examining how different auditory experiences layer or superimpose on each other.

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1. Introduction

The human auditory brainstem is sensitive to many different experiences, ranging from long-term musical training (reviewed in Kraus and Chandrasekaran, 2010) to more limited experiences occurring over the course of a few hours (Skoe and Kraus, 2010a). However, less is known about how different types of experiences interact to influence sensory processing in the auditory brainstem. Following a review of the current literature on experience-dependent auditory brainstem plasticity in Sections 3–13, we present the *Layering Hypothesis*. Our hypothesis diverges from previous models (Kraus and Chandrasekaran, 2010; Krishnan and Gandour, 2009; Patel, 2011) by seeking to explain how multiple experiences, occurring concurrently or consecutively, combine to guide the manner and mechanisms by which the auditory brainstem represents sound. We posit that auditory function is informed by the collective set of auditory experiences that an individual is exposed to or partakes in throughout life, resulting in a 'fingerprint' that reflects an individual's unique set of experiences. This fingerprint captures not only the extent and nature of each type of experience but also the age and the overall metaplasticity of the system. The layering of experiences may explain individual differences in auditory function that can be seen even in typically-developing populations (Chandrasekaran et al., 2012; Hairston et al., 2013; Skoe et al., 2013b). Understanding how experiences combine to shape auditory function is an important first step in designing optimal and individualized training programs (Chandrasekaran et al., 2013a; Perrachione et al., 2011). This approach can be likened to the concept of 'personalized medicine', which is considered one of the most important goals in the medical sciences (Hamburg and Collins, 2010).

This article focuses on experience-dependent plasticity observed in the human auditory brainstem. Until recently, the auditory brainstem had been viewed as a nonplastic site of sensory processing that unlike the auditory cortex did not undergo experience-dependent changes. However, more recent studies focusing on these evolutionarily older structures have revealed that subcortical auditory structures, like cortical ones, are malleable throughout life. Although our spotlight here is on subcortical

Abbreviations: ABR, auditory brainstem response; BOLD, blood-oxygen level dependent; FFR, frequency following) response; IC, inferior colliculus; MOC, medial olivary cochlear; RCT, randomized control training

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structures, the central tenets of the *Layering Hypothesis* can be applied to the auditory system as a whole, not just the subcortical branch. Indeed, there is evidence for the layering of experiences from cortical neuroimaging techniques and also behavioral paradigms (e.g., Bregman et al., 2012; Engel de Abreu et al., 2012; Slevc and Miyake, 2006; Wong et al., 2011b). However, because of the fidelius manner in which specific sound features are captured by the auditory brainstem, this affords greater transparency (compared to cortical responses) into how different auditory experiences have selectively altered the way in which different components of the auditory signal are encoded in the brain.

2. Definition of experience-dependent plasticity

In crafting our operational definition of experience-dependent plasticity, we begin with the notion that our environment is composed of a series of auditory events that have varying durations and behavioral relevance, with some occurring transiently and others occurring on a more regular basis. We then define auditory experience, simply, as the exposure to an auditory event. By this definition, auditory experience could either be the result of passive exposure to sound or it could involve more active (behaviorally-relevant) interactions with sound that engage other modalities, such as vision and somatosensation. This article will survey what we currently know about how the auditory brainstem is changed by *repeated* experience with sound in both unimodal and multimodal settings. This is, however, not to downplay the role of transient events, such as an intense noise or head trauma, and their potential to change auditory brain function. We use the term 'experience-dependent plasticity' to refer to changes in neural circuits and synapses occurring throughout life that result from the environment and the specific ways in which the individual interacts with that environment.

Examinations of experience-dependent plasticity in the auditory system have often examined auditory system development under radically altered environmental conditions (Chang and Merzenich, 2003; Oliver et al., 2011) or described the extent to which the auditory system is modified by sensory deprivation (Tillein et al., 2012) or the reversal of deprivation (Kral and Sharma, 2012). This article instead focuses on human subcortical auditory system plasticity that results from natural variations in language exposure, current and past musical training, and abbreviated yet intensive auditory training.

3. How do we measure experience-dependent plasticity within the subcortical auditory system?

In animal models, experience-dependent plasticity has been examined in the subcortical auditory system using invasive methods (Dean et al., 2005; Luo et al., 2008; Suga et al., 2002). In humans, the two most common (non-invasive) experimental designs for studying experience-dependent plasticity are (1) a descriptive-comparative approach that compares two or more groups of participants who have distinctly different auditory experiences, but are equivalent in other relevant measures. This approach has generally been used to examine lifelong experiences related to language (a cross-language design) or music (reviewed in Krishnan et al., 2009; Strait and Kraus, 2013); and (2) a causality or a causality-descriptive approach that measures subcortical activity before or after the participant undergoes a prescribed auditory experience. In a causality-descriptive approach, a comparison is made to a group that does not undergo the auditory experience or undergoes a different type of auditory experience. For the experimental group, the prescribed experience could be a laboratory-designed training protocol where participants learn a new sound contrast or artificial language (Carcagno and Plack, 2011; Chandrasekaran et al., 2012; Song et al., 2012), it could involve auditory remediation/training performed in school (Hornickel et al., 2012; Tierney et al., 2013) or at home (Anderson et al., 2013a; Song et al., 2012), and/or it could involve augmenting the acoustic input in a specific manner (Hornickel et al., 2013; Munro et al., 2007).

In humans, there are a variety of methods for measuring subcortical function and the plasticity that results from different types of auditory experiences. For example, the efferent pathway between the auditory brainstem and cochlea, called the medial olivocochlear (MOC) system, can be targeted by presenting broadband noise to the contralateral ear. The activation of the MOC bundle is then registered as a change in the otoacoustic emission (reviewed in Guinan, 2010). Using this methodology, de Boer and Thornton reported increases in MOCB activity following a consonant–vowel phoneme-in-noise discrimination task (de Boer and Thornton, 2008; de Boer et al., 2012), lending further support to the idea that efferent function undergoes experience-dependent plasticity (Perrot et al., 1999). Positron emission tomography and functional magnetic resonance imaging are other approaches for studying changes in auditory midbrain (inferior colliculus) function (Rinne et al., 2008; Yu et al., 2009; Zatorre and Halpern, 1996), and recent advances in high resolution imaging and network analysis (Deshpande et al., 2009; Ress and Chandrasekaran, 2013) may lead to greater use of these method for studying experience-dependent subcortical plasticity in humans.

Subcortical auditory function can also be appraised using scalp-electrodes that detect electrical potentials generated by ensembles of intricately-connected subcortical nuclei belonging to the efferent and afferent auditory systems, including the cochlear nucleus, superior olive, lateral lemniscus, and inferior colliculus. Synchronous activity from these populations of neurons is responsive to transient and sustained features of auditory stimuli (Chandrasekaran and Kraus, 2010; Marsh et al., 1975; Moushegian et al., 1973; Skoe and Kraus, 2010b). This response, known as the auditory brainstem response (ABR), provides a means for objectively and non-invasively studying the neural encoding of sound. This review will spotlight experience-dependent plasticity as indexed by the ABR to speech or other sounds commonly encountered in the natural world. For the purposes of this review, we use 'ABR' to refer to both transient and phase-locked responses produced within the upper brainstem (lateral lemniscus, inferior colliculus).

One of the remarkable features of the ABR is that it captures the acoustic features of the sound stimulus (Fig. 1), making it possible to observe how the neural representation of specific sound features, such as the fundamental frequency, harmonics, and temporal envelope, change as a function of experience (Krishnan et al., 2005; Marmel et al., 2011; Parbery-Clark et al., 2009; Strait et al., 2012a). By comparison, functional magnetic resonance imaging (due to the temporal limitations of the hemodynamic response) and cortical-evoked electrophysiological responses (due to the more abstract response function of auditory cortical neurons) provide a more abstract representation of the evoking stimulus.

4. Experience is the engine that guides auditory function

The experience-dependent nature of the auditory brainstem and midbrain are not surprising given that these structures are always 'on'. Whether we are asleep, zoned out in front of the television, or under anesthesia, the auditory soundscape continues to be processed. Not surprisingly, subcortical auditory structures show some of the highest metabolic activity in the brain (Sokoloff, 1977). This steadfast quality has made the ABR (in its many variants) so attractive to medical professionals in the business of