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Review article

Impact of peripheral hearing loss on top-down auditory processing

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ABSTRACT

The auditory system consists of an intricate set of connections interposed between hierarchically arranged nuclei. The ascending pathways carrying sound information from the cochlea to the auditory cortex are, predictably, altered in instances of hearing loss resulting from blockage or damage to peripheral auditory structures. However, hearing loss-induced changes in descending connections that emanate from higher auditory centers and project back toward the periphery are still poorly understood. These pathways, which are the hypothesized substrate of high-level contextual and plasticity cues, are intimately linked to the ascending stream, and are thereby also likely to be influenced by auditory deprivation. In the current report, we review both the human and animal literature regarding changes in top-down modulation after peripheral hearing loss. Both aged humans and cochlear implant users are able to harness the power of top-down cues to disambiguate corrupted sounds and, in the case of aged listeners, may rely more heavily on these cues than non-aged listeners. The animal literature also reveals a plethora of structural and functional changes occurring in multiple descending projection systems after peripheral deafferentation. These data suggest that peripheral deafferentation induces a rebalancing of bottom-up and top-down controls, and that it will be necessary to understand the mechanisms underlying this rebalancing to develop better rehabilitation strategies for individuals with peripheral hearing loss.

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1. Introduction

We effortlessly navigate a world filled with complex sounds. Even under challenging listening situations, our auditory systems routinely extract the meanings of signals corrupted by noise. One cue that may be used to perform this operation is the linguistic or acoustic context within which a sound exists. For example, high-level information about the nature of ambiguous speech sounds

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can dramatically enhance the ability of an organism to recognize these sounds (Davis and Johnsrude, 2007; Liberman and Whalen, 2000; Remez et al., 1981). As such, most real-world hearing is necessarily an inferential process. That is, comprehension of external sounds involves a combination of the detection of the bits and pieces of partially degraded external sound sources, combined with sets of expectations and prior knowledge stored by the listener. It is not yet clear how changes in bottom-up signals from the peripheral auditory system (i.e., in the setting of peripheral hearing loss) alter the top-down mechanisms that influence hearing in noisy environments.

The inferential process of using top-down information to disambiguate noisy signals has been most well described in the domain of speech processing. Here, multiple levels exist in which context can influence the understanding of speech: syntactic, semantic, phonemic and others (Obleser, 2014). Unlike reading tasks, where individuals can control the rate of degraded input by reading more slowly, in hearing, perceptual judgements must be made in real-time, increasing the dependence on contextual information for this process. Therefore, speech perception requires the rapid integration of bottom-up (i.e., signal-related) with top-down (i.e., perceiver-related) factors. Unfortunately, little is known about how bottom-up and top-down signals are integrated in the brain. Nor is it known how loss of bottom-up signals influences the activity of top-down signals. Given the topic of this special issue of *Hearing Research* on plasticity following hearing loss and deafness, this review will focus on the latter, attempting to integrate what is known in the human speech processing literature with the animal literature on sensory system loss. Developing a better understanding of the mechanisms of rebalancing of bottom-up and top-down processing strategies after hearing loss is critical since these strategies will be important in developing new approaches to rehabilitation after hearing loss.

For clarity, we will use the term “top-down” to refer to the cognitive and behavioral manifestations of the use of high-level or contextual information to facilitate sensory processing. The term “descending projection” will be used to refer to anatomical projections originating from sites at upper levels of the sensory hierarchy that project to structures lower in the hierarchy (e.g., from the cortex to the thalamus). One assumption made in this review is that descending projections are important for top-down modulation. This assumption is supported by findings that elimination or stimulation of descending projections dramatically alters receptive field properties of neurons in lower structures (reviewed in (Bajo and King, 2011; Gilbert and Li, 2013; Sillito et al., 2006; Stebbings et al., 2014; Suga, 2012)), as well as altering both their temporal and spatial context-dependent responses (Felsen et al., 2002; Jones et al., 2015). Despite these suggestive findings, there are yet few direct studies available examining the hypothesis that descending projections within sensory systems support behavioral manifestations of top-down modulation. However, given their privileged position to directly modify bottom-up processing based on high-level information, descending projections provide an ideal substrate to mediate top-down cognitive processes. In addition, descending projections are ubiquitous in sensory systems. In some brain structures, such as the thalamus, descending projections outnumber ascending projections by at least 3:1 (Erişir et al., 1997; Van Horn et al., 2000). Descending projections have been described at virtually every level of all sensory systems, ranging from short-range intracortical, to long range from cortex to the brainstem, and, in many cases, extend to the sensory periphery (Guinan, 2006; Heinricher et al., 2009; Matsutani and Yamamoto, 2008; Moga et al., 1990; Repérant et al., 2006). These data suggest that descending projections have the ability to provide high-level cues to influence the earliest stages of sensory processing. See Fig. 1 which summarizes what is known about the organization of descending subcortical projections across sensory systems.

2. Speech perception

It has been known for many decades that speech that is corrupted by noise is made more intelligible by the addition of context (Miller et al., 1951). Fig. 2 shows an intelligibility curve for speech corrupted by noise. This curve may be shifted to the left by any factors that provide some clues to the listener about the nature of the target sound. For example, having heard the sentence prior to it being used as a test item, providing lexical or semantic cues, or limiting the number of choices available to the listener all shift this curve to the left, permitting quantification of contextual advantages (reviewed in (Obleser, 2014)). Another approach to quantify top-down influences on speech perception is to measure the ability to recover missing information in a stream of coherent speech, such as in the phonemic restoration effect. In this effect, phonemes in speech are replaced by noise bursts. Listeners perceive the missing phoneme, often not realizing that these phonemes were replaced by noise. Similar to the speech intelligibility effects described above, the perceived phoneme is dependent upon the context provided by the other phonemes present, and previously stored representations (Shinn-Cunningham and Wang, 2008; Srinivasan and Wang, 2005). It is important to note that paradigms such as the enhancement of word intelligibility by sentence context or phonemic restoration effects, which are commonly attributed to top-down modulatory effects, may also have bottom-up components. For example, coarticulation may alter subtle bottom-up cues for words spoken in sentences and therefore alter their intelligibility (Bonte et al., 2006; Strange, 1989). In addition, the gaps in speech introduced in phonemic restoration paradigms introduce distortions that are mitigated by noise filler, thus providing a bottom up cue to enhance intelligibility (Huggins, 1964). Mitigating these concerns are findings that listener expectation and broader sound context substantially modifies phonemic restoration, suggesting that performance on this task requires top-down modulation (Bashford et al., 1992; Samuel, 1981; Warren and Sherman, 1974).

3. Changes in top-down systems after deafferentation in humans

In the human scientific literature, data describing the influences of bottom-up signals on top-down modulation are derived primarily from studies on two groups of patients with hearing loss: patients with aging-related hearing loss and patients with cochlear implants. Even in the absence of frank hearing loss (measured with pure tone threshold shifts), patients may have auditory deafferentation (e.g., of primarily high-threshold fibers) leading to central reorganization. Such reorganization may lead to auditory perceptual disturbances such as tinnitus and hyperacusis, and top-down mechanisms have been implicated here as well (Song et al., 2015).

Aging is associated with both peripheral hearing loss (Cruickshanks et al., 1998; Moscicki et al., 1985) as well as central changes in auditory processing (Martin and Jerger, 2005; Pichora-Fuller, 2003). Several studies have examined the ability of older listeners with hearing loss to utilize top-down cues to interpret ambiguous or corrupted sounds. These studies have shown a number of effects. First, even when using non-ambiguous speech sounds, aging is associated with disruption of central processing that is not accounted for by a simple decrease in signal to noise ratio of the input sound (Oates et al., 2002; Tremblay et al., 2003).