CellPress

Review

The Neural Consequences of Age-Related Hearing Loss

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During hearing, acoustic signals travel up the ascending auditory pathway from the cochlea to auditory cortex; efferent connections provide descending feedback. In human listeners, although auditory and cognitive processing have sometimes been viewed as separate domains, a growing body of work suggests they are intimately coupled. Here, we review the effects of hearing loss on neural systems supporting spoken language comprehension, beginning with age-related physiological decline. We suggest that listeners recruit domain general executive systems to maintain successful communication when the auditory signal is degraded, but that this compensatory processing has behavioral consequences: even relatively mild levels of hearing loss can lead to cascading cognitive effects that impact perception, comprehension, and memory, leading to increased listening effort during speech comprehension.

Trends

Healthy aging is associated with neurophysiological changes at every stage of the human auditory system, including the cochlea, spiral ganglion neurons, cochlear nuclei, and other midbrain structures up through the auditory cortex.

Despite widespread declines in hearing ability, speech comprehension in older adulthood is generally good.

To maintain high levels of speech comprehension success, hearing-impaired listeners recruit systems outside the canonical speech-processing network to compensate for a poor auditory signal.

The additional cognitive effort required when listening to a degraded speech signal can impact other operations, such as remembering what has been heard.

Hearing: Not All in the Ears

> 'Tout d'abord poussé par ce qui se fait en aviation, j'ai appliqué aux insectes les lois de la résistance de l'air, et je suis arrive. . .à cette conclusion que leur vol est impossible.' (Magnan, 1934) [1]

Some 80 years ago, the French etymologist Antoine Magnan, writing about the wing-size: weight ratio of many flying insects, such as the bumblebee, concluded that these physical limitations would make it impossible for them to fly. How then did they fly? The answer, of course, is that such simple calculations failed to take into account the full complexity of factors related to the structure and movement of the wings of insects that ultimately make flight possible [2].

A similar paradox can be found in older adults' speech recognition. Although substantial variability is seen across individuals, the aging brain shows widespread changes in cortical structure [3] and network dynamics that carry cognitive function [4]. The behavioral consequences of these changes appear in a variety of cognitive 'fundamentals', including slowing in perceptual and cognitive operations, a decline in working memory capacity, and reduced efficiency in executive function and inhibition [5]. Also common in adult aging is hearing loss and increased difficulty processing complex auditory signals [6].

Against this backdrop, consider the challenges for comprehension of natural speech as one hears it on a daily basis. Speech rates in everyday conversation average about 150 words per minute (wpm), ranging from a 'slow' 90 wpm in thoughtful speech to bursts of over 210 wpm as might be heard from a radio or television newsreader working from a prepared script. Furthermore, although it typically goes unnoticed, everyday speech is surprisingly underarticulated, such that many words would be totally unidentifiable if not heard with the support of acoustic and

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linguistic context [7,8].* Adding to the challenges of rapid input rate and variable speech quality, the act of comprehension places a heavy demand on working memory to keep track of a conversation from sentence to sentence and to untangle syntactically complex speech [9].

Given these obstacles, one might reasonably conclude that speech comprehension by older adults would be, if not impossible, at least severely compromised. Yet, in the absence of advanced neuropathology, comprehension of natural speech is typically well maintained in older age. How then can the bumblebee of speech comprehension in older adults not merely fly, but fly so well?

Successful comprehension is possible because the quality of sensory information is only one element to be considered. Balancing age-related deficits in hearing and cognition are compensatory operations supported by cortical networks that extend far beyond the primary auditory system [10,11]. In this review, we trace the impact of hearing loss from the peripheral auditory system to auditory cortex, concluding with its impact on the cognitive processes ultimately required to compensate for the reduced richness of sensory information. Speech comprehension in adult aging is a prime example of systems-level neural flexibility supporting successful behavior.

Changes to the Auditory System in Adult Aging

Although hearing impairment has many etiologies, age-related hearing loss affects 80% of adults over the age of 70 years [12], offering a natural context in which to examine the effects of reduced auditory processing on speech perception. Age-related changes in hearing ability occur at all levels of the auditory system (Figure 1) [13]. We begin with a discussion of age-related changes in auditory physiology, using data from humans and from animal models.

Peripheral and Subcortical Changes

Detection of auditory signals begins with sound-induced vibration of the eardrum (the tympanic membrane) that sets in motion three articulated bones (the ossicles) in the middle ear. The ossicles mechanically amplify these vibrations, transmitting them to a second membrane (the oval window) that separates the middle ear from the inner ear. Vibration of this second membrane produces motion in a fluid located in the cochlea, a snail-shaped structure about the size of a small pea, containing the basilar membrane that runs along its length. Approximately 12 000–15 000 outer hair cells lie along the basilar membrane. Sometimes referred to as 'cochlear amplifiers', movement of the outer hair cells stimulate some 3500 inner hair cells that transduce the acoustic energy to electrical nerve signals [14]. It is here that the most prominent peripheral age-related hearing changes occur due to a decrease in the number of outer hair cells. In aging, outer hair cell loss is preferentially seen at the basal end of the basilar membrane responsible for encoding high-frequency information [15], contributing to the stereotypical pattern of high-frequency hearing loss seen in older adulthood (Box 1).

In addition to hair cell loss, animal models have revealed a more subtle reduction in processing efficiency that stems from synaptic dysfunction and degeneration of cochlear nerve axons. For example, Kujawa and Liberman [16] found that, after a single noise exposure, cochlear afferent nerve terminals can be weakened even in the absence of hair cell loss or long-term hearing threshold shift [17–20] (Figure 1B). This type of cochlear dysfunction has sometimes been referred to as 'hidden hearing loss' because it is not detectable using standard pure-tone

Glossary

Auditory brainstem response (ABR): an electrophysiological signature of auditory processing measured using EEG.
Diffusion tensor imaging (DTI): a type of structural MRI particularly sensitive to white matter.
Electroencephalography (EEG): a noninvasive electrophysiological technique for recording the electrical activity of the brain from the scalp.
Listening effort: additional cognitive resources required to understand acoustically degraded speech.
Otoacoustic emissions (OAE): sounds generated via the hair cells of the inner ear and used to assess cochlear function.
Pure tone average (PTA): a summary measure of hearing thresholds (often reported for a listener's better-hearing ear), and averaged over frequencies important for speech (either 500, 1000, and 2000 Hz, or 1, 2, and 4 kHz). A higher number reflects poorer hearing sensitivity.

*Interestingly, speakers seem to factor this knowledge into their utterances, with speech tending to show a functional adaptation, a principle of least effort, in which the more probable a word is in an utterance, the less carefully we articulate it [112].