Auditory-Processing Malleability

Focus on Language and Music

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ABSTRACT—*Auditory processing forms the basis of humans' ability to engage in complex behaviors such as understanding spoken language or playing a musical instrument. Auditory processing is not a rigid, encapsulated process; rather, it interacts intimately with other neural systems and is affected by experience, environmental influences, and active training. Auditory processing is related to language and cognitive function, and impaired auditory processing negatively affects the quality of life of many people. Recent studies suggest that the malleability of the auditory system may be used to study the interaction between sensory and cognitive processes and to enhance human well-being.*

KEYWORDS—*perceptual learning; plasticity; training*

Auditory processing refers to the broad range of sensory and perceptual skills used to extract meaningful information from sound. Traditionally, the initial stages of auditory processing were attributed to a passive system automatically encoding the physical properties of sound in a bottom-up hierarchical manner (that is, from peripheral to more central structures). Here, we discuss evidence to the contrary: Not only are most stages of auditory processing susceptible to change resulting from either long- or short-term experiences, many of these changes are mediated in a top-down fashion (that is, in a manner consistent with the influence of higher-level cognitive factors such as attention, memory and context), allowing even low levels of the auditory system to encode sound in a context-specific manner. This dynamic processing is achieved through the intricate anatomical and functional connections between auditory and other brain areas and between cortical and subcortical areas within the auditory system.

THE EFFECTS OF LONG-TERM EXPERIENCE ON AUDITORY PROCESSING

Language Experience

A striking example of the effects of experience on auditory processing is that even though human babies are born with the ability to discriminate all possible speech sounds, this ability is constrained by learning their native language, such that older infants can discriminate only sounds from their own language. Kuhl (2004) suggested that language learning results in the infants' brains becoming committed to patterns of a specific language, thus facilitating further learning of that language. An outcome of this process is reduced sensitivity to the sounds of other languages.

Experience with one's native language shapes not only speech perception but auditory processing in general. Thus, native speakers of Mandarin (in which pitch provides meaningful information) were better at processing pitch contours even in a nonlinguistic context, compared to native speakers of English (Bent, Bradlow, & Wright, 2006). At the physiological level, Mandarin speakers show more robust encoding of the pitch content of Mandarin sounds at cortical and subcortical levels of their auditory system, suggesting that language experience fundamentally changes the neural circuitry of the auditory pathway (Krishnan, Xu, Gandour, & Cariani, 2005).

Musical Experience

Striking differences in auditory brain function between musicians and nonmusicians are observed. Not only do musicians' brains respond more strongly to the sound of the instrument they play in comparison to other instruments, they also show stronger responses to simple, artificial tones (Peretz & Zatorre, 2005). Furthermore, as shown in Figure 1, musicians' brains manifest a more robust and faithful encoding of the pitch information contained in speech sounds in subcortical levels of the auditory pathway (Wong, Skoe, Russo, Dees, & Kraus, 2007). These findings suggest that, similar to linguistic experience, intensive music experience affects auditory processing in general.

An alternative explanation is that individuals with better auditory function may be more likely to engage in music training

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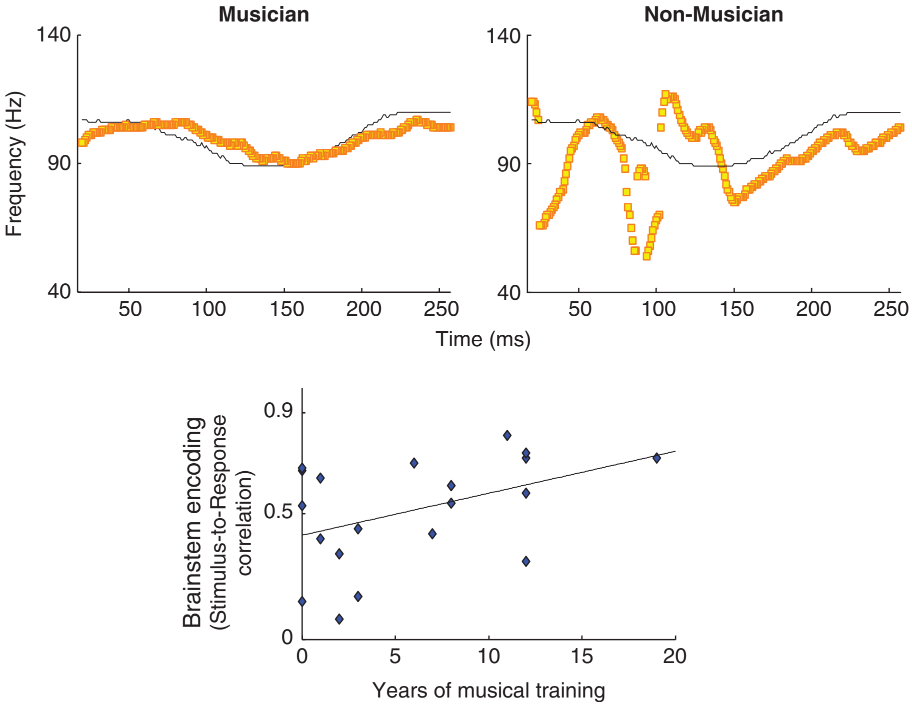

Fig. 1. Effects of prolonged musical experience on brainstem function. The brain of a typical musician encodes the pitch content of Mandarin sounds (top left) more effectively than does the brain of a typical nonmusician (top right). The thin black line on each plot denotes the pitch contour of the stimulus (how the frequency of the stimulus changes over time; in Mandarin and other tonal languages this is an important cue to the meaning of the word); the thick orange line denotes the brainstem response. The musician's brain response follows the frequencies in the stimulus much more precisely, a phenomenon known as pitch tracking. The precision of the brainstem response (brainstem encoding, measured as the degree of correlation between the stimulus and the brainstem response) is associated with the length of musical experience (bottom; re-plotted from Wong, Skoe, Russo, & Kraus, 2007).

to begin with, but recent studies support the first view. Although the brain responses of children about to start music lessons did not differ from those of a control group, after a year of training, researchers did find differences between the two groups in response to violin sounds (Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006). Furthermore, longitudinal data indicate that music training in children results in improved verbal memory (but not visual memory) compared with children who have no musical training (Ho, Cheung, & Chan, 2003).

Reorganization Following Sensory Loss and Injury

Auditory processing changes not only to respond to the auditory environment but also to compensate for visual loss. Provided that the loss happened early in life, visual brain areas can become activated by auditory and tactile stimuli (Neville & Bavelier, 2002). Furthermore, congenitally blind adults are better than sighted controls at detecting sounds occurring at peripheral (as opposed to central) locations in space (Roder et al., 1999). The effects of sensory loss are thus not uniform across the auditory system or across developmental periods; some aspects of auditory processing are more malleable than others. Taken together, these effects demonstrate that auditory processing is dynamic and can be altered according to context.

The effects of sensory loss described above are related to natural experiences; the exact causes of observed effects are hard to decipher. In the following sections, we describe evidence for reorganization and plasticity obtained through controlled studies in animal models. This evidence shows that specific neural loss and environmental inputs affect wide areas of the auditory system and are therefore expected to be important in accounting for sensory and cognitive conditions accompanying these circumstances. Consequently, these studies may help inform effective rehabilitation strategies.

Hearing loss from damage to the inner ear (induced by noise exposure or age) leads to physiological consequences that extend throughout the auditory system. When a region of the cochlea sensitive to a particular frequency is severed, the representation of this frequency in the auditory cortex is also altered; representations of neighboring frequencies in the cochlea replace that of the missing frequency. This means that even in adult animals, higher levels of the auditory system will change their function in response to the type of information received from the auditory periphery. When information related to certain frequencies is no longer received, its representation in the cortex is also lost (Irvine, Rajan, & Brown, 2001). Similar changes, known as cortical-map plasticity, occur following training.

Environmental Manipulations

The adult primary auditory cortex is topographically organized based on sound frequency, such that different cortical areas are optimally sensitive to specific sound frequencies—a phenomenon called *tonotopicity*. Studies by Merzenich and colleagues (reviewed by Wang, 2004) established that during an early critical postnatal period, the acoustics of the auditory environment determine the development of this representation, shaping the auditory cortex to respond preferentially to salient, structured acoustic inputs. The development of tonotopicity in rats can be accelerated if the rats are exposed to appropriate stimuli during the critical period, whereas constant exposure to moderate levels of noise during that same period results in severe disruption in the tonotopic organization, such that the auditory cortices of rats reared in constant noise look like those of younger rats before fine frequency representation is achieved. Whether the auditory cortex can fully recover after normal development is disrupted by exposure to an aberrant acoustic environment is still unknown. Collectively, these studies suggest that the acoustic structure of the auditory environment significantly impacts auditory development, either positively or negatively. Similar effects may operate in human development.

The auditory environment also induces plasticity in the adult rat auditory cortex. Thus, when rats are housed in an enriched acoustic environment in which they are exposed to and can interact with a wide array of natural and artificial sounds, their auditory cortices respond more strongly and become more sensitive (i.e., better able to respond to quiet sounds) and more frequency selective compared to rats housed in standard conditions. These effects disappear shortly after enrichment ceases (Engineer et al., 2004), demonstrating once more the large effects of context on auditory processing.

AUDITORY PROCESSING, LEARNING, AND COGNITION

Perceptual Learning

Here we define perceptual learning as improvement in performance on a perceptual task following practice (training). Studies in animals and humans show that the auditory system can change with practice, even in adulthood. Thus, the perception of simple attributes of sound (pitch, duration) and complex ones (sound patterns, speech sounds) improves with training. Improved perception is accompanied by changes in the auditory cortex, similar to those induced by environmental experience and injury (Irvine et al., 2001).

A typical result is that following active training on a task (e.g., discriminating one sound from another) with a particular target stimulus (e.g., a tone of a given frequency; a speech sound discriminable based on a specific cue such as voicing; a location cue), participants can distinguish stimuli they previously could not. In certain circumstances, learning also transfers to perception of other stimuli that share some features with the stimulus used in training. Learning can be accompanied by a variety of physiological and anatomical correlates. Examples include increased amplitude of the physiological responses to the trained stimuli, improved response precision, sharpening of receptive fields at the level of single neurons (neurons become better tuned to the trained feature), and reorganization of cortical maps (larger cortical areas become sensitive to a trained feature). Exactly how these correlates relate to behavior is unclear and is an important topic for future research (Ohl & Scheich, 2005).

Auditory learning is also context specific. Polley, Steinberg, & Merzenich (2006) trained rats to identify a target sound based on either frequency or intensity using the same set of stimuli and demonstrated a top-down effect on the plasticity of the auditory cortex. In each group of rats, the auditory cortex became more sensitive only to the relevant feature of the target stimuli (either frequency or intensity). Physiological changes were correlated with the magnitude of perceptual learning in both groups, but they were also specific; the rats trained to distinguish frequency did not show learning-related changes when tested for intensity sensitivity, and vice versa. Plasticity of the auditory cortex thus is affected by top-down factors—the "intentional" state of the animal—rather than by sensory factors alone, as the input structure was similar in both groups.

When Auditory Processing Goes Awry

Auditory processing is impaired in several clinical conditions. Obviously, individuals with hearing loss have abnormal auditory processing and, as discussed above, consequences extend beyond the immediate effects of elevated hearing thresholds. Less known is auditory-processing disorder, a condition whose hallmark is unusual difficulty perceiving speech in noisy environments. Children with this disorder have difficulty coping in school. Moreover, about 10% of children suffer from language-based learning problems such as dyslexia, of which a substantial portion (more than 30%) manifest abnormal physiological responses to sound. In this latter population, sound is abnormally encoded at multiple levels of the auditory system—the auditory cortex (Kraus et al., 1996), the auditory brainstem (Johnson, Nicol and Kraus, 2005), or both (Banai, Nicol, Zecker and Kraus, 2005)—suggesting a complex interaction between levels. In the general population, the auditory brainstem represents the acoustic characteristics of speech with exquisite temporal and spectral (that is with respect to frequency information) fidelity. Among the group of individuals with learning problems this fidelity is compromised and timing of the brain response is delayed and imprecise (reviewed in Johnson, Nicol, & Kraus, 2005). Furthermore, timing of the brainstem response is linked

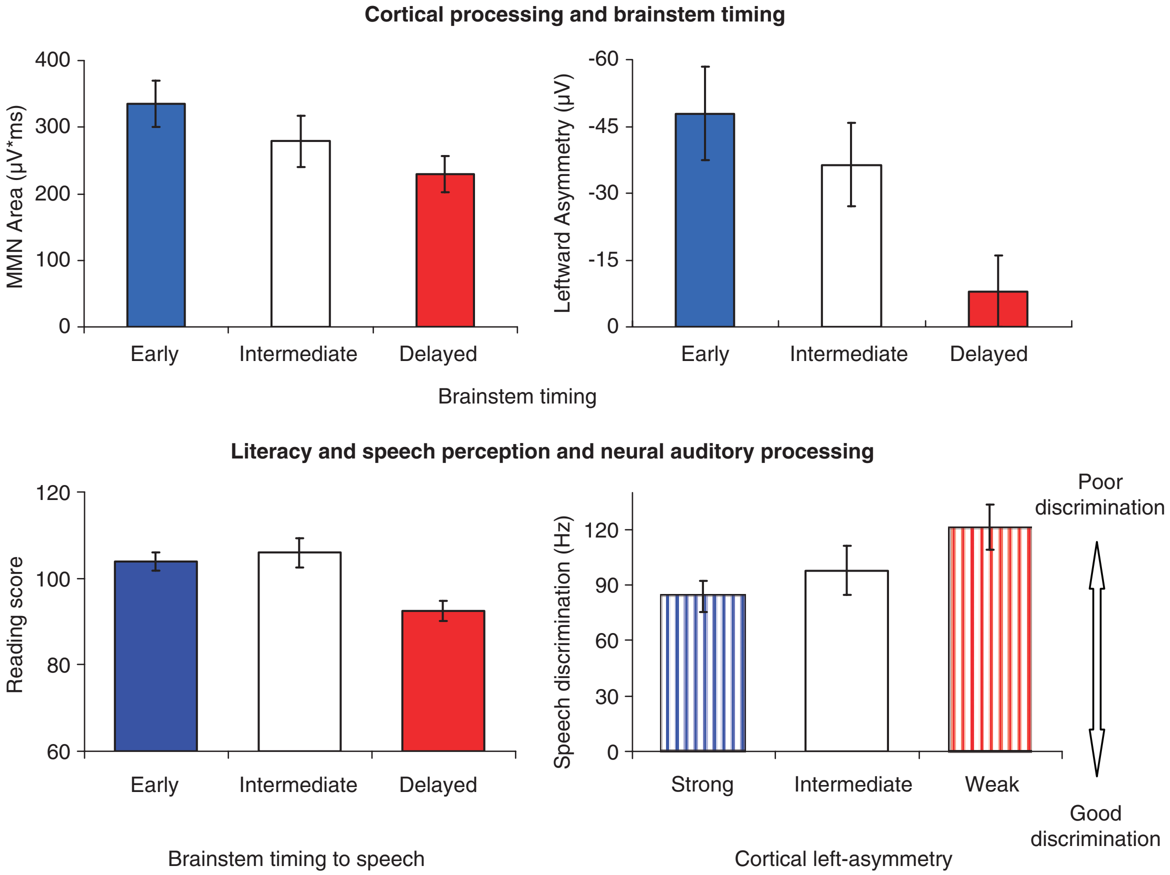

Fig. 2. Cortical processing as a function of subcortical processing in the auditory pathway and physiological processing in relation to reading and speech perception. Auditory processing at the cortex is disrupted in individuals with delayed brainstem timing (red bars) as compared to individuals with early brainstem timing (blue bars). Cortical detection of rare acoustic events among frequent ones (indexed by mismatch negativity, or MMN) is significantly reduced when brainstem timing is delayed (top left). The normal pattern of leftward cortical asymmetry in response to speech sounds is prominent among individuals with early brainstem timing but significantly reduced among individuals with delayed brainstem timing (top right). Individuals with delayed brainstem timing to speech sounds are poorer readers compared to those with early and intermediate timing (bottom left). Individuals with strong cortical asymmetry to speech sounds have better speech perception than those with weak asymmetry (bottom right). (Replotted from Banai, Nicol, Zecker, & Kraus, 2005, and Abrams, Nicol, Zecker, & Kraus, 2006; error bars are ±1 s.e.m.)

to cortical processing of sound. When brainstem timing is delayed, the ability of the cortex to detect acoustic changes is reduced (Fig. 2, top left). In addition, normal cortical processing of speech sounds is asymmetric, with speech being more prominently processed in the left hemisphere. When brainstem timing is delayed, this normal pattern of asymmetry is also disrupted (Fig. 2, top right).

Auditory Processing and Cognitive Function

Compromised auditory processing in auditory-processing disorder and learning and reading disorders is of interest because it suggests a relationship between auditory perception and cognition. Indeed, even in people with normal hearing, performance on perceptual and cognitive tasks is correlated (Deary, 2000). Longitudinal studies further show that auditory processing in infancy is correlated with language, memory, and cognitive function later in childhood (Benasich et al., 2006). Our research suggests that the degree of literacy and speech-perception deficits in school-age children correlates with the degree of physiological deficit in auditory processing (see Fig. 2, bottom panels). Consequently, this work has been translated into a clinical tool, the BioMAP (Biological Marker of Auditory Processing), designed to provide information about auditory encoding during the diagnosis of learning problems (see http://www.communication.northwestern.edu/brainvolts under "Clinical Technologies"). The predictive value of brainstem function will be determined by further longitudinal studies.

Remediation of Auditory Processing Deficits

Taken together, the pattern of auditory-processing deficits in learning problems and the pattern of plastic changes following training suggest that many children (approximately 3% of all children) could benefit from improved auditory processing. Several studies have demonstrated that auditory training can alleviate language problems in some children with language impairments and improve literacy-related skills in normally developing children (c.f. Moore, Rosenberg, & Coleman, 2005). Intensive practice on some auditory skills can thus generalize to untrained, higher-level abilities, attesting to the functional relationships between sensory and cognitive processes. Even in instances in which training does not result in measurable gains to literacy-related skills, normalizing effects on auditory physiology have been observed (Nicol & Kraus, 2005).

The usefulness of training to alleviate learning disabilities is currently limited by the inability to predict who will benefit from training, which could also account for the lack of agreement regarding the efficacy of commercially available programs such as FastForWord and Earobics. For example, some evidence suggests that auditory training is particularly beneficial to the subgroup of children with brainstem-timing deficits (c.f. Johnson, Nicol, & Kraus, 2005). Another limiting factor is incomplete understanding of the causal relationship between auditory processing and literacy and the effects of development on this relationship.

Reciprocal Cognitive–Sensory Function

A theory to account for the interaction between sensory input and top-down processes, discussed previously in the context of perceptual learning and learning disability, is the reverse-hierarchy theory (RHT; Ahissar & Hochstein, 2004). The RHT suggests that learning modifies the neural circuitry governing performance on a given task starting at the highest level that can solve the task, gradually refining lower areas when more fine-grained sensory information is required. The RHT predicts that learning will modify even primary sensory areas in a manner that is consistent with higher-level aspects such as the specific feature attended to during learning or the specific task performed.

The idea that top-down influences guide plasticity in primary sensory areas may be helpful in linking perception, attention, and memory, which are typically thought of as distinct faculties. Recent models suggest that sensory memory is an emergent property of the sensory system used to encode the information to be processed rather than only a product of distinct prefrontal and parietal memory systems (Pasternak & Greenlee, 2005). A memory system tied to a specific sensory modality can be used to effectively guide cognitive, goal-directed behavior in accordance with ongoing sensory input. Similar to the effects of environment and long-term experience, top-down guided plasticity may increase the likelihood that proper percepts, and therefore "good" memory traces, are generated.

SUMMARY

The auditory system is pervasively malleable to experience throughout life. To serve educational and clinical needs, three critical questions must be answered. First, what are the functional relationships between auditory processing and cognition? In particular, it is important to understand how auditory processing interacts with cognitive function across the life span. Second, what is the role of subcortical encoding in perception? Third, which acoustic elements of sounds are critical for language and music, and how are those elements best combined with active engagement with sound in training regimens in order to optimize the use of language and music? For example, although it is known that the acoustic structure of native language shapes auditory processing in infancy, it is not clear how to create acoustic environments that will have similar effects at later developmental stages.

Recommended Reading

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