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Review

Neural circuits underlying adaptation and learning in the perception of auditory space

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ABSTRACT

Sound localization mechanisms are particularly plastic during development, when the monaural and binaural acoustic cues that form the basis for spatial hearing change in value as the body grows. Recent studies have shown that the mature brain retains a surprising capacity to relearn to localize sound in the presence of substantially altered auditory spatial cues. In addition to the long-lasting changes that result from learning, behavioral and electrophysiological studies have demonstrated that auditory spatial processing can undergo rapid adjustments in response to changes in the statistics of recent stimulation, which help to maintain sensitivity over the range where most stimulus values occur. Through a combination of recording studies and methods for selectively manipulating the activity of specific neuronal populations, progress is now being made in identifying the cortical and subcortical circuits in the brain that are responsible for the dynamic coding of auditory spatial information.

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1. Introduction

One of the principal functions of our sensory systems is to indicate the whereabouts of objects and events in the external environment. Although vision generally provides the most accurate spatial information, this is restricted to the visual field of the species in question. By contrast, the auditory system is able to register the presence of stimuli originating from any direction relative to the head. This omnidirectional function, and the capacity to localize sound sources even if they are at least partially occluded by other objects, confers considerable survival value and contributes to the ability of many species to find potential mates or prey or to avoid and escape from approaching predators. More generally, auditory spatial processing plays an important role in redirecting attention, and also helps listeners to pick out particular sources against a background of other sounds emanating from different directions in space (Schnupp et al., 2010).

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Auditory localization relies on the physical separation of the ears on either side of the head. Thus, for sounds located to one side of the midline, the difference in path length to each ear produces an interaural difference in the time of sound arrival whose magnitude is determined by both the distance between the ears and angle subtended by the sound source relative to the head. An interaural difference in the level of the sound may also result from a combination of the spectral filtering effects produced by the external ears and acoustic shadow cast by the head. In mammals, binaural disparity cues are key to localization in the horizontal (or azimuthal) plane, with interaural time differences (ITDs) dominating at low frequencies and interaural level differences (ILDs) at high frequencies, while spectral cues provide the basis for vertical localization, for distinguishing between sources located in front of and behind the subject, and for the normally limited ability to localize sounds using one ear alone (King et al., 2001; Schnupp et al., 2010).

The ITD, ILD and spectral cue values corresponding to a given sound direction are determined by the physical dimensions of the head and external ears, which undergo pronounced changes during development and can also vary quite markedly between individuals within the same age band (Shaw and Teranishi, 1968; Xu and Middlebrooks, 1999; Schnupp et al., 2003; Campbell et al., 2008). Psychophysical studies have shown that humans can localize virtual acoustic space stimuli that simulate real sound sources more accurately when these headphone signals are based on acoustical measurements made from their own ears than from the ears of other subjects (Wenzel et al., 1993; Middlebrooks, 1999). This implies that experience of the cues provided by an individual's own head and ears shapes the functional organization of the brain circuits responsible for spatial hearing. While we might expect such experience-dependent plasticity to be greatest during development, particularly as the cues change in value as these structures grow, it is clear that the capacity for change persists into adulthood. Indeed, this dynamic processing of auditory localization cues seems to play a vital role in enabling listeners to interact effectively with their constantly changing acoustic environments, and provides the basis on which learning can improve their spatial abilities. Here, we review recent studies on the adaptive coding and plasticity of spatial hearing, which have started to reveal the neural circuits involved as well as the nature of the physiological changes that accompany shifts in perception.

2. Short-term adaptive coding

It is well established that the nervous systems of a range of species are adapted to the statistics of their sensory environment. Although some of the tuning of neural circuits to the regularities of the sensory environment has probably occurred over the course of evolution, much of this process seems to take place during development when the heightened plasticity of the nervous system provides the necessary flexibility for sensory experience to exert its effects (Blakemore and Cooper, 1970; Van der Loos and Woolsey, 1973; Zhang et al., 2001). Importantly, the resulting neural representations of the sensory environment appear to minimize redundancy and, thereby, maximize the efficiency with which the encountered signals are processed (Barlow, 1972). To further optimize information processing, sensory systems are also capable of adjusting their coding strategies over much shorter timescales, which allows them to take account of the often considerable fluctuations in input statistics between different sensory scenes.

Most of the evidence for such flexibility in sensory coding can be seen in the way the mature visual system adjusts to changes in the statistics of light intensity fluctuations (Baccus and Meister, 2002; Chander and Chichilnisky, 2001; Dunn and Rieke, 2006; Mante et al., 2005; Smirnakis et al., 1997) or of other visual stimulus dimensions (Brenner et al., 2000; Fairhall et al., 2001). Similarly, electrophysiological studies have shown that the responses of somatosensory (Garcia-Lazaro et al., 2007; Maravall et al., 2007) and auditory (Dean et al., 2005; Kvale and Schreiner, 2004; Nagel and Doupe, 2006; Wen et al., 2009) neurons at different processing levels can change with the composition of their input, such that the most frequently encountered stimuli are encoded most precisely.

Given this evidence from other stimulus dimensions, it would be surprising if the neural processing of auditory space was not optimized in a similar fashion. Indeed, previous work has shown that the sensitivity of neurons in the auditory cortex to interaural phase differences (Malone et al., 2002) and to virtual sound locations (Jenison et al., 2001) depends on the recent history of stimulation. However, it needs to be borne in mind that there are some fundamental differences between the processing of auditory space and, say, light intensity. For the latter, the processing of absolute stimulus values conveys little value – the detection of luminance *differences* across the visual scene is much more important than an accurate representation of a signal's absolute luminance. However, for auditory spatial processing, maintaining a stable representation of the *absolute* stimulus value, i.e. sound-source position, would seem to be more important than accurately registering spatial separations between stimuli.

Recent evidence provides some insight into how the processing of auditory space is affected by spatial input statistics (Fig. 1). By presenting human listeners over headphones with broadband noise sequences whose ILDs fluctuated rapidly according to a Gaussian distribution, and altering the mean or variance of that distribution (Fig. 1A), Dahmen et al. (2010) showed that the perception of auditory space strongly depends on the statistics of the sensory context. When the mean of the ILD distribution was changed, the perceived laterality of a subsequent stimulus was shifted away from the mean (Fig. 1B). Manipulating the variance of the stimulus distribution also affected perception, such that spatial sensitivity improved as the variance was decreased and declined when the variance was increased (Fig. 1C).

Dahmen et al. (2010) also looked for a possible neural substrate for these perceptual changes by presenting essentially the same stimuli to neurons recorded in the inferior colliculus (IC) of anesthetized ferrets. They found that the neurons change their response properties in a way that is highly consistent with the perceptual phenomena. As a result of adaptation to the mean, IC neurons can respond almost identically to very different ILD values, so long as those stimuli lie at the same distance to the mean of the ILD distribution within which they are presented (Fig. 1D, F, H, J). Thus, in the rate–ILD plot shown in Fig. 1H, the neuron produced the same response to ILDs of −30, −15 and −3 dB following adaptation to stimulus distributions with mean ILDs of −15, 0 and +15 dB, respectively. Relying on these neurons for an estimate of the absolute ILD of a signal will therefore result in precisely the type of mean-biased judgements seen psychophysically. IC neurons adjust their gain if the variance of the ILD distribution changes: if the variance goes down, they represent the same difference in input with a larger difference in firing rate (Fig. 1E, G, I, K). Again, the nature of this neural adaptation is consistent with the observed relationship between perceptual sensitivity and stimulus variance.

Further electrophysiological evidence from the same study (Dahmen et al., 2010), as well as other psychophysical results (Getzmann, 2004; Kashino, 1998; Maier et al., 2010; Sach et al., 2000), suggest that an inability to make mean-independent judgements of absolute ILD values may be the cost for the brain's attempt to maintain the highest perceptual sensitivity in that region of space where the majority of stimuli occur. A cost may also be associated with variance adaptation because the observed increase in gain with shrinking variance might produce distortions in the perception of auditory space that, at the same time as improving