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Review

The neurobiology of sound-specific auditory plasticity: A core neural circuit

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ABSTRACT

Auditory learning or experience induces large-scale neural plasticity in not only the auditory cortex but also in the auditory thalamus and midbrain. Such plasticity is guided by acquired sound (sound-specific auditory plasticity). The mechanisms involved in this process have been studied from various approaches and support the presence of a core neural circuit consisting of a subcortico-cortico-subcortical tonotopic loop supplemented by neuromodulatory (e.g., cholinergic) inputs. This circuit has three key functions essential for establishing large-scale and sound-specific plasticity in the auditory cortex, auditory thalamus and auditory midbrain. They include the presence of sound information for guiding the plasticity, the communication between the cortex, thalamus and midbrain for coordinating the plastic changes and the adjustment of the circuit status for augmenting the plasticity. This review begins with an overview of sound-specific auditory plasticity in the central auditory system. It then introduces the core neural circuit which plays an essential role in inducing sound-specific auditory plasticity. Finally, the core neural circuit and its relationship to auditory learning and experience are discussed.

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The central auditory system continuously adapts to changes of acoustic environment throughout the span of a lifetime. The functional organization of the central auditory system can be modified by behaviorally relevant signals and by injuries to the sensory organ or pathway (see reviews by Irvine and Rajan, 1996; Weinberger, 1998; Buonomano and Merzenich, 1998; Suga and Ma, 2003; Yan, 2003; Dahmen and King, 2007; Keuroghlian and Knudsen, 2007; Kral and Eggermont, 2007). This review describes the common neural circuit underlying activity-dependent auditory plasticity in which sound is the cue that prompts or leads to plasticity.

Despite the extensive emphasis of the contribution of synaptic plasticity such as long-term potentiation, one must keep in mind that the fundamental units of the brain are the neurons that combine into neural circuits through synapses. The realization of specific brain function relies heavily on the formation of specific neural circuits. Synaptic plasticity is neurobehaviorally meaningful only when it is placed into a particular neural circuit. To reveal the neural mechanisms of sound-specific auditory plasticity, an inevitable task is the identification of the underlying neural circuit in the brain.

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A common but rarely attended phenomenon is that the plasticity of the neuronal receptive field (RF) and frequency map in the central auditory system can be induced through the judicious use of various training paradigms such as fear conditioning, tone discrimination and reinforced tone stimulation. Although the involved neural substrates can be largely different for various training paradigms, the pattern of plastic changes in the central auditory system is mostly similar. This suggests that different training paradigms induce auditory plasticity through a common neural circuit.

In addition to the long-lasting changes, there are three main common properties that provide us with valuable information on potential neural circuit underlying sound-specific auditory plasticity. One is that the plastic change is highly specific to the frequency characterizing the acquired sound; the RF of a given neuron shifts towards the frequency of an acquired sound so that the tonotopic map is reorganized for the expanded neural representation of the frequency of the acquired sound (Bakin and Weinberger, 1990; Recanzone et al., 1993; Gao and Suga, 2000). Second, the plasticity is prominent so that the changes in neuronal RFs and frequency maps of the auditory cortex are easily detected and measured with electrophysiological recording and neuroimaging (Kilgard and Merzenich, 1998; Pantev et al., 1998; Gao and Suga, 2000; Yan and Zhang, 2005). The last is that the large-scale, sound-specific plasticity is well documented in not only the auditory cortex (AC) but also in subcortical nuclei such as the medial geniculate body (MGB) of the thalamus and the inferior colliculus (IC) of the midbrain (Edeline and Weinberger, 1992; Poon and Chen, 1992; Yu et al., 2007; Gao and Suga, 1998; Zhang et al., 2005; Zhang and Yan, 2008). These properties of sound-specific auditory plasticity allow us to postulate that the underlying circuit must carry or receive accurate auditory information, that it permits reciprocal communication among the auditory cortex and subcortical nuclei, and that it possesses one or more modulators or amplifiers.

This review attempts to explore a common neural circuit that is directly responsible for auditory plasticity in the central auditory system and is relatively independent from training paradigms. Discussion will be centered on plastic changes in the frequency domain since this is the criteria used for the assessment or measurement of auditory plasticity.

1. Sound-specific plasticity in the central auditory system

In nature, numerous sounds are perceived in our daily life but the majority does not affect the function of the central auditory system. Studies on animal have shown that a single sound and/or a behaviorally unrelated sound are not able to change the RFs of auditory neurons. However, the RFs of auditory neurons are dramatically altered if a given sound is repetitively presented or behaviorally relevant (Weinberger, 1998; Buonomano and Merzenich, 1998; Suga and Ma, 2003; Yan, 2003; Dahmen and King, 2007).

Sound-specific auditory plasticity is initially demonstrated in the auditory cortex where neuronal RFs are modified after auditory fear conditioning (Bakin and Weinberger, 1990), a useful training paradigm for studying auditory learning. Auditory fear conditioning consists of a neutral tone stimulus (conditioned stimulus) and an aversive stimulus such as an electric foot shock (unconditioned stimulus). Pairing of conditioned and unconditioned stimuli establishes an association between these two stimuli; an animal shows a conditioned responses to the conditioned stimulus alone (Domjan, 2005). This means that the neutral tone is endowed with behavioral significance following the conditioning. This tone is consequently a powerful cue for guiding neuronal RF changes. For example, in adult animals, auditory fear conditioning (tone-foot shock) shifts the neuronal RFs of the auditory cortex to the frequency of the conditioned tone. The RF shift of cortical neurons results from an increase in responses to the frequency of the conditioned tone and the decrease in responses to other frequencies (Bakin and Weinberger, 1990; Edeline et al., 1993; Gao and Suga, 1998, 2000). More neurons in the auditory cortex consequently tune to the frequency of the conditioned tone. In other words, cortical representation or processing of the conditioned tone is enhanced after auditory fear conditioning. It is important to note that shift in RFs of cortical neurons is not observed if the conditioned tone and unconditioned stimulus are randomly presented or unpaired (Bakin and Weinberger, 1990). In this case, the conditioned tone and unconditioned stimulus are not associated or the neutral tone is not endowed with behavioral significance.

Perceptual learning also appears to induce sound-specific plasticity in the auditory cortex although this finding is somewhat controversial. Following tone frequency discrimination or recognition tasks, animals are able to identify or differentiate trained or acquired tone frequencies. These animals show expanded areas in their auditory cortices that represent the trained or acquired tone frequency (Recanzone et al., 1993; Polley et al., 2006). This suggests that many cortical neurons that originally tune to other frequencies shift their RFs to the frequency of the trained or acquired tone. One study however, contradicts this finding and describes no differences in frequency representation in the auditory cortex following frequency discrimination training; it reports broadened RFs and shortened responses latency of cortical neurons (Brown et al., 2004).

In addition to special training procedures, simple tone stimulation is also able to evoke sound-specific plasticity in the auditory cortex. Functional magnetic resonance imaging demonstrates that the neural representation of piano tones in the auditory cortex is significantly increased in musicians as compared to individuals who have never played the instrument. The size of the representing cortical area is positively correlated to the age at which the musicians began practice (Pantev et al., 1998; Pantev and Lutkenhoner, 2000). These findings suggest that repetitive listening to a particular sound increases the cortical representation of this sound; the population of neurons in the auditory cortex that specifically tune to this particular sound is increased. One may argue however, that the enhanced cortical representation may not only simply result from repetitive listening but also from the movement and sense of the musicians' hands following repetitive practicing. Animal studies involving adult bats confirm that simple tone stimulation does induce sound-specific auditory plasticity; a specific tone burst presented in a behaviourally correlated high repetition rate shifts the RFs of auditory neurons towards the tone frequency (Yan and Suga, 1998; Chowdhury and Suga, 2000; Gao and Suga, 1998, 2000; Ma and Suga, 2001, 2003). Furthermore, sound-specific cortical plasticity induced by simple tone stimulation is more vigorous during early development. Exposure of animals to a specific tone at a young age dramatically increases the cortical representation of this tone frequency whereas exposure to noise disrupts the systematical representation of frequency in the auditory cortex (Zhang et al., 2001, 2002; Chang and Merzenich, 2003; Han et al., 2007).

It is crucial to note that sound-specific auditory plasticity is also demonstrated in subcortical nuclei. In adult animals, auditory fear conditioning shifts the RFs of inferior collicular neurons in the midbrain towards the frequency of the conditioned tone (Gao and Suga, 1998, 2000). The pattern of RF plasticity in the auditory midbrain is identical to that in the auditory cortex. Similarly, early exposure of animals to a specific sound enhances the neural