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Research paper

Auditory cortical plasticity: Does it provide evidence for cognitive processing in the auditory cortex?

Dexter R.F. Irvine *

School of Psychology, Psychiatry, and Psychological Medicine, Faculty of Medicine, Nursing, and Health Sciences, Monash University, Vic. 3800, Australia
Bionic Ear Institute, 384-388 Albert Street, East Melbourne, Vic. 3002, Australia

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Abstract

The past 20 years have seen substantial changes in our view of the nature of the processing carried out in auditory cortex. Some processing of a cognitive nature, previously attributed to higher-order "association" areas, is now considered to take place in auditory cortex itself. One argument adduced in support of this view is the evidence indicating a remarkable degree of plasticity in the auditory cortex of adult animals. Such plasticity has been demonstrated in a wide range of paradigms, in which auditory input or the behavioural significance of particular inputs is manipulated. Changes over the same time period in our conceptualization of the receptive fields of cortical neurons, and well-established mechanisms for use-related changes in synaptic function, can account for many forms of auditory cortical plasticity. On the basis of a review of auditory cortical plasticity and its probable mechanisms, it is argued that only plasticity associated with learning tasks provides a strong case for cognitive processing in auditory cortex. Even in this case the evidence is indirect, in that it has not yet been established that the changes in auditory cortex are necessary for behavioural learning and memory. Although other lines of evidence provide convincing support for cognitive processing in auditory cortex, that provided by auditory cortical plasticity remains equivocal.

Keywords: Cholinergic modulation; Classical conditioning; Cochlear lesion; Perceptual learning; Receptive field; Tonotopic organization

1. Introduction

The last 20 years or so have seen not only a massive increase in our knowledge of auditory cortical processing mechanisms but also a substantial change in the way in which we think about auditory cortical function. An assumption made by most cortical researchers in the early 1980s, so basic that it would not have had to be explicitly formulated, was that the functional response characteristics of auditory cortical neurons, and the functional organization of auditory cortex, were stable features of the adult brain. Any susceptibility of these characteristics to environmental influences was assumed, largely by analogy with the visual and somatosensory cortices, to be restricted to limited "critical" periods during development (Hensch, 2004). A related assumption was that the primary function of auditory cortex is to extract the information contained in the acoustic signal, albeit by mechanisms that are at a greater level of complexity than those at lower levels of the auditory pathway. The cortex was thus seen as the final stage of an essentially hierarchical "bottom up" signal

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Abbreviations: AI, primary auditory cortex; ACh, acetylcholine; BF, best frequency; CF, characteristic frequency; CNS, central nervous system; CS, conditioned stimulus; DCN, dorsal cochlear nucleus; DLF, frequency difference limen; EPSP, excitatory post-synaptic potential; fMRI, functional magnetic resonance imaging; ICC, central nucleus of inferior colliculus; LTD, long-term depression; LTP, long-term potentiation; LPZ, lesion projection zone; MEG, magnetoencephalography; MDF, minimum discharge field; MG_V, ventral division of medial geniculate nucleus; MMN, mismatch negativity; NMDA, *N*-methyl-D-aspartate; PET, positron emission topography; RF, receptive field; S^D, discriminative stimulus; SPL, sound pressure level; STRF, spectro-temporal receptive field; UCS, unconditioned stimulus; V1, primary visual cortex

* Tel.: +61 3 99053963; fax: +61 3 99053948.
E-mail address: d.irvine@med.monash.edu.au.

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processing system. Although our perceptual experience of the auditory world ("hearing" in the normal sense of that word) clearly involves cognitive processes by which the information provided by the environment is interpreted, it was implicitly assumed that this "higher–order" processing takes place in "association" areas beyond the auditory cortex.

A number of lines of evidence have led to substantial changes in this view of the function of auditory cortex. One has been the evidence that auditory cortical response characteristics and organization can in fact be modified in adult humans and animals as a consequence of a variety of changes in the organism's auditory experience (see Weinberger, 1995, 2004a; Irvine and Wright, 2005 for reviews). One manifestation of adult plasticity is associated with auditory learning, and suggests that the auditory cortex contains memory traces of behaviorally significant stimuli (e.g., Weinberger, 2004b). A second line of evidence is that some components of human auditory evoked potentials that are primarily generated in auditory cortex are associated with what have been thought to be higher-order processes. For example, the mismatch negativity (MMN) reflects a form of memory for previous stimuli in the generating structures (e.g., Näätänen et al., 2001). Activity generated by speech sounds in human auditory cortex has also been shown to be influenced by factors such as phonological grammar and intelligibility (e.g., Jacquemot et al., 2003; Obleser et al., 2006). A third line of evidence is that auditory cortex is involved in aspects of auditory scene analysis that have a "top down" flavour (e.g., Näätänen et al., 2001; Nelken, 2004). These (and other) findings have indicated that auditory cortex has the capacity to store some forms of memory and to carry out a range of higher order, or "cognitive", functions (Weinberger, 2004b). As one instance of this changing view of auditory cortical function, Näätänen et al. (2001) referred to some aspects of auditory cortical processing as reflecting "primitive intelligence".

The evidence on adult plasticity in auditory cortex has been complemented by substantial changes in the way auditory cortical receptive fields (RFs) are conceptualized, and the newly recognized characteristics of RFs are in fact among the most important factors that contribute to adult plasticity. In this paper, the evidence for various forms of auditory cortical plasticity in adults will be reviewed, and the extent to which learning-related and other forms of plasticity support the claim that auditory cortex can be considered to carry out cognitive functions will be examined in the light of evidence as to the mechanisms involved.

2. Plasticity in adult auditory cortex

As elaborated in the following sections, plastic changes in the response characteristics of auditory cortical neurons, and in the functional organization of auditory cortical fields, have been demonstrated using a wide range of experimental interventions. Some of these interventions involve manipulation of the organism's sensory environment or of the significance for the organism of particular stimuli in that environment. Others involve the production of changes in auditory input by modifying receptor function or the transmission of information from the receptors to the central nervous system (CNS).

Neural plasticity can be broadly defined as dynamic changes in the structural and functional characteristics of neurons that occur in response to changes in the nature or significance of their input. This definition is intended to distinguish plasticity from changes that occur as *passive* consequences of the altered input or as a direct consequence of changes in the organism's state (e.g. arousal state; age). In the auditory system, for example, changes in the frequency tuning of auditory nerve fibres and central neurons occurs as a direct consequence of destruction of the outer hair cells (e.g., Dallos and Harris, 1978). These changes are passive consequences of the elimination of the cochlear amplifier rather than instances of plasticity, which involves some form of dynamic change in neural properties as a consequence of the altered input. Although the distinction between passive and plastic changes appears straightforward and is usually easily made, there are borderline cases where the distinction is difficult (see Calford, 2002).

2.1. Plasticity induced by restricted cochlear damage

Although there had been earlier reports of sensory cortical plasticity associated with behavioural conditioning, the strongest impetus to recognition that plasticity is not restricted to critical developmental periods was provided by evidence for reorganization of topographic "maps" of receptor surfaces as a consequence of elimination of input from a restricted region of the receptor epithelium. Such reorganization was first demonstrated in somatosensory cortex, but was subsequently described in both auditory and visual cortices after analogous lesions (see Buonomano and Merzenich, 1998; Gilbert, 1998; Kaas and Florence, 2001 for reviews). The impact of these results almost certainly derived from the fact that these maps had long been thought of as simple reflections of orderly projections from receptor surfaces to target structures in the brain, established early in development. As Calford (2002) has pointed out, the orderly nature of these maps also provided a simple metric by which the nature of the reorganization could be quantified.

In the auditory system, unilateral mechanical lesions to a restricted region of the cochlea in adult guinea pigs (Robertson and Irvine, 1989) and cats (Rajan et al., 1993) result in a reorganization of the frequency map in primary auditory cortex (AI) contralateral to the lesioned cochlea. The general form of this reorganization is that the neurons in the region of cortex in which the lesioned section of the cochlea would normally be represented, which has been termed the lesion projection zone (LPZ; Schmid et al., 1996), have new CFs at frequencies represented at the