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Review

Tonotopic mapping of human auditory cortex

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ABSTRACT

Since the early days of functional magnetic resonance imaging (fMRI), retinotopic mapping emerged as a powerful and widely-accepted tool, allowing the identification of individual visual cortical fields and furthering the study of visual processing. In contrast, tonotopic mapping in auditory cortex proved more challenging primarily because of the smaller size of auditory cortical fields. The spatial resolution capabilities of fMRI have since advanced, and recent reports from our labs and several others demonstrate the reliability of tonotopic mapping in human auditory cortex. Here we review the wide range of stimulus procedures and analysis methods that have been used to successfully map tonotopy in human auditory cortex. We point out that recent studies provide a remarkably consistent view of human tonotopic organisation, although the interpretation of the maps continues to vary. In particular, there remains controversy over the exact orientation of the primary gradients with respect to Heschl's gyrus, which leads to different predictions about the location of human A1, R, and surrounding fields. We discuss the development of this debate and argue that literature is converging towards an interpretation that core fields A1 and R fold across the rostral and caudal banks of Heschl's gyrus, with tonotopic gradients laid out in a distinctive V-shaped manner. This suggests an organisation that is largely homologous with non-human primates.

This article is part of a Special Issue entitled <Human Auditory Neuroimaging>.

1. Introduction

Neuroimaging techniques like electro- and magnetoencephalography (EEG, MEG) or positron emission tomography and functional magnetic resonance imaging (PET, fMRI) are painting an increasingly detailed picture about how the human brain is organised. Numerous brain networks have been identified that consistently show coherent patterns of activity during a variety of tasks, and even during rest (Fox et al., 2005; Gazzaniga, 1989). The sensory modalities provide excellent examples of brain networks for which parcellation into subdivisions has been achieved. That is because several sensory systems feature faithful representations of the peripheral sensory epithelia (Kaas, 1997; Weinberg, 1997). For example, neurons in the visual cortex are tuned to particular areas in the visual field of view, and are laid out on the surface of the cerebral cortex in a fashion that can be mapped one-on-one onto the extent of the retina. In fact, multiple such topographic representations exist, each within a distinct subdivision of the visual cortex (Engel et al., 1997; Wandell and Winawer, 2011). Similarly, the somatosensory cortex that is involved in the sense of touch features representations of the various body parts, giving rise to the cortical homunculus. Again, multiple such somatotopic maps appear in parallel in several adjacent cortical subdivisions, and a similar map occurs in neighbouring motor cortex (Mattay and Weinberger, 1999; Narici et al., 1991; Sanchez-Panchuelo et al., 2012).

The auditory system receives input from the organ of Corti in the inner ear. Hair cells are laid out along the length of the basilar membrane, spiralling along the windings of the cochlea. The nerve fibres that synapse with the hair cells retain this essentially one-dimensional cochleotopic organisation, all the way up to the auditory cortex. Because the mechanical properties of the basilar membrane gradually change along its length, hair cells are tuned to progressively higher frequencies when traversing the cochlea from its apex to its base. Thus, the inner ear acts as a sound frequency analyser, and sound information is transmitted centrally along

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numerous frequency channels in parallel (Ellis and Helmholtz, 1885; Fuchs, 2010; Meyer and Moser, 2010; Von Bekesy, 1949). Due to this frequency-place code, cochleotopy is more commonly referred to as tonotopy (τόνος = tone; τόπος = place) in the neuroimaging literature.

The ability to determine tonotopic maps not only serves to gain insight in the functional organisation of the auditory system regarding frequency processing, which may be argued to be one of the most basic functions it performs. Besides that, it provides a tool to parcellate the central auditory system into meaningful subdivisions of which the distinct properties can be studied with regard to acoustic features other than frequency, as well as non-acoustic factors like attention. Multiple tonotopic progressions can be found in various subdivisions of the auditory nuclei in the brainstem, midbrain, and thalamus, and in the auditory cortex of the cerebrum, as illustrated in Fig. 1 (Clopton et al., 1974; Günter Ehret and Romand, 1997; Rees and Palmer, 2010). Currently, frequency is the only acoustic parameter that is unequivocally held to be topographically mapped, although other parameters like sound intensity (Bilecen et al., 2002; Pantev et al., 1989a), tuning bandwidth (Moerel et al., 2012; Seifritz et al., 2006), and modulation rate (Langner et al., 1997; Barton et al., 2012; Herdener et al., 2013) have been suggested to form complementary maps.

Tonotopic mapping of the auditory cortex has proven particularly challenging for human neuroimaging. This is in part due to the small size of auditory cortical fields relative to the spatial resolution of neuroimaging techniques, and in part due to a lack of consensus regarding architectonic definitions of human primary auditory cortex. As a result, neuroimaging studies of human tonotopy have proposed different, even opposing, views regarding the orientation of the primary tonotopic gradients in auditory cortex, which in turn leads to different predictions about the locations of specific auditory fields. However, despite differences in map interpretation and a variety of experimental paradigms, we emphasize that virtually all recent studies show a remarkably *consistent* spatial pattern of frequency preference in human auditory cortex. Here, we review the history of neuroimaging of tonotopy, critically review the differing map interpretations, and describe the range of experimental paradigms used thus far.

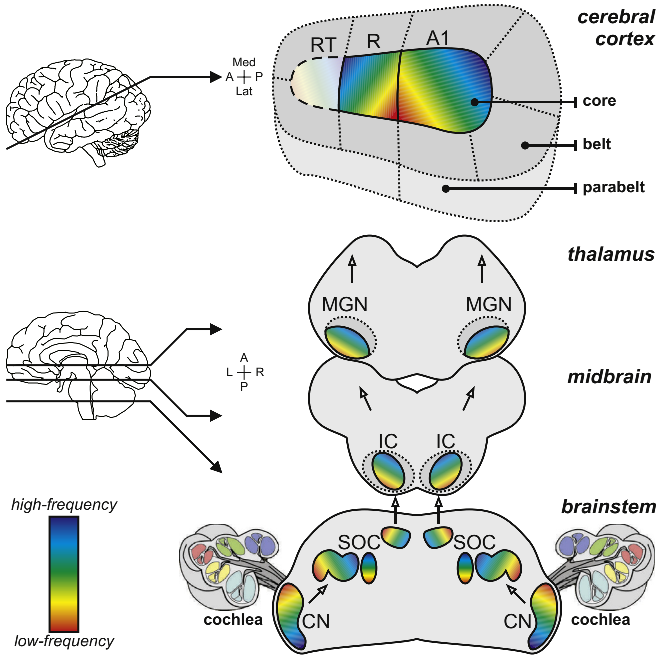

Fig. 1. The central auditory pathway. All nuclei that form part of the classical lemniscal auditory pathway are tonotopically organised. These include various subdivisions of the cochlear nucleus (CN), superior olivary complex (SOC), inferior colliculus (IC), and medial geniculate nucleus (MGN). In the auditory cerebral cortex in the superior part of the temporal lobe, expected divisions of core, belt, and parabelt are based on the non-human primate model of auditory cortical organisation. Human neuroimaging consistently shows at least two primary tonotopic gradients ("high-to-low-to-high") in the auditory cortex, homologous to primary fields A1 and rostral field R in the monkey cortex. In some primate studies, a third rostrotemporal field RT is delineated, but neuroimaging evidence for a similar field in humans is sparse.

2. Tonotopic organisation in humans

2.1. *Extrapolating from animal studies*

By means of invasive animal studies, the existence of tonotopic progressions has been shown for many subdivisions in the central auditory system (Clopton et al., 1974; Ehret and Romand, 1997; Rees and Palmer, 2010). All subdivisions in the brainstem are tonotopically organised (Fig. 1): in the cochlear nucleus, tonotopic progressions exist in the anteroventral subdivision as well as in the dorsal and neighbouring posteroventral divisions, while in the superior olivary complex tonotopic organisations have been reported for both the medial and lateral subdivisions as well as the medial nucleus of the trapezoid body (Kandler et al., 2009; Ryugo and Parks, 2003). In the midbrain, two pathways diverge (Hu, 2003; Møller and Rollins, 2002). One is the lemniscal classical auditory pathway that is tonotopically organised throughout. It comprises the central nucleus of the inferior colliculus and the ventral division of the medial geniculate body, which project to primary areas in auditory cortex. The other is the extralemniscal non-classical auditory pathway that shows a diffuse frequency organisation and provides aspecific sensory information. It comprises the cortex of the inferior colliculus and the dorsal and magnocellular subdivisions of the medial geniculate body, and projects to non-primary auditory cortex as well as various non-auditory brain structures involved in multimodal, associative, and affective processing.

The organisation of the auditory cortex on the superior temporal gyrus of the cerebrum has been most extensively studied. Tonotopic progressions were observed in numerous animal species, including birds (Capsius and Leppelsack, 1999; Cohen and Knudsen, 1996; Terleph et al., 2006), rodents (Hellweg et al., 1977; Kelly et al., 1986; McMullen and Glaser, 1982; Merzenich et al., 1976; Stiebler et al., 1997), primates (Kusmierek and Rauschecker, 2009; Luethke et al., 1989; Morel and Kaas, 1992; Scott et al., 2011), and other mammals (Reale and Imig, 1980; Suga and Jen, 1976). In non-human primates, a hierarchical model of auditory cortical organisation has emerged based on combined knowledge of electrophysiology, cortical architecture, and connectivity. In this model, an elongated *core* (primary regions) is comprised of up to three roughly collinear tonotopic fields (primary auditory field A1, followed by a rostral field R and an even more rostral temporal field RT) surrounded by several *belt* fields (secondary regions), further surrounded by higher-order *parabelt* fields (Kaas and Hackett, 2000).

The elongated core is situated along a posterior-to-anterior axis. Along this axis, neuronal frequency preferences follow a gradient of high to low (A1), followed by a reversed gradient of low back to high (R), followed by a third smaller and perhaps less clearly organised gradient of high back to low (RT). Thus, the overall pattern is a clear "high-to-low-to-high" corresponding to core fields A1 and R followed by a less distinct "high-to-low" corresponding to core-like field RT, with the borders between fields marked by frequency gradient reversals. Architectonic and histochemical markers of the primary core are most pronounced and similar in A1 and R and somewhat less distinct in RT (Imig et al.,

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