Auditory Pathways : Are 'what' and 'where' appropriate?

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New evidence confirms that the auditory system encompasses temporal, parietal and frontal brain regions, some of which partly overlap with the visual system. Common assumptions about the functional homologies between sensory systems may be misleading.

It is widely assumed that the different sensory systems have common organizational principles. For example, the auditory and visual systems engage separate regions of the brain for specialised perceptual processing, and that these inputs later converge for the integration of information across the senses. An important technique for revealing the full extent of the visual and auditory systems in primates uses 2-[^{14}C]deoxyglucose to localise where glucose utilization is greater in an intact hemisphere than in a perceptually-isolated contralateral hemisphere of the same animal, after 45 minutes of stimulation – see Figure A. Applied to the visual system [1,2], the results confirmed extensive activation in the visual cortex. However, visual activation occurs in brain regions much beyond the visual cortex itself, including the inferior temporal cortex, the posterior inferior parietal cortex, prefrontal cortex and the upper bank of the superior temporal sulcus. Recent results applying the same technique to the auditory system [3], have revealed increased glucose utilization across the entire auditory cortex, parts of the inferior parietal cortex, prefrontal cortex, frontal pole (area 10) and the upper back of the superior temporal sulcus. Thus, this work by Mishkin and colleagues [1-3] demonstrates two basic principles of structural organisation; i) both auditory and visual systems involve widespread brain regions, and ii) sensory processing involves modality-specific and modality-free brain regions.

We can compare sensory regions identified by 2-DG functional mapping with those identified by axonal tracing methods. For example, Jones and Powell [4] examined the routes of axonal degeneration after localised cortical lesions in the visual, auditory and somatic systems to reveal a general progression from all sensory areas to similar regions of the frontal and temporal cortices (Figure B). Sites of sensory convergence were also reported in the superior temporal sulcus and prefrontal cortex. The results of Jones and Powell [4] show a marked agreement with those of Mishkin and colleagues [1-3].

The pattern of connectivity has been addressed empirically in both the visual and auditory systems. More than 20 years ago, two major pathways were proposed from the visual cortex; a ventral route projecting to the inferotemporal cortex and dorsal route projecting to the posterior parietal cortex [5]. Each stream is hierarchically organized, with limited cross-talk [6]. This proposal is supported by physiological recordings, anatomical and lesion data, and evidence using functional neuroimaging. Two major pathways have also been confirmed in the auditory system using microinjections of retrograde and anterograde tracers [7,8]. One auditory pathway originates in anterolateral auditory cortex and projects ventrally to the anterior-most tip of the superior temporal gyrus and prefrontal cortex (areas 10, 12, 45 and 46). The other pathway originates in posterolateral auditory cortex and projects dorsally to inferior parietal cortex and prefrontal cortex (areas 8a, 12 and 46). These auditory pathways are illustrated in Figure C and, like the visual pathways, are referred to as the ventral and dorsal routes respectively.

Given the similarities in the basic structural organisation of the visual and auditory systems, the visual system is widely considered to provide an appropriate basis for understanding the auditory system. This inference has been extended not only to the structural organisation, but also to the functional organisation. The pervasive view of the functional divisions between ventral and dorsal visual pathways highlights the requirements for perceptual analysis based on the visual input. The ventral pathway is held to encode object-related (‘what’) features, while the dorsal pathway encodes space-related (‘where’) features [5]. This model has strongly influenced functional descriptions of the ventral and dorsal auditory pathways which are also proposed to encode ‘what’ and ‘where’ information [9]. However, the emphasis on the simple division of function by perceptual input may mislead us about the true functionality of either system. An alternative functional account emphasises the requirements for the control of behaviour, ascribing the role of controlling goal-directed actions to the dorsal pathway [10]. According to this account, both ventral and dorsal pathways can process information about the intrinsic properties of objects and their spatial locations, but the transformations performed upon those properties differ across streams. Empirical support for this proposal includes a recent neuroimaging experiment demonstrating that judgements about the spatial orientation of a grating can be processed either in the ventral or dorsal visual pathway, depending on the cognitive operations required by the task [11]. Several other functional taxonomies have been put forward. For example, Belin and Zatorre [12] posit that the dorsal auditory pathway is primarily involved in processing changes in the frequency spectrum over time and is especially important in the perception of vocalisations. Humphreys [13] has proposed a distinction of within-object and between-object representations, mediated by the ventral and dorsal visual pathways respectively. A dissociation between these two types of object representation has received some support in the domain of audition [14], but its neural basis has not been explored systematically.

Questions about the anatomical independence of the ventral and dorsal routes have also been raised. There are numerous cross-connections between the two visual pathways, most notably in the superior temporal sulcus [15] and the inferior temporal cortex [16]. The inferior parietal lobe might represent an additional link between ventral and dorsal visual routes [17] and may be involved in top-down attention control by biasing information flow within both pathways [18]. By analogy, the superior temporal sulcus and inferior parietal lobe might also provide opportunities for linkage between ventral and dorsal auditory pathways. The superior temporal sulcus has even been proposed to form part of a third visual route [19] and, while the ventral and dorsal routes probably constitute the major pathways for auditory information processing, they may not be the only auditory routes [20].

Summary

In both the visual and auditory systems, two major pathways connect brain regions in the temporal, parietal and frontal cortices, forming the anatomical basis for serial and parallel processing of sensory information. It is becoming increasingly clear that a distinction based on the ‘what’ and ‘where’ features of the stimulus is unlikely to provide a appropriate functional account. Indeed, even the concept of two functionally-isolated pathways may be somewhat simplistic. The first challenge will be to acknowledge that the ‘what/where’ dual route scheme, which has hitherto been so pervasive, is no longer the apotheosis.

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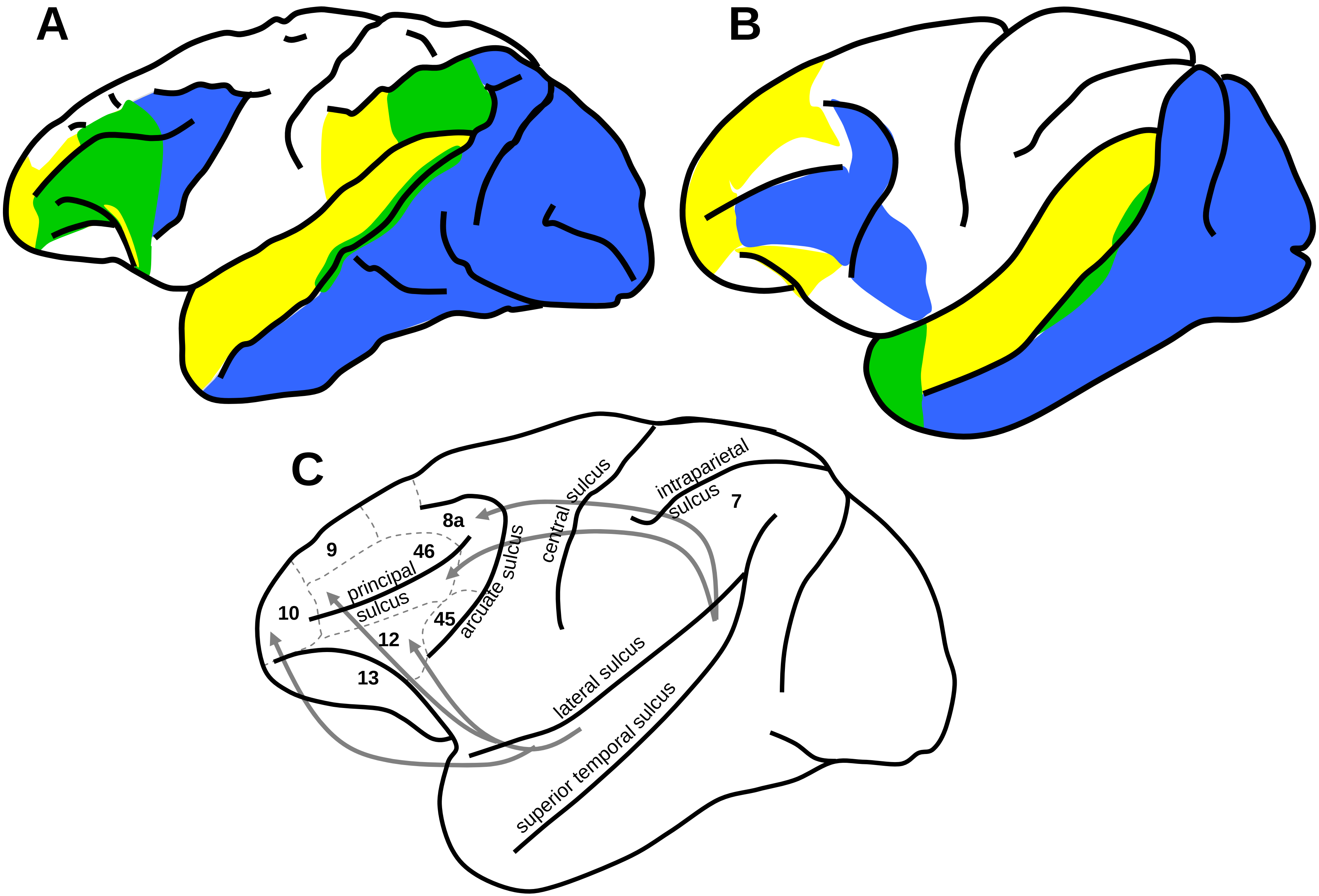
Three different schematic summaries of the auditory system. Figures **A** and **B** illustrate those brain regions engaged in processing auditory stimuli (yellow), visual (blue) stimuli, or both (green). **(A)** shows the activation revealed by 2-DG mapping [1-3]. The frontal pole (area 10) was not assessed in the visual experiment. **(B)** shows the regions of axonal degeneration after circumscribed lesions to different cortical sites [4]. It is unclear why the parietal cortex was not identified as part of the visual system. The absence of parietal degeneration in the auditory system may be explained by the concomitant absence of an ablation placed in the posterior superior temporal cortex (dorsal auditory pathway). Figure **C** describes the termination sites in the prefrontal cortex for the ventral and dorsal auditory pathways [7,8].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