



## Research paper

## Information flow in the auditory cortical network

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## ABSTRACT

Auditory processing in the cerebral cortex is comprised of an interconnected network of auditory and auditory-related areas distributed throughout the forebrain. The nexus of auditory activity is located in temporal cortex among several specialized areas, or fields, that receive dense inputs from the medial geniculate complex. These areas are collectively referred to as *auditory cortex*. Auditory activity is extended beyond auditory cortex via connections with *auditory-related* areas elsewhere in the cortex. Within this network, information flows between areas to and from countless targets, but in a manner that is characterized by orderly regional, areal and laminar patterns. These patterns reflect some of the structural constraints that passively govern the flow of information at all levels of the network. In addition, the exchange of information within these circuits is dynamically regulated by intrinsic neurochemical properties of projecting neurons and their targets. This article begins with an overview of the principal circuits and how each is related to information flow along major axes of the network. The discussion then turns to a description of neurochemical gradients along these axes, highlighting recent work on glutamate transporters in the thalamocortical projections to auditory cortex. The article concludes with a brief discussion of relevant neurophysiological findings as they relate to structural gradients in the network.

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## 1. Auditory and auditory-related areas in cortex

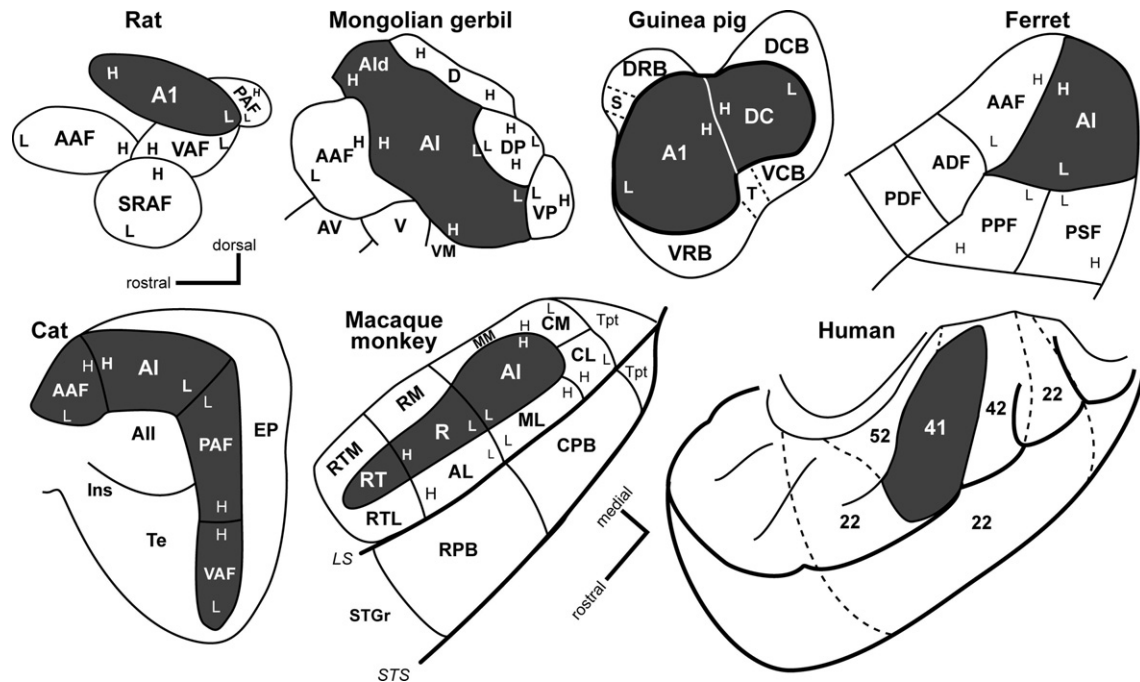
Areas that process sound have been discovered in every lobe of the brain, but are all of these areas part of auditory cortex? The answer depends on how one defines auditory cortex. From an anatomical perspective, *auditory cortex* can be defined as those areas of the cerebral cortex that receive significant thalamic input from one or more divisions of the medial geniculate complex (MGC). By this definition, the auditory cortex of mammals is confined to a group of adjoining areas in the temporal region, as

shown for several mammalian species in Fig. 1. The precise number of areas identified, their arrangement and numerous other features varies by species, but all are considered auditory. In humans, the identity of auditory cortex is less certain, because the projections of the MGC are not known. Therefore, we cannot define auditory cortex in the same way as in other animals. Instead, we rely on comparisons of the neuronal architecture and neurochemistry to identify areas with common features, and then look for support in imaging and electrophysiological studies. At present, it is thought that human auditory cortex occupies the posterior portion of the

*Abbreviations:* AAF, anterior auditory field; AD, anterodorsal division (medial geniculate); A1, auditory area 1; AII, second auditory field; AChE, acetylcholinesterase; AL, anterolateral area; CB, calbindin; CL, caudolateral area; CM, caudomedial area; CO, cytochrome oxidase; CPB, caudal parabelt area; CS, central sulcus; D, dorsal nucleus (medial geniculate); DC, dorsal cortex (inferior colliculus); DD, deep dorsal nucleus (medial geniculate); DS, superficial dorsal nucleus (medial geniculate); DZ, dorsal zone; EP, posterior ectosylvian region; ED, dorsal ectosylvian region; EI, intermediate ectosylvian region; EV, ventral ectosylvian region; FF, feedforward projection; IC, inferior colliculus; ICc, inferior colliculus-central nucleus; Ins, insula; IPS, intraparietal sulcus; L, lateral nucleus (inferior colliculus); LGN, lateral geniculate nucleus; LS, lateral sulcus; LuS, lunate sulcus; M, magnocellular division (medial geniculate); MF, myelinated fibers (axons); MGad, medial geniculate complex, anterodorsal division; MGC, medial geniculate complex; MGd, medial geniculate complex, dorsal division; MGm, medial geniculate complex, magnocellular division; MGpd, medial geniculate complex-posterodorsal division; MGv, medial geniculate complex, ventral division; ML, middle lateral area; MM, middle medial area; Ov, pars ovoidea (of medial geniculate); PAF, posterior auditory field; PD, posterodorsal division (medial geniculate); Pro, proisocortical area; proA, prokoniocortex area; PS, principal sulcus; PV, parvalbumin; R, rostral area; Ri, retroinsular area; RM, rostromedial area; RPB, rostral parabelt area; RT, rostrottemporal area; RTL, rostrottemporal lateral area; RTM, rostrottemporal medial area; Sg, supragenulate nucleus; STG, superior temporal gyrus; Te, temporal auditory field; Tpt, temporal parietotemporal area; VGLuT, vesicular glutamate transporter; V, ventral division (medial geniculate); VAF, ventral posterior auditory field (same as VPAP); VGLuT2, vesicular glutamate transporter 2; VL, ventrolateral nucleus (medial geniculate); VP, ventroposterior nucleus; VPAP, ventral posterior auditory field.

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**Fig. 1.** Schematics of the auditory cortex in selected mammals. Primary (core) auditory areas are darkly shaded. Belt and parabelt areas are unshaded. Tonotopic gradients are indicated by H (high) and L (low) frequency. See text for abbreviations. Redrawn from Polley et al. (2007) (rat); Budinger et al. (2000) (Mongolian gerbil); Bizley et al. (2005) (ferret); Wallace et al. (2000) (guinea pig); Lee et al. (2004b) (cat); Hackett et al. (1998a) (macaque monkey); (Brodmann (1909) (human). Dorsal–rostral axis marker applies to all panels except macaque and human. Schematics are not to scale.

superior temporal cortex, including Heschl's gyrus, the planum temporale, and some portion of the posterior superior temporal gyrus. There is no consensus on the number of areas present or their arrangement.

The network of areas that process auditory information in cortex also includes numerous *auditory-related* areas distributed throughout the forebrain. These areas receive inputs from auditory cortex and often other sensory systems, but *lack* significant inputs from the MGC. This arrangement implies that auditory activity in auditory-related areas depends on inputs from auditory cortex, or perhaps other auditory-related areas. As a whole, then, auditory information in the cerebral cortex is processed by an interconnected network in which auditory areas rely on inputs from the MGC and auditory-related areas largely depend on inputs from the auditory areas. The flow of information within this network is the subject of this article, which draws from past and present studies in several species. For practical reasons, the discussion focuses on cats and primates, but it is acknowledged that such patterns are likely to characterize most if not all mammalian species.

## 2. Information flow in the auditory cortical network

As one reviews the myriad studies of auditory cortex over the last 40 years, a number of common themes stand out. These are based on the structural and functional properties that tend to be the most robust, and are referred to herein as principles of auditory cortical organization (Table 1). Each is related in some way to the flow of information *into*, *within* and *out of* auditory cortex. Perhaps the most fundamental organizational feature is that, in nearly all studied mammals, auditory cortex contains more than one area (Fig. 1). In some models, these areas have been grouped into *regions* based on a set of common features. In cats and primates, where more than ten areas have been identified, the primary areas are grouped into a centrally located “core” region, and the secondary

areas are assigned to “belt” or “parabelt” regions, which tend to be located around the core. Inputs to these areas arise from multiple sources in the forebrain. Subcortical inputs include auditory and other sensory nuclei in the thalamus. Cortical inputs come from intra- and interhemispheric connections within auditory cortex, and reciprocal connections with auditory-related areas. The outputs of auditory cortex include myriad cortical and subcortical structures at all levels of the auditory pathways. Individually and collectively, these patterns frame and constrain the processing of auditory and non-auditory information within the entire auditory cortical network.

### 2.1. Information flow into auditory cortex: thalamocortical projections

Thalamic inputs to auditory cortex are dominated by projections from the MGC (Jones, 2007; Lee and Winer, 2008a). In most species, three major MGC divisions are commonly recognized (v, ventral; d, dorsal; m, medial or magnocellular), each of which can be further subdivided. An important distinction between divisions is that each receives a different blend of inputs from nuclei in the brainstem (Aitkin, 1986; Calford and Aitkin, 1983) and ultimately targets the auditory areas in a specific way (Fig. 2). In cats and monkeys, as in all studied mammals, the principal source of ascending inputs to the ventral division (MGv) is the central nucleus of the tonotopically organized inferior colliculus (ICc), which is part of the primary (lemniscal) ascending pathway. The dorsal divisions (MGd) mainly receive inputs from the dorsal cortex (DC) and lateral (L) nuclei of the inferior colliculus, although the rostral MGd divisions also receive inputs from the ICc. These divisions of the IC are part of the non-tonotopic or diffuse ascending pathway, and do not appear to be tonotopically organized. The magnocellular division (MGm) receives inputs from all three of these IC divisions, and is generally thought to receive additional inputs from vestibular,

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