

Review

Thalamic and cortical pathways supporting auditory processing

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ABSTRACT

The neural processing of auditory information engages pathways that begin initially at the cochlea and that eventually reach forebrain structures. At these higher levels, the computations necessary for extracting auditory source and identity information rely on the neuroanatomical connections between the thalamus and cortex. Here, the general organization of these connections in the medial geniculate body (thalamus) and the auditory cortex is reviewed. In addition, we consider two models organizing the thalamocortical pathways of the non-tonotopic and multimodal auditory nuclei. Overall, the transfer of information to the cortex via the thalamocortical pathways is complemented by the numerous intracortical and corticocortical pathways. Although interrelated, the convergent interactions among thalamocortical, corticocortical, and commissural pathways enable the computations necessary for the emergence of higher auditory perception.

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Introduction

Encoding and processing the rich variety of sounds from the external world requires an equally elaborate and specialized neural processing apparatus. Indeed, the initial sensorineural conversion of sound at the level of the cochlea is a marvel of biophysics (Hudspeth, 1997) and establishes many of the organizing features observed throughout the entirety of the ascending auditory pathway (Trussell, 1999). Multiple brainstem centers, such as the cochlear nuclei (Cant & Benson, 2003) and the superior olivary complex (Moore, 2000; Oliver, 2000; Thompson & Schofield, 2000), parcel the incoming stream into parallel pathways, which eventually converge in the midbrain at the inferior colliculus. From here, ascending tectothalamic pathways project to the auditory thalamus (Wenstrup, 2005), i.e. the medial geniculate body, which in turn projects to the auditory cortex (de la Mothe, Blumell,

Kajikawa, & Hackett, 2006b; Lee & Winer, 2008a). These higher auditory forebrain structures, the thalamus and cortex, establish the circuits necessary for the subsequent extraction and decoding of afferent acoustic information.

This advanced forebrain processing of auditory information, and of other sensory modalities, canonically has been viewed as relying on the numerous corticocortical pathways among areas (Felleman & Van Essen, 1991; Rouiller, Simm, Villa, de Ribaupierre, & de Ribaupierre, 1991). That is, auditory information ascending from the periphery to the medial geniculate body is relayed to a primary auditory cortical area, whereupon after intracortical processing, the transformed information is conveyed to higher cortical areas. From here, higher-level calculations are performed and the process repeats in a hierarchical fashion, until at some stage, putative auditory object, source and higher percepts emerge. Although theoretically attractive, such a wholly corticocentric view ignores the contribution of convergent inputs from thalamic and commissural sources (Lee & Winer, 2011a; Lee & Sherman, 2012), brainstem modulatory inputs (Bao, Chan, & Merzenich, 2001; Miasnikov,

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Chen, & Weinberger, 2008), and feedback and feedforward corticothalamic projections (Sherman & Guillery, 2006; Winer & Prieto, 2001), in particular those to the thalamus. Thus, a more complete account of auditory forebrain processing should encapsulate these pathways into a holistic connective framework.

As a step towards this goal, the patterns of connectivity in the auditory thalamus and cortex are reviewed here with a consideration of the principles organizing the thalamocortical pathways. In particular, we consider two models of thalamocortical connectivity: the core-matrix model proposed by Jones (2001) and the corticothalamic model proposed by Sherman and Guillery (2002). In addition, we examine the corticocortical and commissural connections in relation to their potential roles in auditory information processing.

Thalamocortical pathways

All regions of the neocortex, except those pertaining to olfaction, receive ascending inputs that must first travel through the thalamus

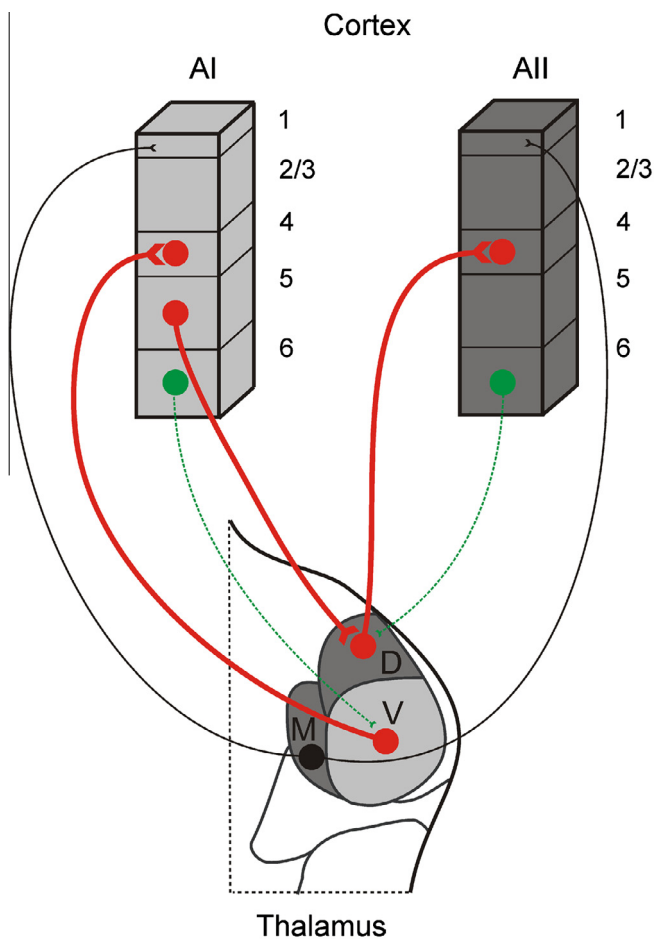


Fig. 1. Thalamocortical connections mediating higher order auditory processing. Primary auditory cortex (AI) receives ascending information from the ventral division of the MGB (V) ending in layer 4, while the secondary auditory cortex (AII) receives information from the dorsal division of the MGB (D) (red thick lines). Feedforward corticothalamic projections from layer 5 (red lines) of AI establish a corticothalamic route for information transfer between AI and AII. In contrast, feedback corticothalamic projections from layer 6 of AI and AII are not primary conduits of information flow, but rather modulate thalamic activity in MGBv and MGBd, respectively (green dashed lines). Calbindin-expressing neurons in the medial division of the MGB (M) project widely to multiple cortical areas (black thin lines), targeting apical dendrites in layer 1 primarily. These projections have the potential to synchronize activity across broad cortical territories. Light gray shading (tonotopic nuclei and areas), dark gray shading (non-tonotopic nuclei and areas).

(Jones, 2007; Sherman & Guillery, 2006). As such, the role of the thalamus in sensory perception generally is construed primarily in relation to its function in the initial transfer of information to the cortex (Felleman & Van Essen, 1991; Olshausen, Anderson, & Van Essen, 1993; Rouiller et al., 1991). However, this view of the thalamus as only a relay has evolved into a more multifaceted view, including roles in mediating intracortical communication and in synchronizing widespread cortical activity (Jones, 2003; Lee & Sherman, 2008, 2009; Sherman & Guillery, 2006).

The medial geniculate body (MGB) is the principle nucleus receiving ascending auditory information and is subdivided into three main divisions: the ventral, dorsal, and medial divisions (Fig. 1) (Calford, 1983; Winer, 1984a). The ventral division is the principal nucleus receiving tonotopic inputs from the central nucleus of inferior colliculus (ICc) and is further subdivided into the ventral nucleus (MGBv), the medial portion forming the *pars ovoidea* (Ov), and the rostral pole nucleus (RP); these project to primary auditory cortical areas (de la Mothe et al., 2006b; Morel & Imig, 1987; Winer, 1984a). The dorsal division (MGBd) is composed of several non-tonotopically organized nuclei, which receive inputs from the dorsal cortex of the inferior colliculus (ICd) (Calford & Aitkin, 1983) and send outputs primarily to secondary non-tonotopic auditory areas (Lee & Winer, 2008a). Finally, the medial division receives non-tonotopic and polymodal inputs from the lateral cortex of the inferior colliculus (ICl) (Rouiller et al., 1989) and sends outputs to all areas of auditory cortex (Lee & Winer, 2008a; Molinari et al., 1995), terminating in non-classical input layers (Fig. 1: black) (Hashikawa, Rausell, Molinari, & Jones, 1991; Huang & Winer, 2000), and to the amygdala (LeDoux, Farb, & Romanski, 1991). Despite the lack of a functional topography in the non-tonotopic thalamic nuclei, each still exhibits highly topographic patterns of thalamocortical connectivity, suggesting that either a metric besides tonotopy organizes these pathways or a general ontogenetic mechanism guides the formation of all auditory thalamocortical connections (Kaas, 1997; Lee & Winer, 2005; Schreiner & Winer, 2007).

Auditory thalamic neurons exhibit a wide range of physiological properties observed at lower stations in the ascending auditory pathway, but vary in their prevalence and distribution. As noted above, frequency tuning differs among the MGB nuclei, with ventral and rostral pole neurons exhibiting the sharpest tuning (Imig & Morel, 1985a; Miller, Escabi, Read, & Schreiner, 2002), while dorsal and medial division neurons have more complex, multipeaked, and sometimes polymodal receptive fields (Imig & Morel, 1985b; Morel, Garraghty, & Kaas, 1993). Intensity coding in the MGB is varied, with a quarter of neurons exhibiting monotonic responses across a range of 60–80 dB and the remaining displaying non-monotonic responses that taper at higher intensities (Rouiller, de Ribaupierre, Morel, & de Ribaupierre, 1983). Temporal coding of auditory information in the ventral division is better than in other nuclei, although phase-locked responses, which are robust at the level of the cochlear nucleus, are limited in the MGB (Lennartz & Weinberger, 1992), with only a tenth of neurons exhibiting a maximum following response of 250 Hz (Rouiller, de Ribaupierre, Toros-Morel, & de Ribaupierre, 1981). Finally, the binaural responses established in the brainstem are manifested in the ventral nucleus, with about half of the neurons exhibiting binaural excitatory responses (EE), and the remaining neurons split roughly evenly among monaural (EO) and excitatory-inhibitory (EI) responses (Calford, 1983; Cetas et al., 2002). The coding of an auditory space map is uncertain in the MGB, although some neurons are responsive to interaural time (ITD) and intensity (IID) differences (Ivarsson, De Ribaupierre, & De Ribaupierre, 1988).

Neurons in the MGB and in other sensory thalamic nuclei exhibit two distinct firing modes, termed the tonic and burst modes (Desc-hènes, Roy, & Steriade, 1982; Jahnsen & Llinas, 1984; Ramcharan, Gnadt, & Sherman, 2000; Sherman, 2001). The transition to the

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