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Auditory thalamocortical transformation: structure and function

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Communicative, predatory, and reproductive behaviors rely on the auditory thalamocortical system, a key nexus that combines, transforms, and distributes virtually all acoustic information relevant to survival. The rules of connectivity for this complex network, both anatomically and functionally, are only beginning to be uncovered. Although the auditory thalamocortical system shares many features with other modalities, its connectivity and information processing principles differ from those of other modalities in many ways. Some physiological and anatomical bases for these differences are the subject of this review.

Introduction

The rustle of grass as a rodent forages for food attracts the attention of an owl. The owl takes flight, using the time and intensity information carried by the displaced foliage to find its next meal. Hearing the owl approach, the rodent has just a few milliseconds to freeze or flee: one strategy leads to survival, the other to near-certain death. How is the prey's location computed in the owl's auditory circuits, and how does the rodent's brain rapidly craft a strategy for survival from sound pressure waves alone [1]? Answering these questions requires extraction of biological meaning from the sound pressure and frequency waves represented in the cochlea. Although medullary and midbrain auditory centers form topographic maps and analyze acoustic parameters underlying this behavior, survival requires that the auditory thalamus and cortex extract and transform information representing biologically and ecologically significant aspects of sound that are essential for perceptual analysis and behavior.

The classic theory of forebrain serial processing considers the thalamus primarily as a relay for ascending information that is propagated to the next hierarchical stage in a point-to-point fashion, enabling perceptual decisions to be made. This simplistic view overlooks the richness of real brains, which is reflected in the many limbic and contextual influences on perception, and the role of descending information, feedback from which interacts nearly continuously with the ascending auditory pathway [2]. A few key nodes – especially the thalamocortical interface – act as arbiters for crucial behavioral decisions that reflect the contextual influences within the acoustic scene and their modification by experience. Thus, limbic circuits influence auditory processing, so that behavioral arousal level is modulated, and sound content and meaning are assessed critically. Corticothalamic input modifies these perceptual inferences and refines ongoing behavior [3]. Transformations of information at the thalamocortical interface have selective, combinatory and encoding roles, and they activate local neural networks [4] to construct global feature maps adapted for essential perceptual tasks [5]. The neural algorithms implementing these transformations embody operations common to all sensory systems [6], in addition to unique, modality-specific processes [7] suitable for the analysis of identity, form, location and motion of auditory objects. Different auditory cortical subregions perform task-related computations in this process [8]. Functional differences underlying these processes are created by thalamic and cortical circuits and by local diversity and specialization in synaptic and cellular mechanisms for specific acoustic stimulus features [9]. This review summarizes recent anatomical and physiological work in the auditory thalamocortical system that illustrates principles common to hearing and other modalities, and notes features of auditory thalamocortical transformation that depart from the classical view of forebrain serial processing. These departures are most marked in the organization and laminar specificity of feedforward connections, and in the rules of functional connectivity that extend classical models of thalamocortical organization.

Thalamocortical networks: specific nuclear origins and laminar targets

Consider first the functional transformations between the ventral division of the medial geniculate body (MGBv) and primary auditory cortex (AI), the core pathway crucial for sound analysis in the classical view of thalamocortical connectivity. This view construes the thalamus as a relay nucleus [10], with point-to-point topographic projections [11] targeting one or two neocortical layers [12], and with a similar organization across modalities [13]. Recent findings suggest that each conclusion requires revision.

Minute deposits of retrograde tracers in AI labeled only a few contiguous MGBv neurons [14]. However, small

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thalamic deposits of sensitive anterograde tracers label thousands of synaptic boutons over many millimeters of cortex [15]. The inference of strict topography in the retrograde studies reflects somatic labeling from tracer deposits that probably involve only some of the many axonal branches of single thalamocortical neurons [16]. By contrast, anterograde experiments reveal the complete axonal deployment, agreeing with results from single axonal injections in other modalities [17]. A few thalamic cells might thus affect large cortical expanses, enabling inheritance models of thalamocortical organization (as will be discussed later) or synchronizing thalamic and cortical activity, so that relatively few thalamic neurons [18] reach widespread cortical regions [19] to permit binding [20] or attentional shifts via the thalamic reticular nucleus. The clustered thalamic labeling in AI could contribute to modular cortical processes in subregions with specific constellations of thalamic (Figure 1c) and corticocortical (Figure 2a) input [21], and their absence elsewhere suggests that AI is specialized physiologically.

The laminar specificity of thalamocortical axons as assessed using biotinylated dextran amines (BDA) is also at odds with degeneration or autoradiographic studies [22,23], which find thalamic input terminating principally in layers III and IV. BDA reveals significant projections to several layers, fills the largest known thalamic axons (which unexpectedly reside in layer I), and labels widespread area-specific laminar projections [15]. Specific inputs could have particular roles; for example, massive layer I thalamocortical axons could interact with corticothalamic neuron apical dendrites before lemniscal input reaches classic intracortical circuits. This might drive corticocortical and corticofugal circuits in tandem [24], synchronizing temporal feedforward and feedback processes. Other layer-specific input might affect intralaminar circuits [25], corticocortical feedforward relationships [26] implicated in hierarchical processes [27], and commissural [28] operations.

The MGB projection pattern is nucleus-specific and thus more complex than point-to-point or one-nucleus-to-area models suggest. Rather, an area receives overlapping input from several nuclei (Figure 1c,ii) that have laminar

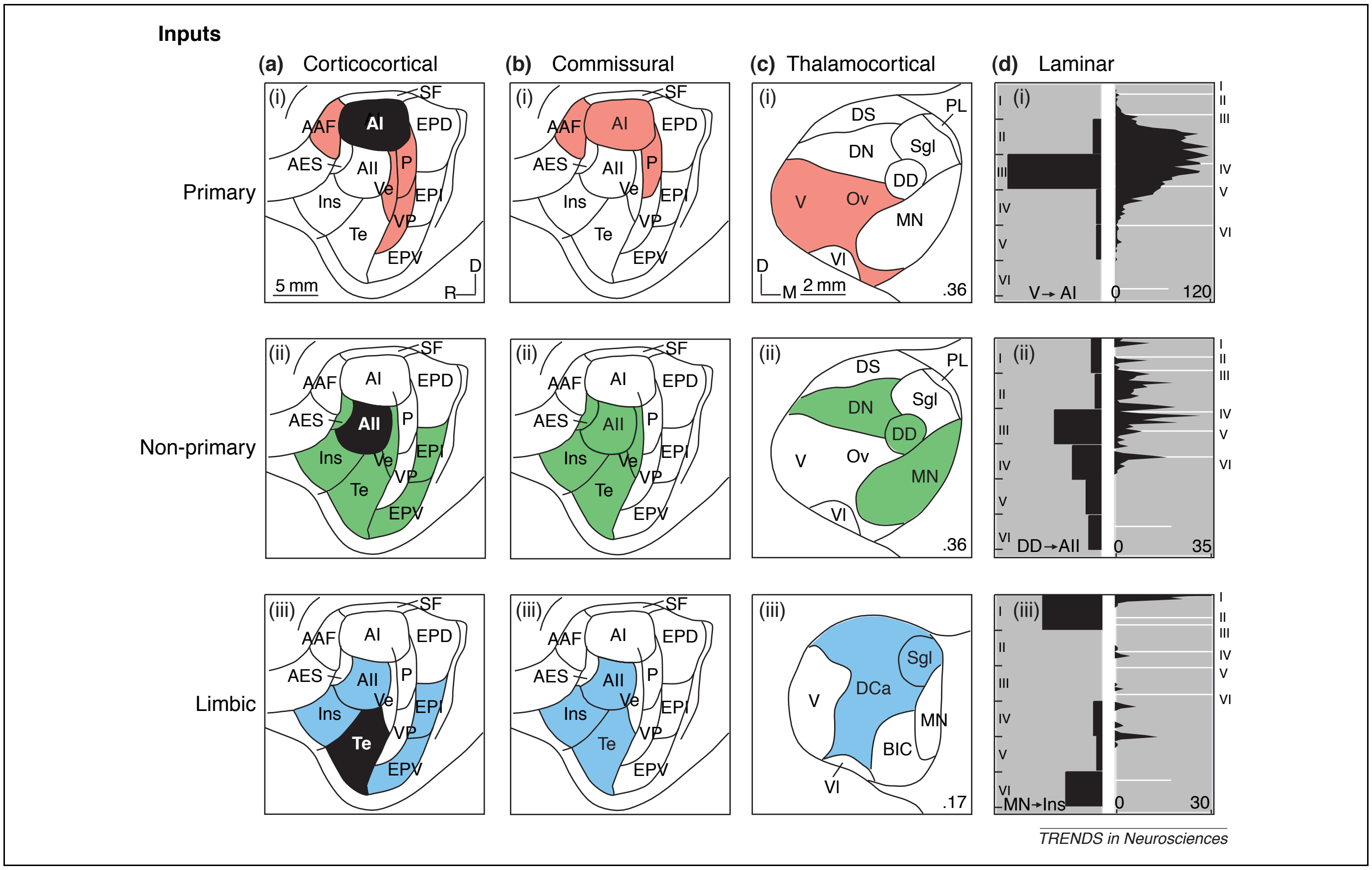

Figure 1. Principal inputs to cat auditory cortex. **(a)** Tracer deposits are shown in black; chief afferents for primary areas are in red, those for non-primary areas are in green, and those for limbic areas are in blue. (i) Corticocortical projections to the primary auditory area (AI) arise from adjoining primary areas, whereas those to the second auditory area AII (ii) and limbic-related cortex (Te) (iii) are mainly from non-tonotopic auditory cortex. **(b)** Commissural afferents follow a similar pattern, with primary afferents in red, non-primary afferents in green and limbic afferents in blue. **(c)** Thalamocortical afferents. Primary medial geniculate body (MGB) afferents are shown in red, non-primary in green and limbic-related in blue. **(d)** Laminar bouton distributions are depicted in two ways: as the percentage of the total number of boutons within a layer in a vertical traverse (left) and as the absolute number of boutons in horizontal bins 50 μm wide, perpendicular to the thickness of the layer and revealing fine-grained sublaminar peaks and valleys at right angles to modular organization (right). Thalamic afferents from the ventral MGB (c,i) concentrate in layers III–IV (d,i), those from deep dorsal nucleus (c,ii) project more broadly (d,ii), and the medial division and caudal dorsal nuclei (c,iii) boutons end mainly in layers I and VI (d,iii). Numbers in lower right in (c) are the percentage distance from the caudal pole. Abbreviations: AAF, anterior auditory field; AES, anterior ectosylvian sulcus; BIC, brachium of the inferior colliculus; D, dorsal; DCa, caudal nucleus of the dorsal division; DN, dorsal nucleus; DD, deep dorsal nucleus; DS, superficial dorsal nucleus; EPD, EPI, EPV, dorsal, intermediate, and ventral parts, respectively, of the posterior ectosylvian gyrus; Ins, insular area; M, medial; MN, medial division of the MGB; Ov, pars ovoidea of the ventral MGB; P, posterior auditory area; PL, posterior limitans nucleus; R, rostral; SF, suprasylvian fringe; Sgl, suprageniculate nucleus; V, ventral division of the MGB; Ve, ventral auditory area; Vl, ventrolateral nucleus; VP, ventroposterior area.

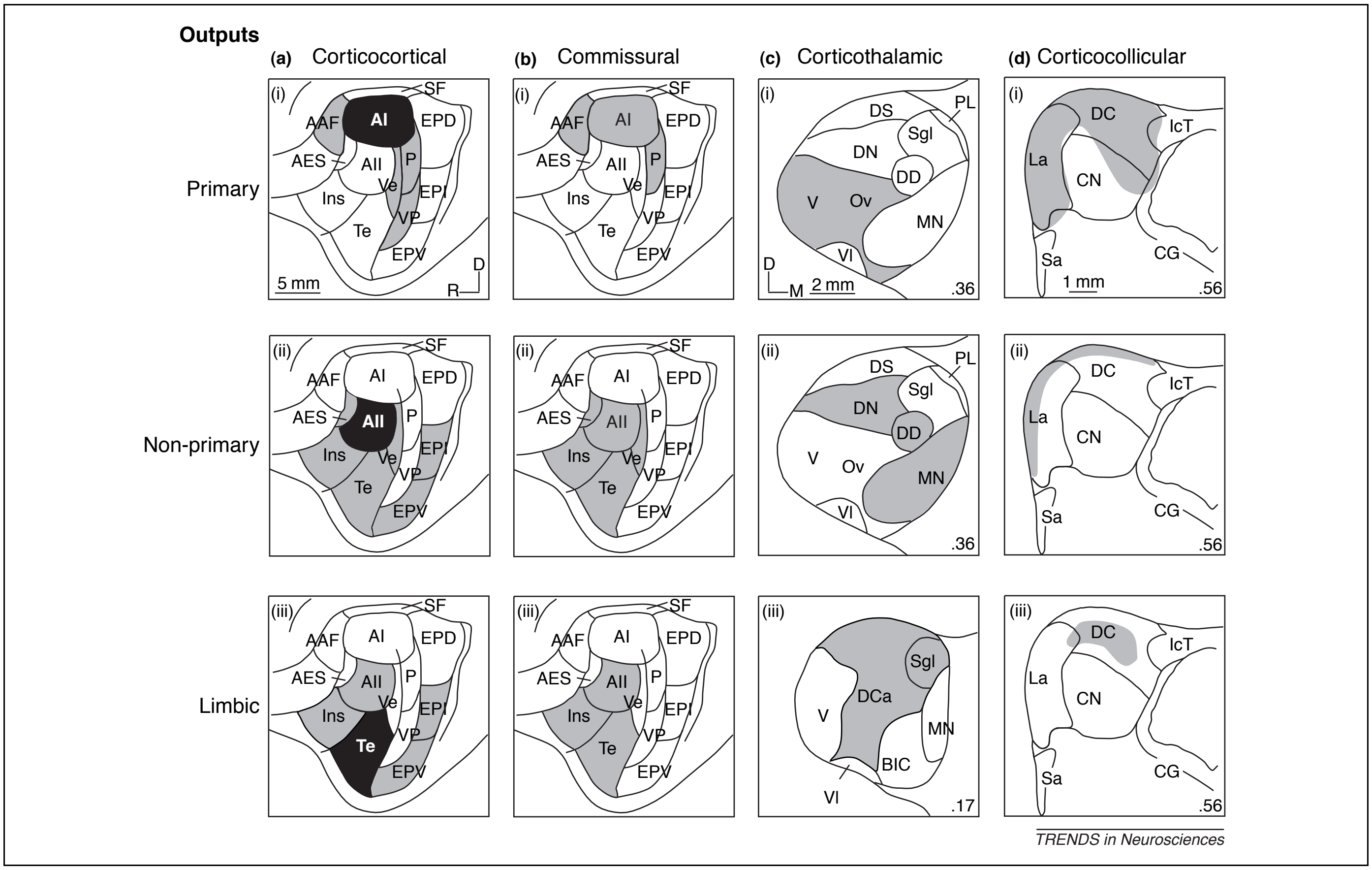

Figure 2. Principal outputs to cat auditory cortex. Tracer deposit sites are in black and targets are in gray. **(a)** Corticocortical targets. **(b)** Commissural targets. **(c)** Corticothalamic targets. **(d)** Corticocollicular targets. Corticocortical projections (a) resemble their input patterns (Figure 1a), as do their commissural targets (b). Corticothalamic projections (c) are likewise segregated in primary (i), non-primary (ii), and limbic (iii) cortical and thalamic territories. By contrast, the corticocollicular projection is strongest outside the lemniscal central nucleus (CN) (d), suggesting a corticothalamic–corticocollicular disjunction. Differential area-specific inputs to the lateral nucleus (LN) (i,ii) and dorsal cortex (DC) (ii,iii) suggest that corticocollicular projections are as topographic and nucleus-specific as their thalamocortical counterparts (c,i). Numbers in lower right in (c,d) are the percentage distance from the caudal pole. Abbreviations as in Figure 1. Additional abbreviations: CG, central gray; DC, dorsal cortex; IcT, intercollicular tegmentum; La, lateral nucleus; Sa, sagulum.

segregation, with each nucleus projecting to multiple laminae in several areas [15]. Thus, axons from MGBv (Figure 2c,i) cluster chiefly in deep layers III and IV (Figure 1d,i), perhaps imparting a driving role [29] onto auditory cortex. They also terminate in layer V, presumably activating intracortical branches and influencing midbrain [30] and thalamic [31] operations. Projections from the dorsal division of the MGB (Figure 1c,ii) are less dense and involve more layers – I, II, V and VI (Figure 1d,ii) – perhaps influencing intracortical feedforward [32] and corticocollicular [33] systems. Finally, projections from the medial division of the MGB (Figure 1c,ii) target layers I and VI principally (Figure 1d,iii), perhaps influencing local circuits [34]. Input to each layer also has an intricate sublaminar distribution (Figure 1d, right) of unknown significance.

These projection patterns argue for further stream segregation in cat auditory cortex, suggesting that primary areas [AI, the anterior auditory field (AAF), the posterior auditory area, the ventral auditory area and the ventroposterior auditory area] are concerned chiefly with spectral and binaural processing [35–37], whereas non-tonotopic areas (the second auditory cortical area and the suprasylvian fringe) have broader tuning curves and duration tuning [38,39], consistent with a role in processing communication signals and non-spectral stimuli [40]. By contrast, limbic-related fields (insular and limbic-related temporal areas) receive polymodal input and link auditory and visceral processes [41,42]. The posterior ectosylvian fields (dorsal, intermediate and ventral parts of the posterior ectosylvian gyrus) interface between audition and vision [43], sharing multisensory thalamic [44] input. Thus, functional subregions of auditory cortex span a continuum, from those specializing in spectrotemporal analysis (primary areas), through those responsible for polymodal integration (non-primary areas) or behavioral repertoire (limbic areas) (Figure 2a,b), to multisensory subregions.

How are the several independent representations of characteristic frequency in auditory cortex achieved? Do they merely propagate along independent tonotopic brain stem channels [45] or do they reflect forebrain convergence and computation? The five cat tonotopic auditory cortical areas [46] might represent different thalamic channels, or branched thalamocortical axons contributing to several MGB frequency maps [47–49]. To investigate this, characteristic frequencies were mapped in AI and AAF and the areas were injected with a different retrograde tracer, at the same frequency in each area. Labeled thalamic and auditory cortical cells formed overlapping, independent topographic arrays, with $<2\%$ double-labeled, confirming parallel spectral streams. Interestingly, 15–35% of the neurons lay outside their predicted thalamic and cortical isofrequency domain, up to several millimeters from their expected position [50]. Perhaps contributions from remote characteristic frequencies influence the various thalamocortical transformations and represent parallel spectral streams in these areas [51], suggesting analogies to X-cell and Y-cell systems, which conserve independent retinal channels in visual cortex [52].

Descending pathways: parallel corticothalamic channels for executive control

Do corticothalamic signals instruct or have advisory and feedback roles? Cooling or inactivating cortex strongly affects thalamic excitability [31], receptive field (RF) structure [53] and oscillations [54]. This influences serial and parallel processing and distinguishes them from the thalamus, despite their reciprocal connections. The classical view of the corticothalamic system [55] was that it was reciprocal to thalamic input. Recent results suggest that this is an oversimplification.

The newer perspective recognizes that some thalamic nuclei do not receive input from their cortical targets [56] and that some cortical regions project beyond thalamic regions that terminate in them [57]. This non-reciprocity [58] suggests functional asymmetry in these pathways. Each scenario entails more than purely reciprocal relationships, and they imply multiple, independent corticothalamic pathways (Figure 2c).

The classical view of the corticothalamic pathway emphasizes its layer VI origin. Other studies reveal that the deepest one-third of layer V is equally involved, with smaller, discontinuous projections from superficial layer V [33,46]. The middle parts of layer V project to the inferior colliculus [59], suggesting complementary corticothalamic and corticocollicular roles.

Another opportunity for cortical–thalamic interactions involves the giant axonal endings from the auditory cortex [60,61], which congregate in thalamic nuclei containing massive GABAergic boutons of local [62], inferior collicular [63] or thalamic reticular nuclear [64] origin. Because many corticothalamic axons are slender and their terminals are smaller than the GABAergic boutons, there might be complementary slow-conducting and fast-conducting streams [57] parallel to the ascending thalamic pathways, and perhaps analogous to drivers and modulators [24].

Functional thalamocortical transformation: rules of cell-to-cell connectivity

A brain stem representation based on acoustic features must be transformed into a representation of the auditory scene that is suitable for interpretation and action. In particular, the ensuing signals, distributed broadly to cortical and subcortical sites, must confer meaning to the complex sounds, unimpeded by the dynamic nature of any acoustic scene, and must prepare biologically appropriate communication and social responses. Such processing is reflected in the robust maps in bat auditory cortex that serve object-specific analyses [65] and suggest the emergence of cortical processes that are either directly object-related [8] or embody processing stages and streams dedicated to specific object features [40,65,66]. How is such a change in processing functionally reflected at the thalamocortical interface?

Despite the analytical advantage of independent, spatially segregated processing stations, few studies have considered the response transformations between individual thalamic and cortical cells [67–72]. Most comparisons rely on group statistics, a powerful tool if the populations are homogeneous or the functional changes are dramatic. Unlike the visual system, neither of these conditions is fulfilled in the auditory thalamocortical system. The RF properties of neither MGB nor AI are homogeneously distributed, nor do these RFs differ dramatically [73]. Consequently, the role and mechanisms of thalamocortical transformation remain unknown.

Simultaneous recording from anatomically connected source and target neurons reveals mechanisms for internuclear transformations. Knowledge of RF attributes is central to their specific signal processing roles. Thus, RFs commonly define and map cortical neural activity into a parametric acoustic feature space that reflects the stimulus or variables for specific auditory tasks [74] or for object attributes (e.g. location or movement) [66]. This reveals single-cell processing capacities and, by comparing the RFs of connected pairs of neurons, the input-to-output transformation. Direct comparisons between auditory thalamic and cortical RF properties reveal types of functional convergence underlying the response, and the transformation of these RFs at the thalamocortical synapse [75–77].

A synthetic, spectrotemporally complex stimulus, the dynamic ripple, shares many properties with natural sounds [78,79] and satisfies formal requirements for deriving spectral–temporal RFs (STRFs) through reverse correlation (Box 1). The dynamic ripple stimulus enables an integrated description of temporal and spectral neural response preferences [80].

Simultaneous single-unit recordings in MGBv and AI, combined with cross-correlation analysis, permit direct comparison of thalamic and cortical RF properties under identical experimental conditions. Comparing MGB and AI STRFs reveals three types of input convergence (Box 2). (i) ‘Inheritance’ occurs when the STRF of a cortical cell is completely determined by thalamic input. Because the RF faithfully reflects thalamic input, opportunities for further processing are preserved. (ii) ‘Constructive convergence’ integrates several thalamic inputs with smaller RFs, in frequency and/or time – a convergence-by-union. It can create selectivity for composite features, such as speech formant combinations or visual oriented lines. (iii) In ‘ensemble convergence’, the thalamic inputs extend beyond the cortical RF domain. This convergence-by-intersection requires cell ensembles that cooperate either to amplify cortical RF regions that are ultimately represented, or to suppress regions that are not. Such cooperation enables more exacting feature selectivity, as for example in the combination sensitivity of bat cortical cells that respond only to specific frequency ratios between biosonar harmonics and their echoes [65]. Convergence

Box 1. Reverse correlation and spectrotemporal receptive fields

Understanding neural function relies on assumptions and biases inherent to methods. When the sensory function of a neuron is unknown, an efficient approach is to make as few assumptions as possible and to explore the largest universe of stimulus attributes in an unbiased way. The reverse correlation technique embodies this principle.

Reverse correlation with action potentials selectively averages some continuous descriptor of stimulus attributes (Figure I of this box). When an action potential occurs, one searches retrospectively ('reverse') for stimulus features that might have elicited it ('corre-correlation'). In the auditory system, many perceptually relevant attributes are captured by the spectrogram, a continuous representation of stimulus energy across time and frequency. Reverse correlation between neural action potentials and the stimulus spectrogram reveals stimulus features that consistently evoke or prevent activity: positive regions denote excitatory features and negative regions indicate inhibitory features. Only stimulus attributes with consistent effects will constructively sum during the averaging process to yield a spectrotemporal receptive field (STRF) [80].

The STRF is a time–frequency representation of neural preferences or filter properties, with unique size, shape and spacing of its excitatory and inhibitory subregions for each neuron. Furthermore, the two-dimensional Fourier transform of an STRF yields a complementary depiction highlighting modulation transfer functions (MTFs) for spectral and temporal stimulus envelopes. These two-dimensional depictions are ripple transfer functions (RTFs). Functionally, temporal and spectral modulations are essential for discriminating complex auditory signals. In speech, for instance, spectral modulations distinguish vowels (e.g. 'eeh' and 'ooh') differing in the spacing of their spectral peaks or formants, and temporal modulations distinguish consonants (e.g. 'buh' and 'puh'). The RTF characterizes neural sensitivity to such distinctions. Reverse correlation is theoretically sound, easy to implement, and widely applicable in the auditory system and in other modalities [70,72]. It requires few assumptions yet provides detailed information about how neurons represent the world. The STRF and its relatives thus remain among our richest unbiased, linear descriptors of neural function.

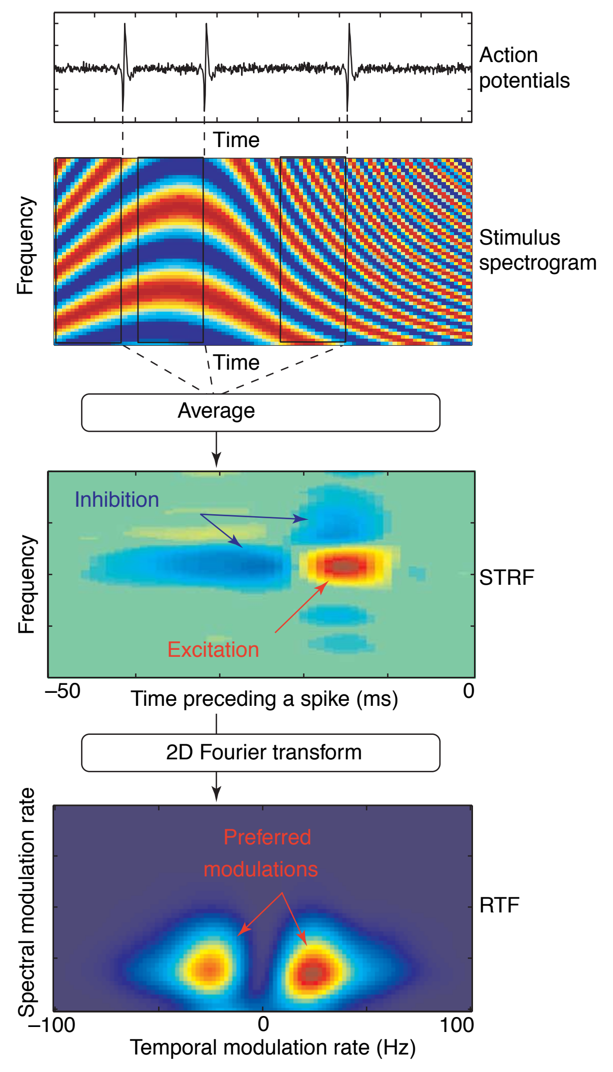

Figure I. Reverse correlation and spectrotemporal receptive fields. The spectrotemporal receptive field (STRF) is created by averaging portions of the stimulus spectrogram preceding each action potential. Positive STRF regions indicate excitatory sound features and negative regions indicate inhibitory features. A complementary depiction, the ripple transfer function (RTF), results from the two-dimensional Fourier transform of the STRF. The RTF highlights the rate of energy fluctuations, in frequency and in time, that strongly affect neural firing. Modified, with permission, from Ref. [76].

types define the space delimited by the three extremes of inheritance, construction convergence and ensemble convergence; some of these convergence types are absent in the visual system, where most thalamocortical connections respect a Hubel–Wiesel type of constructive convergence model [68,70,81].

Functional thalamocortical transformation: spectrotemporal specificity

Thalamocortical STRF specificity is highly focal, spectrally and temporally. Such specific coupling also occurs between the lateral geniculate nucleus and primary visual cortex [68,70,72], suggesting that functional thalamocortical convergence in any modality is precise. In cat hearing, excitatory thalamocortical convergence is constrained to within approximately one-third of an octave [75] or a single critical band, the benchmark psychophysical measure for cross-frequency integration [82].

The prevalence of functional connectivity is strictly determined by tonotopy and overall thalamocortical STRF similarity. Resembling the spatial overlap in the visual system [72], ∼30% of pairs with the same best frequency are functionally connected. The distribution of spectral RF properties between thalamus and cortex, such as excitatory bandwidth or preferred spectral maxima spacing, are very similar [76]. However, connected thalamic and cortical neurons do not correlate well in their broadband spectral properties, such as preferred spectral peak spacing [76]. Temporal response properties differ more systematically between thalamus and cortex. Cortical onset latency is slightly longer owing to axonal and synaptic delay in all modalities [67–70,83,84]. However, the response timing distributions overlap highly. Thus, although the thalamus responds first, it and the cortex are simultaneously active for much of their response, allowing ample opportunity for corticothalamic, or even cortico–colliculo–thalamic, feedback to shape responses at each level [4,31,85–88].

A characteristic difference is that cortical cells respond with precisely timed spikes only to slower temporal

Box 2. Thalamocortical correlation and functional convergence

Sensory neurophysiology has been guided by the question of how individual cells represent the external world. Such representations inform us which ecological functions might be relevant but they shed little light on how the brain constructs and transforms representations through its neural networks. As for any highly parallel machine, the rules of functional connectivity among cells are essential for understanding system-level function.

Most neurons receive converging input from hundreds or thousands of other cells in many different areas. Ideally, recording from all inputs to a neuron would reveal how representations are transformed and transmitted. However, the most powerful techniques available are limited to recording from a target cell plus one or a few of its inputs. The strength and timing of functional coupling is assessed with cross-correlation of action potentials, and the representational roles of neurons can be derived using reverse correlation (Box 1) or analogous methods. The sensory thalamocortical system is ideal for this approach because its basic stimulus preferences and its anatomical connectivity are known in some detail. By comparing the information contributed by input cells with the output of the target cell, rules of functional convergence can be derived.

One way to conceptualize functional convergence is using a heuristic that delineates extreme possibilities of convergence type [75]. In Figure I of this box, colored shapes represent features of a receptive field (RF). The simplest form of functional convergence is inheritance, where the features of a target cell are functionally identical to those of its inputs. Such convergence enables precise representation and the faithful propagation of information to subsequent processing stages. In constructive convergence, the RF of the target cell integrates many smaller, heterogeneous inputs, thereby creating selectivity for emergent features such as formant combinations or oriented lines. Ensemble convergence requires cooperative inputs to amplify some parts of the input and/or suppress others, supporting more exacting feature selectivity than at lower processing levels. In the auditory thalamocortical system, all three convergence types and combinations occur, representing a complex computational network to transform different aspects of sensory representations.

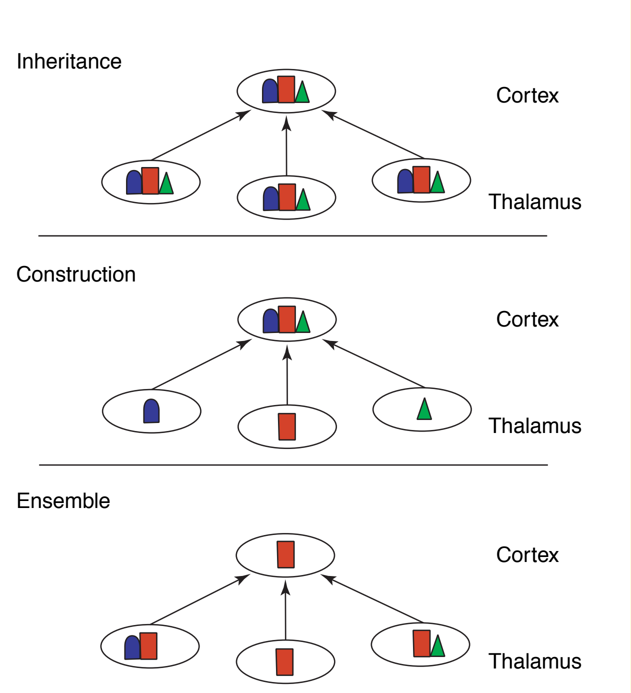

Figure I. Thalamocortical correlation and types of functional convergence. Varieties of functional convergence can be conceptualized as a combination of three possible extremes: inheritance, constructive convergence and ensemble convergence. Modified, with permission, from Ref. [75].

modulation rates [67]. The effective cortical filter for envelope modulations or repetitive signal elements is about half as fast as that for the thalamus (Figure 3) [76]. A few cortical neurons can respond to stimuli with high modulation or repetition rates, although not in a phase-locked manner [89,90].

The thalamocortical transformation of temporal response properties suggests that temporal waveform modulations are represented differently. Connected thalamocortical cell pairs show no rank correlation between preferred modulation frequencies of thalamic inputs and cortical targets: for example, fast thalamic cells do not contribute preferentially to fast cortical cells, nor slow to slow [84] (Figure 3). Therefore, the thalamocortical temporal transformation is not a uniform reduction in rate, which is incompatible with a simple relay role.

The reduction in cortical following rate does not reflect limitations in the timing precision of cortical networks [91]. Cortical plasticity induced by behavioral temporal discrimination training [92] or by nucleus basalis stimulation [93,94] can modulate the preferred cortical rates to values approximating normal thalamic modulation transfer functions. Therefore, the thalamocortical temporal response transformation probably has a specific purpose, such as the perceptual saliency of the lower range of temporal modulations in vocalizations and speech [95,96], which could depend on a preferred cortical representation of lower modulation frequencies. This suggests substantial reconstruction of spectral and temporal modulation properties from MGB to AI in a rigid spectral framework. It shows how some properties are propagated precisely whereas others are significantly transformed or created intracortically. Thalamocortical processing is thus still largely a local, differentiating analysis, rather than a global, integrative one. The precise role of this informational recoding and remapping is unclear. The computed entities probably serve several central processing tasks: (i) allowing construction of a global representation of the acoustic world; (ii) enabling analytical determination of object features such as form, texture and position; (iii) engendering more reliable and stabilized feature representation in the intensity domain and contrast invariance of orientation tuning in the visual cortex, or in maintained response properties of some auditory neurons operating in background noise; (iv) allowing subsequent multi-sensory integration; and (v) permitting the assignment of significance to particular environmental constellations and, ultimately, the emergence of unique perceptual attributes that trigger behavior. Such tasks might take place beyond the primary sensory field.

The features of thalamocortical RF transformations outlined here are likely to be valid only for first-order excitatory cortical cells. Feedforward transformations might differ substantially for inhibitory neurons because

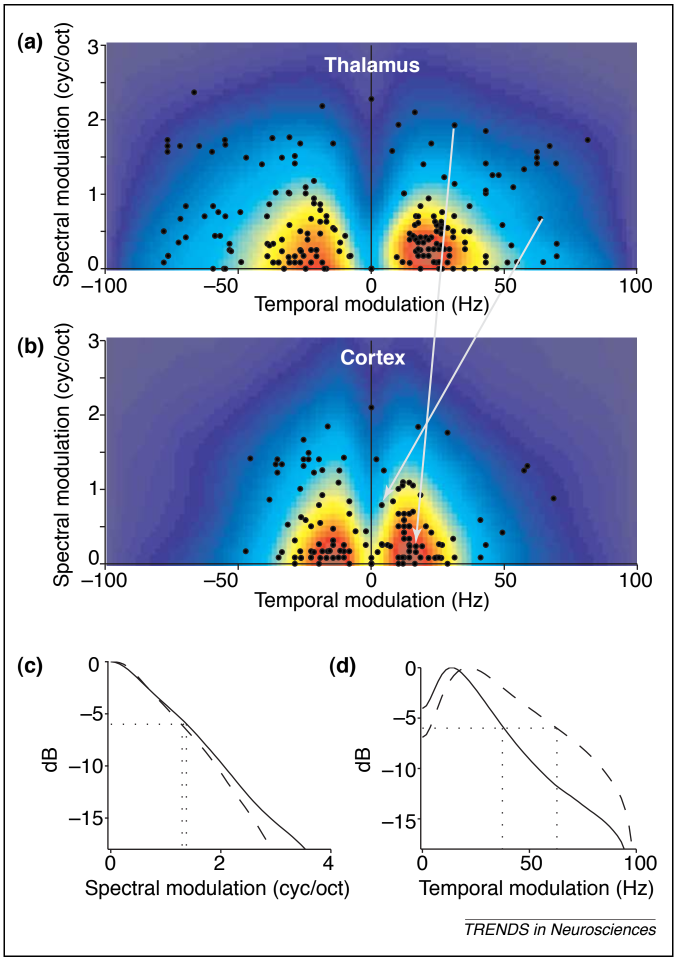

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Figure 3. Spectral–temporal preference of thalamic and cortical auditory neurons. **(a)** Joint spectrotemporal thalamic response properties of the ventral nucleus of the medial geniculate body (MGBv). Color depicts the overall filtering capability of the MGBv preferences from blue to red; points represent preferred modulation parameters for individual neurons. Positive and negative temporal modulation rates designate, respectively, downward and upward spectral features. Note the lack of correlation between spectral and temporal preferences. **(b)** Joint spectrotemporal response properties of primary auditory cortex (AI). Arrows indicate examples of connected thalamocortical neuron pairs as suggested by high cross-correlation. There is no rank-correlation between preferred thalamic and cortical values of connected neurons for either temporal or spectral modulation. **(c)** Composite spectral modulation transfer function (MTF) for MGBv (broken line) and AI (solid line). The plots overlap, indicating that thalamic and cortical cells encode spectral stimulus fluctuations over the same range. **(d)** Composite temporal MTF for MGBv (broken line) and AI (solid line). The plots are offset, indicating that thalamic neurons encode temporal stimulus fluctuations at about twice the rate of cortical cells. Modified, with permission, from Ref. [76].

work in the somatosensory cortex finds unselective, highly divergent and convergent functional networks shaping the RFs of putative inhibitory interneurons [97]. Other transformation processes arise from the two dynamic thalamocortical system states. A quiescent state embodies bursting cell activity, global synchronous oscillations, and presynaptic depression and recurrent inhibition that lead to low-pass sensory information filtering and rapid adaptation [98]. The activated state reflects tonic cell activity, reduced or absent global oscillations, and low-pass filter broadening. The information throughput is profoundly affected by these state-differences [99]. How does this affect the thalamocortical transformation characteristics? As noted, the types of transformation were derived from responses to broad-band, dynamic stimuli. Such stimulation disrupts global oscillatory processes and the resulting neural behavior resembles that in the activated (tonic or alert) state, even though the experiments were in anesthetized preparations [84]. This stimulus-induced state provides a unique opportunity to assess receptive field properties and their transformation under controlled dynamic state conditions.

Concluding remarks

Several types of thalamocortical convergence in AI create distinct streams for cortical sound representation. Construction, inheritance and ensemble coding probably embody parallel transformation streams that create rich analytical substrates for sound representation. Structurally, a much more refined and complex picture of feedforward and feedback connections is emerging. A synthesis of thalamocortical connections and the functional types of input transformation will require integrated electrophysiological and neuroanatomical approaches. Auditory cortex might be concerned less with the representation of specific auditory attributes (a task that we suggest is largely completed in the brain stem) and more with the conjunction and coordination of acoustic, multisensory and limbic frames of reference, each contributing globally to auditory behavior and communication. Ultimately, any 'systems' approach to forebrain auditory performance must include midbrain structures (Figure 2j–l) that concurrently target the MGB and the cochlear nuclei. Such reciprocal and feedforward relationships are absent in the visual and somatic sensory systems and support the idea that there are unique auditory processing schemes.

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