Published in final edited form as:

Hear Res. 2011 April ; 274(1-2): 85–94. doi:10.1016/j.heares.2010.05.008.

Convergence of Thalamic and Cortical Pathways in Cat Auditory Cortex

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Abstract

Cat auditory cortex (AC) receives input from many thalamic nuclei and cortical areas. Previous connectional studies often focused on one connectional system in isolation, limiting perspectives on AC computational processes. Here we review the convergent thalamic, commissural, and corticocortical projections to thirteen AC areas in the cat. Each input differs in strength and may thus serve unique roles. We compared the convergent intrinsic and extrinsic input to each area quantitatively. The intrinsic input was almost half the total. Among extrinsic projections, ipsilateral cortical sources contributed 75%, thalamic input contributed 15%, and contralateral sources contributed 10%. The patterns of distribution support the division of AC areas into families of tonotopic, non-tonotopic, multisensory, and limbic-related areas, each with convergent input arising primarily from within its group. The connections within these areal families suggest a form of processing in which convergence of input to an area could enable new forms of integration. In contrast, the lateral connections between families could subserve integration between categorical representations, allowing otherwise independent streams to communicate and thereby coordinating operations over wide spatial and functional scales. These patterns of serial and interfamilial cooperation challenge more classical models of organization that underestimate the diversity and complexity of AC connectivity.

Keywords

divergence; convergence; nuclear; areal; thalamus; cortex

Introduction

Studies of auditory cortex connections have typically focused on one source of input (e.g. thalamocortical, corticocortical) and a few, usually primary areas (e.g. AI, AAF), and so do not address the relationships between systems or the principles governing connectivity in areas outside primary auditory cortex. In the cat auditory cortex, no model available has placed cortical functions within a conceptual framework that incorporates data from all thirteen areas and all major projection systems. Such a holistic model would have important

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implications for understanding how the arrangements in rodent (Stiebler et al., 1997), primate (Hackett et al., 1998), and human (Woods and Alain, 2009) auditory cortex embody shared and unique elements, and is also significant for visual (Zeki, 1993) and somatic sensory (Kaas, 2008) cortex. In our studies of the connections of cat auditory cortex (Lee and Winer, 2008a, b, c), our goal was to establish such a dataset to enable the development of connectionist principles pertinent to neocortical organization as a whole.

In our studies, we employed several strategies to systematically survey auditory cortex connectivity. First, we analyzed thalamocortical (Lee and Winer, 2008a), commissural (Lee and Winer, 2008b), and corticocortical (Lee and Winer, 2008c) connections to all known areas of cat auditory cortex; in doing so, we found many new connections. Second, we used the most sensitive tracers available (Basbaum and Menetrey, 1987; Llewellyn-Smith et al., 1990; Luppi et al., 1990), tracers capable of revealing minute connections; this demonstrated different patterns of connections than we and others have seen using less sensitive tracers. Third, the use of multiple tracers in tandem allowed us to derive topographic rules of projection for every area (Lee and Winer, 2005); unexpectedly, we found a common set of topographic principles that linked all areas and each projection (Schreiner and Winer, 2007). Fourth, we considered the laminar origins of all projections and found area-specific patterns (Lee and Winer, 2008c). Fifth, the multiple tracer approach allowed us to determine how many thalamic and cortical cells have axons that branch to more than one area (Kishan et al., 2008; Lee et al., 2004a, b), and revealed a pattern at odds with those in the visual cortex (Bullier et al., 1984). Sixth, in addressing the question of why so many areas exist in auditory cortex, we found that small suites of areas are more densely interconnected than others, and may constitute connectionist families and regional subsystems for auditory, limbic, and multisensory processing. Seventh, in each connectional study we found that 15–35% of connections were in topographically unpredicted loci (Lee et al., 2004b; Lee and Winer, 2008a, b, c); this finding could have important implications for frequency-specific plasticity in map organization (Winer et al., 2005). Finally, our approach was semiquantitative, allowing us to estimate the relative strength of thalamic nuclear and cortical areal contributions in each projection; we found striking areal differences in the relative proportion of these inputs.

Here we present a review of the convergent thalamic (Lee and Winer, 2008a), ipsilateral cortical (Lee and Winer, 2008c) and commissural (Lee and Winer, 2008b) input to each of the thirteen AC areas of the cat, revealed with cholera toxin beta subunit (CT β) or a gold bound conjugate (CT β G) to label the origins of projections to each area. The results were quantified to produce a more complete profile of differential thalamic and cortical contributions to AC and to enable comparisons between them.

Assessing Convergent Inputs

To demonstrate how areal convergence was assessed for each of the 13 areas in cat auditory cortex (AC), a representative example with injections in the primary (AI) and secondary (AII) auditory cortical areas (Fig. 1B,C:3) is shown. The ensuing thalamic and AC retrograde labeling was plotted (Fig. 2), and the nuclear and areal boundaries determined in adjacent sections prepared for cytoarchitectonic analysis (see Fig. 3 in Lee and Winer, 2008a, and Fig. 2 in Lee and Winer, 2008b). AI and AII injections elicited different and equally specific patterns of segregated MGB and AC labeling, with AI receiving most of its input from other tonotopic nuclei (V, Ov) (Fig. 2C-E) and cortical areas (AAF, P, VP, Ve) (Fig. 2A-B), while AII was targeted principally by non-tonotopic nuclei (Fig. 2C-E: D, DD, Sl, M) and areas (Fig. 2A-B: AES, ED, EI, Te, In).

Labeled neurons were counted and the distribution divided into intrinsic (within the injected area) or extrinsic thalamic (Fig. 2C-E), ipsilateral (Fig. 2A), and contralateral (Fig. 2B) cortical compartments. Intrinsic projections represent ~50% of the total input in both areas (Table 1), and were clustered anisotropically along the isofrequency contour in AI (Fig. 2A) (Lee and Winer, 2008c), in agreement with the modular physiological organization along this axis (Read et al., 2001). Of the remaining 50% from extrinsic sources, ipsilateral AC sources contributed ~70% (or ~35% of the total combined input) to both areas (Fig. 2F). The thalamic and contralateral inputs were almost an order of magnitude smaller, each contributing about 10% of the extrinsic input (~5% of the total combined input) (Fig. 2F).

On a finer scale, the topographic segregation of input to AI and AII was reflected in their numerical labeling profiles. Thus, AI receives extrinsic input preferentially from tonotopic areas AAF (15%), P (10%), and VP (16%), while AII projections have multisensory (ED: 14%; EI: 10%) and limbic-related (In: 7%) origins (Fig. 2F). Other fields, such as Ve, have nearly equal contribution to both areas (Fig. 3). AI receives its chief MGB input from the ventral division (V; 12%), whereas AII has many more and fewer dorsal division sources (D, DD, DCa; 5%). The contralateral AC has the most stereotyped projections, with >50% from homotypic areas, e.g. AI to AI, AII to AII, etc. This profile reveals that AI and AII receive convergent projections from largely segregated sources, that a few thalamic and cortical inputs are common to each area, that double labeled neurons are rare (Kishan et al., 2008), and that the familial and functional affiliations of areas are consistent with this connectional result. Many of these features of convergent projections to AI and AII are common to the other auditory cortical areas. Below we review these features of convergent inputs from intrinsic and extrinsic sources.

Intrinsic Cortical Projections

In all auditory areas, approximately half of the total input to an area originates from intrinsic cortical sources (Table 1). Topographically, the intrinsic input is distributed <2 mm from the injection sites and densely clustered across all cortical layers (excluding layer I) (Fig. 2A) (Imaizumi et al., 2004; Lee and Winer, 2008c). Among all auditory areas, AES receives the greatest intrinsic input (71%) and Te and Ve have the fewest (37%) (Table 1). However, there is no correlation of input size with anatomical location or functional type ($p>0.05$, ANOVA, $df=2$; Table 3). For example, tonotopic regions have both greater (e.g., AAF) and fewer (e.g., Ve) than average proportions of intrinsic input (Table 1).

Extrinsic Projections

Thalamocortical Contribution

Thalamic input to each area averages ~15% of all extrinsic input (Table 2). Insular cortex (In) receives the strongest thalamic input (24%) and AES the weakest (4%) (Table 2; Fig 3: red), and is independent of either the functional group or anatomical arrangement ($p>0.05$, ANOVA; Table 3; Fig. 3). For example, anatomically remote and functionally unrelated fields (AES: 5% and EV: 7%) receive comparable proportions of input, while functionally related fields have greater (AI: 18%; Ve: 17%) and fewer (P: 9%; AAF: 11%, VP: 11%) than average proportions of thalamic input (Table 2; Fig. 3). The major thalamic input to each area links those with similar functional affiliations, e.g. tonotopic, non-tonotopic, multisensory, and limbic (Fig. 6F-H). Input from functionally dissimilar nuclei provides lesser contributions, e.g. DZ receives projections from non-tonotopic nuclei (D, DD) and from the tonotopic rostral pole nucleus (RP) (Lee and Winer, 2008a).

Corticocortical Contribution

The dominant input to a cortical area is provided by the corticocortical projections (~75%) (Table 2). The three major ipsilateral inputs to an area contribute about half of the total, but these are not always equally distributed. For instance, some areas such as VP (14%: tonotopic), DZ (15%: non-tonotopic), and Te (16%: limbic) receive similarly weighted inputs from their three principal ipsilateral AC sources (Figs. 5C,H, 5A), while others, such as AAF and In, have one dominant input (Figs. 5B, 5E), e.g. area In receives ~28% of its ipsilateral input from Te, and <10% from the next strongest sources (ED: 9%; AES: 7%) (Fig. 5E). Among the areal groups, tonotopic areas are the most preferentially interconnected (Fig. 5A-E). Limbic and multisensory regions have more variable input (Fig. 6A-E), while the non-tonotopic areas receive the widest range of tonotopic, multisensory, and limbic input (Fig. 5F-H), suggesting that they link these three systems.

The numerous corticocortical projections can be used to order auditory areas hierarchically based on the laminar origins of the projections (Felleman and Van Essen, 1991; Hackett, 2010; Lee and Winer, 2008c; Rouiller et al., 1991). Such an analysis results in an eight-stage hierarchy, with the primary auditory cortex (AI) and the anterior auditory field (AAF) at the base and the parahippocampal regions (35/36) at the apex (Fig. 4), respectively (Lee and Winer, 2008c). Such a hierarchical model is consistent with known physiological properties. For example, the complex tuning curves in AII (Schreiner and Cynader, 1984) suggest a higher position than AI or AAF (Carrasco and Lomber, 2009, 2010), whose frequency tuning is sharper (Phillips and Irvine, 1981, 1982). Areas such as AES exhibit multimodal properties (Clarey and Irvine, 1990; Krueger et al., 2009; Meredith and Allman, 2009), consistent with an even higher position in the cortical hierarchy. The limbic and parahippocampal areas occupy the highest positions, consistent with their roles in cognitive, affective and memory processes (Squire et al., 2004).

Commissural Contribution

The commissural input provides ~10% of the total extrinsic input (Table 2), and is independent of functional group ($p>0.05$, ANOVA; Table 3), with tonotopic (9%), non-tonotopic (9%), multisensory (8%), and limbic (7%) areas each receiving similar proportions of input. Area P has the largest (13%) and VP has the smallest (5%) commissural input (Fig. 3). Each area receives its major contralateral input from the homotypic area (Fig. 3: red shade; 5, 6), which is more than half of the total commissural contribution (Lee and Winer, 2008b), and averages 6% (range: 3-11%) of the total extrinsic input, but half the size of the major ipsilateral cortical inputs (Table 2; Figs. 5-6). The remaining (<1%) of commissural input arises from heterotypic sources (Fig. 3), which are generally from functionally related areas (Figs. 5,6), and mirrored many of the same areal sources as the main ipsilateral cortical inputs (Fig. 3) (Lee and Winer, 2008b).

Convergence in auditory cortex

Comparing the relative contributions of thalamic (Lee and Winer, 2008a), ipsilateral (Lee and Winer, 2008c), and contralateral (Lee and Winer, 2008b) projections to each of the thirteen areas in the auditory cortex of the cat, intrinsic projections provide by far the greatest input, contributing nearly half of the total input. The remaining half is provided by extrinsic sources from thalamic and cortical sources, of which the ipsilateral cortical input dominates, providing nearly an order of magnitude greater input than thalamic and contralateral cortical sources.

The robustness of the intrinsic connections supports the idea that these connections play a crucial role in the processing of auditory information (Atencio et al., 2009; Binzegger et al., 2004; Schreiner et al., 2000; Tan et al., 2007; Zhou et al., 2010), which is area specific, since

the relative weights of intracortical connections vary. Such areal differences imply specific adaptations for intrinsic processing in each area and provide an anatomical basis for distinguishing intrinsic circuits in each area, which otherwise are similar. An exception is AI, whose intrinsic projections appear anisotropic and modular (Imaizumi et al., 2004; Middlebrooks et al., 1980; Read et al., 2001).

Extrinsic projections contribute the other half of the total convergent input. The relatively uniform contribution of extrinsic inputs across areas is somewhat remarkable and suggests that functional and developmental constraints (Catalano and Shatz, 1998; Kaas, 1995) from ontogenetic (Kandler et al., 2009; Pallas and Sur, 1993) and experience-dependent (Rutkowski and Weinberger, 2006) processes guide the establishment of extrinsic input.

Among the extrinsic sources, the thalamic projection is the weakest, comprising ~15% of the extrinsic input, which is similar to estimates from the visual (Binzegger et al., 2004) and somatosensory (Benshalom and White, 1986) systems. Despite their relatively small contribution, the thalamic input could have a synaptic impact that may match or exceed that of the much greater corticocortical projections (Gil et al., 1999; Lee and Sherman, 2008; Stratford et al., 1996). In this sense, areas that receive fewer than average thalamic inputs (Miller et al., 2001) might be more affected by selective thalamic damage (Carrera and Bogousslavsky, 2006) while those with greater than average thalamic inputs could compensate for these lost functions more readily, or represent convergent and/or extraauditory streams (Aitkin and Dunlop, 1968; Bordi and LeDoux, 1994).

The near uniform contributions from the major corticocortical sources suggests a common plan for the organization of ipsilateral connections (Winer and Lee, 2007). The sheer number of ipsilateral inputs might explain why selective cortical lesions can have a negligible influence on activity (Kitzes and Hollrigel, 1996). In addition, the widespread connectivity could enable communication among functionally unrelated areas within the ipsilateral cortical system, as compared with the thalamic and commissural systems. In this regard, the non-tonotopic areas have a particularly important role in linking areal groups, given the wide variety of their inputs.

The commissural input is similar in size to the thalamic input, of which the homotypic input provides more than half of the commissural input. The dominant projection from the homotypic contralateral sources can potentially combine interhemispheric auditory information (Gazzaniga, 2000), and may account for the sound localization deficits observed in contralateral inactivation studies (Lomber et al., 2007; Malhotra et al., 2004).

Convergent Networks

The expansive interconnections among auditory thalamic nuclei and cortical areas (Winer and Lee, 2007) can support degenerate functions within the auditory cortical network. For example, a connectional subset may couple functionally at a given time, forming labile nuclear and areal coalitions (Sporns et al., 2002) transiently associating and dissociating them to meet specific computational demands (Izhikevich et al., 2004). In this sense, the functional weight of each anatomical connection is not rigidly constrained, perhaps enabling massive, widespread, specific, and concurrent plastic rearrangements on a global scale (Winer and Lee, 2007). Similarly, multiple degenerate combinations of areas and nuclei can converge upon similar computational outcomes and thereby construct perceptual unity. Such an ensemble scheme is consistent with the immense, continuous, and dynamic demands imposed by the auditory stream (Bregman et al., 2001) and would likely be essential for rapidly and efficiently unifying the otherwise independent 'what' and 'where' streams (Romanski et al., 1999) into a continuous perceptual entity (Winer and Lee, 2007).

The convergent connections of the auditory cortex demonstrate the global nature of computations in the auditory cortex and suggest that functional computations are likely distributed across many forebrain circuits (Kitzes and Hollrigel, 1996). The sheer floridness of these convergent networks underscores the challenges to understanding higher auditory cortical processing, which will eventually require reconciling these anatomical connections with their functional impact. The perspective revealed by convergent connectivity should enable the development of more global models of forebrain acoustic organization.

Acknowledgments

I feel extremely fortunate, privileged and honored to have known, studied, and worked with Jeffery A. Winer. His skills as a neuroscientist were formidable, and his extensive working knowledge of the brain was simply awe-inspiring. Jeff was meticulous, precise, and his attention to detail was unrivaled. His illustrations transcended beyond mere science into art. And, his detailed observations led naturally to synthesis and derivation of the rules and principles guiding the organization of the auditory system.

Yet, those of us who knew Jeff will remember him most for his genuine personality. Jeff was kind, generous, and giving in all the ways that mattered. He had an infectious enthusiasm that he transmitted with ease, a gift that extended to his mentoring, for which I was merely one of many lucky recipients. For me, his most penetrating quality was his sense of humor. He saw beyond the farce of many of life's little travails and was quickly able to make light of them.

I believe that Jeff's best years were yet to come and that he was reaching the heights of his powers as a scientist, and it is simply tragic that he is gone too soon. But, Jeff lived a very fulfilling life, and I know that he would want us to celebrate the time that he was here with us, rather than mourn his passing.

Jeff was more than just my mentor. He was my friend, brother, father, uncle, and teacher combined into one remarkable person. And, I will be forever grateful that he was part of my life.

Jeff, I will miss you.

-Charles Lee

This work could not have been possible without the generosity of Drs. Christoph E. Schreiner and Kazuo Imaizumi for physiological mapping and sharing data from these experiments. David T. Larue and Tania J. Bettis provided histological expertise. Dawn Sung, Richard Lee, Kristen Adams, Haleh Badakoobei, and Esther Yoon assisted with plotting.

Funding: This work was supported by National Institutes of Health grant R01 DC2319-29.

Supported by: National Institutes of Health grant R01 DC2319-28

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Abbreviations

AAF	anterior auditory field
AES	anterior ectosylvian field
AI	primary auditory cortex
AII	secondary auditory cortex
AL	anterior lateral auditory belt, macaque
APt	anterior pretectum
CTβ	cholera toxin beta subunit
CTβG	cholera toxin beta subunit, gold-conjugate
D	dorsal nucleus of the medial geniculate body <i>or</i> dorsal
DCa	caudal dorsal nucleus of the medial geniculate body
DD	deep dorsal nucleus of the medial geniculate body
DS	dorsal superficial nucleus of the medial geniculate body
DZ	dorsal auditory zone
ED	posterior ectosylvian gyrus, dorsal part
EI	posterior ectosylvian gyrus, intermediate part
EV	posterior ectosylvian gyrus, ventral part
III	ocumotor nucleus
In	insular cortex
LD	lateral dorsal thalamic nucleus
LGB	lateral geniculate nucleus
M	medial division of the medial geniculate body
MeV	mesencephalic nucleus of the trigeminal

MRF	mesencephalic reticular formation
Ov	ovoid part of the medial geniculate body
P	posterior auditory cortex
PFC	prefrontal cortex
R	rostral
RP	rostral pole division of the medial geniculate body
SC	superior colliculus
Sl	supragenulate nucleus, lateral part
Sm	supragenulate nucleus, medial part
V	ventral division of the medial geniculate body
Vb	ventrobasal complex
Ve	ventral auditory area
VI	ventrolateral nucleus of the medial geniculate body
VP	ventral posterior auditory area

Figure 1. Summary of experiments. *A*, Cat auditory cortex (AC) contains thirteen areas identified by their functional and connective affiliations. Tonotopic areas (red) receive their principal input from other tonotopic AC and thalamic sources. Non-tonotopic areas (green) adjoin the tonotopic areas and have diverse inputs. The multisensory (blue) and limbic areas (purple) receive chiefly non-tonotopic, multisensory, and limbic inputs. *B*, Summary of injection sites available. In all animals, two different retrograde tracers, cholera toxin β subunit (CT β) (red circles) and cholera toxin β subunit gold conjugate (CT β G) or wheat germ aporhorseradish peroxidase gold conjugate (WAHG) (blue filled circles), were injected into topographically segregated AC loci. Numbers in circles refers to experiments listed in *C*. *C*, Experiments denoted by the number (#), case, and location of injections (font color corresponds to the tracers in *B*). For abbreviations in this and subsequent figures, see the list. Adapted from Fig. 1 in Lee and Winer 2008a.

Figure 2.

Convergent MGB and AC input to areas AI and AII in a representative experiment. Retrograde tracers were injected in two areas, and the labeled cells plotted and counted in the ipsilateral (A) and contralateral (B) cortex, and thalamus (C-E). Labeling was intrinsic (within the injected area) or extrinsic (from other AC and thalamic sources). The proportion of extrinsic input was computed for each thalamic nucleus and AC area (F). A, In a representative experiment, WAHG was injected in AI (light blue ovals) and CTβ in AII (light red ovals). Vertical aliasing of labeling here and in (B) is an artifact of the reconstruction process. Intrinsic projections dominate, arising 1-2 mm from the injection site. Much of the extrinsic ipsilateral AC labeling was highly segregated for both injections. AI projections are in focal clusters in other tonotopic areas (AAf, P, VP, Ve), while AII projections are mainly from other non-tonotopic (AES, DZ), multisensory (ED, EI, EV), and limbic (Te, In) areas (Lee and Winer, 2008c). The ipsilateral AC projection is the largest extrinsic input (~78%; cf Table 1). A, Contralateral projections concentrate in homotopic areas (Lee and Winer, 2008b). Heterotopic projection sources mirrored those in the ipsilateral cortex, but were far smaller. The retrograde labeling in the right hemisphere labeling was represented on the left to facilitate comparison with the ipsilateral labeling. C-E, Thalamic input also had topographically segregated nuclear origins. AI received its principal input from the ventral division, while AII was a target of the dorsal and medial division nuclei (Lee and Winer, 2008a). Decimals, lower left: proportional distance from the MGB caudal pole. F, The nuclear (Thalamus) and areal (Cortex) origin of extrinsic MGB and AC input. The ipsilateral cortical input was ~78%, thalamic was ~14% and contralateral AC ~8%. There is segregation of extrinsic input to both AI and AII from largely independent thalamic and AC (i.e., double labeling <1%) projection sources. Adapted from

Fig. 4 in Lee and Winer 2008a, Fig. 3 in Lee and Winer 2008b, and Fig. 3 in Lee and Winer 2008c.

Figure 3.

Average proportion of convergent extrinsic input to thirteen AC areas. Gray boxes, percent of input from each MGB nucleus and AC area (rows) to its target (columns). Red boxes, the three largest inputs to an area from the MGB, ipsilateral AC, and contralateral AC, respectively. The largest input is typically from ipsilateral AC, while thalamic and commissural sources are much smaller.

Figure 4.

Hierarchical connections of auditory cortical areas according to laminar origins of projections. Auditory areas are ordered from lowest to highest, with AI and AAF at the base and areas 35 and 36 at the top. Connectional strength, line thickness: strong (thick), medium (bold), and weak (thin). When connectional strengths are non-reciprocal, mean strength is indicated. Laminar origins, the line origins on the areal boxes: supragranular (top), bilaminar (side), infragranular (bottom). Areas can also be classified by putative functional relations: dorsal areas (yellow background) may represent auditory space, ventral areas (dusky rose background) may specialize in spectral analysis.

Figure 5.

Summaries of convergence of MGB and AC projections in tonotopic and nontonotopic areas. The three largest inputs to tonotopic and non-tonotopic areas from the MGB, and ipsi- and contralateral AC. Large filled squares, projection targets from MGB (circles), ipsilateral AC (left-side squares), and contralateral AC (right-side squares) sites in tonotopic (red), non-tonotopic (green), multisensory (blue), and limbic (purple) regions. Size of small boxes and circles is proportional to input percentages (numbers). *A-E*, Tonotopic areas (large red boxes) receive their main input from other tonotopic nuclei and areas. In each, the ventral division is among the strongest MGB input, while the homotopic AC is the major contralateral input. Ipsilateral AC input is predominantly from other tonotopic sources. *F-H*, Nontonotopic areas (large green boxes) receive strong MGB dorsal division input, with the homotopic area again the main contralateral AC input. The ipsilateral AC input arises largely from adjacent tonotopic, non-tonotopic, multisensory, and limbic areas.

Multisensory

Figure 6.

Summaries of convergence of MGB and AC projections in multisensory and limbic areas, and group averages. The three largest inputs to multisensory and limbic areas and to each areal group from the MGB and AC. Large filled squares, MGB projection targets (filled circles) and ipsilateral AC (left-side squares) and contralateral AC (right-side squares) sites in tonotopic (red), non-tonotopic (green), multisensory (blue), and limbic (purple) regions. Sizes of small boxes and circles reflects the input percentages (numbers). *A-E*: Multisensory (large blue boxes) and limbic areas (large purple boxes) receive their primary MGB input from shell nuclei (DCa, DS, Sm). The contralateral projections are mainly from the homotopic area, and ipsilateral AC input is from other multisensory and limbic areas. *F-I*: Projection averages for each group capture the self-connected nature of each areal family. Thus, tonotopic (*G*), non-tonotopic (*H*), multisensory (*I*) and limbic (*F*) groups all share strong input from MGB and AC sources within the same family.

TABLE 1
Percentages of intrinsic and extrinsic input

Percentages of intrinsic and extrinsic input from thalamic and cortical sources. Intrinsic and extrinsic sources each provide 50% of the projections.

Area	Intrinsic	Extrinsic ¹
AI	60.2	39.8
AAF	61.1	38.9
P	50.6	49.4
VP	45.2	54.8
Ve	36.9	63.1
AII	42.0	58.0
AES	70.5	29.5
DZ	41.0	59.0
Te	36.3	63.7
In	52.4	47.6
ED	43.0	57.0
EI	48.4	51.6
EV	50.3	49.7
Average ²	49.1	50.9
Std. Dev.	10.1	10.1

¹ Sum of percentage of labeling in thalamus, extrinsic ipsilateral cortex, and contralateral hemisphere.

² $p > 0.05$, paired t -test.

TABLE 2
Sources and percentages of convergent extrinsic input

Percentages of input from the thalamus, ipsilateral, and contralateral cortex. Ipsilateral input dominates (75%); thalamic (15%) and contralateral (10%) sources are nearly an order of magnitude weaker.

Area	Thalamus	Ipsilateral Cortex	Contralateral cortex
AI	18.1	70.2	11.7
AAF	10.9	76.4	12.7
P	9.4	77.6	13.0
VP	11.3	84.2	4.5
Ve	17.1	77.8	5.1
AII	13.1	77.8	9.1
AES	4.5	86.1	9.4
DZ	20.2	70.5	9.3
Te	14.7	78.5	6.8
In	23.8	69.9	6.3
ED	12.0	78.8	9.2
EI	14.8	75.6	9.6
EV	6.7	87.7	5.6
Average	13.6	77.8	8.7
Std. Dev.	5.4	5.7	2.8

TABLE 3
Comparison by group of intrinsic and extrinsic auditory cortex input

Comparison of inputs by functional group. Percentages of extrinsic and intrinsic input are similar and independent of group (ANOVA, $p>0.05$), as is reciprocity (ANOVA, $p>0.05$).

Projection	Tonotopic	Non-tonotopic	Multisensory	Limbic	F	p
Intrinsic	50.8 ± 10.2; 104.8 ¹	51.2 ± 16.8; 280.6	47.2 ± 3.8; 14.4	44.3 ± 11.4; 129.6	0.22 ²	0.88
Extrinsic (total)	49.2 ± 10.2; 104.8	48.8 ± 16.8; 280.6	52.8 ± 3.8; 14.4	55.7 ± 11.4; 129.6	0.22	0.88
Extrinsic (individual)						
Thalamocortical	13.4 ± 4.0; 15.6	12.6 ± 7.9; 61.8	11.2 ± 4.1; 16.9	19.2 ± 6.4; 41.4	0.98	0.44
Corticocortical	77.2 ± 5.0; 24.8	78.1 ± 7.8; 60.9	80.7 ± 6.3; 39.3	74.2 ± 6.1; 37.0	0.47	0.71
Commissural	9.4 ± 4.2; 17.9	9.3 ± 0.2; 0.02	8.1 ± 2.2; 4.9	6.6 ± 0.4; 0.1	0.50	0.69

¹ Values: Mean percentages ± Std. Dev.; Variance

² ANOVA, single factor, df=2