

Decoding the auditory corticofugal systems

Jeffery A. Winer *

*Division of Neurobiology, Department of Molecular and Cell Biology, University of California at Berkeley,
Room 289 Life Sciences Addition, Berkeley, CA 94720-3200, USA*

Received 14 June 2005; accepted 20 June 2005

Available online 8 August 2005

Abstract

The status of the organization of the auditory corticofugal systems is summarized. These are among the largest pathways in the brain, with descending connections to auditory and non-auditory thalamic, midbrain, and medullary regions. Auditory corticofugal influence thus reaches sites immediately presynaptic to the cortex, sites remote from the cortex, as in perolivary regions that may have a centrifugal role, and to the cochlear nucleus, which could influence early central events in hearing. Other targets include the striatum (possible premotor functions), the amygdala and central gray (prospective limbic and motivational roles), and the pontine nuclei (for precerebellar control). The size, specificity, laminar origins, and morphologic diversity of auditory corticofugal axons is consonant with an interpretation of multiple roles in parallel descending systems.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Auditory thalamus; Inferior colliculus; Corticofugal; Corticothalamic; Corticocollicular; Corticopontine

Abbreviations: AA, amygdala, anterior nucleus; AAF, anterior auditory field; ABm, amygdala, basomedial nucleus; ACe, amygdala, central nucleus; AD, dorsal cochlear nucleus, anterior part; AES, anterior ectosylvian sulcus area; AI, auditory cortex, primary area; AII, auditory cortex, second area; ALe, ansa lenticularis; AIP, anterolateral periolivary nucleus; Am, amygdala; Ame, amygdala, medial nucleus; Av, anteroventral cochlear nucleus; AvA, anteroventral cochlear nucleus, anterior division; AvS, anteroventral cochlear nucleus, small cell cap; C, caudal; Ca, caudate nucleus; CC, caudal cortex of the inferior colliculus; Cl, claustrum; CG, central gray; CN, central nucleus of the inferior colliculus; Cu, cuneiform nucleus; D, dorsal nucleus of the medial geniculate body *or* dorsal; DD, deep dorsal nucleus of the medial geniculate body; DC, dorsal cortex of the inferior colliculus; DCa, caudal dorsal nucleus of the medial geniculate body; DF, dorsal cochlear nucleus, fusiform cell layer; DI-DIV, cortex of the inferior colliculus, layers I–IV; DL, dorsal nucleus of the lateral lemniscus; DIP, dorsolateral periolivary nucleus; DM, dorsal cochlear nucleus, molecular layer; DmP, dorsomedial periolivary nucleus; DS, dorsal superficial nucleus of the medial geniculate body; DZ, dorsal auditory zone (suprasylvian fringe); EC, external cortex of the inferior colliculus; ED, posterior ectosylvian gyrus, dorsal part; EI, posterior ectosylvian gyrus, intermediate part; En, entopeduncular nucleus; EV, posterior ectosylvian gyrus, ventral part; GP, globus pallidus; ICa, internal capsule; IL, intermediate nucleus of the lateral lemniscus; In, insular cortex; IT, intercollicular tegmentum; La, amygdala, lateral nucleus; LD, lateral dorsal nucleus; LN, lateral nucleus of the inferior colliculus; LP, lateral posterior nucleus; LS, lateral superior olive; LT, lateral nucleus of the trapezoid body; M, medial division; MR, mesencephalic reticular formation; MS, medial superior olive; MT, medial nucleus of the trapezoid body; NB, nucleus of the brachium of the inferior colliculus; Ov, *pars ovoidea* of the ventral division of the medial geniculate body; P, auditory cortex, posterior area; PA, posterior cochlear nucleus, anterior division; Pu, putamen; Pul, pulvinar nucleus; Pv, posteroventral cochlear nucleus; PvO, posteroventral cochlear nucleus, octopus cell area; Ro, rostral pole nucleus of the inferior colliculus; RP, rostral pole of the medial geniculate body; Sa, nucleus sagulum; SC, superior colliculus; SL, supragenulate nucleus, lateral part; SM, supragenulate nucleus, medial part; SNc, substantia nigra, *pars compacta*; SNr, substantia nigra, *pars reticulata*; Sp, subparafascicular nucleus; SpN, suprapeduncular nucleus; Te, temporal cortex; TL, lateral nucleus of the trapezoid body; TM, medial nucleus of the trapezoid body; TV, ventral nucleus of the trapezoid body; V, *pars lateralis* of the ventral division *or* ventral; Ve, auditory cortex, ventral area; VL, ventral nucleus of the lateral lemniscus; VI, ventrolateral nucleus of the medial geniculate body; VmP, ventromedial periolivary nucleus; VP, auditory cortex, ventral posterior area; 35, parahippocampal cortex, area 35; 36, parahippocampal cortex, area 36

* Tel.: +1 510 642 8227; fax: +1 510 643 6791.

E-mail address: jaw@berkeley.edu.

1. Introduction

The classical view of sensory processing begins with a peripheral receptor epithelium which is topographically organized and whose ganglion cells establish maps in the brain (Weinberg, 1997). At subsequent synaptic stations, the receptive fields (RFs) created at early stages are transformed through divergence and convergence, forms of connectional recombination that permit new features to emerge (Martin, 1994) and which likely enable perceptual decisions (Dykes, 1983). The classical perspective interprets this process of feature extraction and progressive increases in RF size and complexity as integrative, and as a basis for subsequent binding within (Treisman, 1996) and between (Driver and Spence, 1998) modalities. Within the cerebral cortex intricate pathways abound for further analytic purposes and refinement (Read et al., 2002) and these comprise about 85% of the total input to the cortex, with the thalamus accounting for the remaining 15% (Lee et al., 2004a,b; Winer et al., 2005). The finding of equally massive and equally specific descending projections from the cerebral cortex (Diamond et al., 1969) to the medial geniculate body (MGB) (Winer et al., 2001), inferior colliculus (IC) (Winer et al., 1998), superior olivary complex (SOC) (Mulders and Robertson, 2000), cochlear nucleus (CoN) (Weedman and Ryugo, 1996), pons (Brodal, 1972), and basal ganglia (Reale and Imig, 1983) suggests that elements of the ascending pathways themselves receive significant descending input. These manifold connections suggest that the hierarchical model must now accommodate influences from many descending sources. Moreover, physiological studies demonstrate that these descending pathways can affect many aspects of subcortical performance, including filtering (Diamond et al., 1992), sharpness of tuning (Villa et al., 1991), and response plasticity (Ma and Suga, 2001). How the classical model of corticofugal ‘feedback’ might be recast in the light of this new evidence is the subject of this review.

1.1. Roles of the auditory corticofugal systems

As a framework, it is useful to enumerate some candidate processes that the auditory corticofugal systems (ACS) influence. The plural denotes that such inputs to the subcortical forebrain, midbrain, and brain stem may have distinct roles. The model that follows is based chiefly on the cat, with data from rodents, bats, and primates as well; there is no reason yet to suppose differences except in the case of species without neocortex.

1.1.1. Sensory processing

Many facets of RF organization are influenced by the ACS, including threshold, response area, and frequency tuning (Sun et al., 1996). This suggests a powerful, perhaps multisynaptic, role in modulating RF structure

since interneurons as well as principal cells receive such input (Morest, 1975).

1.1.2. Motor behavior

The ACS targets the basal ganglia and other premotor structures (Beneyto and Prieto, 2001), and the pontine nuclei (Schuller et al., 1991), whose output ultimately reaches the cerebellum. This implies that preparatory skeletomotor planning and performance integrates ACS signals.

1.1.3. Autonomic function

Robust ACS projections to the amygdala (Romanski and LeDoux, 1993) and central gray (Winer et al., 1998) permit access, via polysynaptic routes, to the hypothalamus and to tegmental structures implicated in the control of smooth muscle tone. This could affect behaviors as diverse as milk ejection (Deis and Prilusky, 1984) and startle reflexes (Yeomans and Frankland, 1996).

1.1.4. State-dependent changes

The corticothalamic system likely has a central role in the switch from burst-to-tonic firing modes which is proposed to mediate global oscillations that, in turn, modulate discharge synchrony and may embody changes in vigilance (Steriade, 2000).

2. The corticofugal systems

2.1. Thalamus and medial geniculate body

The corticothalamic system is among the largest projections in the brain, comparable to the corticospinal system. Each major MGB subdivision receives massive cortical input from four or more of the 12 areas of AC, and some are a target of every area (Winer et al., 2001). Each of the three principal MGB nuclear groups receives corticothalamic input. Tonotopic AC areas target tonotopic MGB subdivisions preferentially, non-tonotopic areas project largely to non-tonotopic thalamic nuclei, and polymodal associative MGB regions, such as the medial division, receive input from all AC areas and from non-auditory cortex. Thus, the functional families of cortical areas (tonotopic, non-tonotopic, and limbic related) project principally, but not exclusively, to functionally aligned thalamic nuclear groups. In conjunction with robust reciprocal thalamocortical–corticothalamic connectivity (Colwell, 1975), this has shaped the development of three of the basic functional principles ascribed to this system (feedback, reciprocity, and parity; cf. 4). Other descending projections end in the thalamic reticular nucleus, whose γ -aminobutyric acid-containing (GABAergic) cells also receive input from the MGB (Crabtree, 1998) and which has been implicated in attentional modulation (Crick, 1984).

Besides their impressive size, these pathways are topographic. Among tonotopic fields, this takes the form of frequency-specific cortical terminations within tonotopically appropriate MGB loci. The projection of non-tonotopic and polymodal cortical fields is, unexpectedly, equally topographic spatially, though the functional axes for this order remain obscure in both the cortex and thalamus.

Divergence is also a basic feature of the corticothalamic system, with the primary auditory cortex (AI) projecting to six MGB subdivisions, the ventral auditory area (Ve) to three thalamic nuclei, the non-tonotopic second auditory area (AII) to 10, and the temporal area (Te) of limbic cortex has eleven targets. This specificity, as well as the topographic precision of the projections and their various patterns of origin, is consistent with area- and nucleus-specific functional roles, even though such roles have been defined only for primary areas (Villa et al., 1991).

The cortical origins of this system likewise are specific, with AI corticothalamic neurons in the outer part of layer V, in the deepest one-third of layer V, and throughout layer VI (Winer and Prieto, 2001). Such sublaminar precision suggests that there are parallel projections from specific types of neurons within the corticothalamic system.

Finally, the structure of corticothalamic axons is diverse and target-specific, with thin fibers having small boutons ending in the ventral division (tonotopic and lemniscal thalamic zone) and much larger axons with giant terminals in the dorsal and medial divisions (non-tonotopic and extralemniscal) (Winer et al., 1999).

2.2. Midbrain and inferior colliculus

In almost all regards, the corticocollicular projections differ from the corticothalamic system. Where the former is massive and has close relations with lemniscal thalamic nuclei, the latter is smaller and concentrated in extralemniscal IC subdivisions. Parallels include that both projections are topographic, and that their laminar origin is equally specific (Winer and Prieto, 2001).

A primary feature of the corticocollicular projections is that they terminate most heavily in IC regions outside the central nucleus or at its perimeter and proximal portions. Abundant local ipsilateral IC internuclear connections may permit communication across subdivisions (Saldaña and Merchán, 2005); analogous pathways are absent in the MGB (Morest, 1975).

The specificity of corticocollicular projections is comparable to that of the corticothalamic system. Thus, input to the non-lemniscal dorsal cortex, a structure implicated in auditory attention (Jane et al., 1965), arises principally from the five tonotopic areas and ends mainly in layers II–III (Fig. 1D: DII, DIII). In contrast, projections to the central gray (Fig. 1E: CG) are chiefly

from one non-primary area and end in an equally specific fashion.

With respect to divergence, AC tonotopic fields have many more IC targets than does the MGB, while non-primary, limbic-related cortical areas have more limited and specific IC targets. This supports the view that the corticothalamic and corticocollicular systems are independent, as does the sparse population of corticofugal neurons that project jointly to each (Wong and Kelly, 1981).

The laminar origin of the corticocollicular projections complement those of the corticothalamic system: they occupy the central and deep part of layer V, where corticothalamic cells of origin are absent; together, these projections fill most of layers V and VI (Prieto and Winer, 1999), and their pyramidal cells are among the largest corticofugal neurons (Winer, 2005), and their subvarieties have either single spiking or bursting modes of discharge (Hefti and Smith, 2000), patterns whose role in processing information likely differs.

Finally, corticocollicular axons differ from their corticothalamic counterparts: they are more homogeneous, with thin preterminal segments, small boutons (Saldaña et al., 1996) and an en passant neuropil distribution (Winer, 2005).

2.3. Medulla

Less is known about ACS relations with the lower brain stem for several reasons. First, cat AC is about 600 mm² in area, whereas anterograde tracer deposits average 1.5 mm², militating against deriving any global profile readily (Winer et al., 2001). Second, in rodents, in whom proportionally larger deposits can be made (Schofield and Coomes, 2005), cortical areas are fewer and much smaller (Luethke et al., 1989), and there is uncertainty as to their number and precise limits (Doron et al., 2002). Third, only with the advent of sensitive tracers can the full scope of these projections be judged (Bajo et al., 1995). Fourth, the correlative and complementary retrograde studies of corticofugal convergence and laminar origins are available for few areas (Prieto and Winer, 1999).

The proportion of AC cells terminating in the SOC or CoN is estimated at no more than 10% of that projecting to the IC, and the origin of the input was concentrated ipsilaterally with regard to the IC and more bilaterally for the medullary targets (Doucet et al., 2003).

AC axons ending in the SOC concentrated in the ventral nucleus of the trapezoid body, bilaterally, and the heaviest projection ipsilaterally, and a comparable pattern after deposits in different fields; axons in many nuclei have a similar structure (Schofield and Coomes, 2004). In CoN, ipsilateral labeling predominated, and boutons targeted the granule cell domain of the dorsal cochlear nucleus, where small terminals and larger

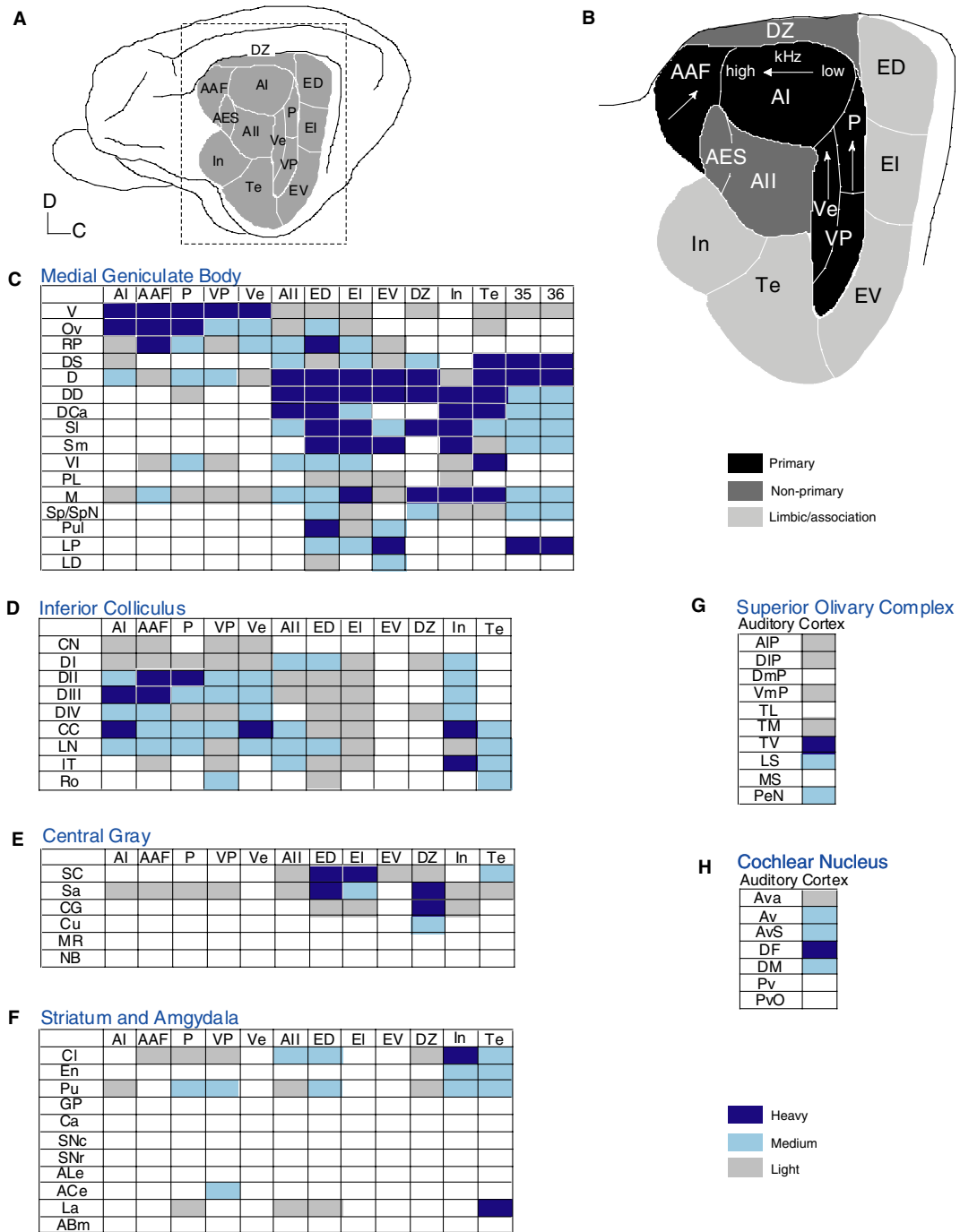


Fig. 1. Cat auditory cortex areas (A and B) and the principal corticofugal targets (C–H). (A) More than 10 auditory fields are recognized in physiological and anatomical studies (Winer, 1992). (B) Primary areas (black) have a systematic representation of characteristic frequency and of other physiologic attributes (Schreiner, 1995), non-primary fields do not, and limbic/association areas are multisensory and have an integrative role. (C–H) Auditory corticofugal projections from specific fields (top) targeting brain stem nuclei (left side). (C) In the medial geniculate body, tonotopic primary cortical areas project chiefly to thalamic areas with similar functional affiliations, whereas non-primary areas have more divergent, and a wider range, of such targets (Winer et al., 2001). (D) The inferior colliculus receives only modest projections in the lemniscal central nucleus, with most corticofugal input to non-tonotopic subdivisions on its perimeter (Winer et al., 1998). (E) The central gray and associated non-auditory midbrain structures are targets of non-primary and limbic-related input (Winer et al., 1998). (F) A wide array of cortical areas project to portions of the striatum (Reale and Imig, 1983). The rat amygdala is a target of highly specific input (Romanski and LeDoux, 1993). (G) Several olivary and periolivary nuclei receive auditory cortex input in the guinea pig (Schofield and Coomes, 2004), as does various (H) cochlear nucleus subdivisions (Schofield and Coomes, 2005). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mossy fiber endings were concentrated (Schofield and Coomes, 2005). Input to granule cells arises from layer V (Weedman and Ryugo, 1996), which is also the origin of projections to the SOC (bilaterally) in both primary and secondary AC, and few cortical cells projected to more than one brain stem target (Doucet et al., 2003). Other AC targets include the sagulum and associated paralemniscal regions (Feliciano et al., 1995).

2.4. Non-auditory brain stem

All AC subdivisions project to the pons, and the principal target is the lateral pontine nucleus (unpublished observations). Individual corticopontine axons have a unique terminal architecture, forming narrow sheets just a few cells wide in which hundreds of boutons cluster. These endings differ entirely from those in the MGB (Bajo et al., 1995), IC (Winer, 2005), and CoN (Schofield and Coomes, 2005), which are smaller, more divergent, and more numerous. These axonal lamellae are solitary and independent, separated by terminal-free spaces even after cortical injections that saturate large areas and whose input to the MGB and IC is larger and more continuous.

2.5. Striatum

The input to the claustrum and entopeduncular nucleus arises from all AC subdivisions (Beneyto and Prieto, 2001), with topographic projections from tonotopic areas to the dorsal putamen and nearby caudate nucleus regions forming zones of dense input interspersed among weaker projections (Reale and Imig, 1983). These axons are slender and delicate compared to those reaching the pons (unpublished observations) and to the range in size of corticothalamic axons (Winer et al., 1999).

3. Principles of the corticofugal projections

The preceding observations on the ACS, while incomplete with respect to the differential contribution of areas and the morphology of axons with regard to their origins and targets, are nonetheless sufficient to support several propositions.

3.1. Density

The projection strength of the ACS is origin- and target-specific. Thus, the IC central nucleus receives a modest projection from many areas, whereas the MGB ventral division is a strong target of tonotopic areas and the recipient of weaker input from non-primary AC. Deciphering the unique relations between source and target is an intriguing question for the future.

3.2. Topography

Topographic ACS projections are the rule, even in targets such as the pons where no topographic functional map is known. Thus, the ACS may be ordered as precisely as the major afferent systems within the cortex (Lee and Winer, 2005).

3.3. Divergence

A given AC area has a complex affiliation with many auditory and non-auditory regions (Figs. 1 and 2). Such divergence supports the parcellation of cat AC and suggests that the descending systems may have targets (and, by implication, functions) equally specific as those of the ascending auditory system.

3.4. Sublaminar origins

The specificity of these projections likewise suggests that, even within cortical layers regarded as homogeneous, their sublaminar corticofugal segregation is consistent with differential function within layers. Supporting evidence is that few corticofugal neurons have multiple brain stem targets (Wong and Kelly, 1981), which again aligns the corticofugal and corticocortical systems (Lee et al., 2004a).

3.5. Axon structure

Diversity in the form of ACS axons is consistent with, and supports, several of the principles enumerated above. Thus, the corticopontine axons are unique within the brain, forming complex, solitary slabs with hundreds of boutons after deposits in all AC areas, while giant terminals are limited to specific MGB subdivisions and arise from all AC areas. Thus, the diverse axon morphology may subserve differential effects on postsynaptic neurons, and it is likely as valid a metric for proposing functional differences as is density or divergence.

4. Thematic perspective

The history of the study of the corticofugal systems is analogous in broad outlines to that of the neurosciences. Both begin with categorical assertions that later require modification (e.g., that the reticular theory only is valid, or that the ascending auditory system alone is responsible for hearing), and both have been refined as new methods reveal novel insights (e.g., the reticular theory is not incompatible with the neuron theory, and the ascending and descending auditory systems are recognized as complementary). A brief history of some principles that have driven this endeavor for the corticofugal system follows.

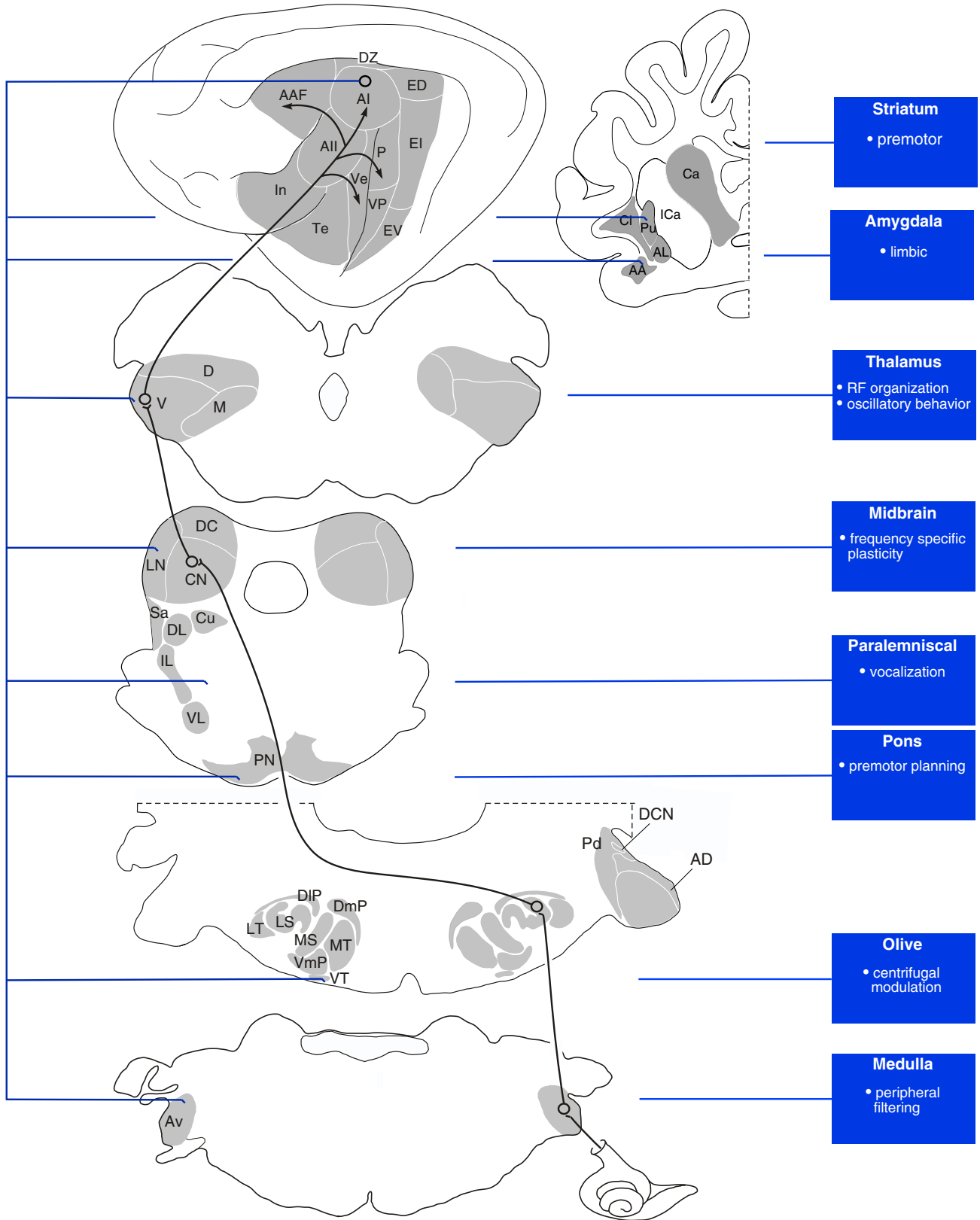


Fig. 2. A schematic of the ascending auditory pathway (black lines) (Winer and Schreiner, 2005), the corticofugal system (blue lines), and some possible functional correlates (blue boxes) from the striatum to the medulla. The chief points are: (i) there are likely several corticofugal systems, (ii) they reach almost all parts of the ascending auditory system, (iii) their actions may be target-specific and, in any case, (iv) are highly diverse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Feedback

Once the existence of the corticofugal system was confirmed, the first roles suggested for it involved the concept of feedback (Frigyesi et al., 1972), and more recent perspectives frame corticothalamic projections within that context (Murphy et al., 1999). Why such feedback is necessary, and the role that it might play, remain elusive.

4.2. Reciprocity

This interpretation of corticothalamic function supports a tight functional coupling between thalamic projections to cortex and the corticothalamic projections. Early studies emphasized the continuity between these systems (Colwell, 1975), and later work specified discontinuities (Winer and Larue, 1987).

4.3. Parity

This was the first approach to formalize the precept that subcortical axonal divergence could underlie some of the discontinuities in descending projections, and to relate these to prethalamic sources and streams (Deschênes et al., 1998).

4.4. Executive control

This perspective emphasized the role of the cortex in signal selection (King, 1997) and in global feature extraction (Przybylski, 1998). These ideas are harbingers that anticipate subsequent studies demonstrating the intricacies of corticofugal control (Suga et al., 2002).

4.5. Hegemony

A most extreme interpretation of ACS function is that it is a dominant agent for sensory-motor control (Winer, 2005). This proposition reflects the idea that the cortex is the sole locus which integrates all subcortical input and its own connections, features which endow it with a unique view of sensory experience that, by definition, is more inclusive than that of the brain stem. Concomitantly, it is presynaptic to much of the ascending pathway, especially to prethalamic structures whose influence on AC is by definition far less direct than that of the ACS upon it.

5. Questions for the future

The present status of understanding the ACS recalls the period preceding the remarkable growth of knowledge about ascending streams on visual cortex function (Hubel and Wiesel, 1977) which has culminated in prin-

cipled models of information flow (Lund et al., 1994). Answers to the questions framed below could encourage steps toward such a model for the descending systems.

5.1. Parallel pathways

If cortical layers are analogous to subcortical nuclei, then the layer VI corticofugal contribution to the thalamus cannot be equivalent to the layer V projections to the IC. Likewise, when several areas converge onto a specific nuclear target, it is an open question if their impact is numerical (winner take all), computational (each making a discrete contribution), or executive (veto-proof).

5.2. Ascending and descending interactions

How tightly, from a synaptic perspective, are the afferent streams and their descending counterparts, linked? How is physiological performance altered when projections are reciprocal (e.g., between area AI and the ventral nucleus of the MGB), and when they are asymmetric (e.g., between AI and the central nucleus of the IC)? How are afferent signals modified by descending influence? Do these transformations (such as changes in RF size or internal dynamics) obey principles analogous to those in the ascending pathways (Winer and Schreiner, 2005).

5.3. Species differences

In species devoid of neocortex, the only descending projections may be from parahippocampal areas to the auditory thalamus (Witter and Groenewegen, 1986), though such connections remain to be demonstrated explicitly. How might thalamic processing of corticofugal input differ in species with many or few Golgi type II cells (Winer and Larue, 1996) or in those whose sensory neocortex is less elaborate than in mammals (Ulinski, 1983)? This question is crucial given species differences in encephalization (Jerison, 1973).

5.4. Anatomical substrates

The cells of origin (Doucet et al., 2002) and the morphology of ACS axons (Bajo et al., 1993) are area- and target-specific (Winer, 2005). This is congruent with, but cannot confirm that, the descending pathways are several in form and function. Data comparing these areal and nuclear patterns are not yet available for any species. Such data precedes any more refined theory of corticofugal operations.

Acknowledgments

This work was supported by National Institutes of Health Grant R01 DC02319-25. Dr. Brett R. Schofield

provided helpful advice on medullary projections. Thanks to Janine P. Beyer for assistance with the figures.

References

- Bajo, V.M., Merchán, M.A., López, D.E., Rouiller, E.M., 1993. Neuronal morphology and efferent projections of the dorsal nucleus of the lateral lemniscus in the rat. *J. Comp. Neurol.* 334, 241–262.
- Bajo, V.M., Rouiller, E.M., Welker, E., Clarke, S., Villa, A.E.P., de Ribaupierre, Y., de Ribaupierre, F., 1995. Morphology and spatial distribution of corticothalamic terminals originating from the cat auditory cortex. *Hearing Res.* 83, 161–174.
- Beneyto, M., Prieto, J.J., 2001. Connections of the auditory cortex with the claustrum and endopiriform nucleus in the cat. *Brain Res. Bull.* 54, 485–498.
- Brodal, P., 1972. The corticopontine projection in the cat. The projection from the auditory cortex. *Arch. Ital. Biol.* 110, 119–144.
- Colwell, S., 1975. Thalamocortical–corticothalamic reciprocity: a combined anterograde–retrograde tracer technique. *Brain Res.* 92, 443–449.
- Crabtree, J.W., 1998. Organization in the auditory sector of the cat's thalamic reticular nucleus. *J. Comp. Neurol.* 390, 167–182.
- Crick, F., 1984. Function of the thalamic reticular nucleus: the searchlight hypothesis. *Proc. Natl. Acad. Sci. USA* 81, 4586–4590.
- Deis, R.P., Prilusky, J., 1984. Participation of the hippocampus in the facilitatory effect of an exteroceptive stimulus on milk ejection. *Exp. Brain Res.* 55, 177–179.
- Deschênes, M., Veinante, P., Zhang, Z.-W., 1998. The organization of corticothalamic projections: reciprocity versus parity. *Brain Res. Rev.* 28, 286–308.
- Diamond, I.T., Jones, E.G., Powell, T.P.S., 1969. The projection of the auditory cortex upon the diencephalon and brain stem of the cat. *Brain Res.* 15, 305–340.
- Diamond, M.E., Armstrong-James, M., Budway, M.J., Ebner, F.F., 1992. Somatic sensory responses in the rostral sector of the posterior group (POM) and in the ventral posterior medial nucleus (VPM) of the rat thalamus: dependence on the barrel field cortex. *J. Comp. Neurol.* 319, 66–84.
- Doron, N., LeDoux, J.E., Semple, M.N., 2002. Redefining the tonotopic core of rat auditory cortex: physiological evidence for a posterior auditory field. *J. Comp. Neurol.* 453, 345–360.
- Doucet, J.R., Rose, L., Ryugo, D.K., 2002. The cellular origin of corticofugal projections to the superior olivary complex in the rat. *Brain Res.* 925, 28–41.
- Doucet, J.R., Molavi, D.L., Ryugo, D.K., 2003. The source of corticocollicular and corticobulbar projections in area Te1 of the rat. *Exp. Brain Res.* 153, 477–485.
- Driver, J., Spence, C., 1998. Crossmodal attention. *Curr. Opin. Neurobiol.* 8, 245–253.
- Dykes, R.W., 1983. Parallel processing of somatosensory information: a theory. *Brain Res. Rev.* 6, 47–115.
- Feliciano, M., Saldaña, E., Mugnaini, E., 1995. Direct projections from the rat primary auditory neocortex to nucleus sagulum, paralemniscal regions, superior olivary complex and cochlear nuclei. *Audit. Neurosci.* 1, 287–308.
- Frigyesi, T., Rinvik, E., Yahr, M.D. (Eds.), 1972. *Corticothalamic Projections and Sensorimotor Activities*. Raven Press, New York.
- Hefti, B.J., Smith, P.H., 2000. Anatomy, physiology, and synaptic responses of rat layer V auditory cortical cells and effects of intracellular GABA_A blockade. *J. Neurophysiol.* 83, 2626–2638.
- Hubel, D.H., Wiesel, T.N., 1977. Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. Lond., Ser. B, Biol. Sci.* 198, 1–59.
- Jane, J.A., Masterton, R.B., Diamond, I.T., 1965. The function of the tectum for attention to auditory stimuli in the cat. *J. Comp. Neurol.* 125, 165–192.
- Jerison, H.J., 1973. *Evolution of the Brain and Intelligence*. Academic Press, New York.
- King, A.J., 1997. Signal selection by cortical feedback. *Curr. Biol.* 7, R85–R88.
- Lee, C.C., Winer, J.A., 2005. Principles governing auditory forebrain connections. *Cereb. Cortex*, in press.
- Lee, C.C., Schreiner, C.E., Imaizumi, K., Winer, J.A., 2004a. Tonotopic and heterotopic projection systems in physiologically defined auditory cortex. *Neuroscience* 128, 871–887.
- Lee, C.C., Imaizumi, K., Schreiner, C.E., Winer, J.A., 2004b. Concurrent tonotopic processing streams in auditory cortex. *Cereb. Cortex* 14, 441–451.
- Luethke, L.E., Krubitzer, L.A., Kaas, J.H., 1989. Connections of primary auditory cortex in a new world monkey, *Saguinus*. *J. Comp. Neurol.* 285, 487–513.
- Lund, J.S., Yoshioka, T., Levitt, J.B., 1994. Substrates for interlaminar connections in area VI of macaque monkey cerebral cortex. In: Peters, A., Rockland, K.S. (Eds.), *Cerebral Cortex. Primary Visual Cortex in Primates*, vol. 10. Plenum Press, New York, pp. 37–60.
- Ma, X., Suga, N., 2001. Plasticity of bat's central auditory system evoked by focal electric stimulation of auditory and/or somatosensory cortices. *J. Neurophysiol.* 85, 1078–1087.
- Martin, K.A.C., 1994. A brief history of the “feature director”. *Cereb. Cortex* 4, 1–7.
- Morest, D.K., 1975. Synaptic relationships of Golgi type II cells in the medial geniculate body of the cat. *J. Comp. Neurol.* 162, 157–194.
- Mulders, W.H.A.M., Robertson, D., 2000. Evidence for direct cortical innervation of medial olivocochlear neurons in rats. *Hearing Res.* 144, 65–72.
- Murphy, P.C., Duckett, S.G., Sillito, A.M., 1999. Feedback connections to the lateral geniculate nucleus and cortical response properties. *Science* 286, 1552–1554.
- Prieto, J.J., Winer, J.A., 1999. Neurons of layer VI in cat primary auditory cortex (AI): Golgi study and sublaminar origins of projection neurons. *J. Comp. Neurol.* 404, 332–358.
- Przybyszewski, A.W., 1998. Does top-down processing help us to see? *Curr. Biol.* 8, R135–R139.
- Read, H.L., Winer, J.A., Schreiner, C.E., 2002. Functional architecture of auditory cortex. *Curr. Opin. Neurobiol.* 12, 433–440.
- Reale, R.A., Imig, T.J., 1983. Auditory cortical field projections to the basal ganglia of the cat. *Neuroscience* 8, 67–86.
- Romanski, L.M., LeDoux, J.E., 1993. Information cascade from primary auditory cortex to the amygdala: corticocortical and cortico-amygdaloid projections of temporal cortex in the rat. *Cereb. Cortex* 3, 515–532.
- Saldaña, E., Feliciano, M., Mugnaini, E., 1996. Distribution of descending projections from primary auditory neocortex to inferior colliculus mimics the topography of intracollicular projections. *J. Comp. Neurol.* 371, 15–40.
- Saldaña, E., Merchán, M.A., 2005. Intrinsic and commissural connections of the inferior colliculus. In: Winer, J.A., Schreiner, C.E. (Eds.), *The Inferior Colliculus*. Springer, New York, pp. 155–181.
- Schofield, B.R., Coomes, D.L., 2004. Projections from the auditory cortex to the superior olivary complex in guinea pigs. *Eur. J. Neurosci.* 19, 2188–2200.
- Schofield, B.R., Coomes, D.L., 2005. Auditory cortical projections to the cochlear nucleus in guinea pigs. *Hearing Res.* 199, 89–102.
- Schreiner, C.E., 1995. Order and disorder in auditory cortical maps. *Curr. Opin. Neurobiol.* 5, 489–496.
- Schuller, G., Covey, E., Casseday, J.H., 1991. Auditory pontine grey: connections and response properties in the horseshoe bat. *Eur. J. Neurosci.* 3, 648–662.
- Steriade, M., 2000. Corticothalamic resonance, states of vigilance and mentation. *Neuroscience* 101, 243–276.
- Suga, N., Xiao, Z., Ma, X., Ji, W., 2002. Plasticity and corticofugal modulation for hearing in adult animals. *Neuron* 36, 9–18.

- Sun, X., Chen, Q.C., Jen, P.H.-S., 1996. Corticofugal control of central auditory sensitivity in the big brown bat, *Eptesicus fuscus*. *Neurosci. Lett.* 212, 131–134.
- Treisman, A., 1996. The binding problem. *Curr. Opin. Neurobiol.* 6, 171–178.
- Ulinski, P.S., 1983. Dorsal Ventricular Ridge. A Treatise on Forebrain Organization in Birds and Reptiles. Wiley, New York.
- Villa, A.E.P., Rouiller, E.M., Simm, G.M., Zurita, P., de Ribaupierre, Y., de Ribaupierre, F., 1991. Corticofugal modulation of the information processing in the auditory thalamus of the cat. *Exp. Brain Res.* 86, 506–517.
- Weedman, D.L., Ryugo, D.K., 1996. Pyramidal cells in primary auditory cortex project to cochlear nucleus in rat. *Brain Res.* 706, 97–102.
- Weinberg, R.J., 1997. Are topographic maps fundamental to sensory processing? *Brain Res. Bull.* 44, 113–116.
- Winer, J.A., 1992. The functional architecture of the medial geniculate body and the primary auditory cortex. In: Webster, D.B., Popper, A.N., Fay, R.R. (Eds.), *Springer Handbook of Auditory Research. The Mammalian Auditory Pathway: Neuroanatomy*, vol. 1. Springer, New York, pp. 222–409.
- Winer, J.A., 2005. Three systems of descending projections to the inferior colliculus. In: Winer, J.A., Schreiner, C.E. (Eds.), *The Inferior Colliculus*. Springer, New York, pp. 231–247.
- Winer, J.A., Larue, D.T., 1987. Patterns of reciprocity in auditory thalamocortical and corticothalamic connections: study with horseradish peroxidase and autoradiographic methods in the rat medial geniculate body. *J. Comp. Neurol.* 257, 282–315.
- Winer, J.A., Larue, D.T., 1996. Evolution of GABAergic circuitry in the mammalian medial geniculate body. *Proc. Natl. Acad. Sci. USA* 93, 3083–3087.
- Winer, J.A., Prieto, J.J., 2001. Layer V in cat primary auditory cortex (AI): cellular architecture and identification of projection neurons. *J. Comp. Neurol.* 434, 379–412.
- Winer, J.A., Schreiner, C.E., 2005. The central auditory system: a functional analysis. In: Winer, J.A., Schreiner, C.E. (Eds.), *The Inferior Colliculus*. Springer, New York, pp. 1–68.
- Winer, J.A., Larue, D.T., Huang, C.L., 1999. Two systems of giant axon terminals in the cat medial geniculate body: convergence of cortical and GABAergic inputs. *J. Comp. Neurol.* 413, 181–197.
- Winer, J.A., Diehl, J.J., Larue, D.T., 2001. Projections of auditory cortex to the medial geniculate body of the cat. *J. Comp. Neurol.* 430, 27–55.
- Winer, J.A., Larue, D.T., Diehl, J.J., Hefti, B.J., 1998. Auditory cortical projections to the cat inferior colliculus. *J. Comp. Neurol.* 400, 147–174.
- Winer, J.A., Miller, L.M., Lee, C.C., Schreiner, C.E., 2005. Auditory thalamocortical transformation: structure and function. *Trends Neurosci.* 28, 255–263.
- Witter, M.P., Groenewegen, H.J., 1986. Connections of the parahippocampal cortex in the cat. III. Cortical and thalamic efferents. *J. Comp. Neurol.* 252, 1–31.
- Wong, D., Kelly, J.P., 1981. Differentially projecting cells in individual layers of the auditory cortex: a double-labeling study. *Brain Res.* 230, 362–366.
- Yeomans, J.S., Frankland, P.W., 1996. The acoustic startle reflex: neurons and connections. *Brain Res. Rev.* 21, 301–314.