

Chapter 2

A Profile of Auditory Forebrain Connections and Circuits

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Abbreviations

AA	amygdala, anterior nucleus	CM	central medial nucleus
AAF	anterior auditory field	CM	central medial/caudomedial auditory cortical area
ABm	basomedial nucleus of the amygdala	CN	central nucleus of the inferior colliculus
ACe	central nucleus of the amygdala	cNB	central narrowband module in AI
AD	anterior part of the DCN	CP	cerebral peduncle
AES	anterior ectosylvian area	Cu	cuneiform nucleus
aes	anterior ectosylvian sulcus	D	dorsal nucleus of the MGB <i>or</i> dorsal narrowband modules in AI
AI	primary auditory cortex	d1–d4	deep dorsal nucleus of the MGB
AIP	anterolateral periolivary nucleus	DD	dorsal cortex of the inferior colliculus
APt	anterior pretectum	DC	caudal pole of the inferior colliculus
AII	second auditory cortex	DCa	dorsal cochlear nucleus
AM	anterior medial nucleus	DCN	dorsal cochlear nucleus, fusiform cell layer
AV	anterior ventral thalamic nucleus	DF	dorsal nucleus of the lateral lemniscus
AV	anteroventral cochlear nucleus	DL	dorsolateral periolivary nucleus
Ava	anteroventral cochlear nucleus, anterior part	DIP	dorsal cochlear nucleus, molecular layer
BB	broadband	DM	dorsomedial periolivary nucleus
BM	amygdala, basomedial nucleus	DmP	dorsoposterior auditory area of cat
BIC	brachium of the inferior colliculus	DP	dorsal superficial nucleus of the MGB
BI	amygdala, basolateral nucleus	DS	Doppler-shifted constant frequency region
C	caudal <i>or</i> C layer of the lateral geniculate body	DSCF	dorsal auditory zone
Ca	caudate nucleus	DZ	posterior ectosylvian gyrus, dorsal part
CBM	cerebellum	ED	excitatory-excitatory binaural interaction
CC	caudal cortex of the inferior colliculus	EE	posterior ectosylvian gyrus, intermediate part <i>or</i> excitatory-inhibitory binaural interaction
CC	corpus callosum	EI	
CF,CF-CF	constant frequency cortical area	En	entopeduncular nucleus
CF	characteristic frequency	EP	posterior ectosylvian gyrus
CI	claustrum	EV	posterior ectosylvian gyrus, ventral part
DF	dorsal fringe auditory cortical area	EW	Edinger-Westphal nucleus
DI–DIV	layers of dorsal cortex of inferior colliculus	FF	fields of Forel
DM	dorsomedial auditory cortical area	FM	frequency modulated
CG	central gray	FM-FM	frequency-modulated auditory cortical area
CIC	commissure of the inferior colliculus	FM ₁ -FM	first harmonic frequency-modulated auditory cortical area
		FM ₁ -FM ₂	first harmonic, second harmonic frequency-modulated auditory cortical area
		FM ₁ -FM ₃	first harmonic, third harmonic frequency-modulated auditory cortical area

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FM ₁ -FM ₄	first harmonic, fourth harmonic frequency-modulated auditory cortical area	Pom	medial part of the posterior group
GP	globus pallidus	Pt	pretectum
Ha	habenula	Pu	pulvinar nucleus
Hip	hippocampus	Pv	posteroventral cochlear nucleus
HiT	habenulointerpeduncular tract	PvO	posteroventral cochlear nucleus, octopus cell layer
IC	inferior colliculus	Py	pyramidal tract
ICa	internal capsule	R	rostral
IcT	intercollicular tegmentum	R	rostral auditory area of squirrel <i>or</i> monkey
IL	intermediate nucleus of the lateral lemniscus	Ra	raphe
In	insular cortex	RF	reticular formation
IIN	intralaminar thalamic nuclei	Rh	rhomboid nucleus
Int	thalamic intralaminar nuclei	RL	rostral lateral auditory are in monkey
IT	intercollicular tegmentum	RN	red nucleus
La	lateral nucleus of the amygdala	RP	rostral pole nucleus of the inferior colliculus <i>or</i> MGB
LC	lateral cortex of the inferior colliculus	Sa	nucleus sagulum
LD	lateral dorsal nucleus	SC	superior colliculus
LGB,LGBd	lateral geniculate body, dorsal part	SCP	superior cerebellar peduncle
LGBv	lateral geniculate body, ventral part	SCPX	decussation of the superior cerebellar peduncle
LM	lateral medial nucleus	SF	suprasylvian fringe area
LMN	lateral mesencephalic nucleus	SF/daz	suprasylvian fringe/dorsal auditory zone
LN	lateral nucleus of the inferior colliculus	SGS	superficial gray layer of superior colliculus
LP	lateral posterior nucleus	SGi	intermediate gray layer of superior colliculus
LS	lateral superior olive	SGP	deep layer of superior colliculus
LT	lateral nucleus of the trapezoid body	Sg	supragenulate nucleus
M	medial division of the MGB	Sgl/SI	supragenulate nucleus, lateral part
MCP	middle cerebellar peduncle	Sgm/S	supragenulate nucleus, medial part
MGB	medial geniculate body	SN	substantia nigra
ML	medial lemniscus	SNC	substantia nigra, <i>pars compacta</i>
MLF	medial longitudinal fasciculus	SNL	substantia nigra, <i>pars lateralis</i>
MR	mesencephalic reticular formation	SNR,SNr	substantia nigra, <i>pars reticulata</i>
MRF	mesencephalic reticular formation	Spf	subparafascicular nucleus
MS	medial superior olive	SpN	suprapeduncular nucleus
MT	medial nucleus of the trapezoid body	TA	temporal auditory area of squirrel
Mv	medioventral thalamic nucleus	TE1	primary auditory cortex of rat
MZ	marginal zone of MGB	TE2	second auditory cortex of rat
NB	narrowband	TE3	third auditory cortex of rat
NBIC	nucleus of the brachium of the inferior colliculus	Te	temporal cortex
NRTP	reticular tegmental nucleus of the pons	TL	lateral nucleus of the trapezoid body
OT	optic tract	TM	medial nucleus of the trapezoid body
OR	optic radiation	TRN	thalamic reticular nucleus
Ov	<i>pars ovoidea</i> of the ventral division of the MGB	Tr	trochlear nerve
P	posterior auditory field	TV	ventral nucleus of the trapezoid body
PC	posterior commissure	V	<i>pars lateralis</i> of the ventral division <i>or</i> ventral <i>or</i> ventral auditory area
Pd	posterodorsal division of the DCN	VA	ventroanterior auditory cortical area
PeN	periolivary nuclei	Vb	ventrobasal complex
PHy	posterior hypothalamus	Ve	ventral auditory area
PL	posterior limitans nucleus	VF	ventral fringe auditory cortical area
PL	posterior lateral auditory area of bushbaby	VL	ventral nucleus of the lateral lemniscus
PLSS	posterior lateral suprasylvian area	VLa	ventral lateral thalamic nucleus
Pl	paralemniscal zone	VI	ventrolateral nucleus of the MGB
PN	pontine nuclei	VM	ventral medial thalamic nucleus
Pol	rostral pole of the MGB		

Vm	mesencephalic nucleus of the trigeminal
VmP	ventromedial periolivary nucleus
VP	ventral posterior auditory area
Vpl	ventral posterolateral nucleus
Vpm	ventral posteromedial nucleus
VT	ventral nucleus of the trapezoid body
wm	white matter
ZI	zona incerta
I-IV	layers of the dorsal cortex of the inferior colliculus
I-VI	layers of cerebral cortex
α	layer IVC α in primary visual cortex
β	layer IVC β in primary visual cortex
c	layer IVc in primary visual cortex
35/36	perirhinal cortex

1 Profiling the Auditory Forebrain

Establishing rules for auditory information processing requires knowledge of the physiology of the neurons, their connections, and of how local circuits shape signals. When available, as in the cochlear nucleus (Cant and Benson 2003), such profiles underlie plausible models of receptive field (RF) genesis (Davis and Young 2000), serial information transfer (Smith et al. 1993), and feature detection (Nelken 2002). Progress in this endeavor in the medial geniculate body (MGB) and auditory cortex (AC) since 1990 is the subject of this review, and it is prerequisite to understanding how auditory thalamic (Senatorov and Hu 2002), cortical (de Ribaupierre 1997; Rouiller and Welker 2000), and sub-cortical sites (Winer 2006) interact. A second theme is the function of massive, focal, and precise corticocortical (Lee and Winer 2005) and corticofugal (Winer 2006) projections. The emerging picture of multiple ascending and descending pathways with intricate convergence and divergence patterns (Smith and Spirou 2002) and robust interneuronal substrates for modulation (Huang et al. 1999) is at odds with more serial models of information flow (Brandner and Redies 1990). Each section summarizes views prevailing circa 1990, then assesses subsequent studies in cat, rodents, bats, and primates. For areas with little change earlier accounts are available (Clarey et al. 1992; Winer 1992).

2 Medial Geniculate Body Organization

The MGB is part of a neuronal network extending from the cochlear nucleus to the cerebral cortex (Winer and Schreiner 2005) (Fig. 2.1). As such, it is no more independent of the midbrain or cortex than the inferior colliculus is from

the cochlear nucleus. A principled analysis of MGB function must therefore integrate the architecture of its neurons, their physiological responses, the main extrinsic influences, the primary neurochemical components, and, when available, comparative functional adaptations.

2.1 Ventral Division

The number of MGB neurons relative to the IC is species specific, ranging from a 1:5 ratio in rat (Kulesza et al. 2002) to structures of more equal volume in the cat (Berman and Jones 1982). Assumptions that a nucleus (or area) is analogous or homologous require caution because of species-specific internal differences of unknown significance (Winer 1984b; Morest and Winer 1986; Winer and Larue 1996).

Many contemporary studies recognize three MGB territories: a large ventral division, which constitutes the principal part, and smaller dorsal and medial divisions; each division differs in size and internal architecture (Winer 1992) (Fig. 2.1). The ventral division can be construed as the thalamic target and representative of the disc-shaped neurons of the central nucleus of the IC, and it contains bushy tufted cells with a characteristic fibrodendritic arrangement. Bushy cells target (McMullen et al. 2005) the non-pyramidal (and other) AC neurons (Winer 1984a; Smith and Populin 2001). Bushy cells share with disc-shaped neurons a morphologically polarized dendritic axis (Oliver 2005), and the tectothalamic axon plexus terminates in ordered arrays (Wenstrup and Leroy 2001) that embody IC tonotopy (Merzenich and Reid 1974) and critical bands (Schreiner and Langner 1997), while enabling novel or enhanced representations of particular physiological features such as species-specific elements of the echolocation call (Wenstrup 1999). This is consistent with bushy cell variability within (Cetas et al. 2003) and between (Winer and Wenstrup 1994) species. Laminar regularity in many species is clearest in the low-frequency (lateral) part of the ventral division, and less so dorsomedially, where passing fibers complicate the neuropil (Morest 1965a) and affect local fibrodendritic patterns.

Ventral division neurons respond to stimulation of the brachium of the IC with single spikes and at the shortest latencies in the MGB (Hu 1995); their membrane properties and response properties contrast with those in the dorsal division (see below). One map of characteristic frequency is present in the cat ventral division, and it spans ~ 9 octaves (Imig and Morel 1985b); neuron types in barbiturate anesthetized animals respond with onset, onset with inhibition, offset, on-off, sustained, and complex responses, of which onset cells were most common and on-off rarest (Cetas et al. 2002). The ventral division contains a further

caudo-rostral gradient of sharpness of tuning (Rouiller et al. 1989) whose significance is unknown. The classes of monaural and binaural responsive MGB neurons resemble those in AC (Samson et al. 2000) and there is evidence for binaural modules (Middlebrooks and Zook 1983) related to AC.

Damage to the ventral division and related thalamic regions has species-specific consequences, leaving rodent sound localization intact (Kelly and Judge 1985), while severely impairing human localization and attention (Wester et al. 2001).

2.2 Dorsal Division

The dorsal division differs from the ventral division: it has more subdivisions, greater neuronal diversity, stellate rather than bushy cells predominate, it contains at least two varieties of interneuron, the principal inputs are from IC and AC subdivisions with less regular tonotopic organization, its cells have broader tuning curves and temporally extended responses to tonal stimuli, damage to it does not affect sound localization, and the neurons are implicated in complex perceptual behaviors.

The dorsal division consists of several nuclei that comprise the caudal, dorsal, dorsomedial, and anterodorsal facets of the MGB (Winer and Morest 1983b). A cardinal feature is the neuronal diversity, including highly tufted cells among which neurons with radiate dendritic fields mingle; this disrupts any laminar pattern. Such heterogeneity extends to the suprageniculate nucleus, where only radiate neurons conspicuously larger are found, and the posterior limitans nucleus, whose major type of principal cell has long, sparsely spinous dendrites. Golgi type II cells are plentiful, with evidence for a small, and a larger, much rarer, class (Huang et al. 1999). Ultrastructural arrangements feature γ -aminobutyric acid-positive (GABAergic) axons presynaptic to immunonegative dendrites, GABAergic profiles postsynaptic to GABA-negative input, and presynaptic dendrites (Coomes et al. 2002), each reminiscent of other thalamic nuclei (Sherman and Guillery 2000).

There is physiological diversity to dorsal division function consonant with its structural complexity. Major features

are a tonotopic organization favoring high frequencies (Bordi and LeDoux 1994a), wide tuning curves (Calford 1983), protracted excitatory–inhibitory oscillations (He 2003), and a bursting rather than the single-spiking firing mode (He and Hu 2002) prevalent in the ventral division (Hu 1995). The intrinsic membrane profile of rat ventral and dorsal division neurons is similar except for a depolarizing sag potential in ventral division cells, while suprathreshold excitatory responses are confined to tufted cells (Bartlett and Smith 1999). This implies continuity among MGB physiological parameters irrespective of the cell's cortical target (Winer et al. 1999b). Moreover, pairs of dorsal division neurons show the most independence of discharge in the MGB (Kvasnak et al. 2000b), suggesting that they may not encode a singular or continuous sensory domain.

2.3 Medial Division

The distinction between lemniscal and extralemniscal streams is embodied by the medial division (Morest 1965b). Auditory input is only one of several modalities that converge upon it, it has no map of characteristic frequency, nor architectonic subdivisions, and it projects to many cortical areas including auditory and non-auditory fields, and subcortically as well.

The medial division comprises the ventromedial aspect of the MGB and extends from nearly the caudal pole almost to the rostral pole. Its neurons are the most diverse in the MGB and comprise a wide range differing in size, shape, and dendritic complexity and which are embedded in heterogeneous axons (Winer and Morest 1983a). Dendritic fields radiate widely or have tufts polarized axially.

Medial division cells in anesthetized preparations respond to pure tones with extended bursts and symmetric interval histograms (Kvasnak et al. 2000a). Single cell tuning is typically broad (Calford 1983), often multisensory and convergent, and potentiated by polymodal activation (Bordi and LeDoux 1994b). Finally, they show more RF plasticity than other MGB cells (Lennartz and Weinberger 1992) and are implicated in autonomic learning paradigms using acoustic cues (McEchron et al. 1996).

Fig. 2.1 (continued) division (DS, D, etc.) has the most nuclei, and the medial division (M) is a single nucleus with several cell types (Huang et al. 1999). **c** Representative MGB neurons. **1**, A thalamocortical (TC) neuron in the ventral division, with highly polarized dendritic tufts. **2**, An elongated cell in the posterior limitans nucleus, with smooth dendrites. **3**, A suprageniculate TC neuron, with sparse appendages and

a soma exceeded only by medial division magnocellular neurons. **4**, A Golgi type II cell with a local axon. **5**, A rare, much larger type II neuron. Rapid Golgi method, planapochromat, N.A. 1.32, $\times 2000$. **d** Canonical MGB circuitry showing multiple, convergent, chemically specific inputs to a typical bushy neuron, including interneuronal contributions (Winer et al. 1996)

3 Auditory Thalamic Neurotransmitter Profile

The discovery of thalamic Golgi type II interneurons (Jacobson 1975) was a watershed in understanding sensory information sent to neocortex is modulated by local circuits (Scheibel and Scheibel 1966). Characterizing these neurons in the MGB (Morest 1971) was a vital step in studying thalamocortical (TC) relations (Sherman and Guillery 1996) and clarified the genesis and control of thalamic oscillations (Jones 2002).

3.1 Excitatory Amino Acids

A major tectothalamic component is glutamatergic axons acting on *N*-methyl-D-aspartate (NMDA) and non-NMDA receptors, in both lemniscal and non-lemniscal streams (Hu et al. 1994).

3.2 Gamma-Aminobutyric Acid

GABA is the principal compound implicated in auditory thalamic inhibition and disinhibition. Immunocytochemical analysis finds a subdivision-specific concentration of GABAergic neurons and axon terminals (puncta), with the cat ventral division having 33% such cells, the dorsal division 26%, and the medial division 18%; ventral division puncta were dense and primarily medium sized, those in the dorsal division were variable, ranging from small to giant, while medial division endings were sparser and heterogeneous (Figs. 2.2 and 2.3). The GABAergic neurons are ~10 μ m in diameter and correspond to neurons in Golgi preparations that have small somata and long, slender dendrites with stringy appendages (Huang et al. 1999); a second, larger and much rarer type II cell is also been recognized (Winer and Morest 1983b).

Three sources of GABA are known: the (two varieties of) intrinsic neurons, the thalamic reticular nucleus projection (Crabtree 1998), and robust feedforward projections from all inferior colliculus (IC) subdivisions (Winer et al. 1996), each contributing to MGB neuropil (Morest 1975). The specific physiological impact of each GABAergic source to function remains unclear. A clue to this complexity is the broad afferent tuning of dorsal (Aitkin and Dunlop 1968) and medial division (Aitkin 1973) neurons, processes which can hardly reflect inhibitory sharpening despite the many GABAergic neurons and extrinsic sources of GABA.

Possible parallels to intrinsic circuit functions in an analogous structure come from the lateral geniculate body, where dendrodendritic synapses between type II cells and principal

neurons modulate TC transmission via metabotropic and ionotropic receptors (Cox and Sherman 2000) and glutamatergic processes (Cox et al. 1998). Analogous mechanisms may operate in the auditory thalamus (Kudoh et al. 2002). A modality-specific role in attentional control is proposed for the thalamic reticular nucleus (McAlonan et al. 2000) that could reflect dynamic shifts in its discharge behavior (Bazhenov et al. 2000). IC GABAergic projections to the MGB evoke a GABA_A-related IPSP/EPSP (inhibitory/excitatory postsynaptic potential) sequence followed by a GABA_B IPSP, suggesting a rapid monosynaptic IC influence on TC transmission. The differential effects of such activation may reflect the several types of GABA-positive IC neurons (Oliver et al. 1994). These observations are compatible with models for bat temporal processing which incorporate parallel GABA_A/GABA_B streams (Llano and Feng 2000).

Lateral geniculate body interneurons studied in vitro show short action potentials, can produce action potentials >500 Hz without robust adaptation of output, and exhibit a regenerative, low-threshold response extending from depolarization below threshold to multiple spikes. They are depolarized by glutamate, kainate, quisqualate, and NMDA, whereas GABA blocked action potentials and baclofen (a GABA_B agonist) hyperpolarized membranes weakly and blocked spontaneous discharge. Acetylcholine hyperpolarized membrane potentials and serotonin affected a subset by enhancing spontaneous discharge, and other compounds have no effect on membrane behavior at rest or spontaneous rate (adenosine, nor adrenaline) or elicit minute, protracted depolarization (histamine). Suggested roles for these interneurons include local inhibitory influences driven by influences arising in the retina, cortex, and brain stem (Pape and McCormick 1995). In the rat ventral division muscarinic agonists induce extended membrane depolarization that block burst responses (Mooney et al. 1995) in a nucleus with few Golgi type II cells (Winer and Larue 1988).

4 Medial Geniculate Body Connections

At least five connectional roles for the MGB can be identified. First, it is the target of IC inputs via convergence and divergence of chemically specific inputs, which it then modifies with intrinsic networks. A second role is redistribution of information to cortical and subcortical targets. Third, brain stem extralemniscal input creates parallel streams. Fourth, the corticothalamic pathways shape MGB representations and may modify ongoing processing. Finally, a small thalamotectal system gives MGB neurons direct access to the IC. These several pathways suggest a view of thalamic

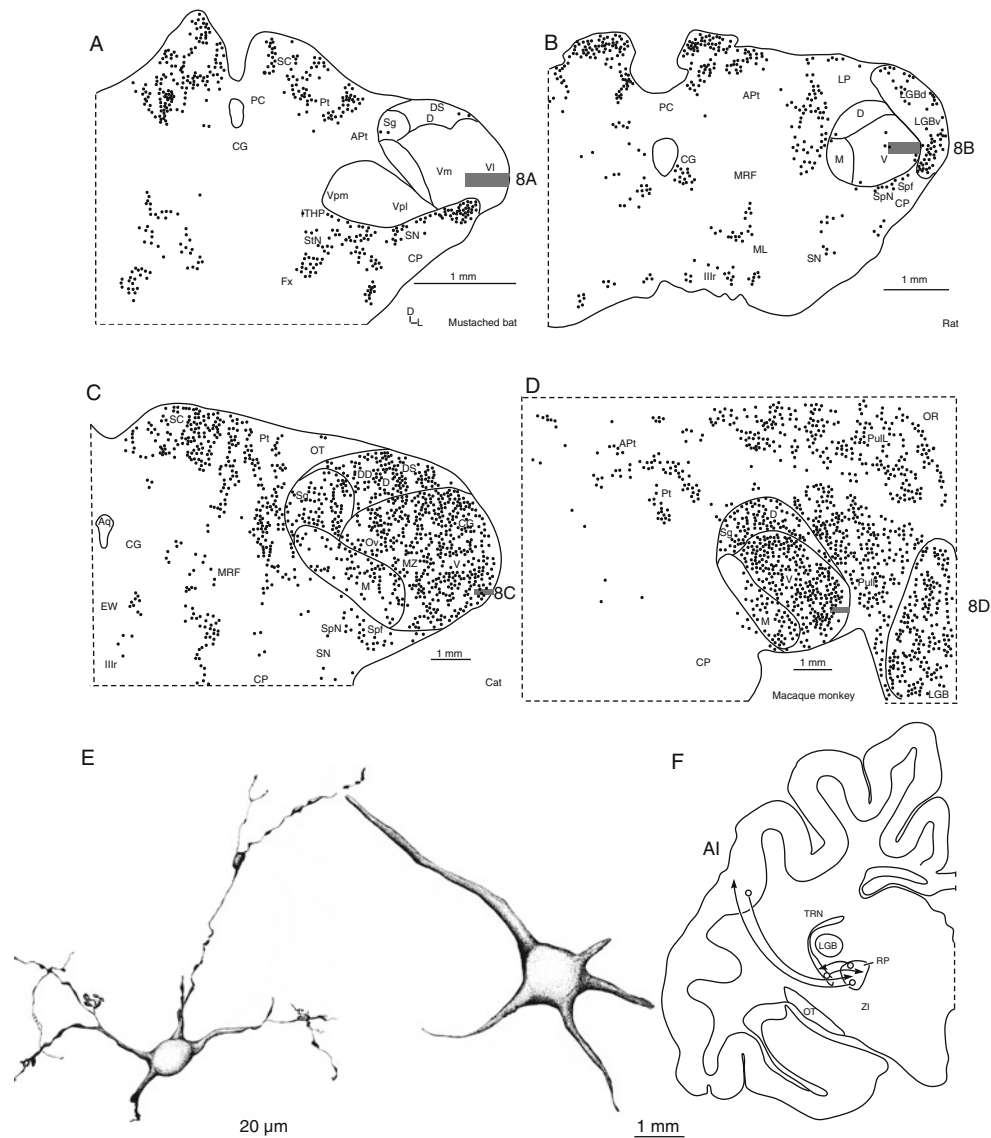


Fig. 2.2 γ -aminobutyric acid-containing (GABAergic) cells in the MGB. **a** In the mustached bat, the few GABAergic neurons present concentrate in the dorsal division, though there are abundant puncta. **b** In the rat, MGB GABAergic neurons are sparse, ~1% of the total, and relatively fewer than in the LGBd. **c** Thalamic GABAergic cells are abundant in the cat, representing ~25% of MGB cells. **d** In the rhesus, the proportion of GABAergic cells is at least equal to that in the cat **c**. **e** Representative GABAergic neurons, showing the more numerous small variety (*left*) corresponding to the classic Golgi type II cell (Fig. 2.1c:4).

The second, much larger type (*right*) is far less common and its somatodendritic profile corresponds to the equally rare large Golgi type II cell (Fig. 2.1c:5). **f** Possible interconnections between the MGB and thalamic reticular nucleus, and TC and corticothalamic circuits. The chemical sign of the specific connections is shown in Fig. 2.1d; TC and corticofugal connections are thought to be excitatory. Plots made from sections 30 μm thick and immunostained with antibodies to glutamic acid decarboxylase (Winer and Wenstrup 1994)

processing incompatible with the concept of the MGB as a relay nucleus.

4.1 Tectothalamic Pathway

This principal ascending input to the MGB is massive, arising from all IC subdivisions and reaching all MGB subdivisions. Projections are origin and target specific, and

there is not a direct relation between a particular IC and MGB division that does not involve other subdivisions of each. Moreover, the tectothalamic projections are bilateral and asymmetrical in density. There are also parallel, chemically specific IC inputs (Wenstrup 2005).

The lemniscal pathway is represented by a massive topographic input from the IC central nucleus that reaches all tonotopic (laminated) parts of the MGB (Calford and Aitkin 1983), where the axons form sheets contributing to restricted

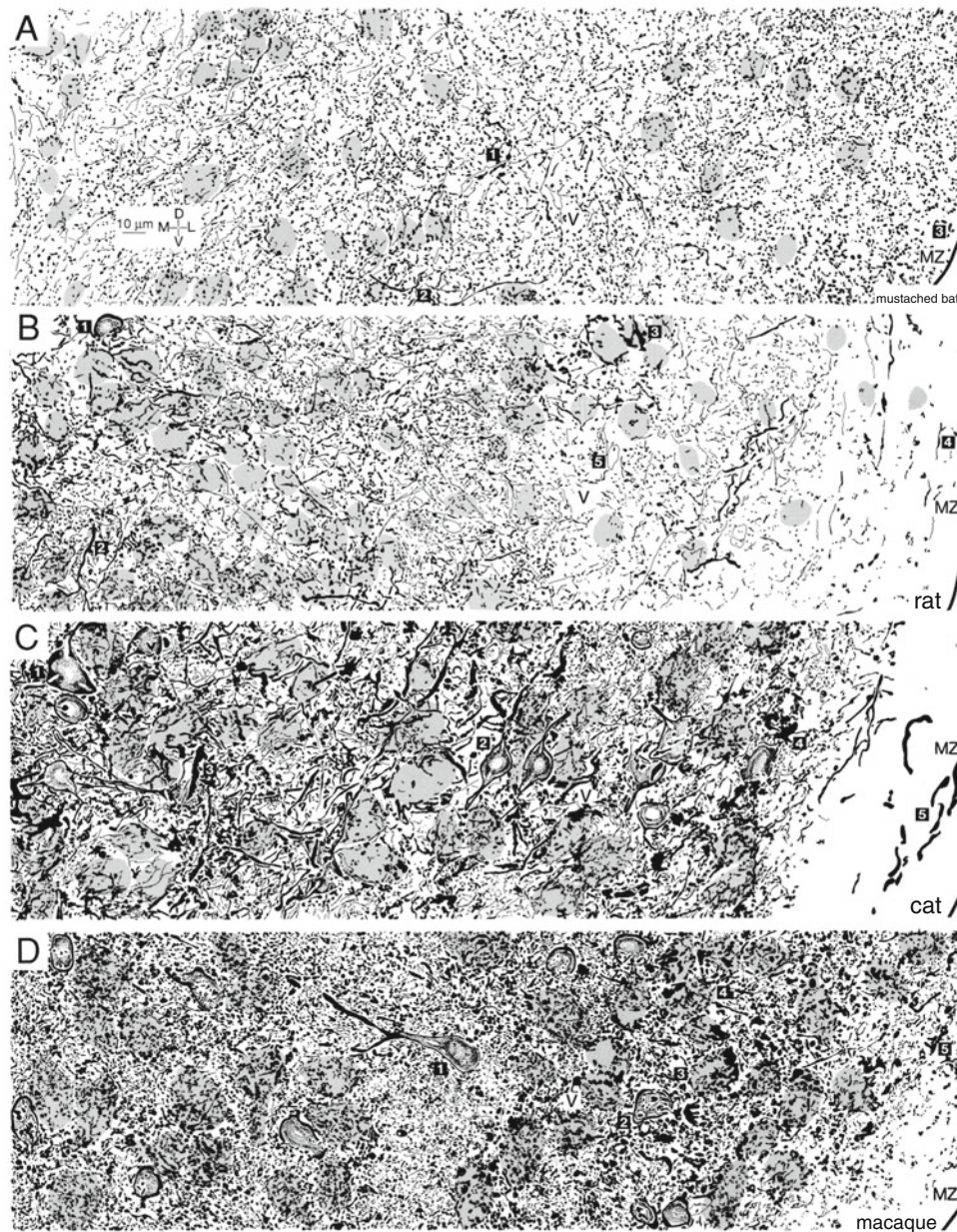


Fig. 2.3 GABAergic axon terminals *fine dots* immunostained neurons (*dark stippled* profiles), and immunonegative MGB neurons in the ventral division in four species; cf. Fig. 2.2 *insets* for loci. Planapochromat, N.A. 1.32, $\times 2000$. (a) The mustached bat ventral division is virtually devoid of GABAergic neurons and contains a fine plexus of puncta. 1, Beaded axons. 2, Axons projecting laterally. 3, The bat marginal zone (MZ) has more puncta than do the other species (b–d). b The rat has a few GABAergic neurons (1), some thick, possibly ascending preterminal fibers (2), some coarse terminals (3), just a few MZ endings, and many extremely fine ($\sim 0.5 \mu\text{m}$ in diameter) fibers (5). c There is a marked increase in neuropil density in

the cat, with an unusually large somatodendritic profile (1) possibly corresponding to a large type II cell (Figs. 2.1c:5 and 2.2e, right). Many GABAergic neurons lie parallel to fibrodendritic laminae (2), some thick axons are present (3) as well as giant ones (4), and the marginal zone has much thicker preterminal fibers (5) than does the rat (b). d The rhesus ventral division has an even denser GABAergic neuropil organization than the cat c. Some GABAergic cells have immunostaining to their secondary dendrites (1), and puncta range from granular to far larger and clustered (2), often virtually engulfing GABA-negative somata (3), and with complex terminal axosomatic architectures (4)

synaptic arrays (McMullen et al. 2005), and other regions (medial division) whose representation of characteristic frequency is far less ordered (Rouiller et al. 1989). Projections from IC subdivisions (lateral cortex and dorsal cortex) with

non-auditory affiliations (Syka et al. 2000) and from lateral tegmental regions (Morest 1965b) reach other MGB subdivisions beside those with a tonotopic representation (Fig. 2.4).

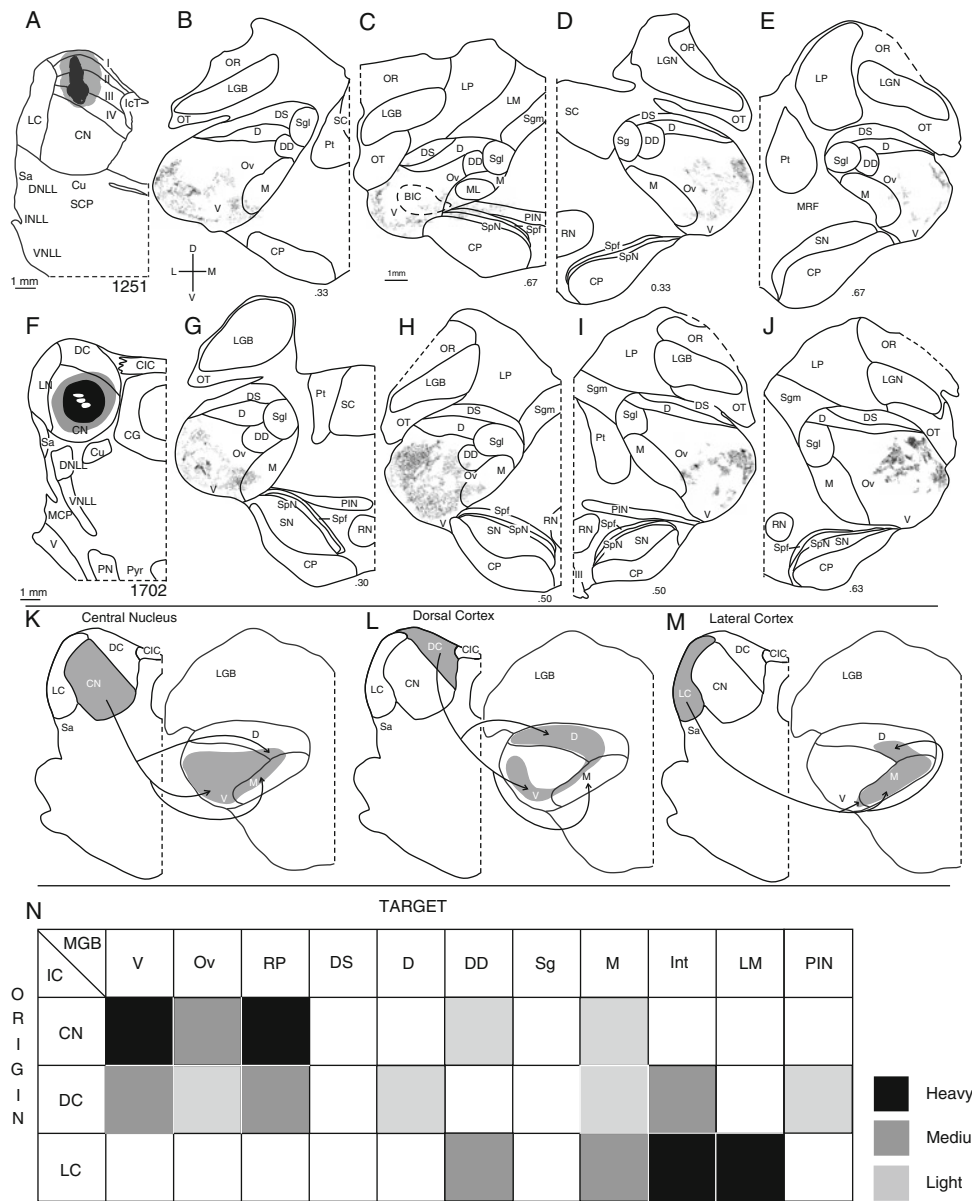


Fig. 2.4 Some inferior colliculus (IC) inputs to the cat MGB. **a–e** A biotinylated dextran amines (BDA) deposit in the IC dorsal cortex (**I–IV**) labels a broad, ipsilateral swath of the ventral division frequency representation in the MGB (Imig and Morel 1985b) (**V**, **Ov**) and a smaller, less continuous, and overlapping crossed projection; note the ipsilateral intralaminar (Spf, **PIN**) input. **f–j** A BDA injection in the central nucleus (CN), extending to its high frequency border (Merzenich and Reid 1974), labels nearly the entire ventral division (**h**)

exclusively, with appreciable contralateral input (**j**). **k–m** Schematics of tectothalamic input showing that each IC targets more than one MGB subdivision and that an MGB target receives convergent input from more than one IC source. **n** A schematic of cat tectothalamic anterograde (present results) and retrograde (Calford and Aitkin 1983) results, showing extensive convergence and divergence suggesting that the tectothalamic transformation is as individuated as the TC system (Winer et al. 2005)

Input from the IC targets principal thalamocortical neurons as well as Golgi type II cells (Morest 1975), a convergence that may well synchronize their temporal discharge behavior for the propagation of thalamic information to the neocortex. The type II neuron’s axon and the dendrites are presynaptic to the thalamocortical cells and might gate transmission as in the visual system (Cox and Sherman 2000). The cholinergic system (Caballero-Bleda et al. 1991) is associated with RF plasticity (Edeline and Weinberger 1992)

and the central adjustments ensuing from peripheral trauma (Kamke et al. 2003).

4.2 Extracollicular Projections

A monosynaptic projection from the small cell cap of the dorsal cochlear nucleus targets the MGB medial division (Malmierca et al. 2002). It may have a role in polymodal

and visuomotor processing and was seen in the chimpanzee (Strominger et al. 1977).

4.3 Thalamocortical System

The MGB may contain a single, complete map of characteristic frequency (Imig and Morel 1985b) or a few such representations (Imig and Morel 1985a), much like the visual thalamus (Malpeli and Baker 1975). How, then, are the (at least) five independent AC maps of the basilar membrane created (Reale and Imig 1980)? In areas AI (primary auditory cortex) and AAF (anterior auditory field), MGB input to the corresponding AC isofrequency contour arises from nearby thalamocortical neurons (Edeline 2003), few of which project to both fields even in experiments designed to maximize this possibility (Lee et al. 2004a). This suggests a conservation of thalamocortical input and its divergence to many areal targets.

As in the tectothalamic system, there is TC convergence and divergence, with single nuclei projecting to many fields and each field receiving input from more than one thalamic nucleus (Huang and Winer 2000) (Fig. 2.5). Such patterns likely contribute to the conservation of thalamic information in AC and to the emergence of new RF architectures and representations (Miller et al. 2001).

Few of the many AC fields have a topographic representation of characteristic frequency (Ehret 1997), implying that thalamic projections to areas without such maps might be less ordered than those to tonotopic fields. In fact, all TC projections to AC (and to non-auditory areas) are equally ordered and specific when assessed with three topographic metrics. Such topographic rules may have developmental implications (Lee and Winer 2005). Other aspects of TC organization are considered below (Section 6.1).

4.4 Thalamoamygdaloid System

Neurons from the MGB dorsal and medial divisions project to the lateral amygdaloid nucleus and nearby polar temporal cortex (Shinonaga et al. 1994). This permits of thalamofugal and corticofugal convergence in the lateral amygdala and confirms the different amygdaloid targets of specific AC subdivisions (Romanski and LeDoux 1993).

4.5 Thalamotectal System

This pathway permits thalamofugal access to midbrain targets. Neurons dispersed widely in the dorsal and medial

divisions of the MGB and in the posterior intralaminar system project to IC dorsal and lateral cortices (Kuwabara and Zook 2000; Senatorov and Hu 2002), regions implicated in multimodal convergence (Aitkin et al. 1994) and attention (Jane et al. 1965) and whose ascending projections reach the same thalamic regions that target non-primary AC (Winer et al. 2001) and the corticoamygdaloid stream (Romanski and LeDoux 1993).

4.6 Corticothalamic System

This is perhaps the largest cortical projection (Winer et al. 2001), rivaling the corticospinal system, and itself part of an even more massive corticofugal system that reaches nearly all levels of the auditory system (Winer 2006). It arises from every AC subdivision and follows many of the same rules that govern thalamocortical connectivity: an area projects to more than one thalamic target, and a thalamic subdivision receives input from more than one AC area. Corticothalamic axons are, likewise, origin and target specific, and comprise giant terminals (Bajo et al. 1995) which might enable thalamic access to cortex (Diamond et al. 1992) and which could interact with equally large GABAergic endings (Winer et al. 1999a). Despite significant exceptions, there is global thalamocortical-corticothalamic reciprocity (Winer and Larue 1987) suggesting powerful coupling between systems.

5 Auditory Cortex

Cortical layers are analogous to subcortical nuclei: each layer has a unique neuronal architecture, individuated connections, a specific neurochemical organization, and a particular functional arrangement. Given the many auditory areas in different species—three in rat (Shi and Cassell 1997), six in gerbil (Thomas and Lopez 2003), thirteen in cat (Lee and Winer 2005), and twelve in monkey (Hackett et al. 1998)—the prospective complexity of forebrain connectional relations is impressive (Fig. 2.6). Amplified as these relations are by sublaminal organization, neurotransmitter receptor diversity and synaptic plasticity, the task of dissecting AC functionally is formidable. It leaves open the question of species differences.

5.1 Supragranular Layers

Layer I has few neurons, >90% are GABAergic, and these are primarily in layer Ib and unexpectedly diverse

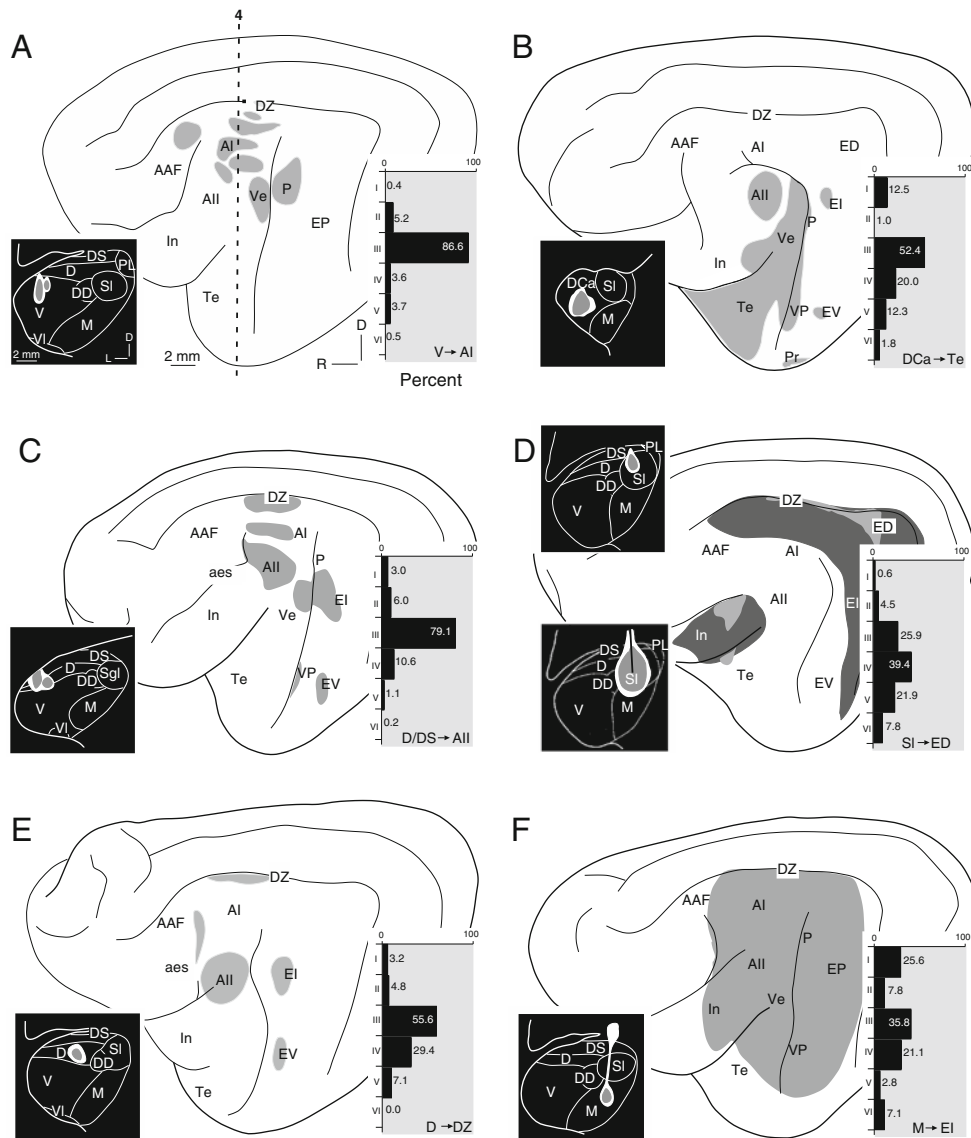


Fig. 2.5 Areal and laminar distribution of TC projections with BDA. **a** A deposit in the central part of the ventral division (*black inset*; V) labels multiple patches in AI and has a more continuous distribution in three other primary fields. *Right inset* on this and subsequent panels: distribution of boutons (cf. Fig. 2.9b) by layers, with >80% in layer III. **b** The caudal dorsal nucleus (DCa) targets primary (Ve) non-primary (EV) and limbic-related (Te) areas, and has a much more variable laminar pattern than the ventral division to AI projection (**a**). **c** The dorsal/dorsal superficial nucleus has as precise, and a similar, laminar organization as the ventral division to AI projection (**a**), but terminates only in non-primary, extralimbic fields. **d** Two experiments

with deposits in the lateral part of the supragenicular nucleus (*black inset*; SI) showing the consistency of TC labeling, its specificity (e.g., in area In but not Te, though both are limbic-related) and unique laminar distribution, with the heaviest input to layer IV in this small series, and significant labeling in 5/6 layers. **e** A deposit in the medial part of the dorsal nucleus (*black inset*; **d**) had a similar labeling pattern as in the lateral dorsal nucleus (**c**) except for AAF involvement, and a more equal layer III/IV distribution. **f** The medial division (*black inset*; M) has the broadest areal suite of projections, and a diverse laminar profile involving all layers in area EI. Modified from prior work (Huang and Winer 2000)

(Winer and Larue 1989). Layer Ia contains the apical dendrites of deep-lying pyramidal cells (Sousa-Pinto 1973) and the largest thalamocortical axons (Huang and Winer 1997).

Layer II is comparatively cell rich, has many pyramidal cells and some unique neurons (Winer 1985), and projects chiefly in the corticocortical system (Fig. 2.7).

5.2 Granular Layers

Layer III is eclipsed in size only by layer V, and pyramidal cells dominate layer IIIa (Winer 1984d) and non-pyramidal cells layer IIIb (Winer 1984c), where MGB input is near-maximal (Hashikawa et al. 1995; Huang and Winer 2000; Linke and Schwegler 2000; Kimura et al. 2003). It contains

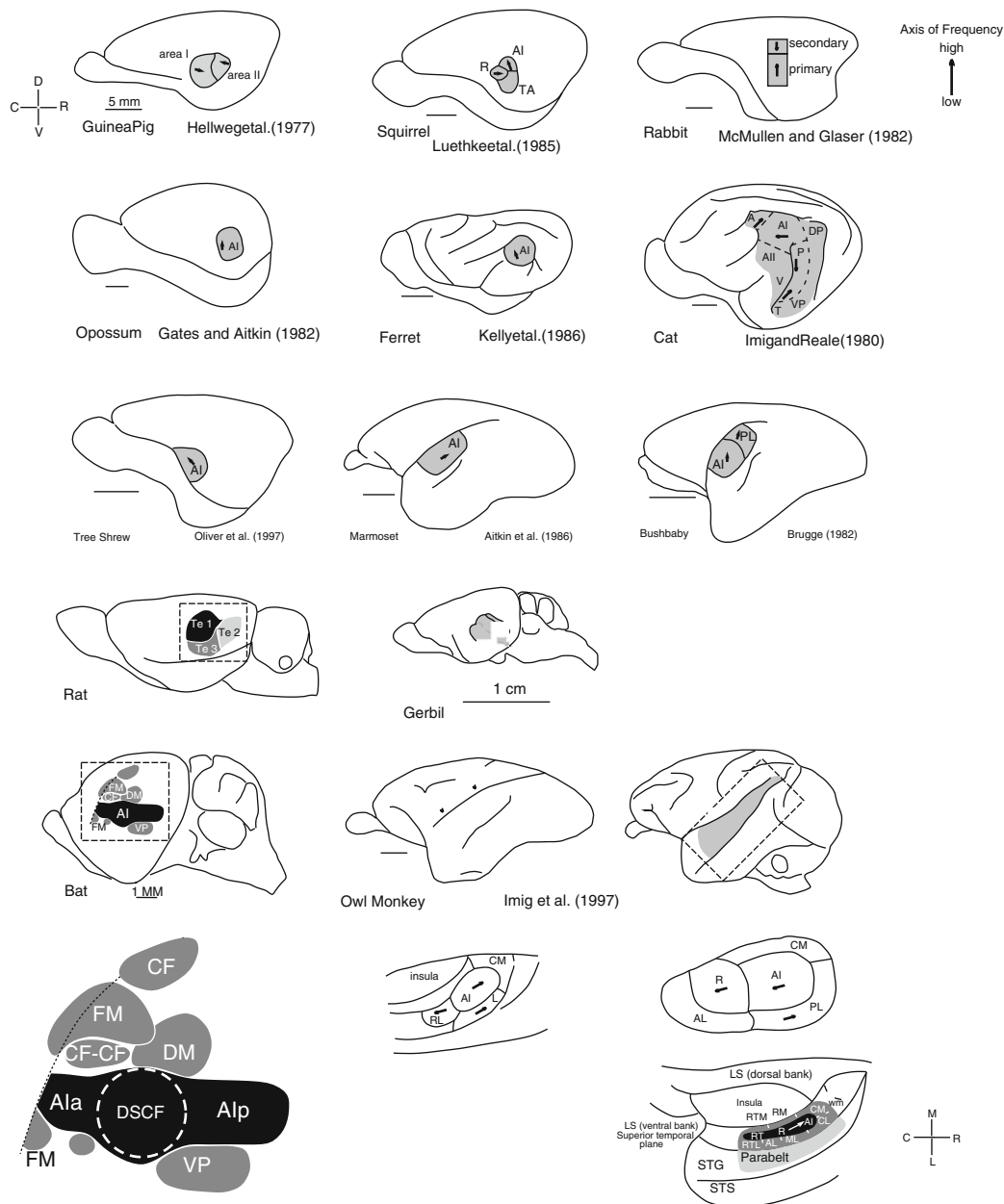


Fig. 2.6 Comparative physiological organization of mammalian AC. Arrows indicate the orientation of the tonotopic organization axis (increase of CF_s)

corticocortical feedforward (Thomas and Lopez 2003) and commissural projection cells and axons (Imig and Brugge 1978).

The major features of layer IV are its non-pyramidal neuronal population (Winer 1984a) (Fig. 2.8) which receives a dense MGB input (Smith and Populin 2001) (Fig. 2.9), and whose primary projection is local (Mitani et al. 1985).

corticocollicular projection cells (Winer and Prieto 2001). The neurons are diverse and the proportion of GABAergic cells is among the lowest in AC (Prieto et al. 1994b).

Layers VI and I are the only AC layers with horizontal cells (Radnikow et al. 2002), layer VI has the lowest proportion of GABAergic cells, and its chief subcortical target is the MGB (Prieto and Winer 1999; Winer et al. 2001).

5.3 Infragranular Layers

Layer V is the thickest AI layer, with three sublaminae: Va and Vc contain corticothalamic neurons, layer Vb has

6 Auditory Cortex Connectivity

The partition of extrinsic connections to AC is approximately 15% from the thalamus, 15% from the contralateral

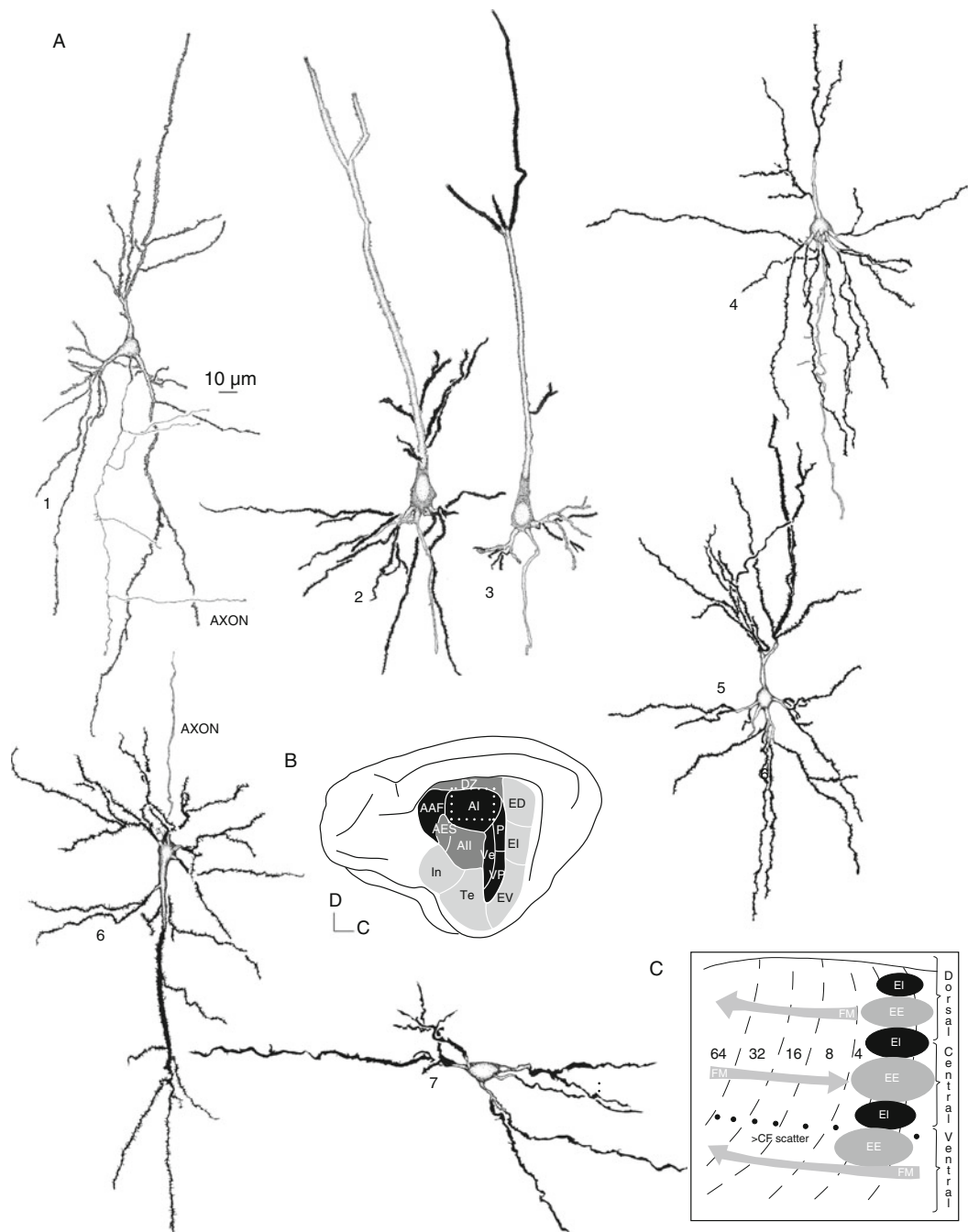


Fig. 2.7 Some types of AI neurons. Protocol for Figs. 2.7 and 2.8: Golgi-Cox method, 140 μm thick section, planachromat, N.A. 1.25, $\times 1000$. **a** 1, A small tufted pyramidal cell in layer Vb with a locally branched axon. 2, 3, Layer II medium-sized pyramidal cells with similar basal and different apical dendritic patterns. 4, A layer II pyramid with stellate basal processes. 5, A small bitufted pyramidal cell in layer V. 6, A layer V spiny inverted pyramidal cell with a vertical axon. 7, A layer VI horizontal cell. **b** Areal subdivisions in cat AC. *Black*,

tonotopic areas; *dark gray*, non-tonotopic areas; *light gray*, multimodal (ED, EI, EV) and limbic-related (In, Te) areas. *Dotted lines*, locus of inset in c. **c** Schematic depiction of AI representations. *Dashed lines*, CF bands; EE, EI, binaural summation and suppression subregions; FM, frequency-modulated preference axis; CF scatter, axis of dispersion of characteristic frequency tuning; dorsal, central, ventral, AI subregions with different tuning properties, of which the sharpest is in the central subarea

hemisphere, and 70% from ipsilateral cortex (Lee et al. 2004a; Lee et al. 2004b), and each source has a similar topography of precision irrespective of the degree of

tonotopic representation in origin or target (Lee and Winer 2005). The corticofugal pathways represent, with the corticocortical projections, the largest projection system (Winer

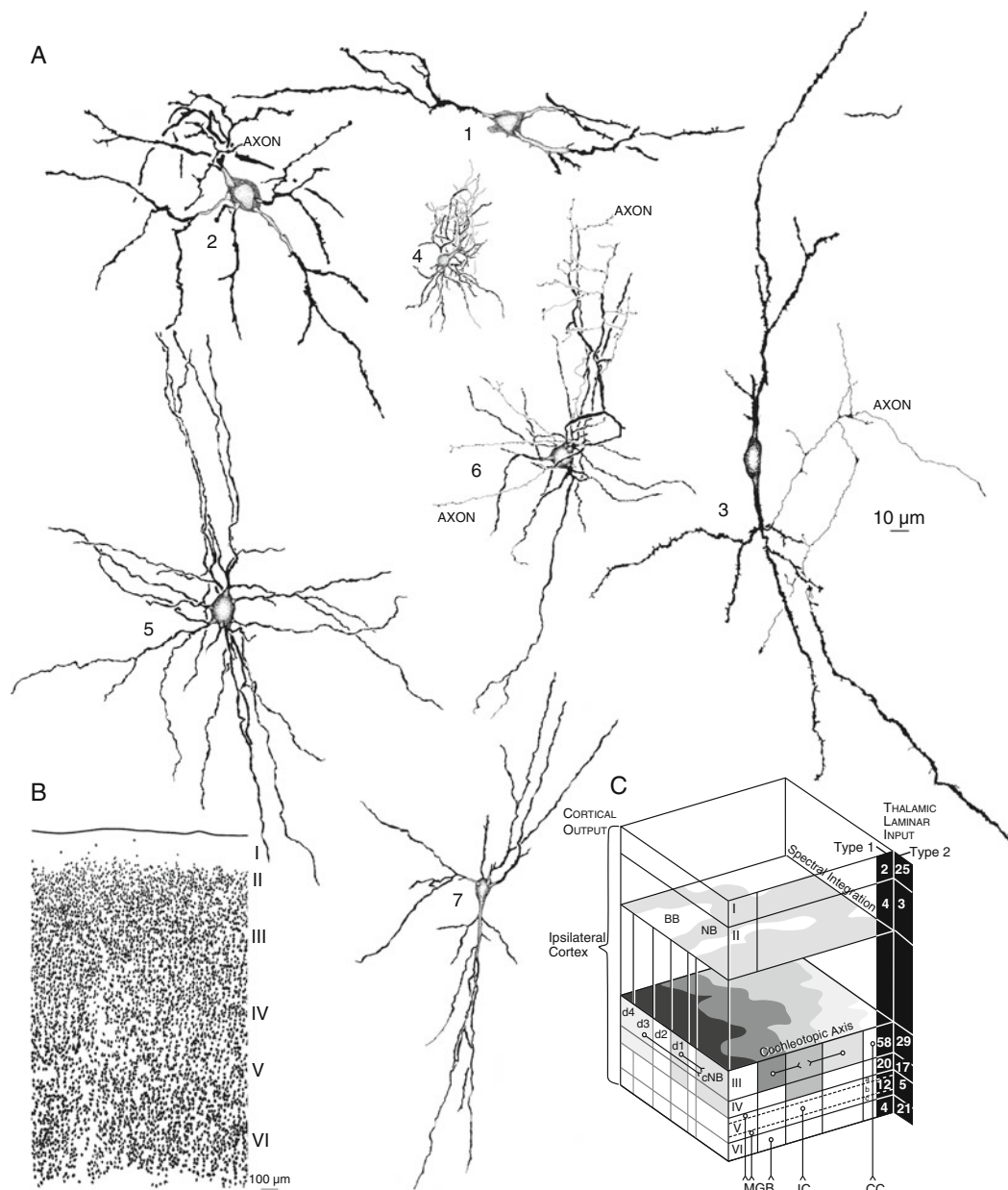


Fig. 2.8 Non-pyramidal AI neurons and AC architectonic and laminar organization. Most, if not all, of these types are GABAergic (Prieto et al. 1994b). Protocol as in Fig. 2.7. **a** 1, A horizontal cell in layer Ib. 2, A sparsely spinous layer I multipolar cell. 3, A layer II bipolar neuron with a local branched axon. 4, A layer III neurogliaform cell whose delicate processes ramify locally. 5, A layer II large multipolar cell with smooth vertical and lateral dendritic fascicles. 6, A layer IV basket cell with aspiny dendrites and a branched local axon. 7, A layer V smooth inverted pyramidal cell. **b** AI cytoarchitecture in a Nissl preparation showing a thick layer I, a small cell-dominated layer II, pyramidal cell-rich layer III, a slender layer IV, a layer V with a wide range of neurons, and a cell-dense layer VI in which horizontal cells dominate the lower half. Celloidin embedded 30 μm thick section,

planapochromat, N.A. 0.65, $\times 500$. **c** A schematic view of a cube of AI integrating some features of structural and functional organization. I–VI, cortical layers. *Light gray shapes*, the spectral integration domains, which include broad- (BB) and narrowband (NB) subregions. cNB, the central narrowband domain; d1–d4, flanking narrowband subregions whose corticocortical projections converge onto the cNB region (Read et al. 2001). Gray-white contours, the cochleotopic axis. Types 1, 2, percentages of MGB boutons in specific thalamic layers after anterograde tracer deposits in the auditory thalamus (Huang and Winer 2000) show three patterns (cf. Fig. 2.11). MGB, IC, and CC refer to the laminar origins of input to, respectively, the medial geniculate, inferior colliculus, and contralateral AC. Feedforward projections (Output) arise from all layers (Unpublished observations)

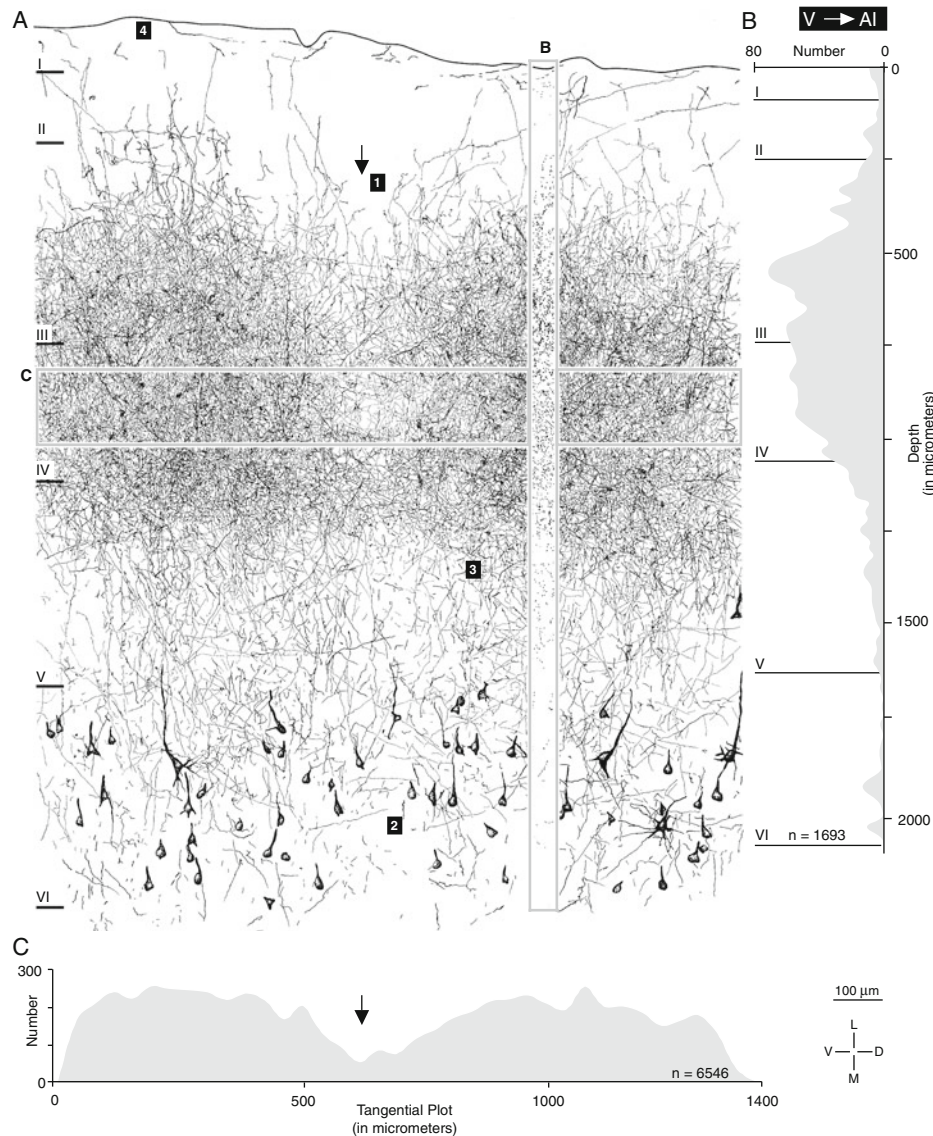


Fig. 2.9 TCC and corticothalamic labeling in AI after a deposit in the ventral division of the MGB (cf. Fig. 2.5a). **a** The TC axonal plexus forms clusters separated by bouton-sparse regions (arrow; 1). Some lateral, preterminal fibers are present (2), and the terminal plexus is heaviest at the base of layer IV; some thick, horizontal fibers (4) are present in layer I. **b** A vertical traverse (gray lines in **a** denote the locus)

in which only boutons were counted shows a peak at the layer IIIa-b border. The corticothalamic neurons are unlikely to have contributed to the bouton profile since their axons were rarely filled. **c** A horizontal traverse confirms the bouton clusters (arrow) and denotes a relatively constant lateral plexus. Modified from prior work (Huang and Winer 2000)

2006). Knowledge of these connectivities is approximately the inverse of their size.

6.1 Thalamic Areal and Laminar Input

All MGB divisions project to AC, and the TC pathway is both nucleus and area specific, with a representative subdivision projecting to half of the fourteen areas identified as auditory (Huang and Winer 2000) (Figs. 2.10 and 2.11).

Ventral division input to primary auditory cortex (AI) is clustered in the cat, rabbit (McMullen and de Venecia 1993), and monkey (Hashikawa et al. 1995), with ~85% of the TC boutons in layers III–IV, and lesser involvement of many other layers; layer II receives only minute input and is thus remote from thalamic influence except via polysynaptic intracortical processes (Fig. 2.9). The dorsal division also concentrates its input to the granular layers, but has more laminar dispersion than the ventral division; the medial division pattern involves layers I and VI in some areas and the granular layers in others. TC axons are diverse and

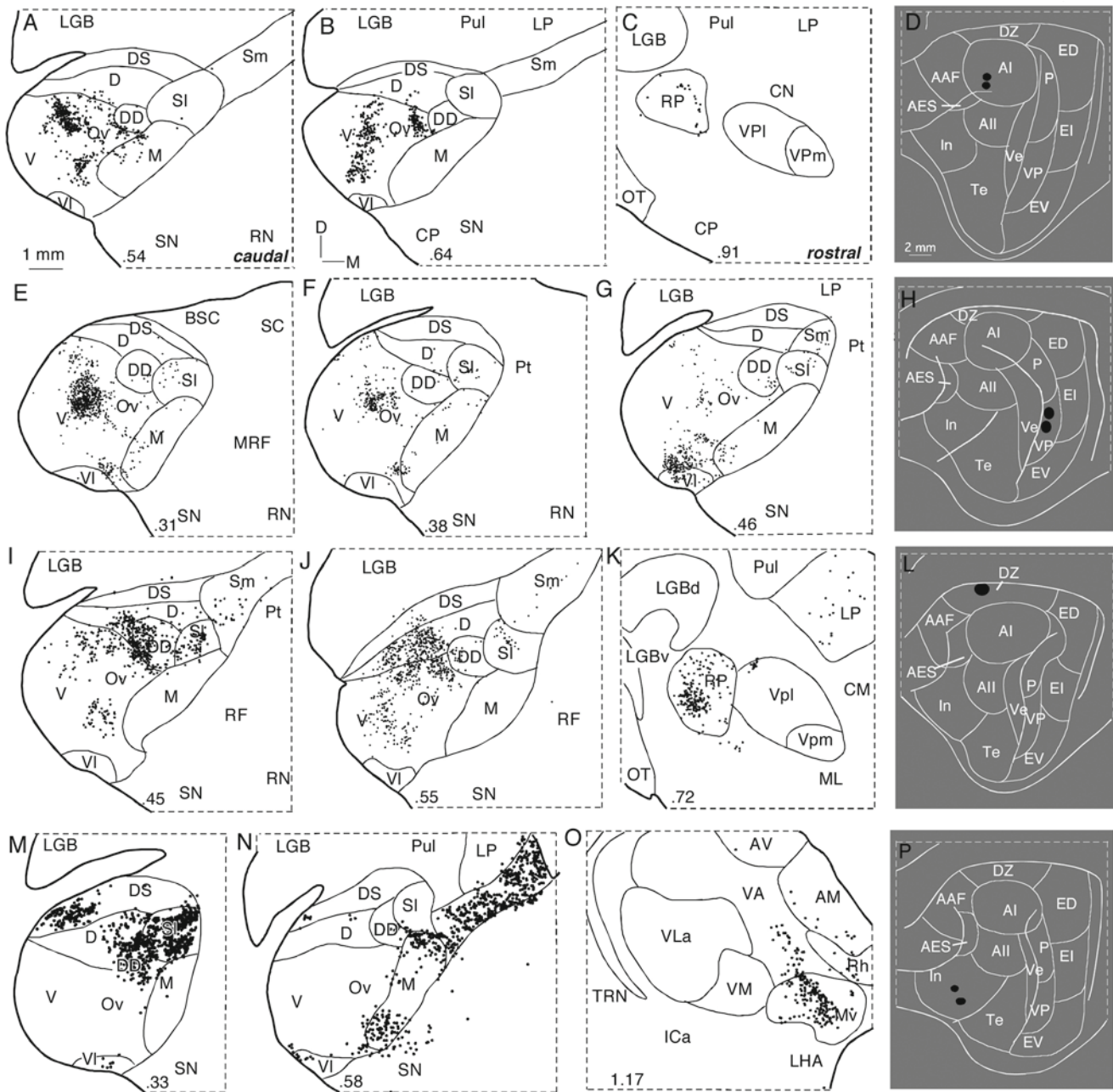


Fig. 2.10 TC input to four AC areas (D,H,L,P) demonstrated with cholera toxin β fragment, and each showing that more than one thalamic nucleus converges to an area and that the projection is topographic. **a–d** Deposits in mid-to-high frequency AI (D) labeled few cells outside the ventral division and rostral pole. **e–h** Injections in area VP label

ventral division neurons and suprageniculate complex (SI, Sm) cells. **i–l** Tracer in the dorsal auditory zone (DAZ) labels mainly dorsal division (DD, Sg) and rostral pole cells, and lateral posterior nucleus (LP) cells. **m–p** Input to In cortex is from nuclei almost wholly outside the lemniscal pathway, yet equally focal and topographic (see **a**)

layer-specific in form, with pronounced lateral plexuses in layers I, IV, and VI, and surprisingly massive fibers in layer I (Huang and Winer 2000), a feature consistent with a projection (Mitani et al. 1984) from magnocellular medial division neurons (Winer and Morest 1983a). Posterior thalamic (suprageniculate, posterior intralaminar, and peripeduncular nucleus) projections to rat AC also target layer Ia, and

the lower part of layer III and layer IV in ectothalamic and visceral areas (Linke and Schwegler 2000). Perhaps layer I intralaminar influences modulate the corticofugal system (Vogt 1991; Cauller 1995) via the distal dendrites of projection neurons (Prieto and Winer 1999; Winer and Prieto 2001). Layer II/III cells have a lower discharge threshold than layer V neurons, permitting the latter neurons

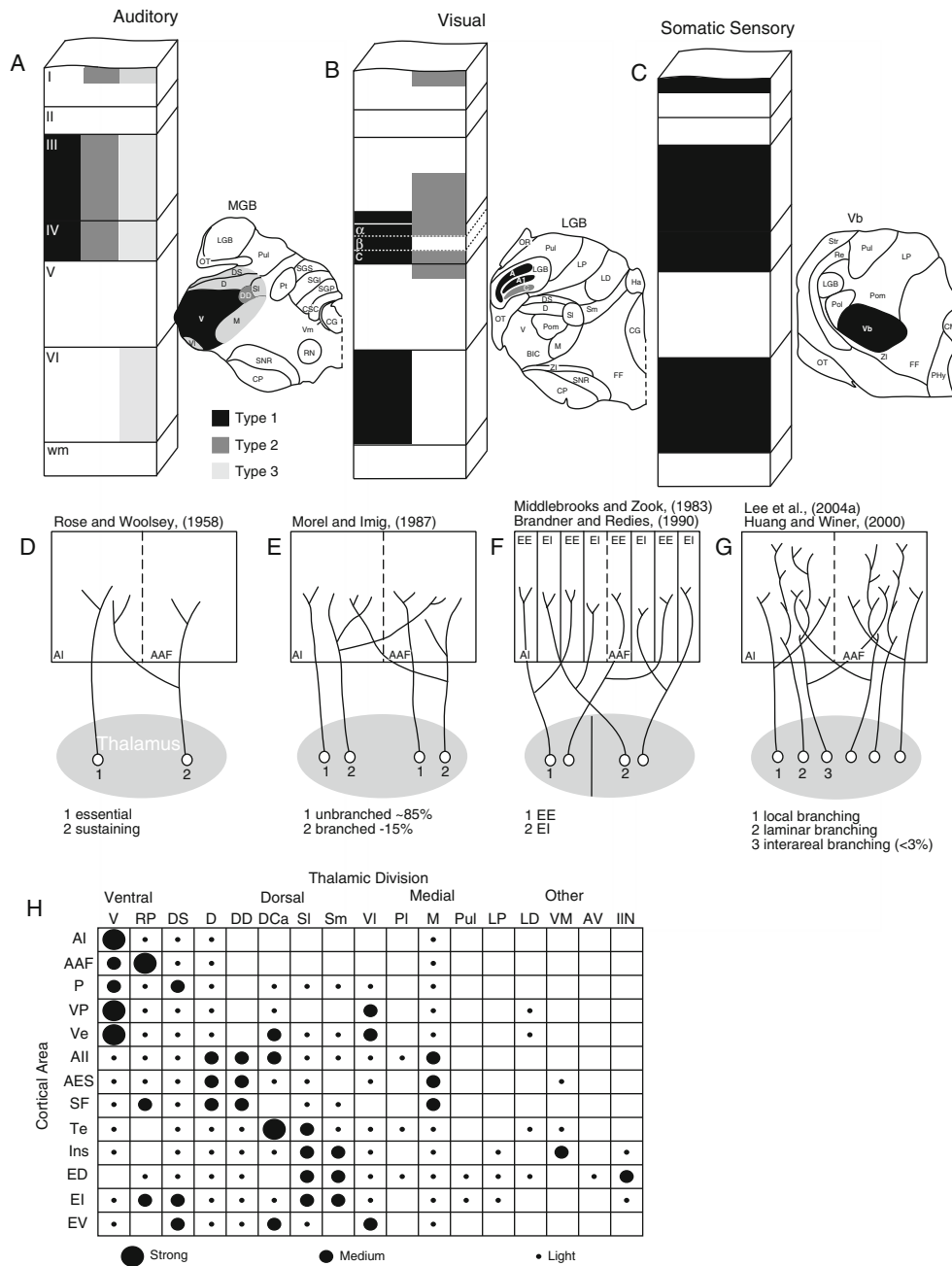


Fig. 2.11 Summary of TC organization and comparison of auditory, visual, and somatic sensory patterns of thalamic organization. **a** Auditory TC input has three arrangements related to the functional affiliations of the parallel streams. Lemniscal input (*black*) targets layers III–IV, dorsal division lemniscal-adjunct (Winer and Morest 1983a) neurons target layers III, IV, and I, and projections from polysensory MGB subdivisions end in all but layer V, many of whose cells receive thalamic input to their distal dendrites (Mitani et al. 1984). **b** In contrast, lateral geniculate projections have only two patterns: those from the *a* layers end in layers IV and VI and those from the *c* layer overlap in the *upper* and *lower parts* of layer IV with those from the *a* layers, but occupy parts of layers I, III, and the *upper part* of layer V (Humphrey et al. 1985). **c** Thalamic input to somatic sensory cortex terminates in all layers except Ib, II, and V (Landry and Deschênes 1981). **d–g** Four models of TC connectivity. **d** Essential projections

(1) are exclusive, while sustaining input accounts for why some thalamic nuclei survive decortication in retrograde degeneration studies (Rose and Woolsey 1958). **e** Most TC axons end in one area (1), and some (2) terminate in more than one (Morel and Imig 1987). **f** Binaural modules in AI receive TC input from MGB neurons with like aural features relating to suppression (EI) or summation (EE) (Middlebrooks and Zook 1983), and TC input is point-to-point (Brandner and Redies 1990). **g** Studies with CT β and CT β G (CT β conjugated to gold) and BDA show that few (<2%) of TC cells have branched projections, that almost all layers receive such input, and that the channels to areas AI and AAF are almost entirely parallel (Huang and Winer 2000; Lee et al. 2004b). **h** Families of auditory TC relations, with lemniscal input the heaviest and most restricted, lemniscal-adjunct lighter and more variable, and multimodal associative projections yet lighter and diverging more

to restrict intracortical processing spatially (Atzori et al. 2004).

Some MGB subdivisions project to area outside AC (Fig. 2.11). The suprageniculate nucleus of the dorsal division (Winer and Morest 1983b), whose neurons respond to acoustic, somatic sensory, and visual stimuli (Benedek et al. 1997), projects to the frontal lobe (Kurokawa et al. 1990) and insular cortex (Winer et al. 1977); other parts of the dorsal division project to AC and perirhinal areas, mainly in layers III/IV (Kimura et al. 2003).

6.2 Corticocortical System

The arrival of parallel streams of thalamic information in AC triggers an immense series of feedforward and feedback intracortical systems which have many essential roles. Among these is the coordination of intrinsic processes with layers and modules in an area; a second facet is the propagation of corticocortical information to areas higher in the presumed sequence and their participation in emergent and parallel processing; finally, these local and remote computations must each converge upon the corticofugal systems to affect subsequent subcortical computations.

Studies with sensitive tracers reveal an area AI intrinsic convergence system with sharpness of tuning as the critical metric, and modules segregated within an isofrequency contour and projecting preferentially to a central, narrowly tuned band (Read et al. 2001; Read et al. 2002). Larger deposits find massive convergent feedback input from many areas, e.g., some fields are the target of all other AC area (Fig. 2.12). The three largest projections often contribute less than half the total input. Tonotopic fields tend to receive input from tonotopic fields, non-tonotopic fields from non-tonotopic fields, and limbic-related fields project preferentially to limbic-related areas; there are significant exceptions, e.g., non-tonotopic area AII (Schreiner and Cynader 1984) projects to limbic-related temporal, but not to insular, cortex (Ch. 7). The feedforward projections likewise are much more elaborate than those seen in degeneration studies (Kawamura 1973) and suggest principles analogous to those noted for the feedback relations. Thus, an area projects to at least three, and up to ten, other fields; feedforward projections have functional affiliative preferences, e.g., tonotopic to tonotopic, etc., but with exceptions; non-primary areas have more divergent, and functionally heterogeneous, targets than tonotopic fields; the projections of adjacent tonotopic fields can be almost entirely independent; and the intricacy and selectivity of the corticocortical projections is consonant with the existence of many, as opposed to a few, AC areas (Fig. 2.13).

In macaque AC, where the areal equivalence the cat includes several tonotopic fields but no obvious equivalent

to AII, there is a comparable richness in the feedforward projections, and an equally marked tendency for the “crossover” of projections from primary to non-primary areas and the converse (Morel and Kaas 1992; de la Mothe et al. 2006). One model for these patterns in primates envisages streams for sound localization and auditory object recognition (Rauschecker et al. 1997; Rauschecker and Tian 2000) analogous to those proposed in visual cortex (Van Essen 2005). Whether such a model extends to other species is uncertain.

6.3 Commissural System

Without exception, the cat interhemispheric connections have an area to area homotopy that sets them apart from the corticocortical system; the strongest single commissural projection is a fraction of the corticocortical input and there are always fewer commissural than ipsilateral inputs (Ch. 7) (Fig. 2.14). Secondary commissural input to an area arises from within families (e.g., tonotopic to tonotopic) or outside (auditory and visual association to limbic areas). The commissural projection originates in layers III and V almost exclusively, though there is no relation between laminar origin and functionality: different primary areas may have a preponderantly supragranular or infragranular origin, and only area Te (temporal field) is bilaminar. In macaque, the commissural projections to non-primary belt cortex arise in belt and parabelt regions only (Hackett et al. 1999), divorcing the commissural core from the belt except via polysynaptic corticocortical pathways. Callosal axonal terminations are modular in AI with considerable anterograde–retrograde reciprocity (Code and Winer 1986), and projection bands vary from 200 to 800 μm wide (Wallace and Harper 1997). Magnetic resonance studies of human primary AC find a symmetrical tonotopic map (Formisano et al. 2003). In macaques damage reveals a functionally asymmetry (Heffner and Heffner 1989).

6.4 Corticothalamic System

This is largest of the corticofugal system and among the largest in the brain, with each AC locus projecting to more thalamic venues than project to it (Winer and Larue 1987; Deschênes et al. 1998). In AI it arises from varieties of layer Va, Vc, and VI pyramidal cells (Winer 1992). The projection is topographic irrespective of the tonotopic status of its AC origin or the MGB target (Winer et al. 2001), suggesting an intrinsic order independent of physiologic topography and analogous to other forebrain connectional systems (Lee and

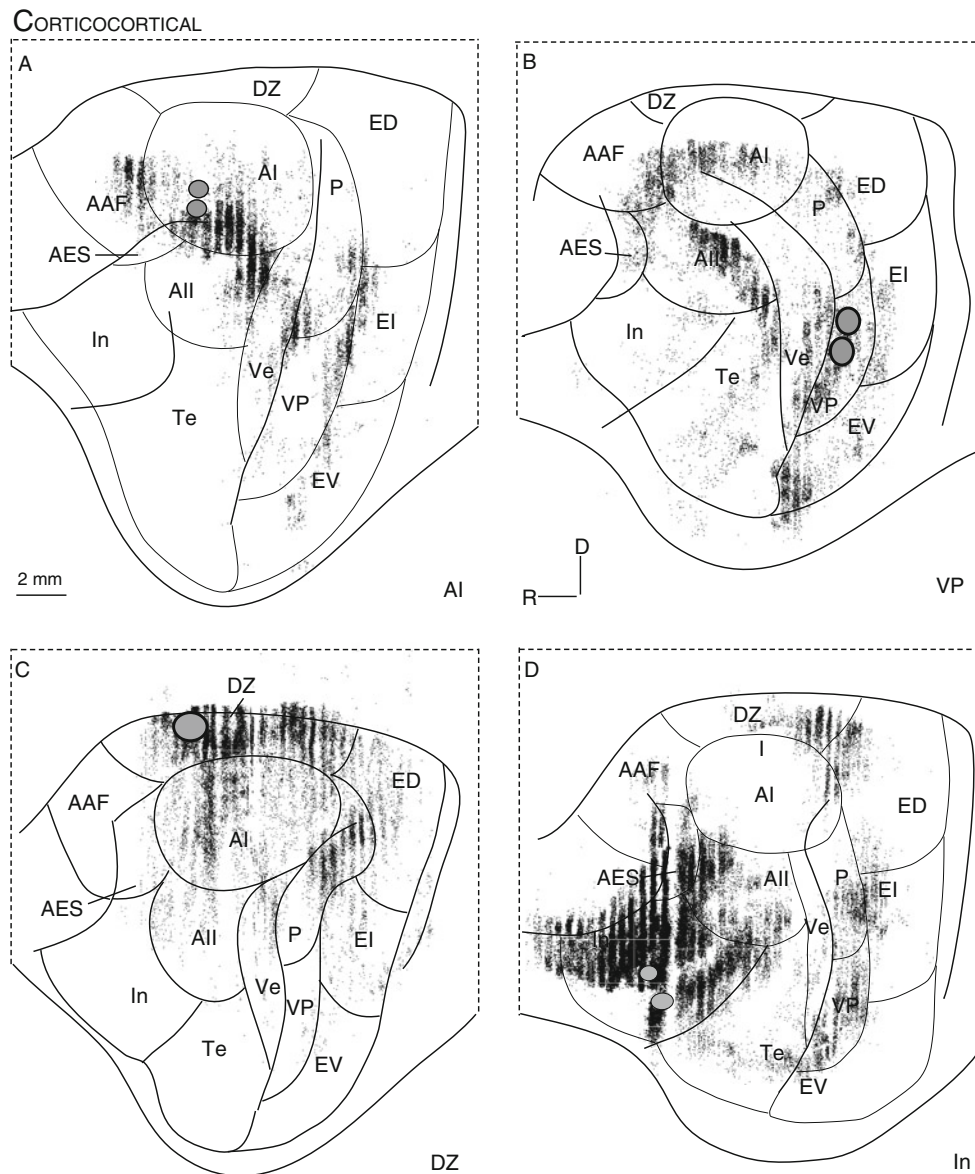


Fig. 2.12 Corticocortical cells of origin revealed with CT β . The vertical banding of labeling is an artifact of collapsing three dimensions onto two. **a** Convergent input to AI arises chiefly from other fields with a tonotopic map (areas AAF, P, VP, Ve), and weak input from the posterior ectosylvian gyrus (EI) and a limbic-related area Te. **b** VP deposits involve label all AC areas significantly,

including both limbic fields (Te, In). **c** Projections to the dorsal auditory zone (DZ) are heaviest from area P, and involve vast expanses of auditory and adjacent suprasylvian territories. **d** Insular cortex is remarkable for having no AI or area P projection, and massive AII and ED projections, attesting to non-tonotopic and multisensory and affiliations

Winer 2005) (Fig. 2.15). The five tonotopic fields in the cat each have fewer MGB targets than non-tonotopic and limbic-related areas, which average three times as many, and these are often discontinuous and widely distributed. Perhaps the corticothalamic system contains parallel streams to specific MGB subdivisions. This is further supported by the existence of small and large corticofugal boutons in cat (Bajo et al. 1995), and monkey (Rouiller and Durif 2004) and other species (Rouiller and Welker 2000); the large endings are among the biggest MGB terminals and may complement a

system of equally large GABAergic endings prominent in cat (Winer et al. 1999a) and sparse in rat (Winer and Larue 1988) MGB, consistent with species-specific neurochemical patterns (Winer and Larue 1996).

6.5 Corticocollicular System

Auditory corticocollicular arrangements differ in almost every respect from their corticothalamic counterparts

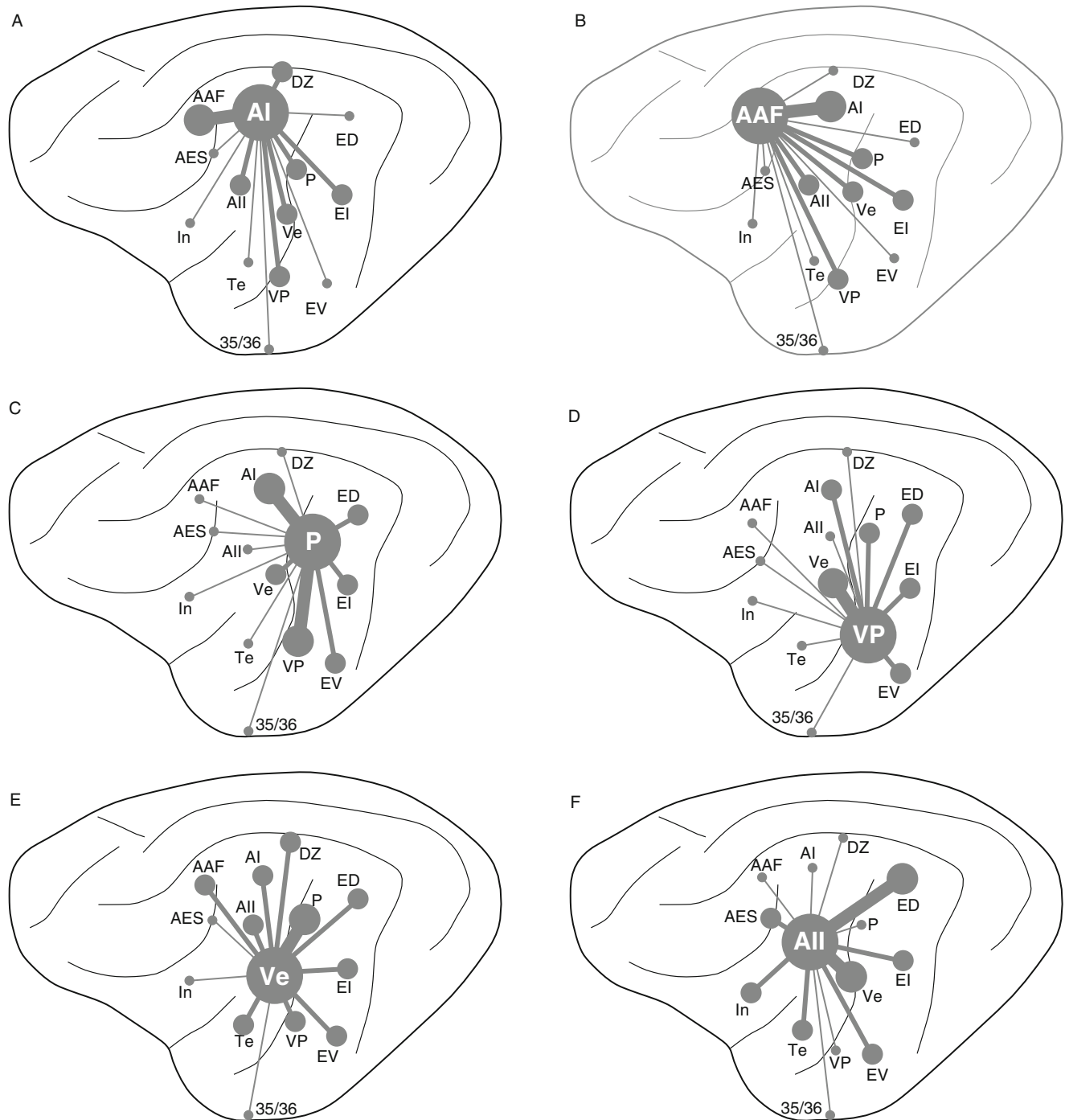


Fig. 2.13 Summaries of corticocortical convergence patterns in Fig. 2.12 converted to density plots in which line thickness is proportional to input strength. The principles are that each area receives projections from many (sometimes all) AC areas and that AI is no more a redistributive hub (Winer 1992) than is any other area. **a** AI resembles other areas in having within-group (i.e., areas with tonotopic affiliations) as its main input. **b** Likewise, AAF is dominated by projections from tonotopic area, but receives substantial input from multimodal

posterior ectosylvian regions. **c** Area P receives a smaller constellation of input than AI, with the heaviest projections from tonotopic areas, consistent with a hierarchical organization. **d** Area VP has a special relationship with area Ve, with second tier input from multiple primary and perivisual fields. **e** Area Ve has many second tier projections, and a differential limbic-related input. **f** AII is hardly a target of AI, and receives area-specific primary input (from Ve but not AAF) and substantial posterior ectosylvian projections (ED, EI, EV)

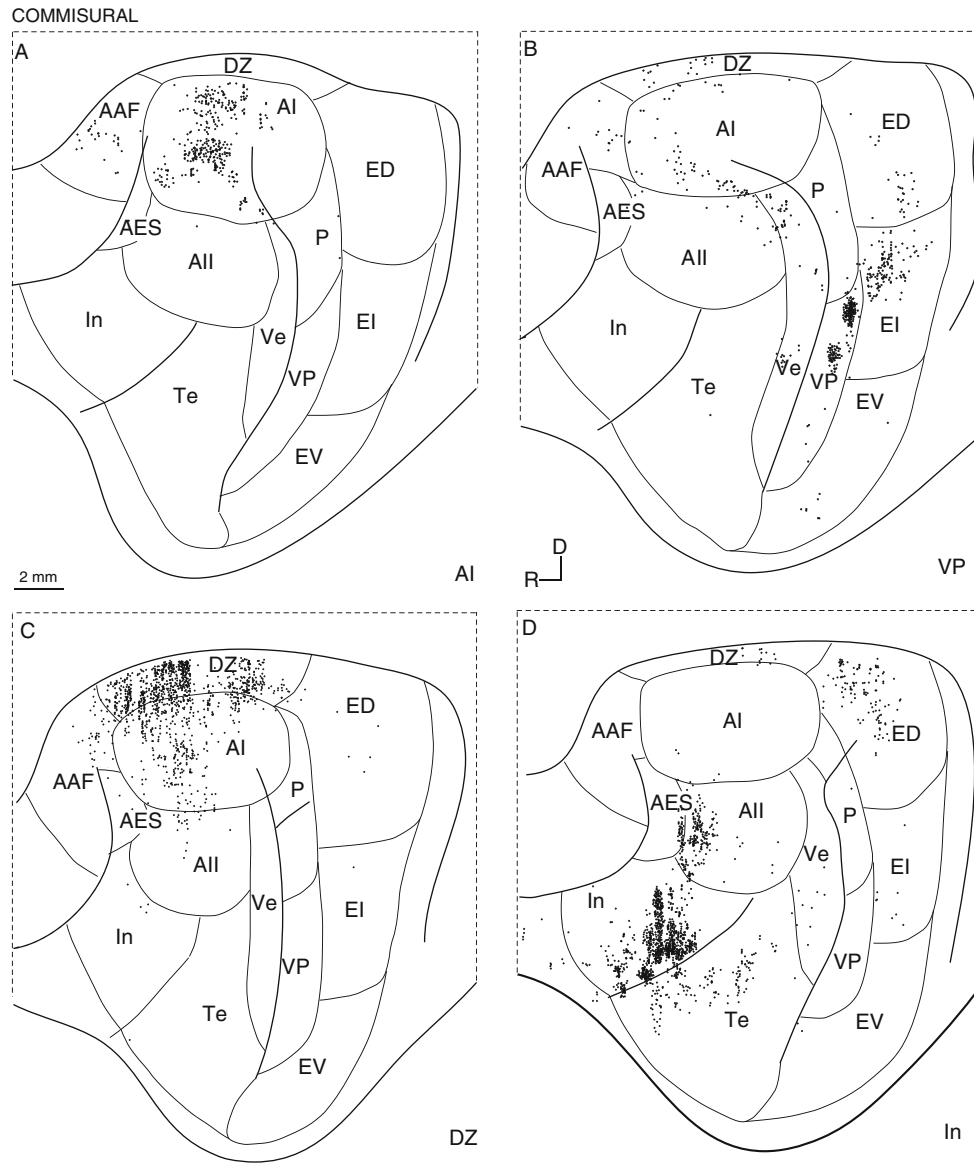


Fig. 2.14 Commissural projections from the experiments in Fig. 2.12. These differ from the corticocortical projections is being smaller, more reciprocal, and within-family (e.g., limbic to limbic) though selectively (only some tonotopic areas project). **a** Input to AI is the most symmetrical in this series, with little involvement of areas P, VP, and VE, and moderate AAF projections. **b** Area VP receives

significant input from AI but does not project to it (**a**), and unexpected projections from periauditory posterior ectosylvian fields. **c** Area DZ receives input from nearly all of contralateral DZ and substantial, topographic AI projections. **d** Area In is a commissural target of areas ED, Te, and AII/AES, suggesting a widespread integrative role

(Fig. 2.16). Their laminar origins are limited to layer Vb (Winer and Prieto 2001), and few corticofugal cells project to both the MGB and the inferior colliculus (IC) (Wong and Kelly 1981), a pattern consistent with the virtual absence of branched forebrain auditory projections (Lee et al. 2004a, b). The input to the IC central nucleus is a mere fraction of that to the MGB ventral division. The chief targets of the tonotopic fields are, rather, the dorsal and caudal cortices, and regarded as outside the primary auditory pathway (Winer 2005). In contrast, non-tonotopic areas project only weakly to these venues, and moderately

to the central nucleus, implying extralemniscal influences on the lemniscal stream; AC areas with perivisual affiliations project to the superior colliculus. The limbic-related auditory association fields have a unique projection pattern which includes non-tonotopic IC subdivisions and motor affiliated extracollicular targets perhaps related to vocalization and other behaviors (Jürgens 2002). Finally, corticocollicular axon morphology differs from that of corticogeniculate axons, suggesting different spatiotemporal dynamics (Winer et al. 1998; Winer et al. 2001; Winer 2005).

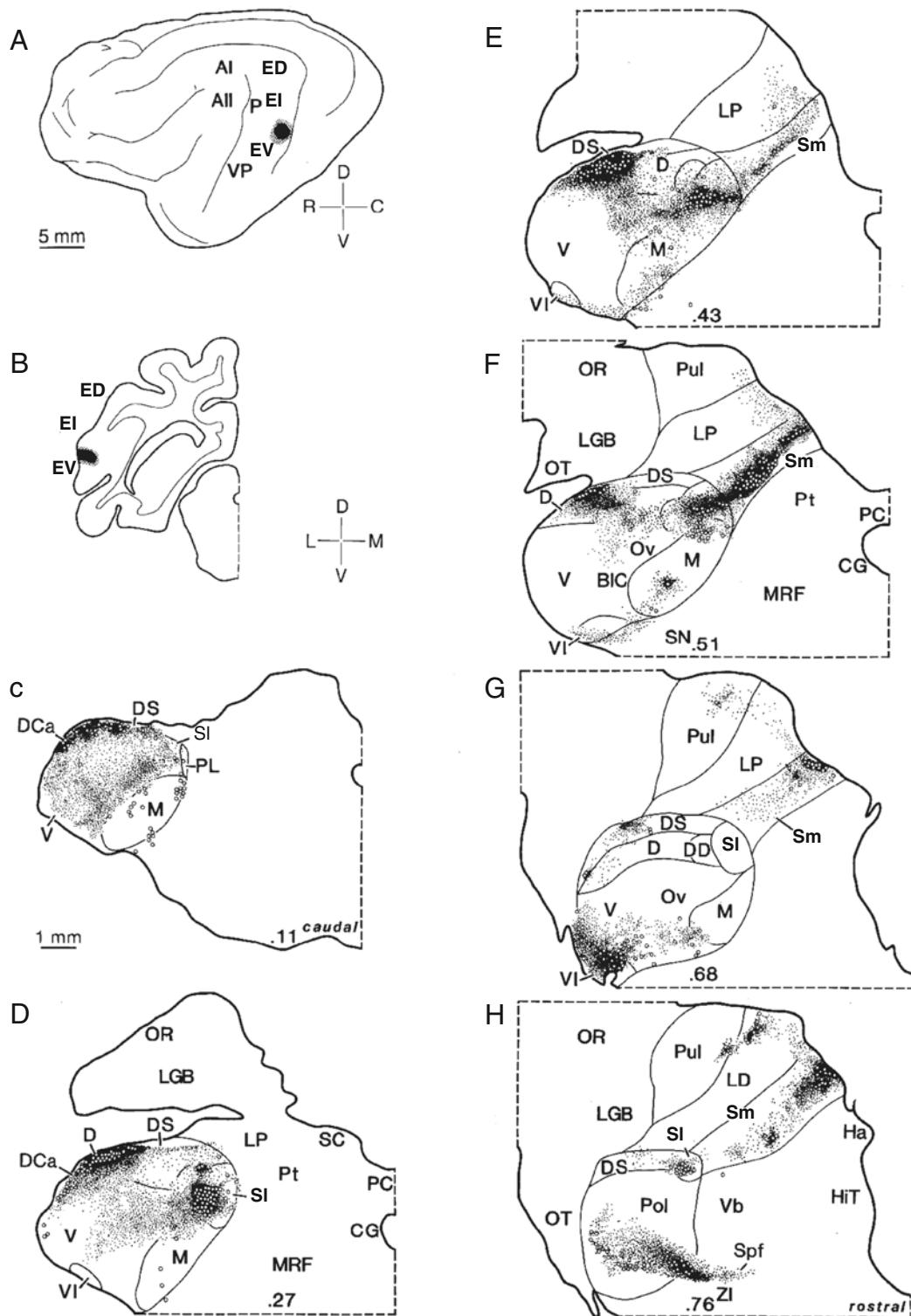


Fig. 2.15 AC projections to MGB subdivisions studied with a tracer transported bidirectionally (wheat germ agglutinin conjugated to horseradish peroxidase; WGA). *Fine dots*: corticofugal axon terminals; *circles*, TC neurons. **a, b** The deposit was at the EI-EV border and did not enter the white matter. **c** Non-tonotopic MGB divisions were principally involved, especially the dorsal nuclei. **d** Independent projection foci target the dorsal division (D, DCa) and the supragenulate (SI) nuclei. This implies multimodal-to-auditory crosstalk in the descending

system. **e** Extraauditory targets include the lateral posterior (LP) and supragenulate nucleus medial part (Sm). **f** The medial division receives AC input as specific and focal as that to the ventral division in other experiments (not shown). **g** Even a small part of the dorsal division, the ventrolateral nucleus (VI) has a massive and reciprocal projection. **h** The labeling extends nearly to the rostral tip of the MGB and terminates in the posterior intralaminar system (Spf) (Winer et al. 1988)

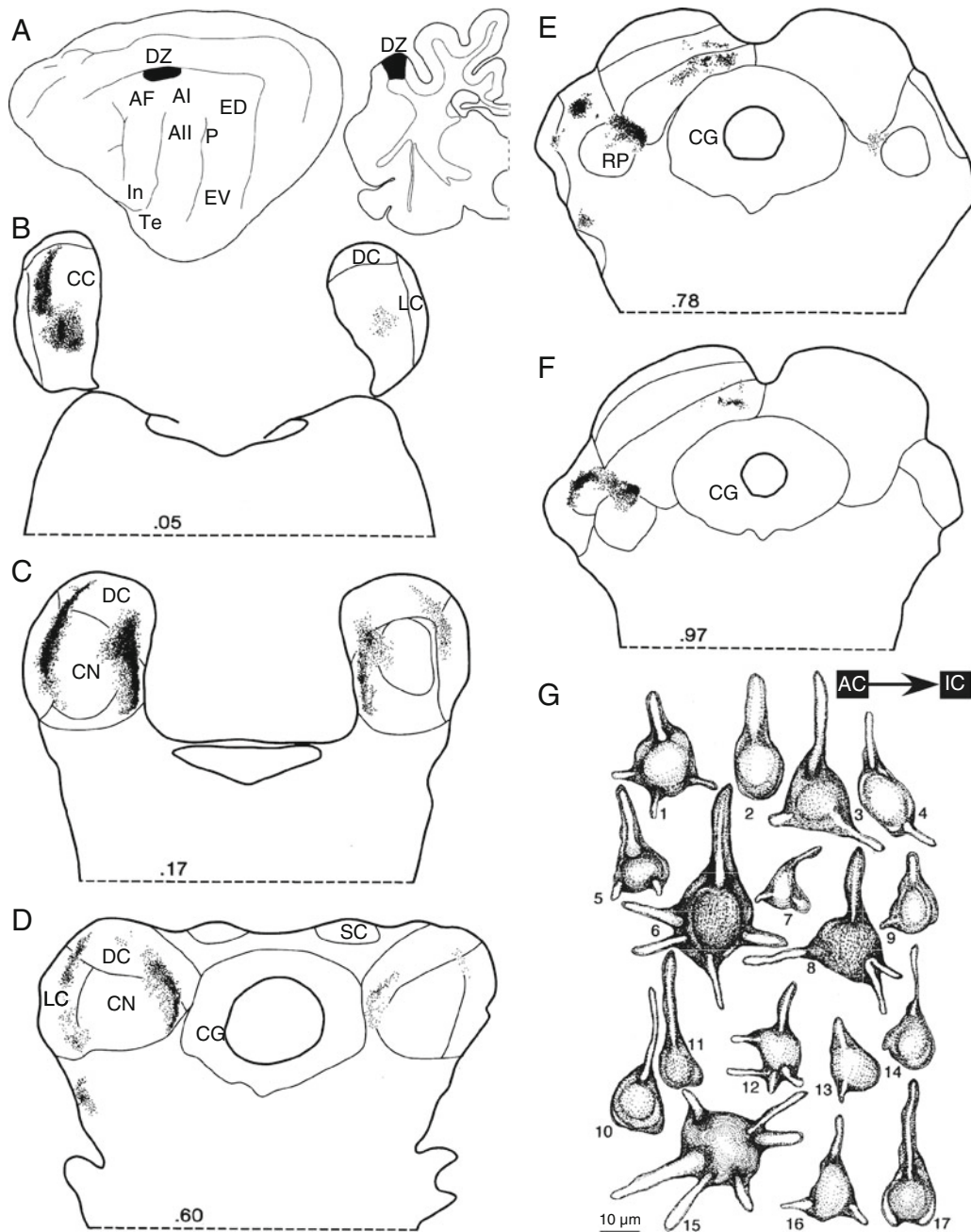


Fig. 2.16 AC axon terminals in the midbrain labeled with WGA. **a**, **b** A deposit on the crest of the ectosylvian gyrus does not encroach into medial perivisual areas. **c** The caudal inferior colliculus cortex receives the bulk of input. **d** The projection is bilateral, and symmetrical, and largely outside the central nucleus. **e** The lateral nucleus (La)

and sagulum (Sa), both regarded as outside the primary auditory pathway (Casseday et al. 2005), each receive input. **f** The deep layers of the superior colliculus (SCx) receive bilateral projections. **g** Axons extend from virtually the caudal tip to the inferior colliculus rostral pole (RP), and are focal and dense

6.6 Corticopontine System

Like the corticocollicular pathway, the corticopontine system arises from layer V cells that do not project to the cochlear nucleus or superior olivary complex (Doucet et al. 2003). This projection comes from all AC areas and, like the corticogeniculate (Winer et al. 2001) and corticocollicular

systems (Winer et al. 1998), is topographic and reaches most pontine subdivisions. A given AC locus, which labels a discrete IC target, may span much larger pontine territories, suggesting an area- and target-specific pattern of corticofugal divergence. Corticopontine axons have an architecture entirely different from the other corticofugal axons, forming narrow sheets 200–300 μm long whose preterminal

segments fill a narrow subdomain with boutons concentrated focally. Single deposits label strongly focal and discontinuous domains, suggesting a mosaic of interdigitating terminal architectures (Perales et al. 2006) perhaps contributing ultimately to fractured somatotopy in cerebellar cortex (Arends 1997).

6.7 Other Corticofugal Systems

Other regions beside the thalamus and midbrain receive AC input (Fig. 2.17). Thus, the caudate and putamen both are targets and the projections are organized topographically, forming sheets (Reale and Imig 1983) resembling corticopontine axons (Perales et al. 2006).

Corticoclastral projections arise from all AC areas, are reciprocal, and may be bilateral, with the principal input from insular cortex and the posterior ectosylvian gyrus, and the intermediate claustrum receiving auditory input preferentially and projecting to AC. The nearby endopiriform nucleus is dominated by limbic-related AC input (Beneyto and Prieto 2001) and is implicated, with parts of the MGB and other structures, in fear conditioning (Campeau et al. 1997).

Temporal cortex projections reach the superior olivary complex bilaterally, preferentially ipsilaterally, mainly in the ventral nucleus of the trapezoid body, with axons either branching widely or ending focally (Schofield and Coomes 2004). Cochlear nucleus input likewise was ipsilateral-dominant, ending mainly in the granule cell domain, the dorsal cochlear nucleus, and magnocellular regions of the posteroventral and dorsal cochlear nucleus (Schofield and Coomes 2005). Like other corticofugal projections, these arise from pyramidal neurons (Weedman and Ryugo 1996b), and they end on granule cell dendrites (Weedman and Ryugo 1996a).

7 Neurochemical Profile

In the visual cortex there is a vast array of chemically specific circuits and cell types (Lund et al. 1995; Gonchar et al. 2002) contributing to local microcircuitry (Callaway 1998). Such a profile is not available for AC.

7.1 Gamma-Aminobutyric Acid

GABAergic neurons and axons in AC influence RF architecture (Foeller et al. 2001), intensity tuning (Sutter and Loftus 2003), excitatory–inhibitory interactions (Volkov and Galazjuk 1991), and tuning curve shape (Chen and Jen

2000), to name just a few, and GABA antagonists selectively interfere with frequency discrimination (Riquimaroux et al. 1992). The richness and robustness of these GABA-mediated responses is consistent with the layer-specific distribution of immunopositive neurons and puncta (Prieto et al. 1994a, b) (Fig. 2.18). GABAergic networks are probably largely local or limited to a few millimeters (Winer 1986) except GABAergic inverted pyramidal cells (Bueno-López et al. 1990; Reblet et al. 1992) which may project farther. In visual cortex, many GABAergic local circuit neurons project ~1 mm or less and target pyramidal cells (Freund et al. 1983). GABAergic arrangements elsewhere in AC are unknown, though there are marked regional patterns in non-auditory areas (Hendry et al. 1987) and evidence for area-specific patterns of GABA-mediated effects, e.g., posterior auditory area neurons have a more intricate inhibitory sideband structure than AI cells (Loftus and Sutter 2001). Perhaps GABAergic inhibition is site and species specific (Winer et al. 1995; Pollak et al. 2003) and even TC transmission may have system-specific features (Atzori et al. 2001).

7.2 Other Neurotransmitters

Cholinergic projections largely from nucleus basalis (Jones et al. 1976; Kamke et al. 2005) ramify widely in AC and may have roles in TC and intracortical transmission (Hsieh et al. 2000) as well as modifying the tonotopic map (Kamke et al. 2003). Influences from noradrenergic locus ceruleus neurons might modulate the level of vigilance (Foote et al. 1983). Both GABA and noradrenalin affect vocalization related AC discharge in primate (Foote et al. 1975).

7.3 Aspects of Auditory Cortex Physiology

Stimulating the white or gray matter can evoke a wide range of diverse AC synaptic responses, including a rapid EPSP followed sequentially by an early IPSP, late EPSP, and late IPSP; each was sensitive to specific pharmacologic blockade (e.g., a quisqualate/kainate receptor antagonist abolished the early EPSP, while the late EPSP was affected by an NMDA receptor antagonist, etc.) (Cox et al. 1992).

EPSPs evoked in young mouse AC slices by thalamic stimulation are reliable and have little temporal variation, with both regular- and fast-spiking cells receiving TC input; the EPSPs can also summate to elicit multisynaptic activity modulated by NMDA receptors (Rose and Metherate 2005). This is in accord with observations that the postsynaptic targets of TC neurons are heterogeneous (Smith and Populin 2001), a pattern of diversity that could subserve the several motifs of TC transformation (Winer et al. 2005). Tracing

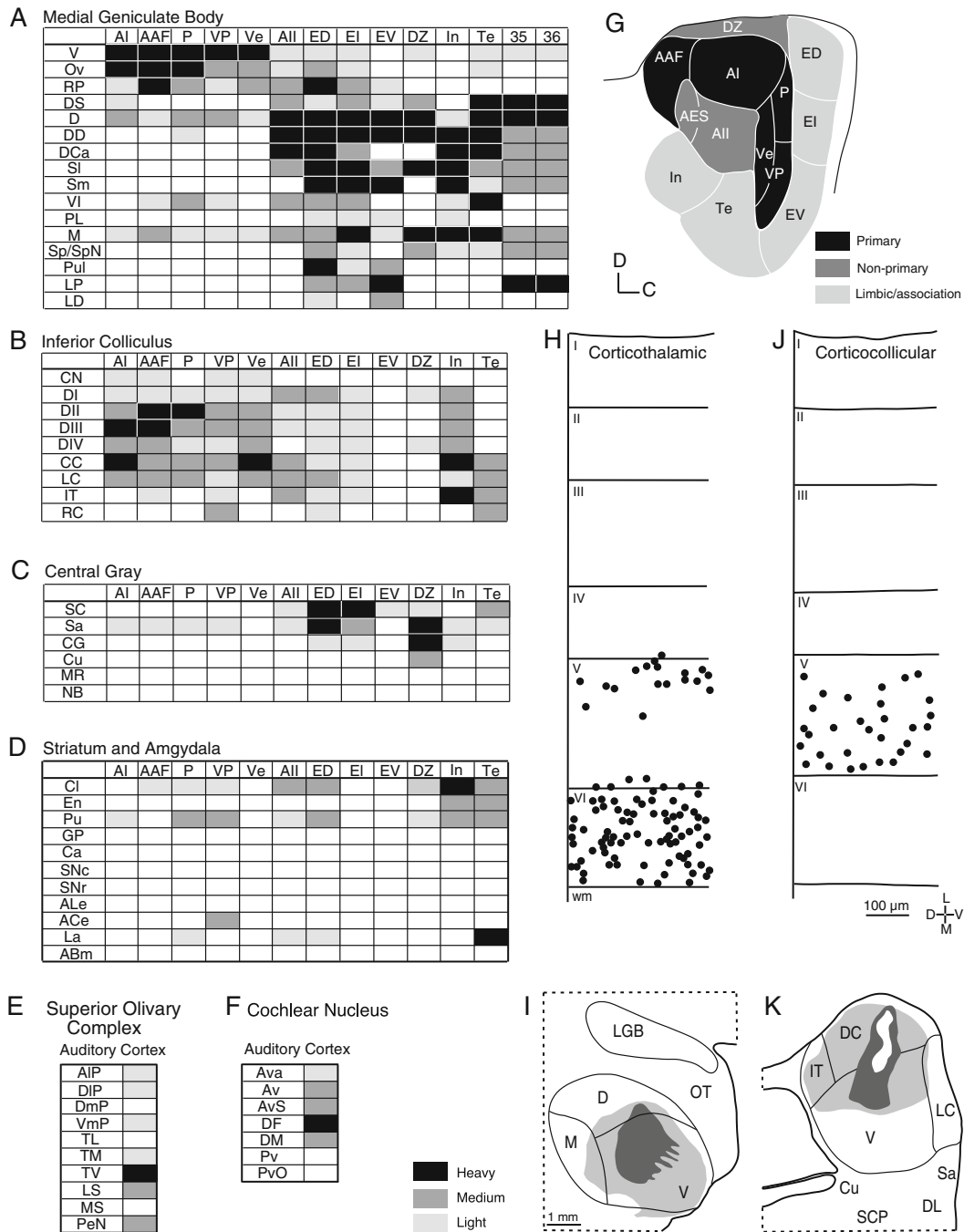


Fig. 2.17 Targets of the auditory corticofugal system. The main points are that the system is highly divergent, that all levels of the central auditory pathway receive some descending projections, that the projection patterns are areally and target specific, and that the axons (not shown) are also related to their targets. **a** Corticofugal projections from 14 cortical areas to the MGB and adjoining thalamic nuclei. Primary areas have the most limited projections, non-primary (e.g., AII) the most diverse, and limbic-related (e.g., In) areas have projections as focal as those of primary areas but little nuclear overlap. This suggests area-specific parallel corticothalamic pathways (Winer et al. 2001). **b** Corticocollicular projections are principally to targets outside the central nucleus, few are as heavy as those to the MGB, and the divergence is comparable to that of the corticogeniculate system. **c** Central gray input is restricted and supports a functional distinction between limbic-related areas (In,

Te) and specificity in their corticofugal role (Winer et al. 1998). **d** Corticolimbic and corticostriatal projections are more widespread than those to the central gray, and involve different areas (EV and DZ in the latter and not in the former), again supporting a functional disjunction among areas whose roles remain uncertain. **e** Near all rodent superior olivary subdivisions receive AC input (Schofield and Coomes 2004), as does the (f) cochlear nucleus with the conspicuous exception of the posteroventral (Pv) and octopus cell (PvO) regions, which suggests differential corticofugal influence. **g** Principal AC areas recognized in the cat. **h, i** Laminar distribution of corticothalamic projections to the ventral division (i), showing that layers Va, Vc, and VI project. **j, k** The contrasting corticocollicular projection arises from different parts of layer V after a central nucleus deposit (k) (Winer et al. 2001) and has few targets (b)

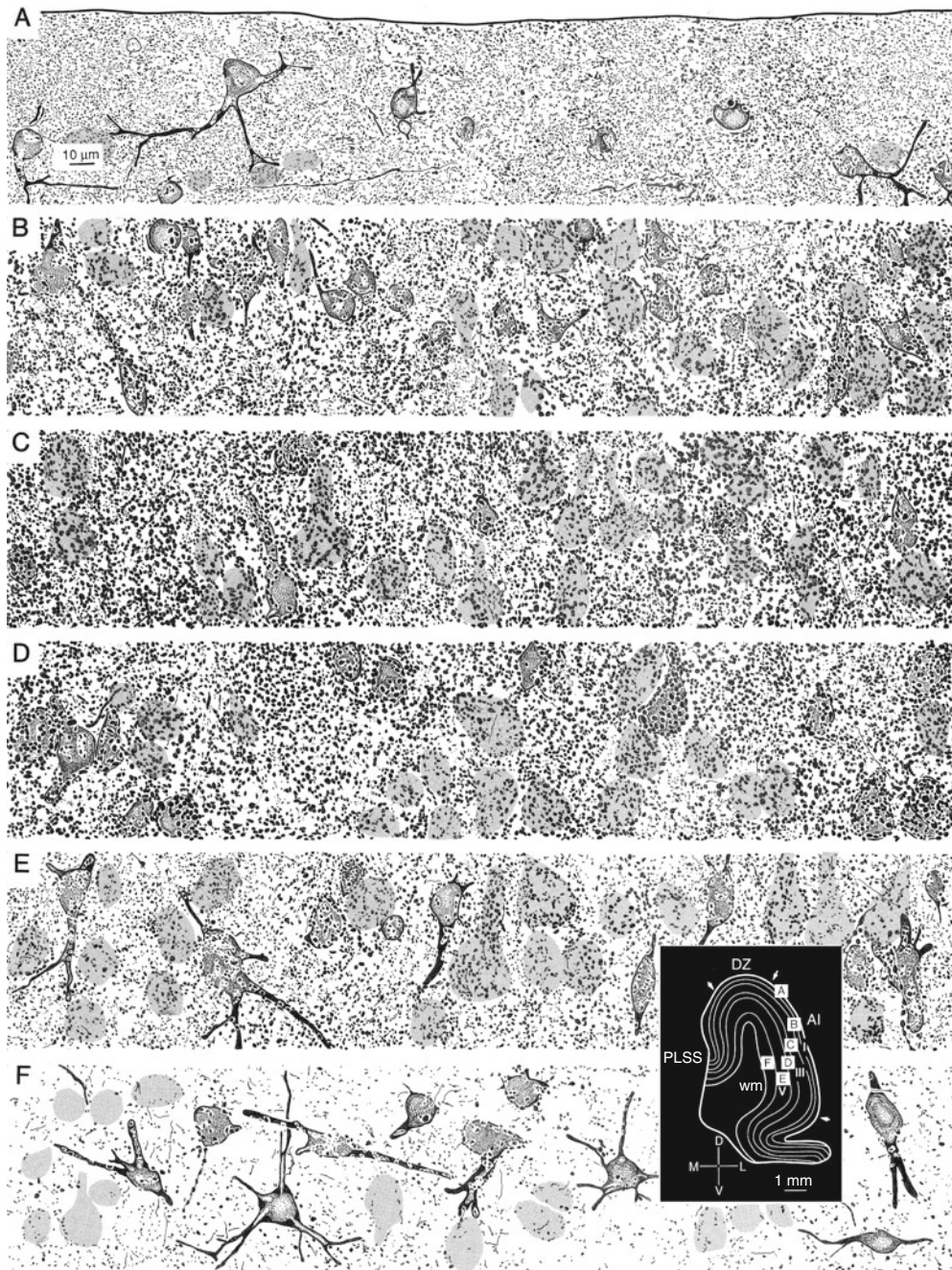


Fig. 2.18 Glutamic acid decarboxylase-positive AI neurons (*heavy stipple*) and puncta (*fine dots*) and immunonegative somata (*gray stipple*). Frozen section, 30 μm thick, planapochromat, N.A. 1.32, $\times 2000$. Each layer has a unique organization, a pattern consistent with the proposition that cortical layers have as specific an organization as sub-cortical nuclei. **a** Layer I puncta are finer than in any other layer, with few GABAergic layer Ia cells. **b** Layer II puncta are coarser and target

both immunopositive and immunonegative somata. **c** Layer III puncta cover triangular, immunonegative somata and their apical processes. **d** Layer IV neurons are almost entirely non-pyramidal and the puncta are larger than those in layer II. **e** Layer V puncta are finer than those in layer IV and sparser, and cluster on all somata. **f** Layer VI terminals are as fine and delicate as those in layer I, and often less numerous on immunonegative somata (Prieto et al. 1994a)

the further intracortical distribution of these signals using current source density analysis reveals strong early sinks in layers III and IV, while stimuli far (3 octaves from CF) preferentially activated primarily infragranular sinks, and later overlap presumed to reflect lemniscal and non-lemniscal

influence. MGB stimulation in vitro in rat elicits horizontal dispersion of excitation and sinks in layers III and IV (Kaur et al. 2005). Such dispersion is consistent with estimates of the size of TC axonal plexuses (Huang and Winer 2000; McMullen et al. 2005). In anesthetized rats muscimol

greatly attenuated local field potentials and RF size, but did not affect threshold at characteristic frequency or the timing of the onset response, consistent with an effect on intracortical rather than TC processes. Subthreshold EPSPs and local field potentials were unexpectedly broad (Kaur et al. 2004), consistent with models of TC input emphasizing intracortical dispersion (Lee et al. 2004b). Other evidence suggests coactivation of primary and non-primary areas in tandem from different MGB subdivisions (Barth et al. 1995).

AI neurons have heterogeneous tuning curves which may embody a continuous rather than a categorical distribution of response types, ranging from classic V- to U-shaped to sloped or slanted RF profiles, many showing pronounced sharpening (Sutter 2000) and a range of responses consistent with diverse roles for GABAergic neurons (Prieto et al. 1994b). Convergent excitatory–inhibitory interactions find an exclusively early-stage inhibitory contribution to excitatory intensity tuning (Sutter and Loftus 2003) consistent with the specificity of intracortical inhibition (Prieto et al. 1994a). In awake marmosets AC cells exposed to preferred stimuli can fire for longer than expected periods, consistent with a model in which neural ensembles have extended representational-computational roles (Bendor and Wang 2005).

More complex stimulus representations are also found in AC, with primate vocalizations eliciting considerable response specificity. Thus, responses concentrate in supra-granular layers and neuron pairs discharge independently, with phrase-specific temporal release, and excitatory–inhibitory events reflect sound frequency and energy (Eliades and Wang 2005). The dispersion of TC projections in cat (Huang and Winer 2000; Lee et al. 2004b) is in accord with the distributed spatial arrangement.

8 Toward a Theory of Auditory Forebrain Operations

The premise explored here is that the auditory forebrain (and perhaps the auditory system) is comprised of several streams which have evolved interdependently and which interact cooperatively. The concept of an “auditory system” is thus a synthetic construct whose value is mainly heuristic and whose objective correlative may not exist.

8.1 Forebrain Auditory System

A classical view of the auditory forebrain views it as an extension of systems arising in the cochlear nucleus and olivary complex and which are exquisitely adapted for

analyzing interaural time and intensity differences. Signals arising in the cochlea are propagated to hindbrain, midbrain, thalamic and cortical levels, presumably for further analysis of complex features, before corticocortical feedforward input to higher areas for more global processing, to provide descending output for ongoing activity, and for perceptual purposes (Bregman 1990). While this view might be pertinent to the function of end bulbs of Held, bushy cells in the anteroventral cochlear nucleus, the superior and medial superior olives, and disc shaped or bushy cells in the central nucleus of the IC, the ventral nucleus of the MGB, and the several tonotopic areas of AC, it says little about the explicit roles of much (perhaps most) of the midbrain and forebrain. Areas omitted include five of six IC subdivisions (dorsal cortex, lateral cortex, caudal cortex, intercollicular tegmentum, and rostral pole nucleus), vast MGB regions (dorsal division, caudal cortex, medial division, and rostral pole), and all of AC except the five tonotopic areas (omitting nine others connected with the MGB and IC). This view is insufferably parochial.

8.2 Multimodal Interactions

Trigeminal somatic sensory information reaches the granule cell domain of the cochlear nucleus (Haenggeli et al. 2005), and eye position signals influence RFs in primate IC (Groh et al. 2001). In the IC extensive non-auditory connections establish multimodal representations (Syka et al. 2000), and convey auditory input to other systems (Linke 1999; Harting and Van Lieshout 2000) and this pattern is elaborated in the MGB (Wepsic 1966).

8.3 Auditory-Motor Relations

Motor activity influenced by audition includes somatic, visceral, vocal behavior, and movement planning components. Acoustic startle and its inhibition are shaped by sensory input that requires integration across these four domains (Fig. 2.19a). Substantia nigra projections to the IC (Olazábal and Moore 1989) may coordinate motor orientation to sounds, while AC input to the basal ganglia (Reale and Imig 1983) could provide a premotor signal essential for cross-modal calibration (Fig. 2.19a). Analogous corticofugal circuits (Feliciano et al. 1995) might subserve auditory influence on vocalization (Schuller et al. 1997).

8.4 Auditory-Limbic Interactions

Circuits linking the MGB and the amygdala (LeDoux et al. 1985) bidirectionally (Marsh et al. 2002) could

shape autonomic responses to sound (LeDoux et al. 1986) (Fig. 2.19b). A massive AC projection to the amygdala (Romanski et al. 1993; Shi and Cassell 1997) testifies to this strong relation.

9 Directions for Future Research

It will suffice here to point out a few directions in which future research may be most helpful in providing a stronger underpinning for the development of a theory of auditory forebrain function. Further thoughts are expressed in Chapters 10 and 32.

1. What rules (construction, combination, etc.) govern the tectothalamic transformation?
2. Are the principles for information transfer similar among MGB subdivisions?
3. How does reversible inactivation of MGB subdivisions affect behavioral performance?
4. Are different MGB and AC subdivisions equally plastic from a physiologic perspective?
5. How is forebrain plasticity related to synaptic processes of facilitation and depression?
6. What do interneurons do in the MGB and AC? Is their performance nucleus and layer specific, or do they serve more general processes?
7. What is the significance—physiologically and behaviorally—of the several-fold species differences in the proportion of interneurons in the MGB and AC?

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References

- Aitkin L, Tran L, and Syka J (1994) The responses of neurons in subdivisions of the inferior colliculus of cats to tonal, noise and vocal stimuli. *Experimental Brain Research* **98**:53–64.
- Aitkin LM (1973) Medial geniculate body of the cat: responses to tonal stimuli of neurons in medial division. *Journal of Neurophysiology* **36**:275–283.
- Aitkin LM and Dunlop CW (1968) Interplay of excitation and inhibition in the cat medial geniculate body. *Journal of Neurophysiology* **31**:44–61.
- Arends JJ (1997) Sensory representation in the cerebellum and control circuits of motion. *European Journal of Morphology* **35**:234–245.
- Atzori M, Flores Hernández J, and Pineda JC (2004) Interlaminar differences of spike activation threshold in the auditory cortex of the rat. *Hear Res* **189**:101–106.
- Atzori M, Lei S, Evans DI, Kanold PO, Phillips-Tansey E, McIntyre O, and McBain CJ (2001) Differential synaptic processing separates stationary from transient inputs to the auditory cortex. *Nature Neuroscience* **4**:1230–1237.
- Bajo VM, Rouiller EM, Welker E, Clarke S, Villa AEP, de Ribaupierre Y, and de Ribaupierre F (1995) Morphology and spatial distribution of corticothalamic terminals originating from the cat auditory cortex. *Hearing Research* **83**:161–174.
- Barth DS, Goldberg N, Brett B, and Di S (1995) The spatiotemporal organization of auditory, visual, and auditory-visual evoked potentials in rat cortex. *Brain Research* **678**:177–190.
- Bartlett EL and Smith PH (1999) Anatomic, intrinsic, and synaptic properties of dorsal and ventral division neurons in rat medial geniculate body. *Journal of Neurophysiology* **81**:1999–2016.
- Bazhenov M, Timofeev I, Steriade M, and Sejnowski T (2000) Spiking-bursting activity in the thalamic reticular nucleus initiates sequences of spindle oscillations in thalamic networks. *Journal of Neurophysiology* **84**:1076–1087.
- Bendor D and Wang X (2005) The neuronal representation of pitch in primate auditory cortex. *Nature* **436**:1161–1165.
- Benedek G, Perényi J, Kovács G, Fischer-Szátmári L, and Katoh YY (1997) Visual, somatosensory, auditory and nociceptive modality properties in the feline supragenulate nucleus. *Neuroscience* **78**:179–189.
- Beneyto M and Prieto JJ (2001) Connections of the auditory cortex with the claustrum and endopiriform nucleus in the cat. *Brain Research Bulletin* **54**:485–498.
- Berman AL and Jones EG (1982) *The Thalamus and Basal Telencephalon of the Cat: A Cytoarchitectonic Atlas with Stereotaxic Coordinates*. University of Wisconsin Press, Madison.
- Bordi F and LeDoux JE (1994a) Response properties of single units in areas of rat auditory thalamus that project the amygdala. I. Acoustic discharge patterns and frequency receptive fields. *Experimental Brain Research* **98**:261–274.
- Bordi F and LeDoux JE (1994b) Response properties of single units in areas of rat auditory thalamus that project the amygdala. II. Cells receiving convergent auditory and somatosensory inputs and cells antidromically activated by amygdala stimulation. *Experimental Brain Research* **98**:275–286.
- Brandner S and Redies H (1990) The projection of the medial geniculate body to field AI: organization in the isofrequency dimension. *Journal of Neuroscience* **10**:50–61.
- Bregman AS (1990) *Auditory Scene Analysis. The Perceptual Organization of Sound*. MIT Press, Cambridge.
- Bueno-López JL, Reblet C, López-Medina A, Gómez-Urquijo SM, Grandes P, Gondra J, and Hennequet L (1990) Targets and laminar distribution of projection neurons with ‘inverted’ morphology in rabbit cortex. *European Journal of Neuroscience* **3**:415–430.
- Caballero-Bleda M, Fernandez B, and Puelles L (1991) Acetylcholinesterase and NADH-diaphorase chemoarchitectonic parahippocampal areas that have strong reciprocal amygdaloid connections (Shinonaga et al. 1994). This enables monosynaptic auditory corticoamygdaloid pathways and disynaptic and reciprocal corticothalamoamygdaloid and corticoamygdalothalamic streams. (Adapted from Winer and Lee 2007)

Fig. 2.19 (continued) sites (Clascá et al. 2000). Robust corticoamygdaloid input may mediate visceromotor and appetitive behavior (Romanski and LeDoux 1993). These pathways also have reciprocal and extended connections with the distributed AC. Corticogeniculate projections target MGB divisions receiving input from

- subdivisions in the rabbit medial geniculate body. *Journal of Chemical Neuroanatomy* **4**:271–280.
- Calford MB (1983) The parcellation of the medial geniculate body of the cat defined by the auditory response properties of single units. *Journal of Neuroscience* **3**:2350–2364.
- Calford MB and Aitkin LM (1983) Ascending projections to the medial geniculate body of the cat: evidence for multiple, parallel auditory pathways through the thalamus. *Journal of Neuroscience* **3**:2365–2380.
- Callaway EM (1998) Local circuits in primary visual cortex of the macaque monkey. *Annual Review of Neuroscience* **21**:47–74.
- Campeau S, Falls WA, Cullinan WE, Helmreich DL, Davis M, and Watson SJ (1997) Elicitation and reduction of fear: behavioural and neuroendocrine indices and brain induction of the immediate early gene *c-fos*. *Neuroscience* **78**:1087–1104.
- Cant NB and Benson CG (2003) Parallel auditory pathways: projection patterns of the different neuronal populations in the dorsal and ventral cochlear nuclei. *Brain Research Bulletin* **60**:457–474.
- Casseday JH, Schreiner CE, and Winer JA (2005) The inferior colliculus: past, present, and future. In: Winer JA and Schreiner CE (eds). *The Inferior Colliculus*. Springer, New York, pp. 626–640.
- Caulier L (1995) Layer I of primary sensory neocortex: where top-down converges upon bottom-up. *Behavioural Brain Research* **71**:163–170.
- Cetas JS, Price RO, Crowe J, Velenovsky DS, and McMullen NT (2003) Dendritic orientation and laminar architecture in the rabbit auditory thalamus. *Journal of Comparative Neurology* **458**:307–317.
- Cetas JS, Price RO, Velenovsky DS, Crowe JJ, Sinex DG, and McMullen NT (2002) Cell types and response properties of neurons in the ventral division of the medial geniculate body of the rabbit. *Journal of Comparative Neurology* **445**:78–96.
- Chen QC and Jen PH (2000) Bicuculline application affects discharge patterns, rate-intensity functions, and frequency tuning characteristics of bat auditory cortical neurons. *Hearing Research* **150**:161–174.
- Clarey JC, Barone P, and Imig TJ (1992) Physiology of thalamus and cortex. In: Popper AN and Fay RR (eds). *Springer Handbook of Auditory Research*, volume 2, *The Mammalian Auditory Pathway: Neurophysiology*. Springer, New York, pp. 232–334.
- Clasca F, Llamas A, and Reinoso-Suarez F (1997) Insular cortex and neighboring fields in the cat: a redefinition based on cortical microarchitecture and connections with the thalamus. *Journal of Comparative Neurology* **384**:456–482.
- Code RA and Winer JA (1986) Columnar organization and reciprocity of commissural connections in cat primary auditory cortex (AI). *Hearing Research* **23**:205–222.
- Coomes DL, Bickford ME, and Schofield BR (2002) GABAergic circuitry in the dorsal division of the cat medial geniculate nucleus. *Journal of Comparative Neurology* **453**:45–56.
- Cox CL, Metherate R, Weinberger NM, and Ashe JH (1992) Synaptic potentials and effects of amino acid antagonists in the auditory cortex. *Brain Research Bulletin* **28**:401–410.
- Cox CL and Sherman SM (2000) Control of dendritic outputs of inhibitory interneurons in the lateral geniculate nucleus. *Neuron* **27**:597–610.
- Cox CL, Zhou Q, and Sherman SM (1998) Glutamate locally activates dendritic outputs of thalamic interneurons. *Nature* **394**:478–482.
- Crabtree JW (1998) Organization in the auditory sector of the cat's thalamic reticular nucleus. *Journal of Comparative Neurology* **390**:167–182.
- Davis KA and Young ED (2000) Pharmacological evidence of inhibitory and disinhibitory neuronal circuits in dorsal cochlear nucleus. *Journal of Neurophysiology* **83**:926–940.
- de la Mothe L, Blumell S, Kajikawa Y, and Hackett TA (2006) Cortical connections of the auditory cortex in marmoset monkeys: core and medial belt regions. *Journal of Comparative Neurology* **496**:27–71.
- de Ribaupierre F (1997) Acoustic information processing in the auditory thalamus and cerebral cortex. In: Ehret G (ed). *The Central Auditory System*. Oxford University Press, New York, pp. 317–397.
- Deschênes M, Veinante P, and Zhang Z-W (1998) The organization of corticothalamic projections: reciprocity versus parity. *Brain Research Reviews* **28**:286–308.
- Diamond ME, Armstrong-James M, Budway MJ, and Ebner FF (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. *Journal of Comparative Neurology* **319**:66–84.
- Doucet JR, Molavi DL, and Ryugo DK (2003) The source of corticocollicular and corticobulbar projections in area Te1 of the rat. *Experimental Brain Research* **153**:477–485.
- Edeline J-M and Weinberger NM (1992) Associative retuning in the thalamic source of input to the amygdala and auditory cortex: receptive field plasticity in the medial division of the medial geniculate body. *Behavioral Neuroscience* **106**:81–105.
- Edeline JM (2003) The thalamo-cortical auditory receptive fields: regulation by the states of vigilance, learning and the neuromodulatory systems. *Experimental Brain Research* **153**:554–572.
- Ehret G (1997) The auditory cortex. *Journal of Comparative Physiology A* **181**:547–557.
- Eliades SJ and Wang X (2005) Dynamics of auditory-vocal interaction in monkey auditory cortex. *Cerebral Cortex* **15**:1510–1523.
- Feliciano M, Saldaña E, and Mugnaini E (1995) Direct projections from the rat primary auditory neocortex to nucleus sagulum, paralemniscal regions, superior olivary complex and cochlear nuclei. *Auditory Neuroscience* **1**:287–308.
- Foeller E, Vater M, and Kössl M (2001) Laminar analysis of inhibition in the gerbil primary auditory cortex. *Journal of the Association for Research in Otolaryngology* **2**:279–296.
- Foote SL, Bloom FE, and Aston-Jones G (1983) Nucleus locus ceruleus: new evidence of anatomical and physiological specificity. *Physiological Reviews* **63**:844–914.
- Foote SL, Freedman R, and Oliver AP (1975) Effects of putative transmitters on neuronal activity in monkey auditory cortex. *Brain Research* **86**:229–242.
- Formisano E, Kim DS, Di Salle F, van de Moortele PF, Ugurbil K, and Goebel R (2003) Mirror-symmetric tonotopic maps in human primary auditory cortex. *Neuron* **40**:859–869.
- Freund TF, Martin KAC, Smith AD, and Somogyi P (1983) Glutamate decarboxylase-immunoreactive terminals of Golgi-impregnated axo-axonic cells and of presumed basket cells in synaptic contact with pyramidal neurons of the cat's visual cortex. *Journal of Comparative Neurology* **221**:263–278.
- Gonchar Y, Turney S, Price JL, and Burkhalter A (2002) Axo-axonic synapses formed by somatostatin-expressing GABAergic neurons in rat and monkey visual cortex. *Journal of Comparative Neurology* **443**:1–14.
- Groh JM, Trause AS, Underhill AM, Clark KR, and Inati S (2001) Eye position influences auditory responses in primate inferior colliculus. *Neuron* **29**:509–518.
- Hackett TA, Stepniowska I, and Kaas JH (1998) Subdivisions of auditory cortex and ipsilateral cortical connections of the parabelt auditory cortex in macaque monkeys. *Journal of Comparative Neurology* **394**:475–495.
- Hackett TA, Stepniowska I, and Kaas JH (1999) Callosal connections of the parabelt auditory cortex in macaque monkeys. *European Journal of Neuroscience* **11**:856–866.
- Haenggeli CA, Pongstaporn T, Doucet JR, and Ryugo DK (2005) Projections from the spinal trigeminal nucleus to the cochlear

- nucleus in the rat. *Journal of Comparative Neurology* **484**:191–205.
- Harting JK and Van Lieshout DP (2000) Projections from the rostral pole of the inferior colliculus to the cat superior colliculus. *Brain Research* **881**:244–247.
- Hashikawa T, Molinari M, Rausell E, and Jones EG (1995) Patchy and laminar terminations of medial geniculate axons in monkey auditory cortex. *Journal of Comparative Neurology* **362**:195–208.
- He J (2003) Slow oscillation in non-lemniscal auditory thalamus. *Journal of Neuroscience* **23**:8281–8290.
- He J and Hu B (2002) Differential distribution of burst and single-spike responses in auditory thalamus. *Journal of Neurophysiology* **88**:2152–2156.
- Heffner HE and Heffner RS (1989) Unilateral auditory cortex ablation in macaques results in a contralateral hearing loss. *Journal of Neurophysiology* **62**:789–801.
- Hendry SHC, Schwark HD, Jones EG, and Yan J (1987) Numbers and proportions of GABA-immunoreactive neurons in different areas of monkey cerebral cortex. *Journal of Neuroscience* **7**:1503–1519.
- Hsieh CY, Cruikshank SJ, and Metherate R (2000) Differential modulation of auditory thalamocortical and intracortical synaptic transmission by cholinergic agonist. *Brain Research* **880**:51–64.
- Hu B (1995) Cellular basis of temporal synaptic signalling: an in vitro electrophysiological study in rat auditory thalamus. *Journal of Physiology (London)* **483**:167–182.
- Hu B, Senatorov V, and Mooney D (1994) Lemniscal and non-lemniscal synaptic transmission in rat auditory thalamus. *Journal of Physiology (London)* **479**:217–231.
- Huang CL, Larue DT, and Winer JA (1999) GABAergic organization of the cat medial geniculate body. *Journal of Comparative Neurology* **415**:368–392.
- Huang CL and Winer JA (1997) Areal and laminar distribution of cat auditory thalamocortical projections. *Proceedings of the Society for Neuroscience* **24**:185.
- Huang CL and Winer JA (2000) Auditory thalamocortical projections in the cat: laminar and areal patterns of input. *Journal of Comparative Neurology* **427**:302–331.
- Humphrey AL, Sur M, Uhlrich DJ, and Sherman SM (1985) Projection patterns of individual X- and Y-cell axons from the lateral geniculate nucleus to cortical area 17 in the cat. *Journal of Comparative Neurology* **233**:159–189.
- Imig TJ and Brugge JF (1978) Sources and terminations of callosal axons related to binaural and frequency maps in primary auditory cortex of the cat. *Journal of Comparative Neurology* **182**:637–660.
- Imig TJ and Morel A (1985a) Tonotopic organization in lateral part of posterior group of thalamic nuclei in the cat. *Journal of Neurophysiology* **53**:836–851.
- Imig TJ and Morel A (1985b) Tonotopic organization in ventral nucleus of medial geniculate body in the cat. *Journal of Neurophysiology* **53**:309–340.
- Jacobson M (1975) Development and evolution of type II neurons: conjectures a century after Golgi. In: Santini M (ed). *Golgi Centennial Symposium: Perspectives in Neurobiology*. Raven Press, New York, pp. 147–160.
- Jane JA, Masterton RB, and Diamond IT (1965) The function of the tectum for attention to auditory stimuli in the cat. *Journal of Comparative Neurology* **125**:165–192.
- Jones EG (2002) Thalamic circuitry and thalamocortical synchrony. *Philosophical Transactions of the Royal Society of London, series B, Biological Sciences* **357**:1659–1673.
- Jones EG, Burton H, Saper CB, and Swanson LW (1976) Midbrain, diencephalic and cortical relationships of the basal nucleus of Meynert and associated structures in primates. *Journal of Comparative Neurology* **167**:385–420.
- Jürgens U (2002) Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Reviews* **26**:235–258.
- Kamke MR, Brown M, and Irvine DR (2003) Plasticity in the tonotopic organization of the medial geniculate body in adult cats following restricted unilateral cochlear lesions. *Journal of Comparative Neurology* **459**:355–367.
- Kamke MR, Brown M, and Irvine DR (2005) Origin and immunolabeling of cholinergic basal forebrain innervation of cat primary auditory cortex. *Hearing Research* **206**:89–106.
- Kaur S, Lazar R, and Metherate R (2004) Intracortical pathways determine breadth of subthreshold frequency receptive fields in primary auditory cortex. *Journal of Neurophysiology* **91**:2551–2567.
- Kaur S, Rose HJ, Lazar R, Liang K, and Metherate R (2005) Spectral integration in primary auditory cortex: laminar processing of afferent input, in vivo and in vitro. *Neuroscience* **134**:1033–1045.
- Kawamura K (1973) Corticocortical fiber connections of the cat cerebrum. I. The temporal region. *Brain Research* **51**:1–21.
- Kelly JB and Judge PW (1985) Effects of medial geniculate lesions on sound localization by the rat. *Journal of Neurophysiology* **53**:361–372.
- Kimura A, Donishi T, Sakoda T, Hazama M, and Tamai Y (2003) Auditory thalamic nuclei projections to the temporal cortex in the rat. *Neuroscience* **117**:1003–1016.
- Kudoh M, Sakai M, and Shibuki K (2002) Differential dependence of LTD on glutamate receptors in the auditory cortical synapses of cortical and thalamic inputs. *Journal of Neurophysiology* **88**:3167–3174.
- Kulesza RJ, Viñuela A, Saldaña E, and Berrebi AS (2002) Unbiased stereological estimates of neuron number in subcortical auditory nuclei of the rat. *Hearing Research* **168**:12–24.
- Kurokawa T, Yoshida K, Yamamoto T, and Oka H (1990) Frontal cortical projections from the supragenicular nucleus in the rat, as demonstrated by the PHA-L method. *Neuroscience Letters* **120**:259–262.
- Kuwabara N and Zook JM (2000) Geniculate-collicular descending projections in the gerbil. *Brain Research* **878**:79–87.
- Kvasnak E, Popelar J, and Syka J (2000a) Discharge properties of neurons in subdivisions of the medial geniculate body of the guinea pig. *Physiological Research* **49**:369–378.
- Kvasnak E, Suta D, Popelar J, and Syka J (2000b) Neuronal connections in the medial geniculate body of the guinea-pig. *Experimental Brain Research* **132**:87–102.
- Landry P and Deschênes M (1981) Intracortical arborizations and receptive fields of identified ventrobasal thalamocortical afferents to the primary somatic sensory cortex in the cat. *Journal of Comparative Neurology* **199**:345–372.
- LeDoux JE, Ruggiero DA, and Reis DJ (1985) Projections to the subcortical forebrain from anatomically defined regions of the medial geniculate body in the rat. *Journal of Comparative Neurology* **242**:182–213.
- LeDoux JE, Sakaguchi A, Iwata J, and Reis DJ (1986) Interruption of projections from the medial geniculate body to an archi-neostriatal field disrupts the classical conditioning of emotional responses to acoustic stimuli. *Neuroscience* **17**:615–627.
- Lee CC, Imaizumi K, Schreiner CE, and Winer JA (2004a) Concurrent tonotopic processing streams in auditory cortex. *Cerebral Cortex* **14**:441–451.
- Lee CC, Schreiner CE, Imaizumi K, and Winer JA (2004b) Tonotopic and heterotopic projection systems in physiologically defined auditory cortex. *Neuroscience* **128**:871–887.
- Lee CC and Winer JA (2005) Principles governing auditory forebrain connections. *Cerebral Cortex* **15**:1804–1814.
- Lennartz RC and Weinberger NM (1992) Frequency-specific receptive field plasticity in the medial geniculate body induced by Pavlovian fear conditioning is expressed in the anesthetized brain. *Behavioral Neuroscience* **106**:484–497.

- Linke R (1999) Differential projection patterns of superior and inferior collicular neurons onto posterior paralamina nuclei of the thalamus surrounding the medial geniculate body in the rat. *European Journal of Neuroscience* **11**:187–203.
- Linke R and Schwegler H (2000) Convergent and complementary projections of the caudal paralamina thalamic nuclei to rat temporal and insular cortex. *Cerebral Cortex* **10**:753–771.
- Llano DA and Feng AS (2000) Computational models of temporal processing in the auditory thalamus. *Biological Cybernetics* **83**:419–433.
- Loftus WC and Sutter ML (2001) Spectrotemporal organization of excitatory and inhibitory receptive fields of cat posterior auditory field neurons. *Journal of Neurophysiology* **86**:475–491.
- Lund JS, Wu Q, Hadingham PT, and Levitt JB (1995) Cells and circuits contributing to functional properties in area V1 of macaque monkey cerebral cortex: bases for neuroanatomically realistic models. *Journal of Anatomy (London)* **187**:563–581.
- Malmierca MS, Merchán MA, Henkel CK, and Oliver DL (2002) Direct projections from cochlear nuclear complex to auditory thalamus in the rat. *Journal of Neuroscience* **22**:10891–10897.
- Malpeli JG and Baker FH (1975) The representation of the visual field in the lateral geniculate nucleus of *Macaca mulatta*. *Journal of Comparative Neurology* **161**:569–594.
- Marsh RA, Fuzessery ZM, Grose CD, and Wenstrup JJ (2002) Projection to the inferior colliculus from the basal nucleus of the amygdala. *Journal of Neuroscience* **22**:10449–10460.
- McAlonan K, Brown VJ, and Bowman EM (2000) Thalamic reticular nucleus activation reflects attentional gating during classical conditioning. *Journal of Neuroscience* **20**:8897–8901.
- McEchron MD, Green EJ, Winters RW, Nolen TG, Schneiderman N, and McCabe PM (1996) Changes of synaptic efficacy in the medial geniculate nucleus as a result of auditory classical conditioning. *Journal of Neuroscience* **16**:1273–1283.
- McMullen NT and de Venecia RK (1993) Thalamocortical patches in auditory neocortex. *Brain Research* **620**:317–322.
- McMullen NT, Velenovsky DS, and Holmes MG (2005) Auditory thalamic organization: cellular slabs, dendritic arbors and tectothalamic axons underlying the frequency map. *Neuroscience* **136**:927–943.
- Merzenich MM and Reid MD (1974) Representation of the cochlea within the inferior colliculus of the cat. *Brain Research* **77**:397–415.
- Middlebrooks JC and Zook JM (1983) Intrinsic organization of the cat's medial geniculate body identified by projections to binaural response-specific bands in the primary auditory cortex. *Journal of Neuroscience* **3**:203–225.
- Miller LM, Escabi MA, Read HL, and Schreiner CE (2001) Functional convergence of response properties in the auditory thalamocortical system. *Neuron* **32**:151–160.
- Mitani A, Itoh K, Nomura S, Kudo M, Kaneko T, and Mizuno N (1984) Thalamocortical projections to layer I of the primary auditory cortex in the cat: a horseradish peroxidase study. *Brain Research* **310**:347–350.
- Mitani A, Shimokouchi M, Itoh K, Nomura S, Kudo M, and Mizuno N (1985) Morphology and laminar organization of electrophysiologically identified neurons in primary auditory cortex in the cat. *Journal of Comparative Neurology* **235**:430–447.
- Mooney DM, Hu B, and Senatorov VV (1995) Muscarine induces an anomalous inhibition of synaptic transmission in rat auditory thalamic neurons in vitro. *Journal of Pharmacology and Experimental Therapeutics* **275**:838–844.
- Morel A and Imig TJ (1987) Thalamic projections to fields A, AI, P, and VP in the cat auditory cortex. *Journal of Comparative Neurology* **265**:119–144.
- Morel A and Kaas JH (1992) Subdivisions and connections of auditory cortex in owl monkeys. *Journal of Comparative Neurology* **318**:27–63.
- Morest DK (1965a) The laminar structure of the medial geniculate body of the cat. *Journal of Anatomy (London)* **99**:143–160.
- Morest DK (1965b) The lateral tegmental system of the midbrain and the medial geniculate body: study with Golgi and Nauta methods in cat. *Journal of Anatomy (London)* **99**:611–634.
- Morest DK (1971) Dendrodendritic synapses of cells that have axons: the fine structure of the Golgi type II cell in the medial geniculate body of the cat. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **133**:216–246.
- Morest DK (1975) Synaptic relationships of Golgi type II cells in the medial geniculate body of the cat. *Journal of Comparative Neurology* **162**:157–194.
- Morest DK and Winer JA (1986) The comparative anatomy of neurons: homologous neurons in the medial geniculate body of the opossum and the cat. *Advances in Anatomy, Embryology and Cell Biology* **97**:1–96.
- Nelken I (2002) Feature detection by the auditory cortex. In: Oertel D, Popper AN and Fay RR (eds). *Springer Handbook of Auditory Research*, volume 15, *Integrative Functions in the Mammalian Auditory Pathway*. Springer, New York, pp. 359–416.
- Olazábal UE and Moore JK (1989) Nigroreticular projection to the inferior colliculus: horseradish peroxidase transport and tyrosine hydroxylase immunohistochemical studies in rats, cats, and bats. *Journal of Comparative Neurology* **282**:98–118.
- Oliver DL (2005) Neuronal organization of the inferior colliculus. In: Winer JA and Schreiner CE (eds). *The Inferior Colliculus*. Springer, New York, pp. 69–114.
- Oliver DL, Winer JA, Beckius GE, and Saint Marie RL (1994) Morphology of GABAergic cells and axon terminals in the cat inferior colliculus. *Journal of Comparative Neurology* **340**:27–42.
- Pape HC and McCormick DA (1995) Electrophysiological and pharmacological properties of interneurons in the cat dorsal lateral geniculate nucleus. *Neuroscience* **68**:1105–1125.
- Perales M, Winer JA, and Prieto JJ (2006) Focal projections of cat auditory cortex to the pontine nuclei. *Journal of Comparative Neurology* **497**:959–980.
- Pollak GD, Burger RM, and Klug A (2003) Dissecting the circuitry of the auditory system. *Trends in Neurosciences* **26**:33–39.
- Prieto JJ, Peterson BA, and Winer JA (1994a) Laminar distribution and neuronal targets of GABAergic axon terminals in cat primary auditory cortex (AI). *Journal of Comparative Neurology* **344**:383–402.
- Prieto JJ, Peterson BA, and Winer JA (1994b) Morphology and spatial distribution of GABAergic neurons in cat primary auditory cortex (AI). *Journal of Comparative Neurology* **344**:349–382.
- Prieto JJ and Winer JA (1999) Layer VI in cat primary auditory cortex (AI): Golgi study and sublamina origins of projection neurons. *Journal of Comparative Neurology* **404**:332–358.
- Radnikow G, Feldmeyer D, and Lübke J (2002) Axonal projection, input and output synapses, and synaptic physiology of Cajal-Retzius cells in the developing rat neocortex. *Journal of Neuroscience* **22**:6908–6919.
- Rauschecker JP and Tian B (2000) Mechanisms and streams for processing of “what” and “where” in auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America* **97**:11800–11806.
- Rauschecker JP, Tian B, Pons T, and Mishkin M (1997) Serial and parallel processing in rhesus monkey auditory cortex. *Journal of Comparative Neurology* **382**:89–103.
- Read HL, Winer JA, and Schreiner CE (2001) Modular organization of intrinsic connections associated with spectral tuning in cat auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America* **98**:8042–8047.
- Read HL, Winer JA, and Schreiner CE (2002) Functional architecture of auditory cortex. *Current Opinion in Neurobiology* **12**:433–440.
- Reale RA and Imig TJ (1980) Tonotopic organization in auditory cortex of the cat. *Journal of Comparative Neurology* **192**:265–291.

- Reale RA and Imig TJ (1983) Auditory cortical field projections to the basal ganglia of the cat. *Neuroscience* **8**:67–86.
- Reblat C, López-Medina A, Gómez-Urquijo SM, and Bueno-López JL (1992) Widespread horizontal connections arising from layer 5/6 border inverted cells in rabbit visual cortex. *European Journal of Neuroscience* **4**:221–234.
- Riquimaroux H, Gaioni SJ, and Suga N (1992) Inactivation of the DSCF area of the auditory cortex with muscimol disrupts frequency discrimination in the mustached bat. *Journal of Neurophysiology* **68**:1613–1623.
- Romanski LM, Clugnet M, Bordi F, and LeDoux JE (1993) Somatosensory and auditory convergence in the lateral nucleus of the amygdala. *Behavioral Neuroscience* **107**:444–450.
- Romanski LM and LeDoux JE (1993) Information cascade from primary auditory cortex to the amygdala: corticocortical and corticoamygdaloid projections of temporal cortex in the rat. *Cerebral Cortex* **3**:515–532.
- Rose HJ and Metherate R (2005) Auditory thalamocortical transmission is reliable and temporally precise. *Journal of Neurophysiology* **94**:2019–2030.
- Rose JE and Woolsey CN (1958) Cortical connections and functional organization of thalamic auditory system of cat. In: Harlow HF and Woolsey CN (eds). *Biological and Biochemical Bases of Behavior*. University of Wisconsin Press, Madison, pp. 127–150.
- Rouiller EM and Durif C (2004) The dual pattern of corticothalamic projection of the primary auditory cortex in macaque monkey. *Neuroscience Letters* **358**:49–52.
- Rouiller EM, Rodrigues-Dagaëff C, Simm GM, de Ribaupierre Y, Villa AEP, and de Ribaupierre F (1989) Functional organization of the medial division of the medial geniculate body of the cat: tonotopic organization, spatial distribution of response properties and cortical connections. *Hearing Research* **39**:127–146.
- Rouiller EM and Welker E (2000) A comparative analysis of the morphology of corticothalamic projections in mammals. *Brain Research Bulletin* **53**:727–741.
- Samson FK, Barone P, Irons WA, Clarey JC, Poirier P, and Imig TJ (2000) Directionality derived from differential sensitivity to monaural and binaural cues in the cat's medial geniculate body. *Journal of Neurophysiology* **84**:1330–1345.
- Scheibel ME and Scheibel AB (1966) Patterns of organization in specific and nonspecific thalamic fields. In: Purpura DP and Yahr MD (eds). *The Thalamus*. Columbia University Press, New York, pp. 13–46.
- Schofield BR and Coomes DL (2004) Projections from the auditory cortex to the superior olivary complex in guinea pigs. *European Journal of Neuroscience* **19**:2188–2200.
- Schofield BR and Coomes DL (2005) Auditory cortical projections to the cochlear nucleus in guinea pigs. *Hearing Research* **199**:89–102.
- Schreiner CE and Cynader MS (1984) Basic functional organization of second auditory cortical field (AII) of the cat. *Journal of Neurophysiology* **51**:1284–1305.
- Schreiner CE and Langner G (1997) Laminar fine structure of frequency organization in auditory midbrain. *Nature* **388**:383–386.
- Schuller G, Fischer S, and Schweizer H (1997) Significance of the palelemniscal tegmental area for audio-motor control in the mustached bat, *Pteronotus p. parnellii*: the afferent and efferent connections of the palelemniscal area. *European Journal of Neuroscience* **9**:342–355.
- Senatorov VV and Hu B (2002) Extracortical descending projections to the rat inferior colliculus. *Neuroscience* **115**:243–250.
- Sherman SM and Guillery RW (1996) Functional organization of thalamocortical relays. *Journal of Neurophysiology* **76**:1367–1395.
- Sherman SM and Guillery RW (2000) *Exploring the Thalamus*. Academic Press, Orlando.
- Shi C-J and Cassell MD (1997) Cortical, thalamic, and amygdaloid projections of rat temporal cortex. *Journal of Comparative Neurology* **382**:153–175.
- Shinonaga Y, Takada M, and Mizuno N (1994) Direct projections from the non-laminated divisions of the medial geniculate nucleus to the temporal polar cortex and amygdala in the cat. *Journal of Comparative Neurology* **340**:405–426.
- Smith PH, Joris PX, and Yin TCT (1993) Projections of physiologically characterized spherical bushy cell axons from the cochlear nucleus of the cat: evidence for delay lines to the medial superior olive. *Journal of Comparative Neurology* **331**:245–260.
- Smith PH and Populin LC (2001) Fundamental differences between the thalamocortical recipient layers of the cat auditory and visual cortices. *Journal of Comparative Neurology* **436**:508–519.
- Smith PH and Spirou GA (2002) From the cochlea to the cortex and back. In: Oertel D, Fay RR and Popper AN (eds). *Springer Handbook of Auditory Research*, volume 15, *Integrative Functions in the Mammalian Auditory Pathway*. Springer, New York, pp. 6–71.
- Sousa-Pinto A (1973) The structure of the first auditory cortex (A I) in the cat. I. — Light microscopic observations on its structure. *Archives Italiennes de Biologie* **111**:112–137.
- Strominger NL, Nelson LR, and Dougherty WJ (1977) Second order auditory pathways in the chimpanzee. *Journal of Comparative Neurology* **172**:349–366.
- Sutter ML (2000) Shapes and level tolerances of frequency tuning curves in primary auditory cortex: quantitative measures and population codes. *Journal of Neurophysiology* **84**:1012–1025.
- Sutter ML and Loftus WC (2003) Excitatory and inhibitory intensity tuning in auditory cortex: evidence for multiple inhibitory mechanisms. *Journal of Neurophysiology* **90**:2629–2647.
- Syka J, Popelar J, Kvasnak E, and Astl J (2000) Response properties of neurons in the central nucleus and external and dorsal cortices of the inferior colliculus in guinea pig. *Experimental Brain Research* **133**:254–266.
- Thomas H and Lopez V (2003) Comparative study of inter- and intra-hemispheric cortico-cortical connections in gerbil auditory cortex. *Biological Research* **36**:155–169.
- Van Essen DC (2005) Corticocortical and thalamocortical information flow in the primate visual system. *Progress in Brain Research* **69**:215–237.
- Vogt BA (1991) The role of layer I in cortical function. In: Peters A (ed). *Cerebral Cortex*. Plenum Press, New York, pp. 49–80.
- Volkov IO and Galazjuk AV (1991) Formation of spike response to sound tones in cat auditory cortex neurons: interaction of excitatory and inhibitory effects. *Neuroscience* **43**:307–321.
- Wallace MN and Harper MS (1997) Callosal connections of the ferret primary auditory cortex. *Experimental Brain Research* **116**:367–374.
- Weedman DL and Ryugo DK (1996a) Projections from auditory cortex to the cochlear nucleus in rats: synapses on granule cell dendrites. *Journal of Comparative Neurology* **371**:311–324.
- Weedman DL and Ryugo DK (1996b) Pyramidal cells in primary auditory cortex project to cochlear nucleus in rat. *Brain Research* **706**:97–102.
- Wenstrup JJ (1999) Frequency organization and responses to complex sounds in the medial geniculate body of the mustached bat. *Journal of Neurophysiology* **82**:2528–2544.
- Wenstrup JJ (2005) The tectothalamic system. In: Winer JA and Schreiner CE (ed). *The Inferior Colliculus*. Springer, New York, pp. 200–230.
- Wenstrup JJ and Leroy SA (2001) Spectral integration in the inferior colliculus: role of glycinergic inhibition in response facilitation. *Journal of Neuroscience* **21**:RC124 (121–126).
- Wepsic JG (1966) Multimodal sensory activation of cells in the magnocellular medial geniculate nucleus. *Experimental Neurology* **15**:299–318.
- Wester K, Irvine DRF, and Hugdahl K (2001) Auditory laterality and attentional deficits after thalamic haemorrhage. *Journal of Neurology* **248**:676–683.

- Winer JA (1984a) Anatomy of layer IV in cat primary auditory cortex (AI). *Journal of Comparative Neurology* **224**:535–567.
- Winer JA (1984b) The human medial geniculate body. *Hearing Research* **15**:225–247.
- Winer JA (1984c) The non-pyramidal neurons in layer III of cat primary auditory cortex (AI). *Journal of Comparative Neurology* **229**:512–530.
- Winer JA (1984d) The pyramidal cells in layer III of cat primary auditory cortex (AI). *Journal of Comparative Neurology* **229**:476–496.
- Winer JA (1985) Structure of layer II in cat primary auditory cortex (AI). *Journal of Comparative Neurology* **238**:10–37.
- Winer JA (1986) Neurons accumulating [3H]gamma-aminobutyric acid (GABA) in supragranular layers of cat primary auditory cortex (AI). *Neuroscience* **19**:771–793.
- Winer JA (1992) The functional architecture of the medial geniculate body and the primary auditory cortex. In: Webster DB, Popper AN, and Fay RR (eds). *Springer Handbook of Auditory Research, volume 1, The Mammalian Auditory Pathway: Neuroanatomy*. Springer, New York, pp. 222–409.
- Winer JA (2005) Three systems of descending projections to the inferior colliculus. In: Winer JA and Schreiner CE (ed). *The Inferior Colliculus*. Springer, New York, pp. 231–247.
- Winer JA (2006) Decoding the auditory corticofugal systems. *Hearing Research* **212**:1–8.
- Winer JA, Diamond IT, and Raczkowski D (1977) Subdivisions of the auditory cortex of the cat: the retrograde transport of horseradish peroxidase to the medial geniculate body and posterior thalamic nuclei. *Journal of Comparative Neurology* **176**:387–418.
- Winer JA, Diehl JJ, and Larue DT (2001) Projections of auditory cortex to the medial geniculate body of the cat. *Journal of Comparative Neurology* **430**:27–55.
- Winer JA and Larue DT (1987) Patterns of reciprocity in auditory thalamocortical and corticothalamic connections: study with horseradish peroxidase and autoradiographic methods in the rat medial geniculate body. *Journal of Comparative Neurology* **257**:282–315.
- Winer JA and Larue DT (1988) Anatomy of glutamic acid decarboxylase (GAD) immunoreactive neurons and axons in the rat medial geniculate body. *Journal of Comparative Neurology* **278**:47–68.
- Winer JA and Larue DT (1989) Populations of GABAergic neurons and axons in layer I of rat auditory cortex. *Neuroscience* **33**:499–515.
- Winer JA and Larue DT (1996) Evolution of GABAergic circuitry in the mammalian medial geniculate body. *Proceedings of the National Academy of Sciences of the United States of America* **93**:3083–3087.
- Winer JA, Larue DT, Diehl JJ, and Hefti BJ (1998) Auditory cortical projections to the cat inferior colliculus. *Journal of Comparative Neurology* **400**:147–174.
- Winer JA, Larue DT, and Huang CL (1999a) Two systems of giant axon terminals in the cat medial geniculate body: convergence of cortical and GABAergic inputs. *Journal of Comparative Neurology* **413**:181–197.
- Winer JA, Larue DT, and Pollak GD (1995) GABA and glycine in the central auditory system of the mustache bat: structural substrates for inhibitory neuronal organization. *Journal of Comparative Neurology* **355**:317–353.
- Winer JA and Lee CC (2007) The distributed auditory cortex. *Hearing Research* **229**:3–13.
- Winer JA, Miller LM, Lee CC, and Schreiner CE (2005) Auditory thalamocortical transformation: structure and function. *Trends in Neurosciences* **28**:255–263.
- Winer JA and Morest DK (1983a) The medial division of the medial geniculate body of the cat: implications for thalamic organization. *Journal of Neuroscience* **3**:2629–2651.
- Winer JA and Morest DK (1983b) The neuronal architecture of the dorsal division of the medial geniculate body of the cat. A study with the rapid Golgi method. *Journal of Comparative Neurology* **221**:1–30.
- Winer JA, Morest DK, and Diamond IT (1988) A cytoarchitectonic atlas of the medial geniculate body of the opossum, *Didelphys virginiana*, with a comment on the posterior intralaminar nuclei of the thalamus. *Journal of Comparative Neurology* **274**:422–448.
- Winer JA and Prieto JJ (2001) Layer V in cat primary auditory cortex (AI): cellular architecture and identification of projection neurons. *Journal of Comparative Neurology* **434**:379–412.
- Winer JA, Saint Marie RL, Larue DT, and Oliver DL (1996) GABAergic feedforward projections from the inferior colliculus to the medial geniculate body. *Proceedings of the National Academy of Sciences of the United States of America* **93**:8005–8010.
- Winer JA, Sally SL, Larue DT, and Kelly JB (1999b) Origins of medial geniculate body projections to physiologically defined regions of rat auditory cortex. *Hearing Research* **130**:42–61.
- Winer JA and Schreiner CE (2005) The central auditory system: a functional analysis. In: Winer JA and Schreiner CE (eds). *The Inferior Colliculus*. Springer, New York, pp. 1–68.
- Winer JA and Wenstrup JJ (1994) The neurons of the medial geniculate body in the mustached bat (*Pteronotus parnellii*). *Journal of Comparative Neurology* **346**:183–206.
- Wong D and Kelly JP (1981) Differentially projecting cells in individual layers of the auditory cortex: a double-labeling study. *Brain Research* **230**:362–366.



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