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Thalamic and amygdaloid connections of the auditory association cortex of the superior temporal gyrus in rhesus monkey (*Macaca mulatta*)

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Abstract. Thalamic and amygdaloid connections of three association auditory areas (AA1, AA2, AA3) of the superior temporal gyrus (STG) were investigated. In order to define the projections of the particular areas, injections of fluorescent tracers were made in three monkeys. Distribution of labeling indicates that area AA1 differs from areas AA2 and AA3 in patterns of both thalamo-cortical and amygdalo-cortical connections. Area AA1 receives its predominant inputs from the ventral and dorsal nuclei of the medial geniculate body (MGB). The amygdaloid projection to the area AA1 originates from the basal nuclei, whereas input from the lateral nucleus was not found. The characteristic thalamic projections to areas AA2 and AA3 originate from the dorsal MGB nucleus and the polymodal nuclei of the posterior thalamus. The density of projections from the dorsal nucleus gradually decreases from area AA1 to area AA3 while projections from the Plm, Sg and Lim nuclei increase in the same direction. Areas AA2 and AA3 are the source of strong connections with the lateral nucleus of amygdala, which density increases progressively when injections shift from area AA2 to AA3. The basal and accessory basal nuclei are the source of a less significant amygdalofugal projections to both cortical areas. Thus, our experimental data indicate that influence of the polymodal thalamic nuclei increases substantially in the direction of the higher order association areas. The strong relation of the same cortical areas with the lateral amygdaloid nucleus might suggest that areas AA2 and AA3, in addition to auditory input are the site of transfer of complex sensory information to the amygdala.

Key words: auditory association cortex, thalamic connections, amygdala connections, fluorochrome dyes

INTRODUCTION

The superior temporal gyrus (STG) lying above the superior temporal sulcus (STS) is involved in processing auditory input and contains both primary and associative auditory cortices. Localization of the primary auditory fields within the lower bank of the lateral sulcus has been recently reinvestigated on the basis of sensory representation, cellular architecture and distribution of the acetylcholinesterase (AChE) and cytochrome oxidase (CO) activity (Morel et al. 1993). The auditory association cortex involved in higher integrative functions, like sound localization or recognition of complex auditory patterns (Rauschecker et al. 1995) and also in the auditory memory process (Leinonen et al. 1980, Colombo et al. 1990), has been studied relatively little in comparison to the primary auditory cortex.

The auditory association cortex used to be divided into several subfields on the basis of differences in the regional cytoarchitectonics and the pattern of connections (thalamic, cortical intrinsic and long-distance association). Depending on the criteria used by different authors, both the nomenclature and boundaries of these subfields differ to some degree (see Table I). On the basis of cytoarchitectonic differences and distribution of thalamo-cortical connections, Burton and Jones (1976) divided the superior temporal gyrus into T1, T2 and T3 fields arranged in concentric belts around the primary auditory cortex. Among them, field T2, situated mainly on the surface of the gyrus, forms an elongated strip along the whole postero-anterior axis of STG. Another parcelation of STG was based on cytoarchitectonic trends in the differentiation of cortical layers. On the basis of progressive rostro-caudal differentiation of the third cortical layer along STG (belt line according to Pandya and Sanides 1973), cytoarchitectonic fields Pro, Ts1, Ts2, Ts3, paAlt and Tpt were distinguished. The sequence of intrinsic connections determined that STG cortex is involved in the transfer of auditory information through the successive STG cytoarchitectonic fields towards the temporal pole (Pandya and Sanides 1973, Seltzer and Pandya 1978, Galaburda and Pandya 1983, Pandya and Yeterian 1985). Distant, topographically organized cortical connections with the frontal cortex, parietotemporal region and paralimbic cortex constituted the basis of STG division into three association areas: AA1, AA2, AA3 situated on the STG surface in the postero-anterior order (Chavis and Pandya 1976, Seltzer and Pandya 1978, Pandya and Yeterian 1985).

Early studies of the thalamo-cortical connections determined a general topography of projection between STG and the posterior part of the thalamus defined as systems of separated connections (Burton and Jones 1976). According to that, fields T1 and T2 receive projection from the dorsal division of MGB, whereas field T3 receives projections from the medial pulvinar (Plm). Additionally, STG cortex was defined as related to the posterior group of the thalamus - suprageniculate (Sg), limitans (Lim) and posterior (Po) nuclei (Trojanowski and Jacobson 1975). The group is considered to be associative in function because of its relation to various sensory modalities and a widespread corticopetal projection (Fitzpatrick and Imig 1978, Morel and Kaas 1992, Morel et al. 1993, Pandya et al. 1994).

On the other hand, the sensory related temporal neocortex has also significant connections with the amygdaloid complex (Herzog and Van Hoesen 1976, Aggleton et al. 1980, Turner et al. 1980, Van Hosen 1981, Amaral and Price 1984, Markowitsch et al. 1985, Aggleton and Mishkin 1986, Baylis et al. 1987, Amaral et al. 1992, Rolls 1992). It has been found that the most dense reciprocal connections link the amygdala with the cortical fields localized outside the unimodal sensory representation: in the polymodal cortex of the superior temporal sulcus, temporal pole and perirhinal cortex. Some amygdalopetal projections, however, were found to originate within the modality-specific association areas (Aggleton et al. 1980, Amaral and Price 1984, Iwai and Yukie 1987, Amaral et al. 1992). In this way sensory information may influence and modify emotional behavior (Aggleton and Mishkin 1986, LeDoux 1992, Aggleton 1993) and memory processes (Kesner 1992, Murray 1992, LeDoux 1994).

Data concerning the extent of the cortex in which amygdalopetal connections originates as well as the topography and reciprocity of connections are not consistent. Although the reviewed data consistently link the rostral STG cortex with the lateral nucleus (Herzog and Van Hoesen 1976, Aggleton et al. 1980, Turner et al. 1980, Van Hoesen 1981, Amaral et al. 1992), it still remains an open question whether the amygdalopetal projection originates mainly from the polymodal cortex of the temporal pole ,or the unimodal auditory association areas participate in it as well. Another question is, whether the cortex connected with the amygdala receives a distinct thalamic projection.

The aim of this study was to determine the topography of both thalamo-cortical and cortico-amygdaloid con-

nections of particular areas of the auditory association cortex . The indirect thalamo-cortico-amygdaloid connections may constitute the morphological background of inflow of sensory information reaching the amygdala through the superior temporal cortex.

METHODS

The housing, care and surgical procedures followed the quidelines established by the Ethical Committee on Animal Research of the Nencki Institute, based on a decree of the President of Polish Republic.

Three adult male rhesus monkeys (*Macaca mulatta*), designated as M1, M2 and M3, were used in this study.

The auditory association cortex situated on the surface of the superior temporal gyrus was injected with the fluorochrome dyes; fluoro ruby (FR) which is transported in both retrograde and anterograde directions, fast blue (FB) and diamidine yellow (DY), which are transported retrogradely and label perikarya and neuronal nuclei, respectively. Injecting of three retrogradely transported tracers into three succesive auditory fields in one experiment allowed us to determine spatial distribution of the labeled neurons in the thalamus and amygdala. Comparing the density of labeling among three dyes, we observed that the FR injections were more effective than DY or FB. In addition, the diffusion of FR, or spread of the injection site were very restricted. It did not generate cortical necrosis around the site of injection as was often the case with FB and DY (cf. D and E in Fig. 1).

Prior to surgery the animals were initialy anesthetized with ketamine hydrochloride (10 mg/kg) and atropine (0.04 mg/kg), and supplemented with injections of sodium pentobarbital (Nembutal) (15 to 25 mg/kg). Surgery was performed under aseptic conditions. Multiple pressure-injections of ca 50 nl of the dye at one site of the cortex were made through a glass micropipette attached to picospritzer (General Valve Corporation). Most of these injections involved the whole thickness of the cortex. The total amount of the dye injected varied depending on the kind of fluorochrome used and on the cortical area injected. Twelve days after the injections of tracers animals were deeply reanesthetized with Nembutal and perfused transcardially with 0.9 % saline mixed with heparin followed by a solution of 4 % formaldehyde in 0.1 M phosphate buffer (pH 7.4) and 5% glycerol in the same buffer.

The brain blocks were processed according to the cryoprotection method for frozen sections which produced no freezing artifacts (Rosene et al. 1986), and then 50 μm thick coronal sections were cut on a freezing microtome. Five separate sets of consecutive histological sections were collected in phosphate buffer. The distance between two sections in a series was 500 μm. Two sets were used for examination of cells and axons labeled with fluorochrome dyes. Two other sets were processed for acetylcholinesterase (AChE) activity according to the method of Genser-Jensen and Blackstad (1971). Different times of incubation with the acetylothiocholine iodide and ethopropasine (a pseudocholinesterase inhibitor) were used for staining the cortex and subcortical structures (3 h and 30 min, respectively). The remaining sets were dehydrated and stained according to the standard Nissl method with thionine. Sections examined with a fluorescence microscope were not counterstained and the dehydration process was omitted. Sections were coverslipped with the Fluoromount (Serva).

Distribution of labeled neurons was observed with a Nikon fluorescent microscope, and their approximate number was estimated. Cells labeled retrogradely with FB were identifiable by blue fluorescence of their perikarya, whereas those labeled with DY - by green-yellow fluorescence of their neuronal nuclei (excitation filter EX 380-425). The FR retrogradely labeled cells and anterogradely labeled axons were identified by red fluorescence (excitation filter EX 510-560). Location of labeled cells and terminal parts of axons was established by matching with the position of blood vessels charted onto drawings prepared from sections. Identification of the exact location of labeled cells in our material was based on the analysis of three neighboring histological sections. Unstained fluorochrome sections were compared with the cellular arrangement in the Nissl-stained sections and this comparison was corroborated by the distribution of AChE activity.

RESULTS

Localization of injections

Area AA1 was injected in one monkey - M3 with FB dye, (Table I and Fig. 1C). This large multiple injection spread additionally into a small dorsal part of area AA2. Diffusion of the dye merged particular points of injections. The injection penetrated to some extent the underlying white matter (Table I; Fig. 1C,3 and E).

Area AA2 was injected in two monkeys, M1 and M3. In M1 the FR dye was injected into a central part of the

TABLE I

Localization of injections in three monkeys in reference to cytoarchitectonic and functional divisions of the STG

Monkey (number and dye injected)	Jones and Burton (1976)	Galaburda and Pandya (1983)	Chavis and Pandya (1976)
M1 - FR	T2/T1	Ts3/Ts2 dors.	AA2
M2 - FR	T2/T3	Ts1/Pro, Ts2	AA3
M3 - FB	T1/T2	Ts3/paAlt	AA1/AA2
- DY	T2	Ts2/Ts3 ventr.	AA2
- FR	T2	Ts1/Pro	AA3

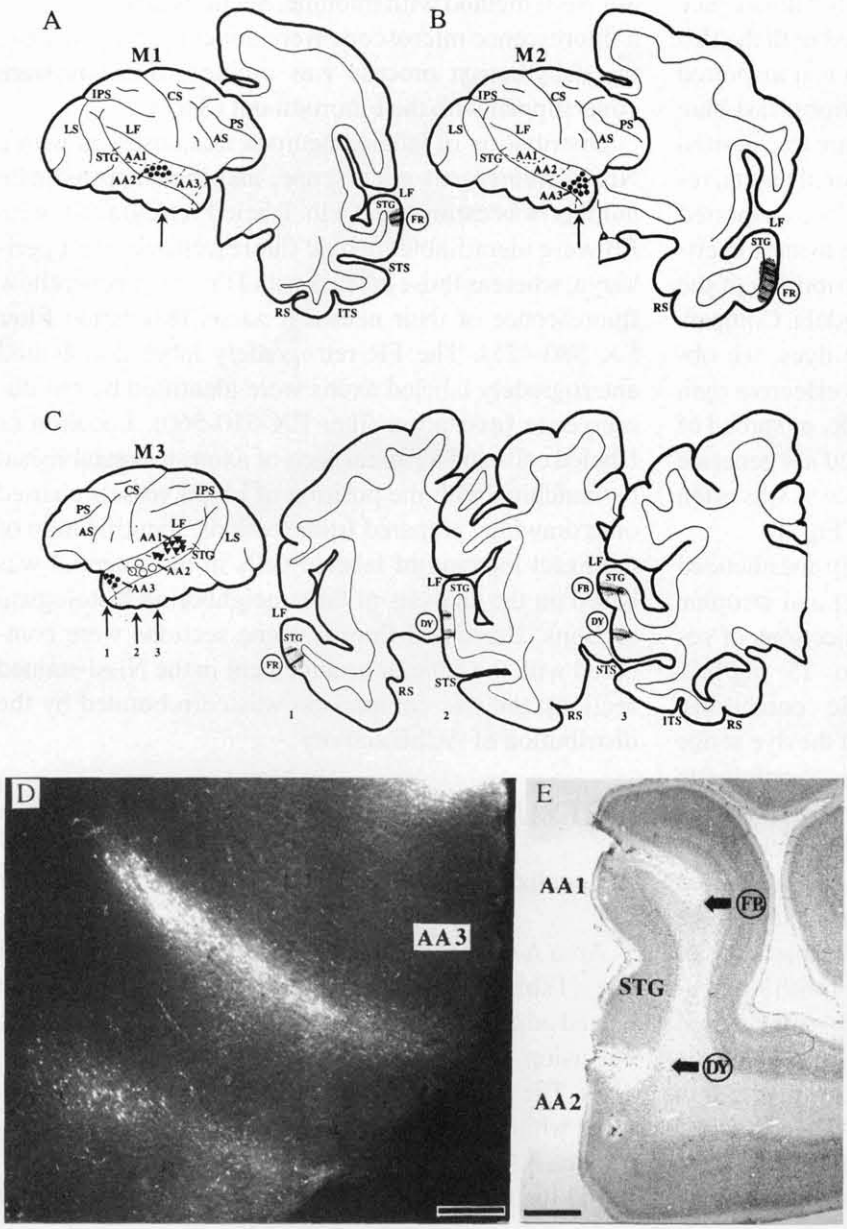

Fig. 1. Localization of injections in monkeys M1-M3, shown on the lateral view of the right (M1 and M2) and left (M3) hemispheres. The extent and depth of particular injections are illustrated in coronal sections. Arrows indicate the levels of coronal sections. A, in monkey M1, fluoro-ruby (FR) injections were located in the area AA2 (solid circles). In the coronal section sites of injections into STG cortex and the diffusion of the dye through the cortical thickness are marked as a shaded area. B, in monkey M2, FR injections were placed in area AA3 of the rostral most part of STG. In the coronal section, the site of injections and diffusion of the dye through the cortical thickness is shown as a shaded area. C, localization of three injections: fast blue (FB) into the area AA1 (solid triangles), diamidine yellow (DY) -into area AA2 (open circles), and FR into AA3 (solid circles) in the monkey M3. Positions and depths of particular injections are shown at three successive coronal sections from the rostral (1) to the caudal (3) extent of STG. The FB injection into area AA1 (section C3) penetrates the underlying white matter. D, low-power fluorescent photomicrograph of FR injection in monkey M2. It corresponds to the level of coronal section shown in B. Scale bar = 0.3 mm. E, low-power photomicrograph of Nissl-stained coronal section of monkey M3 showing the positions and depths of the FB and DY injections. This photomicrograph corresponds to section C3. Notice a small area of necrosis in and around the pipette tracks in both FB and DY injections. Scale bar = 2 mm.

area (Fig. 1A). In M3, a small DY injection was located in its ventral part (Table I; Fig. 1C,2,3 and E).

Area AA3 was injected in two monkeys, M2 and M3 with FR. In M2, the injection covered a fairly large anterior part of the area AA3, slightly affecting the dorsal extent of the temporal pole (Fig. 1B). Injection in monkey M2 (Fig. 1D) illustrates limited diffusion of FR, which is typical for the dye, forming separate bands across the cortical thickness for particular injection sites. In M3, a small injection was placed in the anterior part of AA3 below the lateral fissure (Table I and Fig. 1C,1).

Thalamic projections

Three main nuclear groups projecting to STG cortex were distinguished in the posterior thalamic region: the medial geniculate body, the posterior complex, and the pulvinar. For analysis and description of our results, the cytoarchitectonic divisions of the posterior thalamic nuclei were adopted according to Burton and Jones (1976). In agreement with that description, and observation of cytoarchitecture in present material (Fig. 2A), in the medial geniculate body the principal division and the mag-

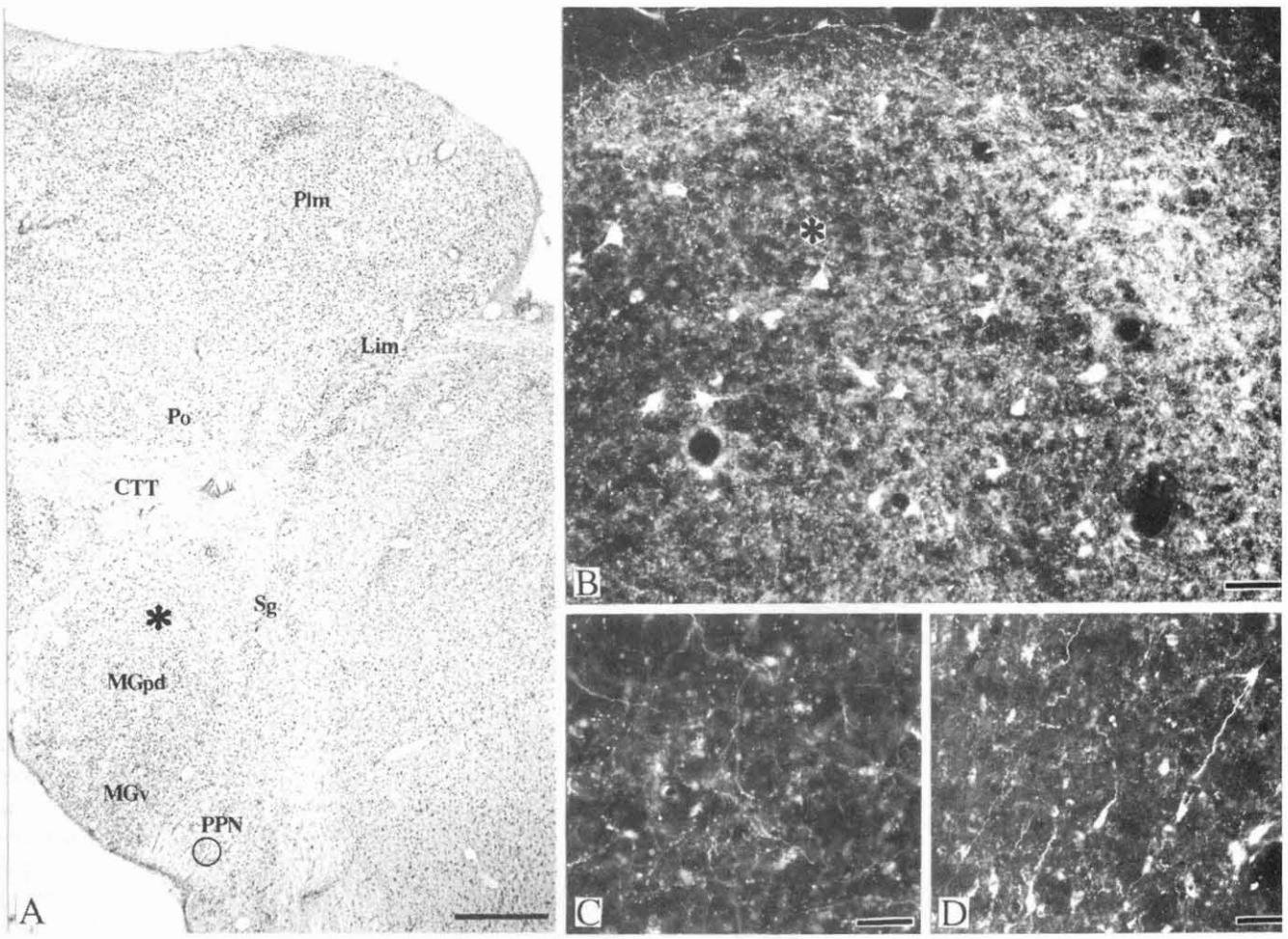

Fig. 2. Cytoarchitecture of the posterior thalamus and results of labeling in monkey M3. A, low-power photomicrograph of the Nissl-stained coronal section illustrating the cytoarchitectonic subdivisions of the posterior thalamus; list of abbreviations in the text. Asterisk indicates the part of MGpd that is magnified in B; open circle indicates the site of PPN that is magnified in D. Scale bar = 1 mm. B, fluorescent photomicrograph showing the cells retrogradely labeled with FR and the anterogradely labeled axon terminals in MGpd, after injection into area AA3. Notice the area with very high density of labeled terminals situated in the dorsomedial part of the nucleus. In the central area of the nucleus only sparse terminals are seen. Scale bar = 0.1 mm. C, higher magnification view of sparse axonal terminals seen in the central area of MGpd marked with an asterisk in B. Scale bar = 50 μm. D, high-power fluorescent photomicrograph of scattered cells labeled retrogradely with FR and sparsely distributed labeled axons in PPN. Approximate position of the photomicrograph is marked as an open circle in A. Scale bar = 50 μm.

nocellular medial nucleus (MGm) were distinguished. The principal division consisted of the ventral (MGv) and dorsal nuclei. In the Nissl-stained sections the ventral nucleus of MGB is distinguishable by a population of small, densely packed neurons (MGv; Fig. 2A), but its border with the dorsal nuclei is rather unclear. The dorsal nucleus was further subdivided into the posterodorsal (MGpd) and anterodorsal (MGad) nuclei. Both dorsal nuclei were generally formed by a group of slightly larger and not so tightly packed cells as in the ventral nucleus (MGpd; Fig. 2A). The magnocellular medial nucleus of the medial geniculate body was recognized by the presence of large cells scattered among the smaller ones. It was situated in the medial region of the complex.

The posterior complex consisted of the suprageniculate (Sg), limitans (Lim) and posterior (Po) nuclei (Fig. 2A). The Sg nucleus is situated dorsomedially to the principal MGB divisions and it is continuous dorsally with a narrow belt of Lim nucleus, located at the ventromedial limit of medial pulvinar nucleus. The Po nucleus is formed by an ill-defined population of cells scattered in the part of the thalamus situated dorsolaterally to the MGB complex and below the pulvinar Ventrally, MGB borders with a population of small scattered cells of the peripeduncular nucleus (PPN). The pulvinar was cytoarchitectonically divided into four subnuclei: anterior or oral (Pla), lateral (Pll), inferior (Pli), and medial (Plm). Among these subnuclei only the medial pulvinar nucleus projected to the STG cortex. The Plm is situated at the dorsomedial limit of the thalamus (Figs. 2A and 9A).

CORTICOPETAL THALAMIC CONNECTIONS

Retrograde labeling after injections into the area AA1

Among the principal MGB nuclei the FB labeled cells in the monkey M3 were observed predominantly in the ventral and posterodorsal nuclei. The density of retrograde labeling was similar in both nuclei and composed approximately 80% of the total number of FB labeled cells.

In the ventral nucleus, the main group of labeled cells was found at the middle of the antero-posterior extent of the complex (v; Fig. 3B,b). This group of cells extended

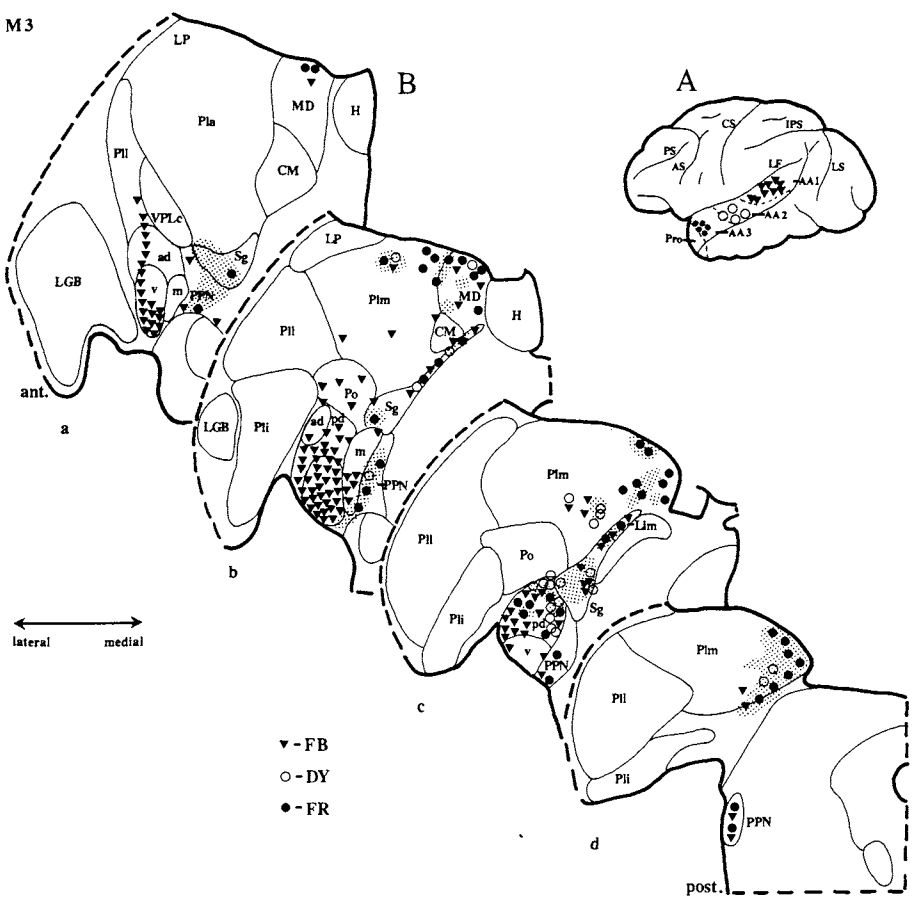

Fig. 3. Results of labeling in monkey M3. A, localization of injections into the areas AA1, AA2 and AA3 is marked on the lateral view of the left hemisphere. Area covered with solid triangles shows the FB injection into the area AA1; open circles, DY injection into AA2; solid circles, FR injection into AA3. B, distribution of retrogradely labeled cells after injections of three fluorochromes (marked with respective symbols) and anterogradely labeled axonal terminals (shaded areas) are shown in four drawings of coronal sections of the posterior thalamus, presented in antero-posterior order (a-d); v, ad, pd, m indicate positions of the particular MGB nuclei; list of abbreviations in the text.

slightly into the anteroventral part of the nucleus (Fig. 3B,a) and caudally, where only single FB labeled cells were seen in the ventral nucleus (Fig. 3B,c). In the dorsal nuclei, numerous labeled cells were observed mainly in the posterodorsal subdivision of the nucleus (pd; Fig. 3B,b,c). At the caudal limit, labeled cells were arranged in a closely packed group situated at the lateral border of the nucleus which gradually scattered into its central part (Fig. 4A). In the anterodorsal nucleus, only single labeled cells were scattered in a narrow band extending dorsally from MGv (ad; Fig. 3B,a). Moreover, a few FB labeled cells were found in the ventral part of MGm nucleus at its intermediate level (m; Fig. 3B,b).

In the posterior thalamic complex FB labeled cells were found in Sg and Lim as well as in PPN and Po nuclei. Their numbers equalled approximately 10% of the total number of the FB labeled cells. Among these nuclei slightly more cells were found in the posteromedial Sg part (Figs. 3B,c and 4C).

A limited number of labeled cells (approx. 6%) were observed in the posteromedial and central parts of the medial pulvinar nucleus. In addition, a few cells appeared in the mediodorsal (MD) thalamic nucleus adjacent to Plm (Fig. 3B,b-c).

Retrograde labeling after injections into the area AA2

In both cases of AA2 injections (M1-FR, M3-DY), large numbers of labeled cells (approx. 17% of the total number of labeled cells in the posterior thalamus) were found predominantly in the posterodorsal nucleus of the medial geniculate body. After a FR injection in monkey M1, labeled cells were mainly grouped along the medial and dorsal borders of the caudal most limit of the MGpd nucleus (Fig. 5B,b). At the successive anterior levels the cells formed two separate aggregations in the medial and lateral regions of the nucleus (Fig. 5B,c). Generally, in M3 less numerous DY labeled neurons were found in the comparable postero-medial extent of MGpd (cf. Fig. 3B, c and Fig. 5B, c).

Comparison of the distribution of labeled cells in MGpd after injections into AA1 and AA2 shows that the projection to AA1 was formed mainly by neurons located in the lateral part of the nucleus, whereas projection to area AA2 originated in cells of its posteromedial extent (Fig. 4A and B). Only single labeled cells were observed in the medial nucleus of the medial geniculate body (Fig. 5B,d). It is important to emphasize that in both

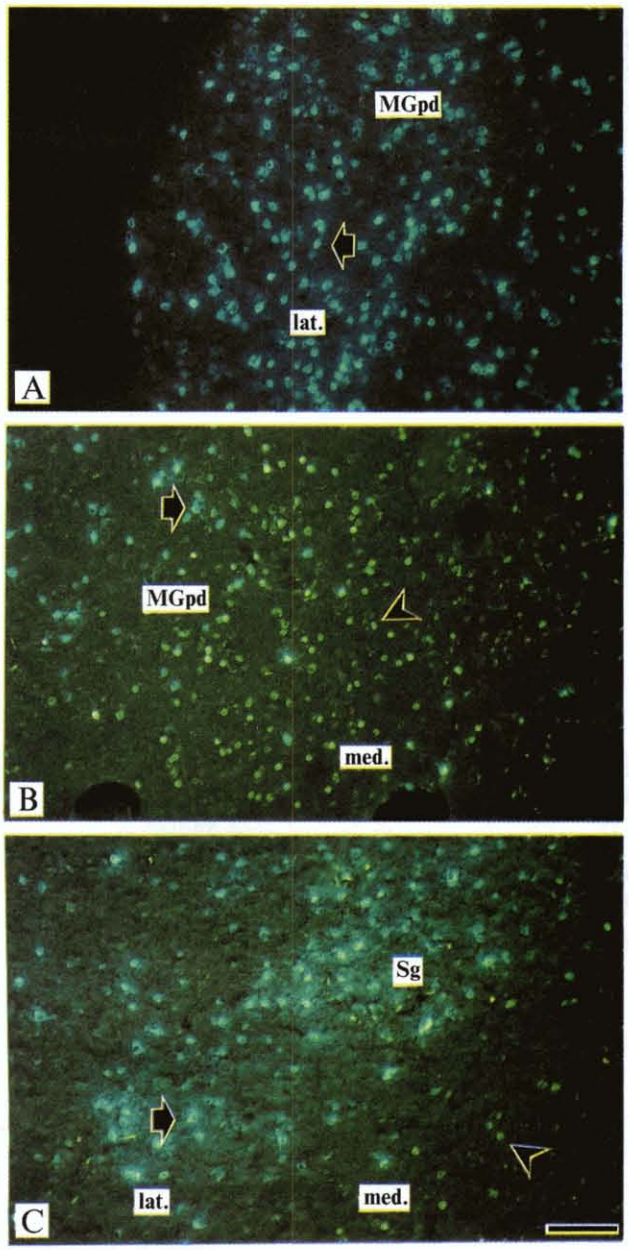

Fig. 4. Fluorescent photomicrographs illustrate the localization and density of cells projecting to areas AA1 and AA2 in monkey M3. A, homogeneous population of FB labeled neurons located in the lateral part of MGpd nucleus, projecting to the area AA1. Localization of these cells corresponds to Fig. 3B,b. Arrow shows one of the FB labeled cells. B, the DY labeled neuronal nuclei (arrowhead) located mainly in the medial part of MGpd projecting to the area AA2. Less numerous FB labeled cells (arrow) send their axons to the area AA1. Localization of these cells corresponds to Fig. 3B,c. C, a group of FB labeled cells (arrow) in the medial part of Sg and less numerous DY labeled neuronal nuclei (arrowhead) situated medially to the FB labeled cells. Localization of these cells corresponds to Fig. 3B,c.

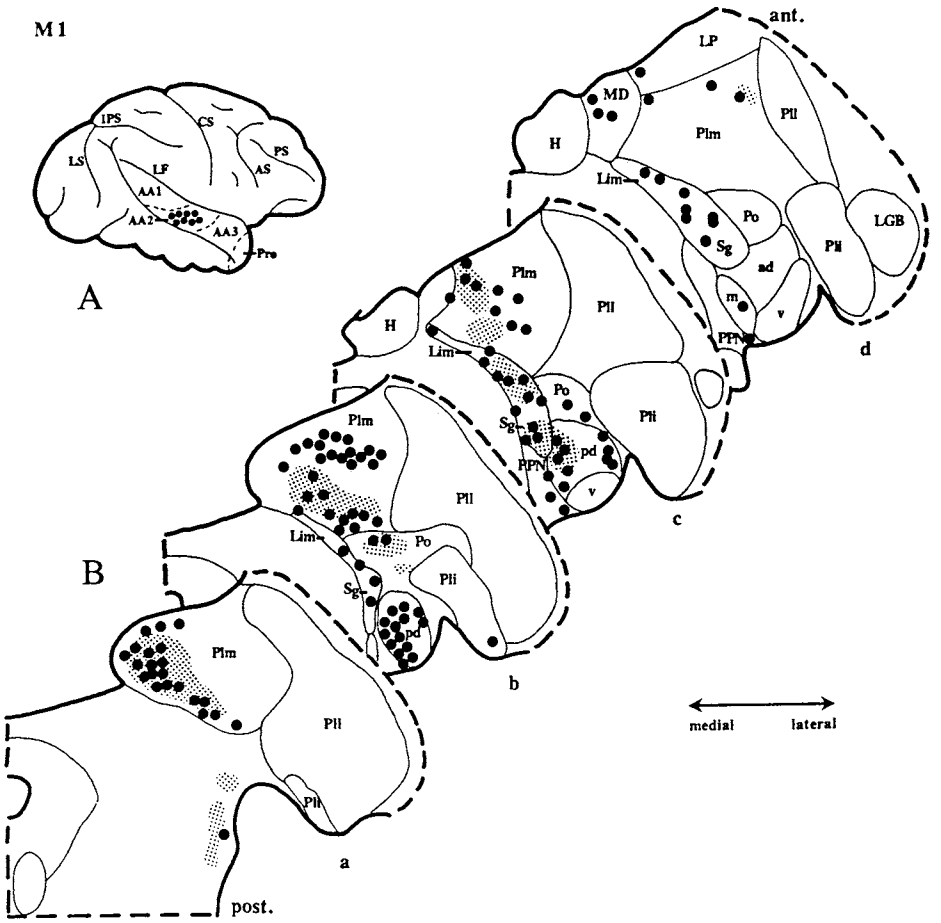

Fig. 5. Results of labeling in monkey M1. A, localization of FR injections into the area AA2 is marked with solid circles on the lateral view of the right hemisphere. B, distribution of retrogradely labeled cells (solid circles) and anterogradely labeled axonal terminals (shaded areas) are shown on four drawings of coronal sections through the posterior thalamus, presented in the postero-anterior order (a-d); v, ad, pd, m indicate positions of the particular MGB nuclei; see list of abbreviations.

cases of the area AA2 injections, there were no labeled neurons in the ventral MGB nucleus.

In the other parts of the posterior thalamus labeled cells were observed in Sg and Lim nuclei. The cells were fairly numerous in the monkey M1 (approx. 15% of all neurons labeled in the posterior thalamus), where they occupied the whole ventro-dorsal extent of both nuclei (Fig. 5B, b-d). The same tendency as in the topography of Sg projection to areas AA1 and AA2 was noticed in the MGpd projection. The cells of origin of projection to the AA1 (FB labeled cells in Figure 4C) were located more laterally in comparison to those forming connections to area AA2 (DY labeled cells in Fig. 4C).

A large group of labeled cells (approx. 58% of all neurons labeled in the posterior thalamus) occupied the posterior region of the medial pulvinar nucleus. The cells were found predominantly at the medial most limit of the nucleus and along its ventral border. In the successive anterior sections, the cells were scattered into the dorsal and central parts of the nucleus (Fig. 5B,a-d). Some labeled cells appeared also in the caudal most part of the mediodorsal thalamic nucleus, adjacent to Plm (MD; Figs. 3B,b and 5B,d,e). Moreover, in both cases single cells were found in the PPN and Po nuclei of the posterior thalamus (Figs. 3B,c and 5B,b-c).

When the injections in area AA1 are compared with these in AA2 it is evident that the population of the MGB neurons projecting to the area AA2 is less numerous, whereas the numbers of neurons of the posterior thalamus nuclei , particularly of the Plm, projecting to this area are significantly higher.

Retrograde labeling after injections into the area AA3

In both cases of the AA3 injections (M2, M3-FR), the number of labeled cells in MGpd (approx. 4-8% of the total number of labeled neurons in the posterior thalamus) was lower in comparison to that following the AA2 injections. However, the cells were scattered in the same posterior region of the nucleus (Figs. 3B,c and 6B,a-c).

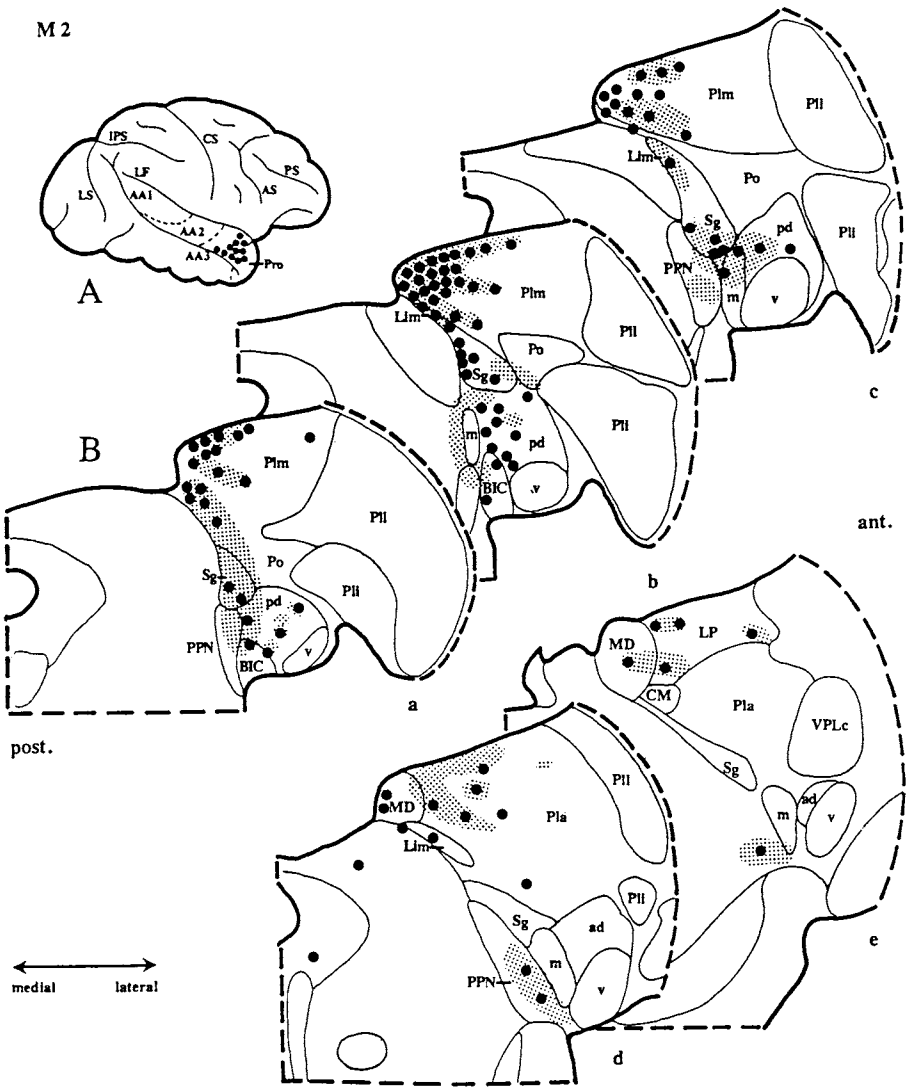

Fig. 6. Results of labeling in monkey M2. A, localization of FR injections into the area AA3 is marked with solid circles on the lateral view of the right hemisphere. B, distribution of retrogradely labeled cells (solid circles) and anterogradely labeled axonal terminals (shaded areas) are shown in five drawings of coronal sections through the posterior thalamus, presented in the postero-anterior order (a-e); v, ad, pd, m indicate positions of the particular MGB nuclei; see list of abbreviations.

In the nuclei of the posterior thalamic region most of the labeled neurons (approx. 56-62% of the total number of labeled neurons) were observed in the posteromedial part of Plm (Figs. 3B,c,d and 6B,a-c). Their location resembles that after injections into area AA2. However, the cells were mainly aggregated in the medial most limit of the nucleus. The large group of labeled cells (14-19%) was found within Sg and Lim, particularly in the dorsal parts of these nuclei (Fig. 6B,a-c). A few labeled cells were observed in the posterior part of MD bordering Plm. They were in a similar location to those observed after injections into areas AA1 and AA2 (Figs. 3B,a,b, 5B,d and 6B,d,e). Only single cells were found in the PPN nucleus (Figs. 3B,a-d and 2D).

The main features of the thalamo-cortical projection can be drawn by comparison of distributions of labeled cells after injections into the three auditory association areas. There are no sharp boundaries between locations of particular cell populations in the thalamic nuclei sending axons to the three association areas. The topography of projection is marked by the ventro-dorsal arrangement of thalamic cells giving rise to connections reaching successive areas of the superior temporal gyrus. In accordance with this topography, area AA1 receives a dominant projection from the principal nuclei of the medial geniculate body, whereas connections from the nuclei of the posterior thalamic region were less substantial. In contrast, the projection to area AA3 originated predominantly in the posteromedial pulvinar nucleus as well as the posterior thalamic nuclei (Sg and Lim), whereas the projection from nuclei of the medial geniculate body was minimal. Area AA2, which occupies an intermediate position in STG, apart from its most substantial projection from the Plm, receives

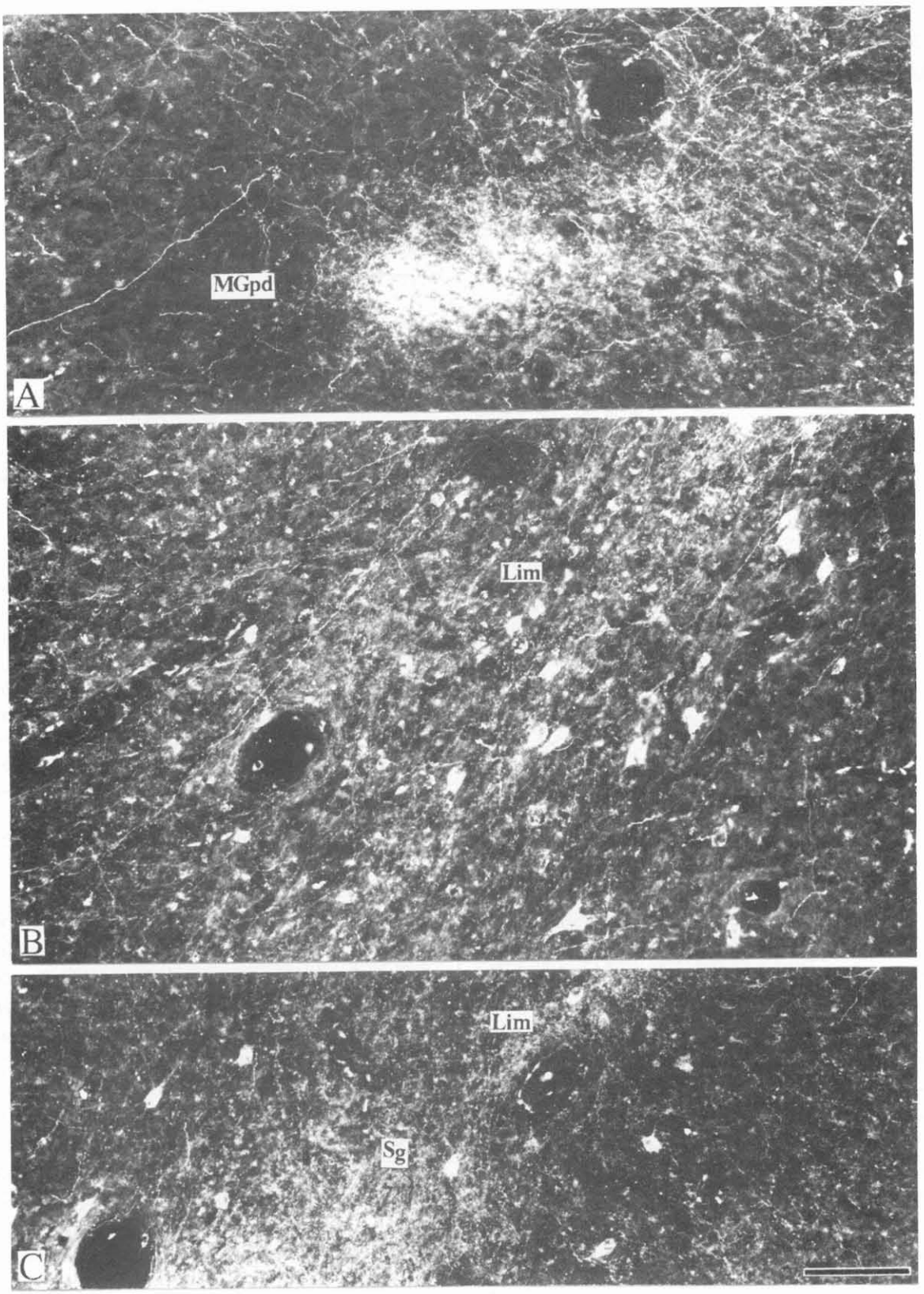

Fig. 7. Fluorescent photomicrographs illustrating examples of FR labeling in monkey M3 after injections into the area AA3. A, a small area of dense axonal terminals labeled in Mgpd. B, axonal terminals overlap the area of retrogradely labeled cells in Lim. C, the border between the Sg and Lim nuclei is characterized by a density of axonal terminals. Scale bar for A, B, C = 0.1 mm.

equally strong projections from MGpd as from the Sg and Lim nuclei.

CORTICOFUGAL THALAMIC CONNECTIONS AND RECIPROCITY OF PROJECTIONS

Anterograde labeling of axons observed after FR injections into areas AA2 (M1) and AA3 (M2 and M3) provided an opportunity to determine the thalamic nuclei in which the corticofugal projection terminates. Comparison of the distribution of axonal terminals with locations of retrogradely labeled cells allowed us to study the reciprocity of connections.

Anterograde labeling after the FR injections into the area AA2 and reciprocity of projections

Labeled axons of the area AA2 neurons were followed to the medial geniculate body, as well as to the posterior thalamic nuclei and the medial pulvinar nucleus. Their axonal terminals formed a wide strip in the medial region of thalamus extending through a few adjoining thalamic nuclei. The ventral part of the strip involved a small dorsomedial region of the posterodorsal MGB nucleus (Fig. 5B,c). Dorsally, terminals were distributed throughout the adjacent Sg (Fig. 5B,c), Po (Fig. 5B,b), Lim (Fig. 5B,c) and a large extent of Plm (Fig. 5B,a-c). The terminal plexus largely overlapped with the areas of retrogradely labeled cells showing the reciprocity of the thalamo-cortical projection. However the total area covered by axonal terminals was smaller than the area in which retrogradely labeled cells were found. Occasionally, the thalamic regions where retrogradely labeled cells were seen did not overlap with the labeled axonal terminals, e.g. in the MGpd nucleus (Fig. 5B,b), in the most caudal and rostral limits of Sg-Lim (Fig. 5B,b,d) and in the central part of Plm (Fig. 5B,b,c). Single axonal

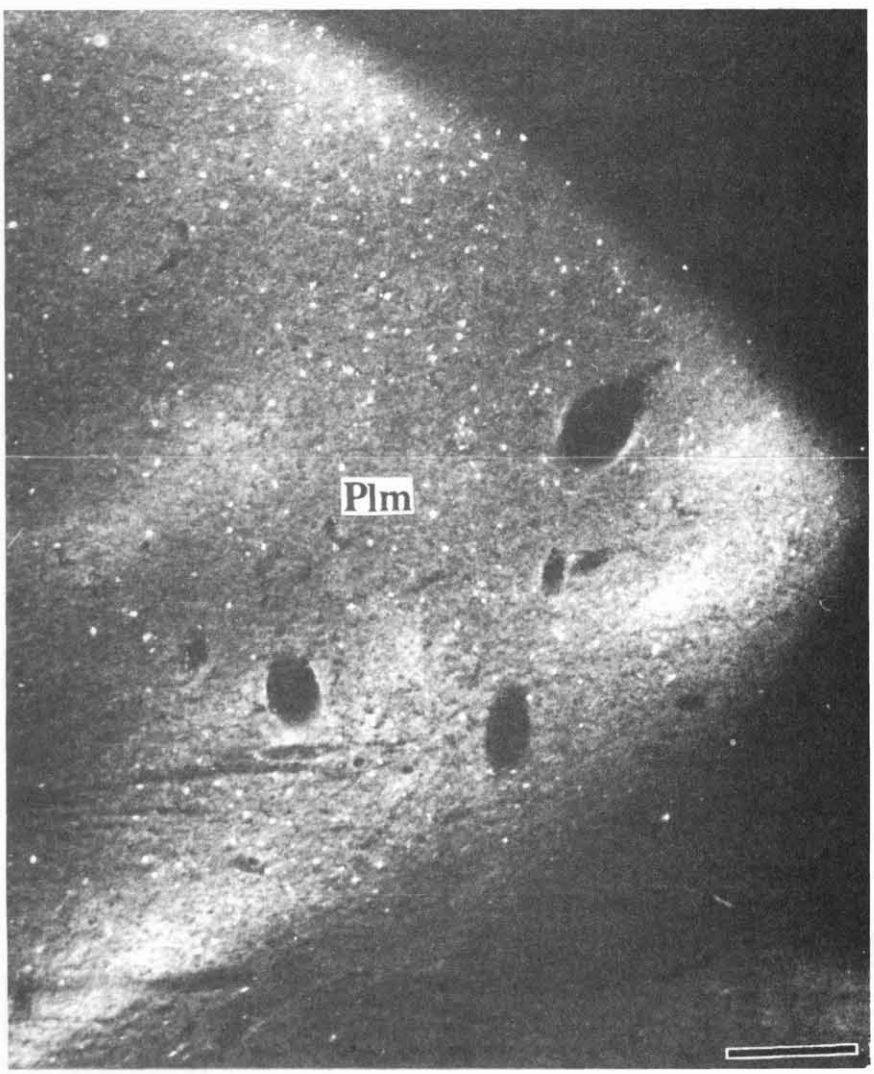

Fig. 8. Low-power fluorescent photomicrograph illustrating distribution of FR labeling in the posteromedial territory of Plm after injections into the area AA3 of monkey M3. Anterogradely labeled axonal terminals are seen as medio-lateral, longitudinal white strips. They overlap the retrogradely labeled cells scattered through the Plm. Scale bar = 0.5 mm.

terminals were seen in the medioventral part of Plm (Fig. 5B,c) and the caudal part of PPN (Fig. 5B,a).

Anterograde labeling after the FR injections into the area AA3 and reciprocity of projections

Anterogradely labeled axons after injections into the area AA3 were distributed through the same thalamic nuclei as in the case of AA2 injection. In the MGpd nucleus terminals of the corticofugal axons were very dense and formed a band of labeling at the dorso-medial border of the nucleus (Fig. 2B), whereas more sparse terminals occurred in its central part (Fig. 2C). Occasionally, at the border of MGpd and Sg nuclei, corticofugal axons were focused into a small area of extremely dense terminals (Fig. 7A).

In both cases of AA3 injections, extremely dense terminals were observed at the caudal most level of the medial pulvinar nucleus (Figs. 3B,c,d and 6B,a-d). Large patches of dense labeling were distributed along the ventral Plm border, and also in its dorsal and central regions in the form of parallel strips (Figs. 6B,a-d and 8). Sparse axonal terminals were observed between them. Another area of dense terminal labeling was seen at the border of the medial pulvinar and mediodorsal nuclei (Figs. 3B,b, 6B,d,e and 9B,C). Less dense anterograde labeling was distributed throughout the Sg and Lim nuclei (Figs. 3B,a-c; 6B,a-c and 7B,C).

Overlapping areas of labeled neurons and axonal terminals indicate the reciprocity of projections in the majority of the thalamic nuclei involved (Fig. 7B,C). Throughout the entire antero-posterior extent of the Plm, both retrograde and anterograde labelings were arranged in characteristic longitudinal strips (Fig. 8) which may reflect a peculiar organization of these cortico-thalamic connections.

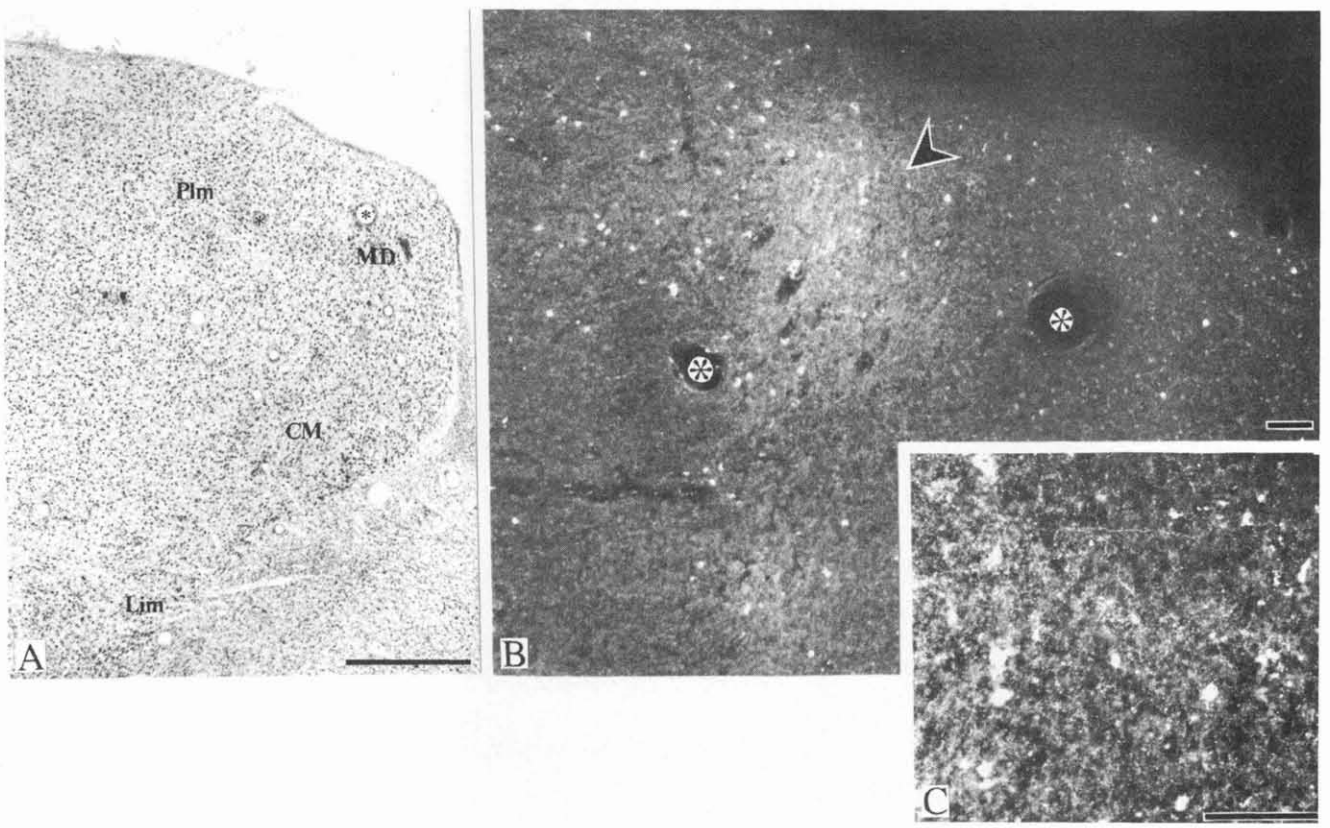

Fig. 9. Cytoarchitecture of the posterior thalamus at the level of distribution of labeling after FR injections into the area AA3 in monkey M3. A, low-power photomicrograph of the Nissl-stained coronal section through the posterior thalamus at the level of junction of the caudal MD part and Plm nucleus. Small asterisks indicate the positions of blood vessels seen at higher magnification in B. Scale bar = 1 mm. B, fluorescent photomicrograph illustrates distribution of retrogradely labeled cells and dense anterograde labeling of axonal terminals situated at the junction of MD and Plm. Arrowhead indicates localization of the higher power photomicrograph in C. Blood vessels corresponding to those in A are marked with asterisks. Scale bar = 0.1 mm. C, higher magnification of dense labeling of axonal terminals, in the site marked with arrowhead in B. Scale bar = 0.1 mm.

Amygdaloid projections

The terminology of Amaral et al. (1992) was adopted for the description of amygdaloid nuclei. The cytoarchitecture of the amygdala at the intermediate level of its antero-posterior extent is illustrated in Figs. 12A and 14A.

CORTICOPETAL AMYGDALOID CONNECTIONS

Retrograde labeling after injection into the area AA1

As a result of injections into the area AA1 (M3-FB), retrograde labeling of cells was observed in the basal nuclei (Bmc, Bi, Bpc, Fig. 10A-C) of the amygdala. A majority of cells, consisting of approx. 61% of all cells labeled with FB in the amygdala, were located in the basal magnocellular nucleus at the intermediate A-P level of amygdala (Fig. 10C). Smaller numbers of labeled cells were found in the magnocellular (ABmc; Fig. 10B-D) and parvocellular (ABpc; Fig. 10B) subdivisions of the accessory basal nucleus (approx. 33%). A few labeled cells appeared also in the periamygdaloid cortex (PAC; Fig. 10C).

It is important to note that despite of the large injection into the area AA1, labeled cells were virtually absent in the lateral amygdaloid nucleus except for one cell in the medial part of the nucleus, found close to its border with the basal nucleus (Fig. 10B).

Retrograde labeling after injections into the area AA2

Injections into the area AA2 (M1-FR and M3-DY) produced a substantial retrograde labeling in the lateral amygdaloid nucleus (approx. 69-87% of the total number of labeled cells). In both cases, labeled cells were found in the dorsolateral part of the nucleus at the intermediate and caudal levels of the antero-posterior extent of the amygdala (Figs. 10C,D and 11B-D). In monkey M1, labeled cells were more widely distributed in com-

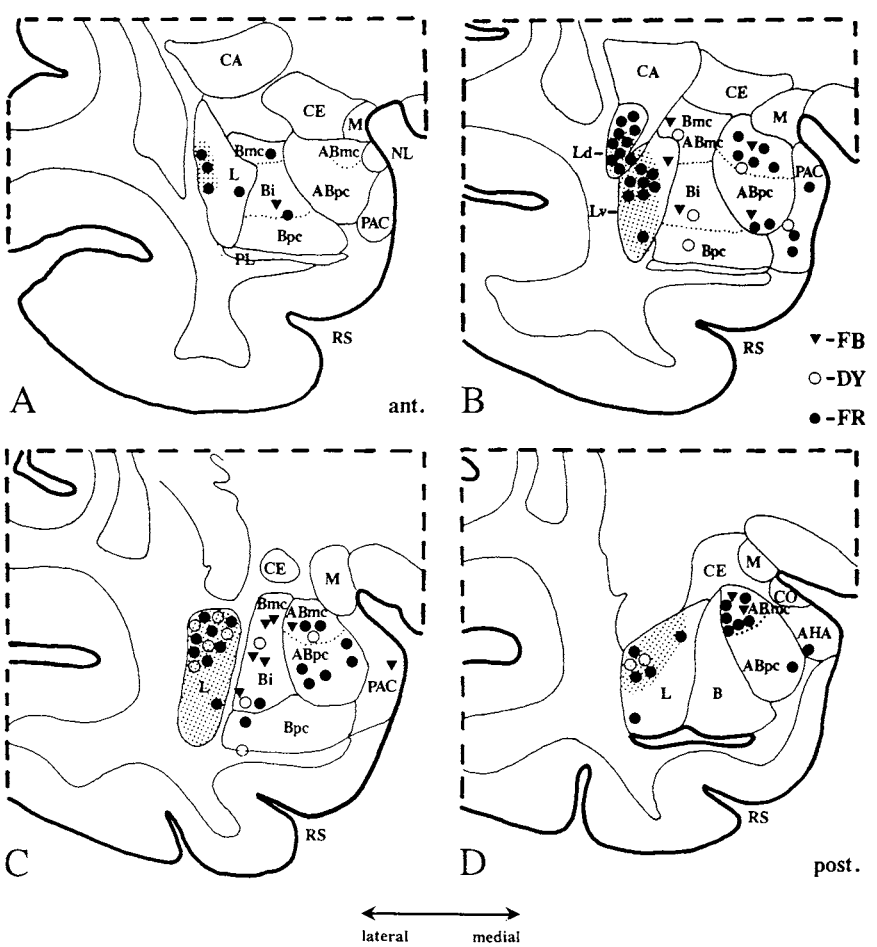

Fig. 10. Results of labeling in the amygdala after injections of three fluorochromes into the area AA1 (FB, solid triangles), AA2 (DY, open circles) and AA3 (FR, solid circles) in monkey M3. Distribution of retrogradely labeled neurons (marked with respective symbols) and anterogradely labeled axonal terminals (shaded areas) are shown in four drawings of coronal sections through the left amygdala, presented in the antero-posterior order (A-D). Notice that retrograde and anterograde labeling overlaps in the lateral nucleus (L) only.

parison to M3, into the anterior and ventral extent of the nucleus (Fig. 11B). Large numbers of labeled cells were clustered dorsolateraly between bundles of fibers passing the lateral nucleus. More dense labeling in monkey M1 seems to result predominantly from a more effective axonal transport of FR dye in comparison to DY labeling in the monkey M3. There was no overlap of the location of labeled cells with the area of high AChE activity in the lateral nucleus (cf. Figs. 10C and 12B).

In contrast to the resulting labeling after injections into the area AA1, only single retrogradely labeled cells were scattered in the basal and accessory basal amygdaloid nuclei in both cases of AA2 injections (Figs.10B,C and 11C,D).

Retrograde labeling after injections into the area AA3

Injections of FR into the area AA3 (M2 and M3) revealed a prominent corticopetal projection originating in the lateral nucleus of amygdala. In both cases, cells forming this projection consisted of the dominant group (approx. 68-72% of the total number of labeled cells in one case), aggregated at the intermediate and posterior levels of the dorsolateral part of the nucleus (Figs. 10B,C; 12C and 13B-D). A specific feature of this labeling was the distribution of the labeled cell groups between fibers passing through the dorsolateral part of the lateral nucleus which corresponds to the localization of retrograde labeling found after AA2 injections (cf. Figs. 10B, 11B, 13B and 14A,B,D).

Small numbers of the retrogradely labeled cells were found in the accessory basal and basal nuclei (Fig. 12D). Most of them (approx. 22-23%) were present in both subdivisions of the accessory basal nucleus (ABmc, ABpc; Figs. 10B-D and 13B,C), whereas only single cells were scattered around the basal nucleus (Figs. 10A-D and 13A-C), the periamygdaloid cortex (PAC; Fig. 10B) and amygdalo-hippocampal area (AHA; Fig. 10D).

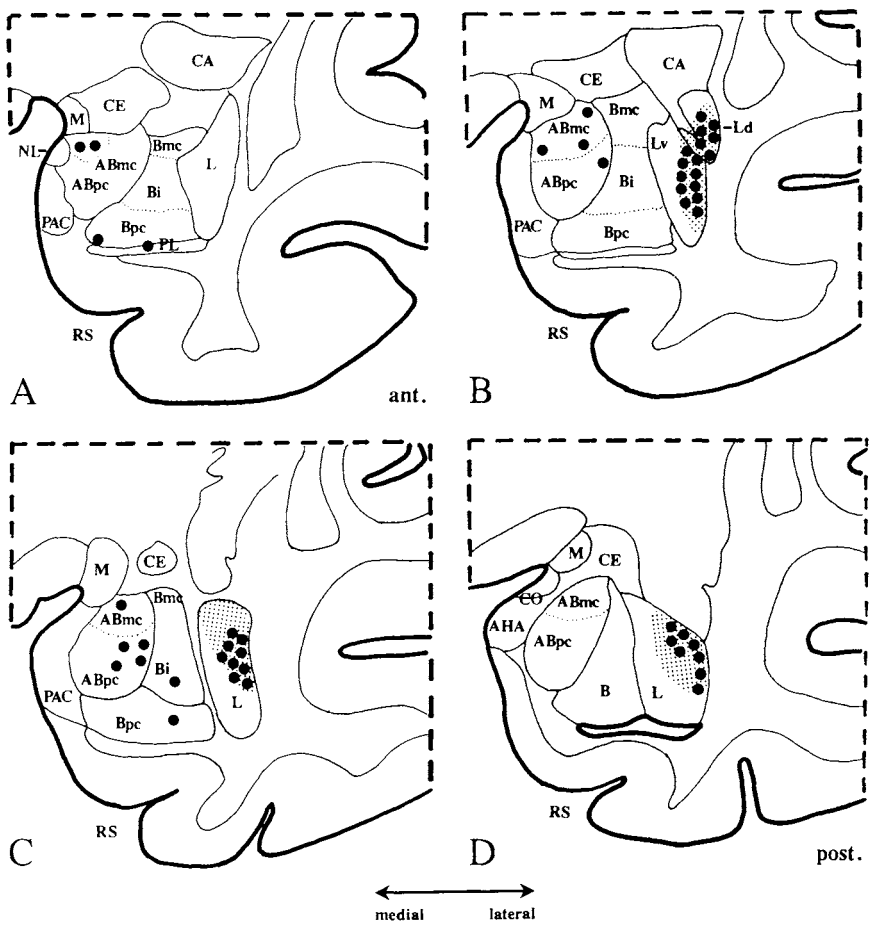

Fig. 11. Results of labeling in the amygdala following FR injections into the area AA2 in monkey M1. Distribution of retrogradely labeled neurons (solid circles) and anterogradely labeled axonal terminals (shaded areas) are illustrated in four drawings of coronal sections through the right amygdala, presented in the antero-posterior order (A-D).

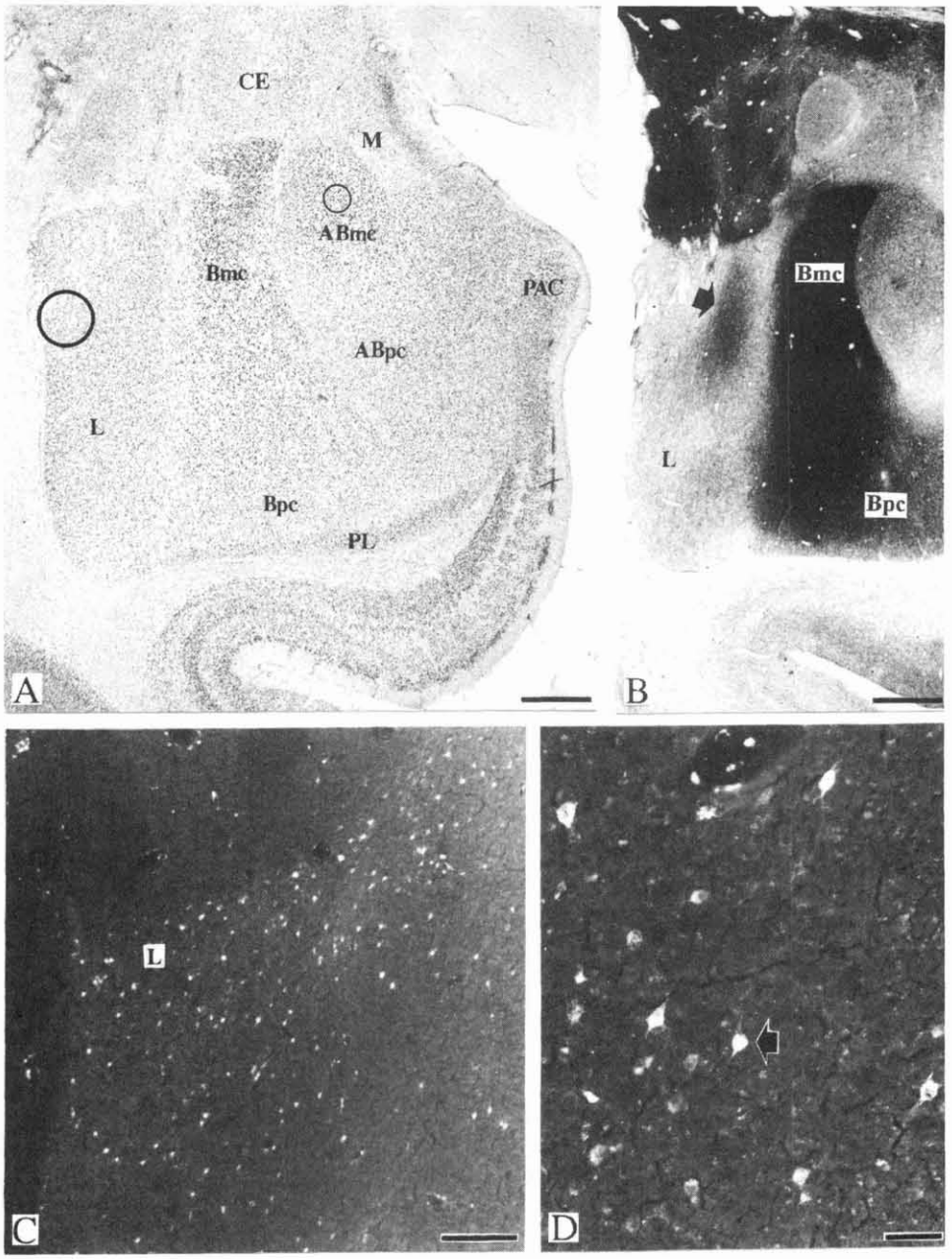

Fig. 12. Cyto- and chemoarchitecture of the amygdala of the left hemisphere and examples of retrograde labeling in monkey M3. A, low-power photomicrograph of the Nissl-stained coronal section illustrating the cytoarchitectonic division of the amygdala at its intermediate level (see list of abbreviations). Large open circle indicates the site of the lateral nucleus corresponding to the magnified fluorescence photomicrograph in C. Small open circle indicates the part of the accessory basal nucleus corresponding to the magnified fluorescence photomicrograph in D. Scale bar = 1 mm. B, photomicrograph of a coronal section processed for AChE histochemistry at the level corresponding to section presented in A. Photomicrograph illustrate the distribution of AChE activity in the basolateral amygdaloid part. Notice a differentiation of AChE activity in the lateral amygdaloid nucleus. The area of high AChE activity (stained black) is seen in the dorsomedial part of the nucleus (arrow). Scale bar = 1 mm. C, low-power fluorescent photomicrograph illustrating an aggregation of cells retrogradely labeled with FR (injection into the area AA3), located in the dorsolateral part of the lateral nucleus. Approximate localization of cells is marked with the large open circle on the corresponding Nissl-stained section in A. Scale bar = 0.25 mm. D, fluorescent photomicrograph of cells retrogradely labeled with FR (arrow) in the accessory basal nucleus, after injection into the area AA3. Approximate localization of cells is marked with the small open circle on the corresponding Nissl-stained section in A. Notice the lack of anterograde labeling in the nucleus. Scale bar = 0.1 mm.

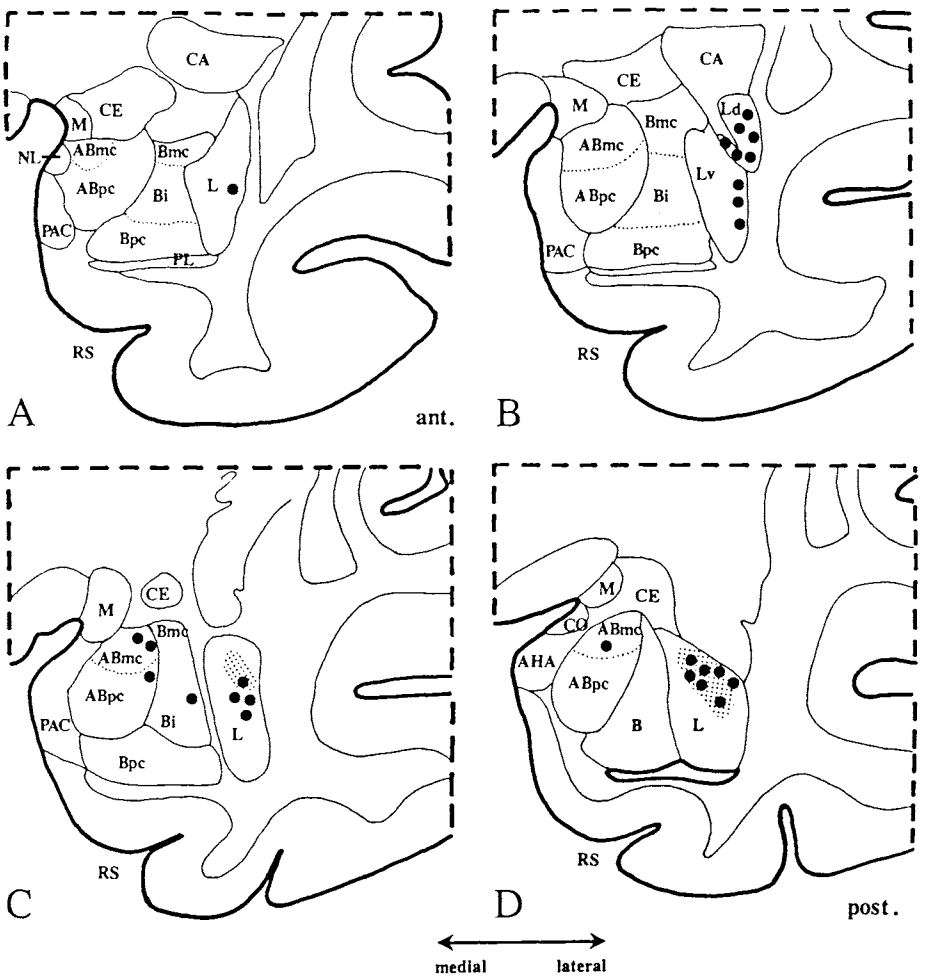

Fig. 13. Results of labeling in the amygdala following FR injection into the area AA3 in monkey M2. Distribution of retrogradely labeled neurons (solid circles) and anterogradely labeled axonal terminals (shaded areas) are shown in four drawings of coronal sections through the right amygdala, presented in the antero-posterior order (A-D).

CORTICOFUGAL AMYGDALOID CONNECTIONS AND THE RECIPROCITY OF PROJECTIONS

Distribution of the cortico-amygdaloid projection was defined on the basis of anterograde labeling of axons observed after FR injections into areas AA2 (M1) and AA3 (M2 and M3). The terminals of these axons were observed exclusively in the lateral amygdaloid nucleus.

Anterograde labeling after injections into areas AA2 and AA3 and reciprocity of projections

After injections into area AA2, a plexus of thin, moderately dense axon terminals was seen in the dorsolateral part of the lateral amygdaloid nucleus, at the middle antero-posterior extent of the nucleus (Fig. 11C and D). The most dense amygdalopetal projection originated, however, in the area AA3. Its injections resulted in dense labeling of thin axons covering a larger extent of the nucleus, than the injection into area AA2 (Fig. 14C). Dorsolateraly, dense terminals overlap the cells clustered between bundles of fibers located similarly as in the case of the AA2 injections (Fig. 14A,B,D). At the successive posterior level the anterograde labeling extended ventrally and caudally in the lateral nucleus covering additionally the most ventral part of the nucleus which was free of labeling in monkey M2 (Figs. 10B,C and 13B,C). Comparison between neighboring sections has shown that labeled neurons were located in the region of a low AChE activity (Fig. 14A and B).

Axonal terminals overlapped to a great extent with areas of retrogradely labeled cells showing the reciprocity of cortico-amygdaloid connections. The most intense reciprocity was found in the dorsolateral part of the lateral nucleus (Fig. 14A,D), whereas in the remaining part of the nucleus large areas were covered only by axonal terminals. In cases of the AA3 injections they were found in different parts of the nucleus. In monkey M2 such terminals were found in the dorsal part (Fig. 13C), whereas in monkey M3 were found in the ventral part of the nucleus (Fig. 10B,C). Difference may be the result of different uptaking of the dye in the sites of injections.

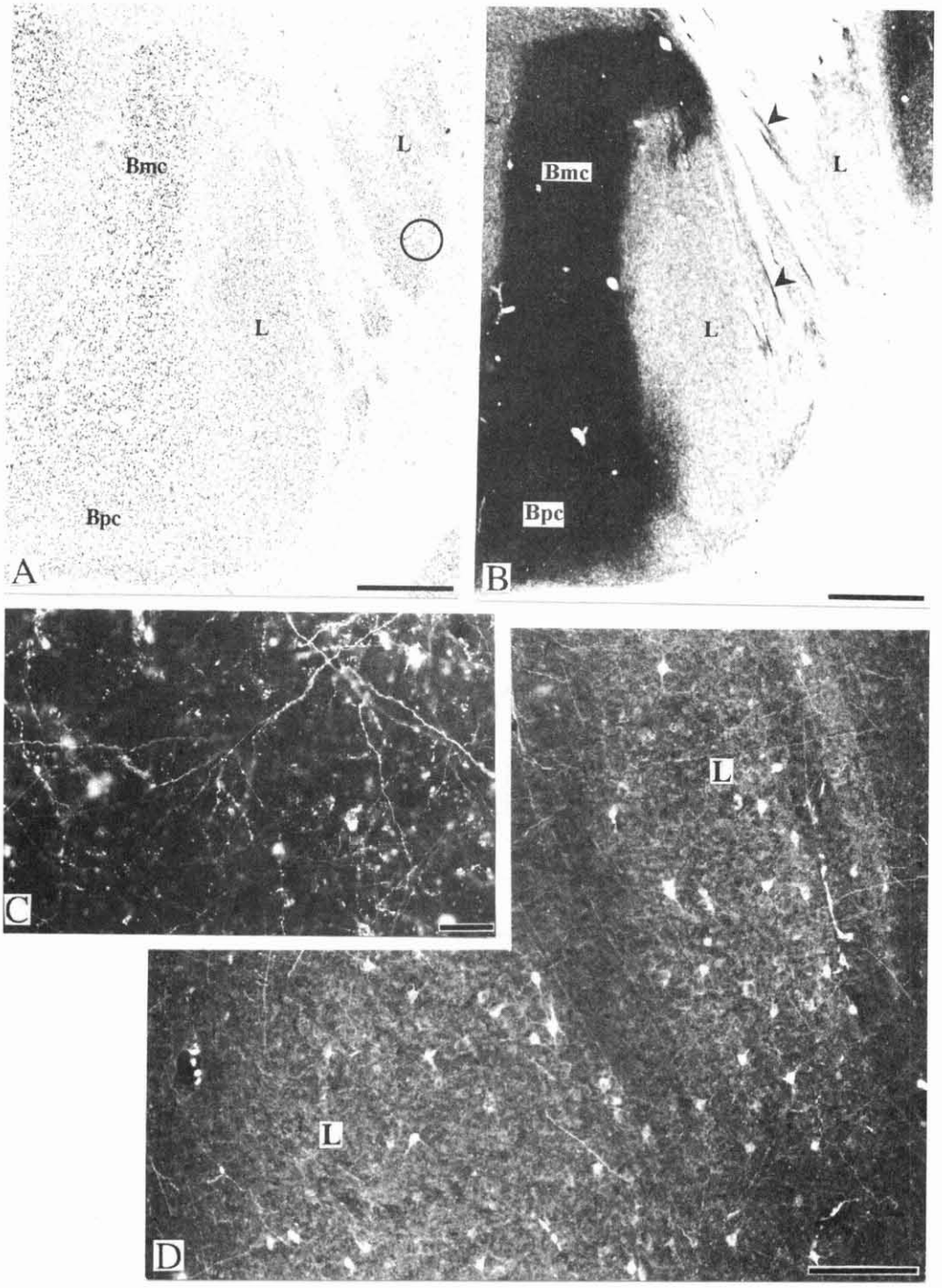

Fig. 14. Cyto- and chemoarchitecture of the lateral amygdaloid nucleus of the right hemisphere, at the rostral level to that in Fig. 11 and examples of FR labeling in monkey M2. A, photomicrograph of a Nissl-stained coronal section showing the architecture of the lateral nucleus (L). Bundles of bypassing fibers between groups of neurons are seen at the level corresponding to Fig. 13B. Scale bar = 1 mm. B, photomicrograph of the coronal section processed for AChE histochemistry at the level corresponding to A. AChE activity is low in almost entire lateral nucleus, except for the narrow strips of high AChE activity (stained black) distributed along bundles of fibers (arrowheads). Scale bar = 1 mm. C, fluorescent photomicrograph of anterogradely labeled axons entering the dorsal part of the lateral nucleus. Scale bar = 50 μm. D, fluorescent photomicrograph of retrogradely labeled cells and dense anterogradely labeled axonal terminals in the dorsolateral part of the lateral nucleus. Approximate localization of this area is marked with the open circle in A. Scale bar = 0.2 mm.

The above observations provide evidence that the AA2 and AA3 auditory association areas have substantial reciprocal connections with the lateral amygdaloid nucleus. The density of projections gradually increased from area AA2 to area AA3. Other amygdaloid nuclei (basal, accessory basal and periamygdaloid cortex) are sources of an amygdalo-cortical projection which is much weaker in comparison to the projection originating in the lateral nucleus. The magnocellular divisions of both basal and accessory basal nuclei seem to be the main source of projection to the STG cortex. Projections from the basal nucleus are preferentially directed to the area AA1, whereas these from the accessory basal nucleus are to areas AA2 and AA3.

DISCUSSION

In the present study we have investigated the organization of the thalamo-cortical and cortico-amygdaloid connections through which auditory and polymodal information from the posterior thalamic region through the auditory association areas of STG reaches the amygdala.

We found, that area AA1 is characterized by a dominant projection originating in the principal MGB nuclei (summary diagram, Fig. 15). Area AA2 is supplied by auditory input from the MGpd afferents and from more dense input from the polymodal nuclei of the posterior thalamic region, predominantly from Plm. Area AA3 receives most of its projections from the polymodal thalamic nuclei.

Among the three auditory association areas, AA2 and AA3 have profuse reciprocal connections with the lateral amygdaloid nucleus, whereas the basal amygdaloid nuclei are source of the amygdalofugal projection that is not reciprocated. The density of the amygdalopetal projection to the lateral nucleus increases gradually in the direction of area AA3.

All cortico-thalamic connections terminate in the same thalamic nuclei which are the source of projection in the opposite direction, whereas among the amygdaloid nuclei substantial reciprocal connections were observed only in the lateral nucleus.

Thalamic connections of the association STG cortex

Early descriptions of the thalamo-cortical connections suggested a high degree of segregation of MGB projections to the temporal cortex. According to Burton

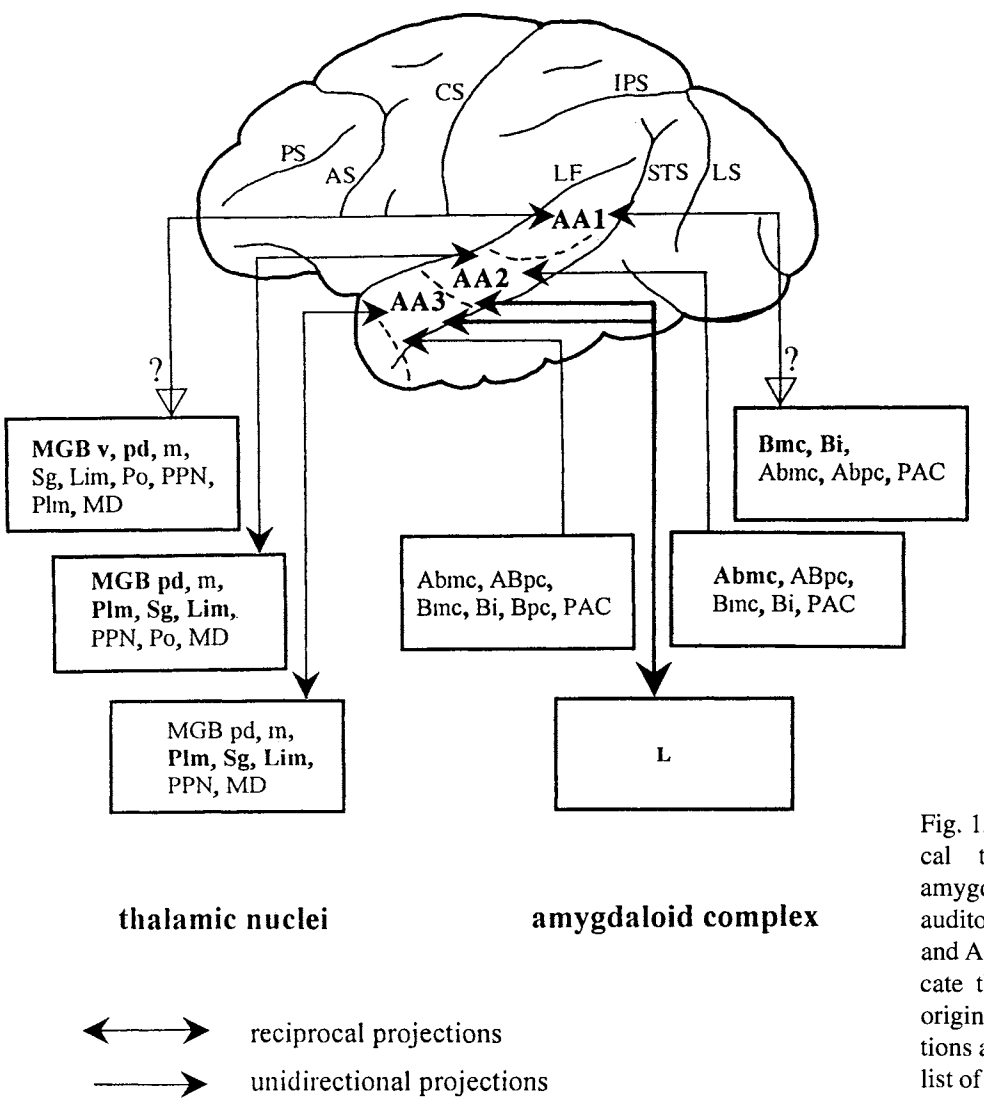

Fig. 15. Summary diagram of reciprocal thalamo-cortical and cortico-amygdaloid connections of three auditory association areas AA1, AA2 and AA3. Abbreviations in boxes indicate the nuclei in which projections originate. Nuclei of dominant projections are marked with bold letters. See list of abbreviations.

and Jones (1976), the ventral nucleus of MGB sends projections to the primary auditory area (A1), whereas the dorsal MGB nuclei project to cytoarchitectonic fields T1 and T2 of postauditory cortex which might correspond to the associative auditory fields. Recent studies of thalamo-cortical connections, with more sensitive anatomical methods, show that projections originating in particular MGB nuclei might involve wider cortical region than previously supposed. For instance, projections derived from the tonotopic ventral MGB nucleus do not seem to be limited to area A1, but additionally involve adjacent lateral cortical regions (field PL; Morel et al. 1993). Some discrepancies in defining the extent of projections from the vMGB may be related to differences in delineation of territories of v and pd nuclei, which are defined either on the basis of cytoarchitecture in the Nissl-stained sections, or distribution of the cytochrome oxidase activity (Morel et al. 1993). Recent studies of populations of the MGB neurons stained immunocytochemically for calcium-binding proteins helped to define the extents of particular nuclei. However, they too show that sharp borders between different populations of cells do not exist (Morel et al. 1993, Molinari et al. 1995). The presence of the labeled cells in the ventral MGB nucleus resulting from our injections might support the opinion that wider than previously suspected corticopetal projection leaves the ventral nucleus, but may also be the result of damage to the white matter fibers below the PL field, when the injection was made.

Functional features of neurons of the dorsal nucleus of MGB differ from those in the tonotopic ventral nucleus. They are characterized by less specific responses to the acoustic stimulation. Many of them do not respond to pure tones and do not always discharge spontaneously (Gross et al. 1974). Moreover, at least in the cat, large numbers of broadly tuned neurons display longer latencies than those in the ventral nucleus (Calford 1983, Calford and Aitkin 1983). The dorsal nucleus seems to contain a mixed population of narrowly as well as broadly tuned neurons which form a component of diffuse auditory pathway projecting to the primary and associative areas of the auditory cortex (Calford and Aitkin 1983). In monkey it was found that the projection of the posterodorsal nucleus was directed to the large part of STG (T1 and T2 fields of Burton and Jones 1976). Our results support observations that the whole STG is connected with the posterodorsal nucleus of MGB, but the projection directed towards areas AA1 and AA2 is particularly dense. The anterodorsal nucleus of MGB sends only a minor projection to AA1. Thus, both association areas AA1 and AA2, but not AA3, receive substantial auditory input derived predominantly from the posterodorsal MGB nucleus. These connections are reciprocated by corticofugal projections, which were especially dense at the posterior limit of the posterodorsal MGB nucleus. Similar distribution of the cortico-thalamic projection originating in the cytoarchitectonic areas of the belt line was demonstrated by Pandya et al. (1994).

The next MGB source of the thalamo-cortical projection is the Mgm. In electrophysiological experiments performed in the cat, no evidence of tonotopic organization of this nucleus has been found (Calford 1983). The nucleus is considered to be polysensory, since it receives afferents from both the auditory and somatosensory pathways (Wepsic 1966, Winer and Morest 1983). In the cat, the medial geniculate nucleus sends projections to all subdivisions of the auditory cortex (Winer et al 1977, Anderson et al. 1980) with some preference to the tonotopic anterior field (Morel and Imig 1987). Widespread distribution of the MGm corticopetal projection in the monkey involves primary auditory (Morel and Kaas 1992, Morel et al. 1993) and surrounding cortices (Trojanowski and Jacobson 1975). However, the main projection of this nucleus in the monkey seems to be directed towards the secondary auditory (AII) cortex (Mesulam and Pandya 1973). Sparse projection from this nucleus reaching the three auditory association areas in our material is consistent with the previously defined diffuse character of that projection.

The nuclei of the posterior thalamic complex, which were found to be a source of projection to the STG cortex are located dorsally and medially to the medial geniculate body. Because they receive afferent projections from various sensory pathways, they used to be considered polysensory nuclei. The Sg and Lim connections in the monkey were claimed to be widespread throughout the auditory cortex. They were identified as directed to the primary auditory fields (Morel and Kaas 1992, Morel et al. 1993) and to the temporal pole (Markowitsch et al. 1985). They seem to be focused however on the granular insular cortex (Burton and Jones 1976). While in the monkey Sg neurons appear to be involved in the transfer of multimodal information, in the cat a dominance of visually responsive neurons was strongly suggested (Hicks et al. 1984, 1986, Abramson and Chalupa 1988), supported by observations of the specific Sg and Lim projections to the visual, anterior ectosylvian area (Olson and Graybiel 1987). Our observations agree with previous data about widespread

distribution of Sg and Lim projections over a large extent of the auditory association cortex.

The Po nucleus is a differentiated structure, related to various sensory modalities. The projections of neuronal groups of this nucleus, studied in the brush-tailed possum (Neylon and Haight 1983) and in the cat (Morel and Imig 1987), were directed not only to the auditory cortex, but also to the motor, somatosensory and parietal association cortices (Neylon and Haight 1983). In monkey the lateral part of Po was previously defined as a source of projection to the postauditory cortex (Burton and Jones 1976). A sparse labeling in the Po nucleus, found in our material after injections into the STG areas, indicates its weak relation to the auditory association cortex.

Distribution and density of labeling observed in our experiments indicate that one of the most prominent projections to the superior temporal cortex originates in the medial pulvinar nucleus. The topography of reciprocal connections between the medial pulvinar nucleus and STG cortex resembles that, which was previously defined in the squirrel monkey, where the ventro-dorsal gradient of projection was shown (Trojanowski and Jacobson 1975). We found the main aggregation of labeled cells forming projections to areas AA2 and AA3 in the dorsomedial cell populations located at the posteromedial most limit of the Plm nucleus. The intensity of relations between the STG and the Plm was also visualized by dense cortico-thalamic connections originating in both rostral areas of the auditory association cortex. The axonal terminals, which overlapped retrogradely labeled cells were distributed in the form of patches and longitudinal strips oriented medio-lateraly in Plm. Such an arrangement of axonal terminals derived from the STG cortex, resembles that observed by Pandya et al. 1994. Thus, the Plm neurons supply both the unimodal auditory STG cortex and polymodal fields involving the cortex situated at the dorsal bank of STS (field T3, Burton and Jones 1976), as well as the temporal pole (Markowitsch et al. 1985). Moreover, it was found in the owl monkey, that the Plm projection extends as far as the cortex of the supratemporal plane, bordering the primary auditory fields (Morel and Kaas 1992). The different populations of the Plm neurons also form projections to the inferior temporal and parietal cortices (Baizer et al. 1993).

Amygdaloid connections of the association STG cortex

Results of previous experiments show that the cortico-amygdaloid projection is predominantly derived from the polymodal fields located in the temporal pole and the superior temporal sulcus (Aggleton et al. 1980), whereas connections originating in the unimodal association cortex of the superior temporal gyrus were less known and were defined as rather weak (Herzog and Van Hoesen 1976, Turner et al. 1980, Van Hoesen 1981, Amaral et al. 1992). Injections of HRP centered on the lateral nucleus, led to labeling of neurons in the rostral part of STG, adjacent to the temporal pole (Aggleton et al. 1980). Our observations of the profuse cortico-amygdaloid projection, originating in both areas AA2 and AA3, seems to be evidence of a more substantial projection of axons from the auditory association cortex to the lateral amygdaloid nucleus than was previously supposed. On the basis of the cytoarchitectonic similarities, the dorsolateral granular subdivision of the temporal pole, involved in some of our injections, is considered to be a rostral extension of the area AA3. Moreover, axons of the temporopolar neurons terminate in the lateral nucleus of the amygdala similar to the projection of the auditory association areas (Markowitsch et al. 1985, Moran et al. 1987). This pattern of connections strongly suggests that the auditory association and the dorsal temporopolar areas constitute subsequent steps in the cortical processing of auditory information.

In all previous studies the cortico-amygdaloid connections were consistently followed to the lateral amygdaloid nucleus, and the site of termination was determined in the ventral or ventrolateral part of the nucleus (Herzog and Van Hoesen 1976, Aggleton et al. 1980, Turner et al. 1980, Van Hoesen 1981). In addition to this, we found the site of abundant labeling in the dorsolateral region of the lateral nucleus. Dense axonal terminals overlap with neuronal groups clustered between the bundles of fibers leaving the external capsule. This part of the lateral nucleus was named by Turner et al. (1980) the claustral area of the amygdala. The distribution of labeling which extends from the dorsolateral to the more ventral region of the nucleus strongly suggests an integrity of both parts. In the AChE stained sections both dorsolateral and ventral parts the nucleus show similar, low level of AChE activity. The capsular nuclei described in *Macaca fascicularis* (Amaral and Bassett 1989) are similarly located among the bundles of fibers at the rostral level of amygdala, but they are characterized by the high AChE activity. We were able to find only narrow belts of high AChE activity distributed along the bundles of fibers which pierce the dorsolateral part of the lateral nucleus. They were not related to the

sites of labeling. Thus, the correspondence of capsular nuclei to the sites of the most rostral labeling in our material remains unclear and could be related to species differences. The dorsal part of the lateral nucleus was additionally recognized as a target of visual information transferred by the inferior temporal gyrus (Iwai and Yukie 1987, Baizer et al. 1993). It appears that at least the auditory and visual information converge in this part of the nucleus.

Whereas connections of the lateral nucleus with areas AA2 and AA3 show distinct reciprocity by overlapping of dense retrograde and anterograde labeling, the basal nuclei appear to send predominantly the amygdalofugal projection. The basal and accessory basal nuclei were usually considered to be a source of widespread corticopetal projections to the inferior temporal and occipital (Iwai and Yukie 1987, Baizer et al. 1993), as well as the prefrontal, cingular and insular cortices (Porrino et al. 1981, Amaral and Price 1984, Amaral et al. 1992). Thus, our findings that the amygdalofugal projection of the basal and accessory basal nuclei reach the whole superior temporal cortex, seems to be in agreement with the pattern of widespread projection directed to the large extent of neocortex.

It is known that in primates the direct thalamo-amygdaloid pathway seems to be rather weak because among the monkeys thalamic nuclei only PPN was found to project to the lateral amygdaloid nucleus (Jones et al. 1976, Aggleton et al. 1980, Mehler 1980). In the rat MGm and Sg nuclei as well as the posterior intralaminar nucleus (PIN), which is regarded as an equivalent of the peripeduncular nucleus of monkey (PPN), were recently defined as a source of direct thalamo-amygdaloid projection which reaches the lateral amygdaloid nucleus (Romanski and LeDoux 1992). These connections in the rat are considered to be rapid routes for acoustic signals of emotional significance (LeDoux et al. 1990, Bordi and LeDoux 1994). In primates the direct thalamo-amygdaloid projection seems to be less substantial in comparison to that reaching amygdala via the STG cortex.

Our data indicate that the entire superior temporal cortex is a target of differential input from the nuclei of the posterior thalamic region. A striking feature of the topography of thalamo-cortical projection is an alternate contribution of connections originating in the auditory nuclei of the medial geniculate body, *versus* polymodal nuclei of the posterior thalamic region. The contribution of the auditory thalamic nuclei decreases along the STG cortex, whereas projections of the polymodal nuclei progressively increases from area AA2 to AA3. Taking into account the strong relation of the same STG areas with the lateral amygdaloid nucleus it seems justified to regard them as the site of transfer of both auditory and complex sensory information to the amygdala.

ABBREVIATIONS

ABmc	- accessory basal nucleus of the amygdala, magnocellular division
ABpc	- accessory basal nucleus of the amygdala, parvocellular division
AHA	- amygdalo-hippocampal area
AS	- arcuate sulcus
B	- basal nucleus of the amygdala
Bi	- basal nucleus of the amygdala, intermediate division
Bmc	- basal nucleus of the amygdala, magnocellular division
Bpc	- basal nucleus of the amygdala, parvocellular division
BIC	- brachium of the inferior colliculus
CA	- commissura anterior
CE	- central nucleus of the amygdala
CM	- centrum medianum
CO	- cortical nucleus of the amygdala
CS	- central sulcus
H	- habenula
IPS	- intraparietal sulcus
L	- lateral nucleus of the amygdala
Ld	- lateral nucleus of the amygdala, dorsal division
LF	- lateral fissure
LGB	- lateral geniculate body
Lim	- nucleus limitans of the thalamus
LP	- lateroposterior nucleus of the thalamus
LS	- lunate sulcus
Lv	- lateral nucleus of the amygdala, ventral division
M	- medial nucleus of the amygdala
MD	- mediodorsal nucleus of the thalamus
MGB	- medial geniculate body
MGad	- anterodorsal nucleus of MGB
MGm	- medial nucleus of MGB
MGpd	- posterodorsal nucleus of MGB
MGv	- ventral nucleus of MGB
NL	- nucleus of the lateral olfactory tract
PAC	- periamygdaloid cortex
PL	- paralaminar nucleus of the amygdala
Pla	- anterior pulvinar nucleus
Pli	- inferior nucleus of the pulvinar

Pll - lateral nucleus of the pulvinar
Plm - medial nucleus of the pulvinar
Po - posterior nucleus of the thalamus
PPN - peripeduncular nucleus
Pro - proisocortical area
PS - principal sulcus
RS - rhinal sulcus
Sg - suprageniculate nucleus of the thalamus
SN - substantia nigra
VPLc - ventroposterolateral nucleus of the thalamus, caudal part

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