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Organization of Projections From the Basomedial Nucleus of the Amygdala: A PHAL Study in the Rat

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ABSTRACT

The organization of axonal projections from the basomedial nucleus of the amygdala (BMA) was examined with the *Phaseolus vulgaris* leucoagglutinin (PHAL) method in adult male rats. The anterior and posterior parts of the BMA, recognized on cytoarchitectonic grounds, display very different projection patterns. Within the amygdala, the anterior basomedial nucleus (BMAa) heavily innervates the central, medial, and anterior cortical nuclei. In contrast, the posterior basomedial nucleus (BMAp) sends a dense projection to the lateral nucleus, and to restricted parts of the central and medial nuclei. Extra-amygdalar projections from the BMA are divided into ascending and descending components. The former end in the cerebral cortex, striatum, and septum. The BMAa mainly innervates olfactory (piriform, transitional) and insular areas, whereas the BMAp also innervates inferior temporal (perirhinal, ectorhinal) and medial prefrontal (infralimbic, prelimbic) areas and the hippocampal formation. Within the striatum, the BMAa densely innervates the striatal fundus, whereas the nucleus accumbens receives a heavy input from the BMAp. Both parts of the BMA send massive projections to distinct regions of the bed nuclei of the stria terminalis. Descending projections from the BMA end primarily in the hypothalamus. The BMAa sends a major input to the lateral hypothalamic area, whereas the BMAp innervates the ventromedial nucleus particularly heavily.

Injections were also placed in the anterior cortical nucleus (COAa), a cell group superficially adjacent to the BMAa. PHAL-labeled axons from this cell group mainly ascend into the amygdala and olfactory areas, and descend into the thalamus and lateral hypothalamic area. Based on connections, the COAa and BMAa are part of the same functional system.

The results suggest that cytoarchitectonically distinct anterior and posterior parts of the BMA are also hodologically distinct and form parts of distinct anatomical circuits probably involved in mediating different behaviors (for example, feeding and social behaviors vs. emotion-related learning, respectively).

Indexing terms: anterograde tracer, emotion, hypothalamus, anterior cortical amygdalar nucleus

The amygdala has been implicated in a wide variety of functions, from sexual and social behaviors to emotion and sensory-associative learning (see Discussion). It is becoming clear that specific amygdalar nuclei contribute differentially to the various functions associated with this part of the inferior temporal lobe, and an appreciation of these contributions and how they are interrelated is essential for understanding the organization of the amygdala as a whole. In fact, a large body of anatomical evidence has clarified the major input-output relationships of most amygdalar nuclei in the rat, although the basomedial nucleus (BMA) is an exception, in part because it has never been the object of a systemic analysis, and in part because of inconsistencies in the way its boundaries have been drawn.

In the rat, two parts of the BMA have been recognized on cytoarchitectonic grounds: anterior (BMAa) and posterior (BMAp; De Olmos et al., 1985; Swanson, 1992), and they occupy a considerable fraction of the amygdala. Unfortunately, almost nothing is known about the function of the BMA based on specific physiological manipulations. Interestingly, however, recent work demonstrated a heavy projection from the ventral subiculum to the BMAp (Canteras and Swanson, 1992), which also seems to receive the bulk of

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Abbreviations

AAA	anterior amygdaloid area
ab	angular bundle
ac	anterior commissure
ACAd	anterior cingulate area, dorsal part
ACB	nucleus accumbens
aco	anterior commissure, olfactory limb
act	anterior commissure, temporal limb
ADP	anterodorsal preoptic nucleus
AHA	anterior hypothalamic area
AHNa, c, d, p	anterior hypothalamic nucleus, anterior, central, dorsal, posterior parts
AId, p, v	agranular insular area, dorsal, posterior, ventral parts
alv	alveus
AONpv	anterior olfactory nucleus, posteroventral part
ARH	arcuate nucleus hypothalamus
AUDd, p, v	auditory, dorsal, primary, ventral areas
AVP	*anteroventral* preoptic nucleus
AVPV	anteroventral periventricular nucleus hypothalamus
BA	bed nucleus accessory olfactory tract
BAC	bed nucleus anterior commissure
BLAa,p	basolateral nucleus amygdala, anterior, posterior parts
BMAa, p	basomedial nucleus amygdala, anterior, posterior parts
BST	bed nuclei stria terminalis
ad, al, av	anterodorsal, anterolateral, anteroventral areas
d, dl, dm	dorsal, dorsolateral, dorsomedial nuclei
fu, if, ju	fusiform, interfascicular, juxtacapsular nuclei
mg, ov, pr	magnocellular, oval, principal nuclei
tr, v, rh	transverse, ventral, rhomboid nuclei
sc, se	subcommissural zone, strial extension
CA1-3	field CA1-3, Ammon's horn
slm, so	stratum lacunosum-moleculare, stratum oriens
sp, spd, sps	pyramidal layer, deep, superficial
sr, slu	stratum radiatum, stratum lucidum
cc	corpus callosum
ccr	corpus callosum, rostrum
CEAm, l, c	central nucleus amygdala, medial, lateral, capsular parts
CLA	claustrum
CLI	central linear nucleus raphe
CM	central medial nucleus thalamus
COAa, p, pl, pm	cortical nucleus amygdala, anterior, posterior, posterior lateral, posterior medial parts
CP	caudoputamen
cpd	cerebral peduncle
DGcr	dentate gyrus, crest
DGlb	dentate gyrus, lateral blade
mo, po, sg	molecular, polymorph, granule-cell layers
DMHa, p, v	dorsomedial nucleus hypothalamus, anterior, posterior, ventral parts
ec	external capsule
ECT	ectorhinal area
ee	extreme capsule
ENT	entorhinal area
ENTl1-6	entorhinal area, lateral part, layers 1-6
ENTm1-6	entorhinal area, medial part, dorsal zone, layers 1–6
ENTmv	entorhinal area, medial part, ventral zone
EPd, v	endopiriform nucleus, dorsal, ventral parts
fi	fimbria
fr	fasciculus retroflexus
FS	fundus of the striatum
fx	columns of the fornix
GPl, m	globus pallidus, lateral, medial segments
GU	gustatory area
hf	hippocampal fissure
IA	intercalated nuclei amygdala
ILA	infralimbic area
IMD	intermediodorsal nucleus thalamus
int	internal capsule
isl	islands of Calleja (olfactory tubercle)
islm	major island of Calleja (olfactory tubercle)
LA	lateral nucleus amygdala
LH	lateral habenula
LHA	lateral hypothalamic area
LM	lateral mammillary nucleus
lot	lateral olfactory tract
LPO	lateral preoptic area
LSd, i, v	lateral septal nucleus, dorsal, intermediate, ventral parts
MA	medial accessory nucleus
MDm, c, l	mediodorsal nucleus thalamus, medial, central, lateral parts
MEAad, av,pv	medial nucleus amygdala, anterodorsal, anteroventral, posteroventral parts
MEApd-a,b,c	medial nucleus amygdala, posterodorsal part, sublayers a–c
MEPO	median preoptic nucleus
MM	medial mammillary nucleus
MPNc, l, m	medial preoptic nucleus, central, lateral, medial parts
MPO	medial preoptic area
MRN	mesencephalic reticular nucleus
MS	medial septal nucleus
mtt	mammillothalamic tract
NC	nucleus circularis
NDB	nucleus of the diagonal band
NLOT1, 2, 3	nucleus of the lateral olfactory tract, molecular layer, pyramidal layer, dorsal cap
och	optic chiasm
opt	optic tract
ORBvl	orbital area, ventrolateral part
OT1, 2, 3	olfactory tubercle, molecular, pyramidal, polymorph layers
PA	posterior nucleus amygdala
PAA	piriform-amygdaloid area
PAG	periaqueductal gray
PAR1-6	parasubiculum, layers 1-6
pc	posterior commissure
PD	posterodorsal preoptic nucleus
PERI	perirhinal area
PH	posterior hypothalamic nucleus
PIR	piriform area
PIR1, 2, 3	piriform area, molecular, pyramidal, polymorph layers
PL	prelimbic area
PMd	dorsal premammillary nucleus
PMv	ventral premammillary nucleus
PRE1–6	presubiculum, layers 1–6
PS	parastrial nucleus
PT	parataenial nucleus
PTLp	parietal region, posterior association areas
PVH	paraventricular nucleus hypothalamus
am, ap	anterior magnocellular, anterior parvicellular parts
d, f, p	descending, forniceal, parvicellular part
dp, lp	dorsal parvicellular, lateral parvicellular parts
mm, mp	medial magnocellular, medial parvicellular parts
mpd, mpv	medial parvicellular part dorsal, ventral zone
pm, pml, pmm	posterior magnocellular, lateral, medial zone
pv	periventricular part
PV	periventricular nucleus hypothalamus
a, i, po	anterior, intermediate, preoptic parts
PVT	paraventricular nucleus thalamus
RCH	retrochiasmatic area
REm	nucleus reuniens, median part
rf	rhinal fissure
RR	mesencephalic reticular nucleus, retrorubral area
SBPV	subparaventricular zone hypothalamus
SCH	suprachiasmatic nucleus
SEZ/RC	subependymal zone/rhinocoel
SI	substantia innominata
sm	stria medullaris
SO	supraoptic nucleus
PFp	subparafascicular nucleus thalamus, parvicellular part
st	stria terminalis
SUBv	subiculum, ventral part
SUBm, sp, sr	subiculum, molecular, pyramidal layers, stratum radiatum
SUMl,m	supramammillary nucleus, lateral, medial parts
sup	supraoptic commissures
TEP	temporal pole
TEv	ventral temporal association areas
TMv	tuberomammillary nucleus, ventral part
TR	postpiriform transition area
TT	taenia tecta
TTd1-4	taenia tecta, dorsal part, layers 1-4
TTv1-3	taenia tecta, ventral part, layers 1-3
VISC	visceral area
VMHa, c, dm, vl	ventromedial nucleus hypothalamus, anterior, central,dorsomedial, ventrolateral parts
VTA	ventral tegmental area

projections from the lateral amygdalar nucleus (Krettek and Price, 1978b; Pitkanen et al., 1995). The latter in turn receives inputs (apparently sensory-related) from the cerebral cortex and thalamus (Ottersen, 1982; McDonald and Jackson, 1987; LeDoux et al., 1990; Turner and Herkenham, 1991; Romanski and LeDoux, 1993; Mascagni et al., 1993).

Thus, we have examined the overall pattern of projections from the BMA and its two very distinct parts by using the PHAL anterograde tracing method. The results, considered together with other information in the literature, suggest possible distinct roles played by the BMAa and BMAp in the functional organization of the amygdala as a whole.

MATERIALS AND METHODS

Thirty-six adult male Harlan Sprague-Dawley rats (300–350 g) were used for tracer injections. Each animal was anesthetized with a mixture of ketamine and xylazine (v/v; 1 ml/kg body weight) and received a single injection of a 2.5% solution of PHAL (Vector Laboratories, Burlingame, CA), prepared in 0.01 M sodium phosphate-buffered saline (NaPBS), into the region of the BMA. Injections were made iontophoretically through a stereotaxically positioned glass micropipette (tip diameter: 10–15 μm) by applying a positive current (5 μA, 7 seconds off/on intervals) for 10–15 minutes.

After a survival time of 14–16 days, the rats were deeply anesthetized with pentobarbital and perfused transcardially with 150 ml of 0.9% NaCl followed by 300 ml of ice-cold 4% paraformaldehyde in 0.1 M borate buffer (pH 9.5). The brains were removed and postfixed overnight at 4°C in the same paraformaldehyde solution containing 10% sucrose. The brains were then frozen, and serial 30 μm thick sections were cut in the frontal plane on a sliding microtome. Sections were usually collected in four series, and an additional series was collected through the region of the BMA and stained quickly (immunofluorescence; Simerly and Swanson, 1988) for confirmation of injection site location.

PHAL was detected by using the immunohistochemical procedure described elsewhere (Gerfen and Sawchenko, 1984; Canteras et al., 1992). In brief, one complete series of sections was processed for immunohistochemistry with an antiserum against PHAL (Dako Laboratories; dilution 1:1,000) and a solution containing avidin-biotin-horseradish peroxidase (HRP) complex (ABC Elite Kit, Vector Laboratories, Burlingame, CA). Staining was obtained by processing the peroxidase histochemistry with a solution containing 0.05% diaminobenzidine and 0.01% hydrogen peroxide. The sections were then mounted on gelatin-coated slides and treated with osmium tetroxide (0.01%) to enhance the intensity of the enzymatic reaction product (Gerfen and Sawchenko, 1984). Slides were then dehydrated and coverslipped with DPX. An adjacent series was always stained with thionin for cytoarchitectonic purposes.

Sections were examined under the microscope with bright-field and darkfield illumination. PHAL-containing cells (in the injection sites) and fibers were plotted with the aid of a camera lucida onto cytoarchitectonic drawings of an adjacent thionin-stained sections. For illustration purposes, the distribution of anterogradely labeled fibers was then transferred onto a series of standard drawings of the rat brain (Swanson, 1992) with the aid of a computer (Apple, Macintosh Quadra 700; Adobe Illustrator 5); photomicrographs were composed with Adobe Photoshop 3 by using the standard tools. The parcellation and nomenclature of the rat brain adopted here follows Swanson (1992), unless otherwise indicated.

RESULTS

Parcellation

Before describing the projections of the BMA, it is important to consider the boundaries adopted here for the nucleus and its two parts because they have not been defined precisely or consistently by earlier workers, and different nomenclatures have been used.

The BMA, as defined here, is present throughout most of the rostrocaudal length of the amygdala. The two parts we recognize in the rat, the BMAa and BMAp, were originally defined on cytoarchitectonic grounds (De Olmos et al., 1985; Swanson, 1992).

The BMAp is located in the caudal half of the amygdala. It is an oval-shaped region that contains primarily small- to medium-sized, medium- to darkly-stained neurons (Fig. 1). It first appears as a group of cells located dorsal to the lateral posterior cortical nucleus and extends to the caudal pole of the amygdala. It is limited by the posterior basolateral nucleus laterally, the lateral part of posterior cortical nucleus and piriform-amygdaloid area ventrally, and the posterior nucleus medially (at caudal levels) (Swanson, 1992). The BMAp seems to correspond to the basomedial nucleus described by Krettek and Price (1978b), the posterior basomedial nucleus of De Olmos et al. (1985), and the accessory basal nucleus of Price et al. (1987). Furthermore, it corresponds roughly to the basomedial nucleus described originally by Brodal (1947) and only vaguely to the medial part of the basal nucleus ("AB4") of Turner and Zimmer (1984). Comparison of work done in different mammals is problematic because of differences in nomenclature and a lack of adequate connectional information. The term "accessory basal nucleus," first applied to monkey (Lauer, 1945), was recently applied to the cat and rat basomedial nucleus (specifically the BMAp, Price et al., 1987). However, connectional data reviewed in the Discussion indicate that the equivalence of the accessory basal nucleus in the rat and monkey remains to be established.

The BMAa is located in the rostral half of the amygdala (De Olmos et al., 1985; Swanson, 1992). It contains small, moderately tightly packed neurons that are lightly stained in Nissl preparations (Fig. 1). The BMAa is trapezoid shaped and begins at the level of the nucleus of the lateral olfactory tract and extends to mid-rostrocaudal levels of the amygdala. It is followed by the slightly larger, darker, and more loosely arranged neurons of the BMAp. In Nissl-stained material it is easily distinguished from the large, darkly stained, loosely packed cells of the anterior part of the basolateral nucleus, located dorsolaterally, and from the small, darkly stained and tightly packed cells of the intercalated nuclei dorsomedially. Laterally, the BMAa shares a border with the darker, slightly larger, and more loosely packed cells of the ventral part of the endopiriform nucleus. The rostral border of the BMAa is least clear because it gradually fuses with the anterior amygdaloid area (containing just slightly larger and darker neurons).

The BMAa corresponds to the anterior subdivision of the basomedial nucleus of De Olmos et al. (1985) and in part to the accessory basal nucleus ("ABA") of Turner and Zimmer

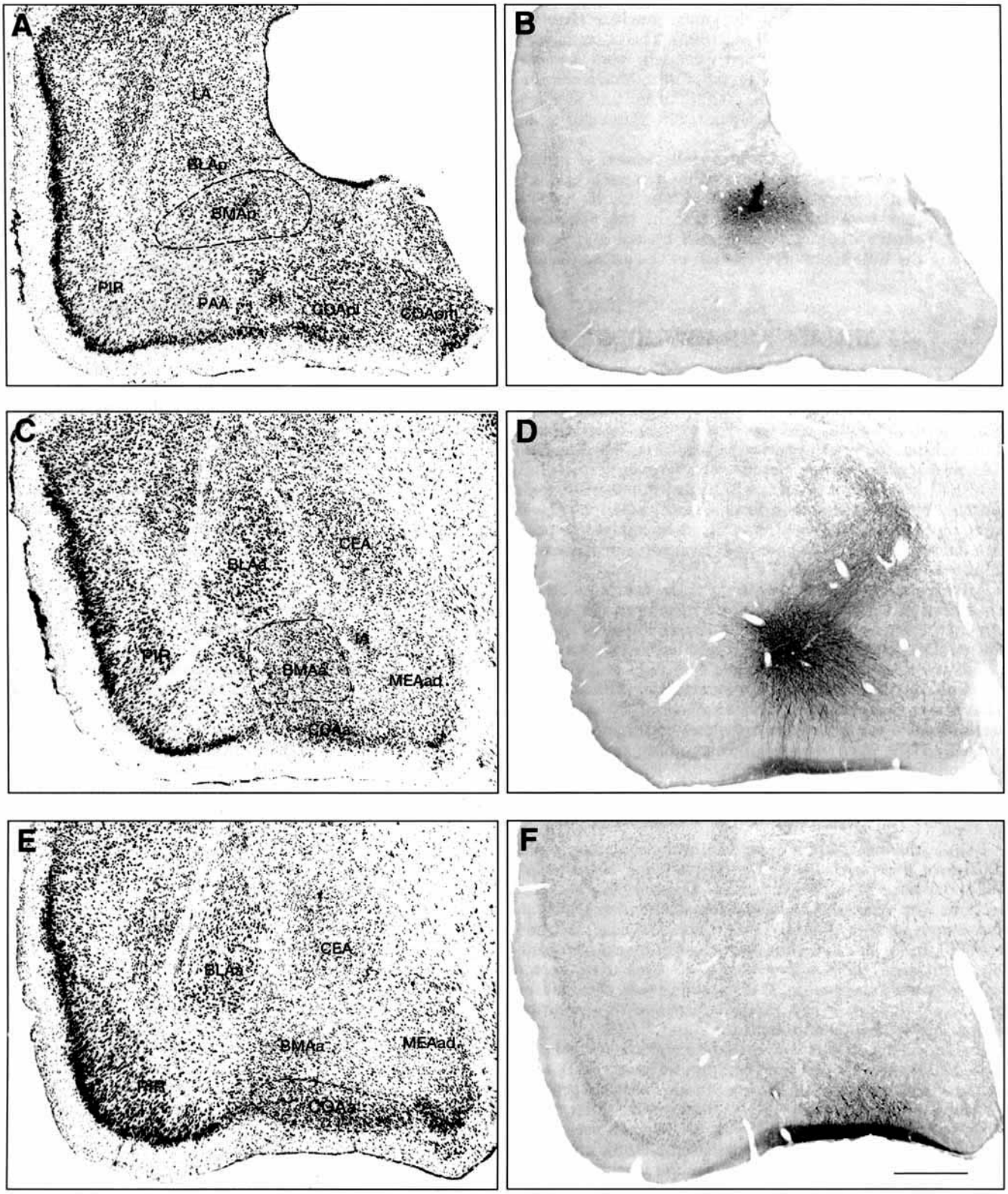


Fig. 1. **B,D,F:** Brightfield photomicrographs illustrating the appearance of the *Phaseolus vulgaris* leucoagglutinin (PHAL) injection site in experiments BMAp number 28 (B), BMAa number 60 (D), and COAa number 73 (F). **A,C,E:** Brightfield photomicrographs of caudally adjacent thionin stained sections for the BMAp (A), BMAa (C), and COAa (E) injection sites. Dark staining in the molecular layer of the COAa in D and particularly in F represents dendritic PHAL-labeling. Scale bar = 500 μm.

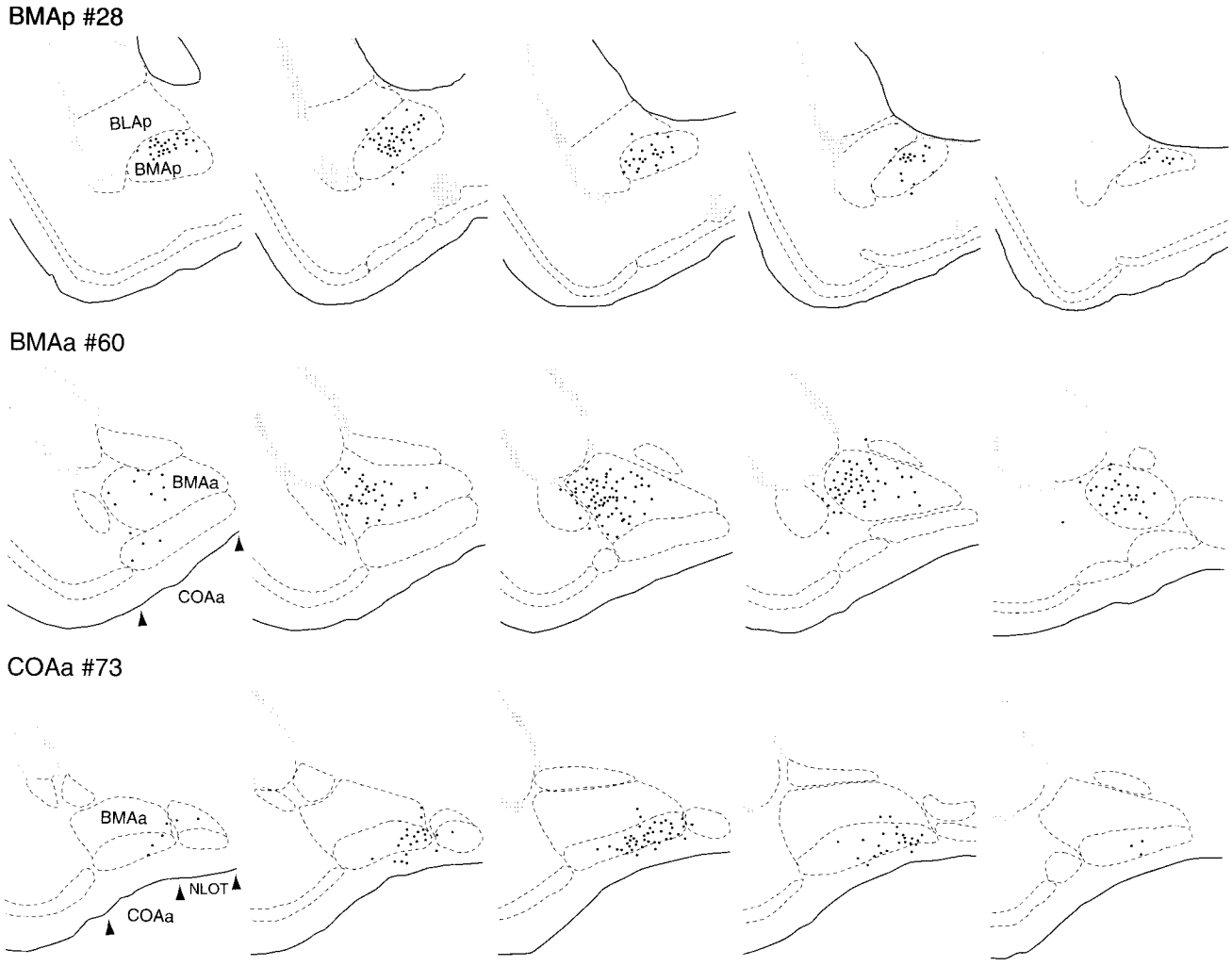


Fig. 2. Camera lucida plots of labeled cells following PHAL injections into the BMAp, BMAa, and COAa. Sections are arranged from rostral (left) to caudal (right). The distribution of labeled axons projecting from these injection sites is illustrated in Figures 3, 4, and 5.

(1984); it was also recognized as a "loosely structured cell mass" dorsal to the anterior cortical amygdalar nucleus (COAa), labeled "C?" by Brodal (1947). Furthermore, some authors consider the BMAa as a deep part (third layer) of the COAa (Scalia and Winans, 1975; Krettek and Price, 1978b; Pitkanen et al., 1995). The BMAa does appear to be closely related to the COAa, which accompanies it ventrally. According to the interpretation adopted here, the COAa (Fig. 1) consists of two layers, molecular (plexiform) and neuronal (pyramidal) (De Olmos et al., 1985; Swanson, 1992). The second layer contains small to medium-sized, tightly packed neurons that are moderately stained in Nissl material. The cell density decreases dorsally near the border with the BMAa. The COAa is limited medially by the nucleus of the lateral olfactory tract at rostral levels, and by the anteroventral part of the medial nucleus and bed nucleus of the accessory olfactory tract at caudal levels. Laterally, it is bordered by the piriform area and lateral part of the posterior cortical nucleus. Interestingly, some neurons are present in the molecular layer, especially near layer 2. The COAa corresponds to the anterior cortical nucleus described by Brodal (1947) and De Olmos (1985), and also to the first and second layer of the COAa described by Krettek and Price (1978b).

Projections from the BMAp

In seven experiments the PHAL injection labeled many neurons within the BMAp and of these, five injection sites were confined almost entirely to this part of the BMA. Dorsal regions of the nucleus contained the majority of PHAL-labeled neurons in two experiments: medial and ventral parts of the nucleus were labeled in one experiment, one injection was centered in the rostral half and one in the caudal half of the nucleus, and two injections labeled neurons throughout most of the nucleus. The projections of one of the latter experiments, number 28 (Figs. 1 and 2), will be described in detail because the injection was restricted to the BMAp, and because the projection pattern is typical of those labeled in other experiments with an injection in the BMAp. Other injections labeled projections that can be attributed to labeled cells in adjacent nuclei.

Intra-amygdalar projections

Within the amygdala, the BMAp provides dense inputs to the central and lateral nuclei, and moderate inputs to the medial nucleus and piriform-amygdaloid area. The BMAa, anterior amygdaloid area, nucleus of the lateral olfactory tract, posterior basolateral nucleus, and lateral and medial parts of the posterior cortical nucleus receive a light input, while the anterior basolateral nucleus, intercalated nuclei, and COAa are only very sparsely innervated.

From the injection site, many labeled fibers course dorsally through the posterior basolateral nucleus (Fig. 3M,N) to end in the central and lateral nuclei. The BMAp appears to innervate mainly the capsular part of the central nucleus, whereas the lateral and most of the medial part contain only a few labeled terminals (see Risold et al., 1994, their Fig. 4, for definition of axonal structures labeled with PHAL). Ventral (Fig. 3J–M) and more caudodorsal regions (Fig. 3L,M) of the capsular part of the central nucleus contain a dense plexus of anterogradely labeled axons with numerous branches displaying terminal boutons. Interestingly, a thin ventral strip (Fig. 3J,K) of the medial part of the central nucleus, bordering the capsular part, receives a dense input, while the rest of the medial (Fig. 3H–M), and the lateral (Fig. 3K–N), parts of the central nucleus receive only a sparse input.

The ventral region of the lateral nucleus (Fig. 3M–O) receives a dense plexus of fibers and terminals from the BMAp, while, curiously, more rostral (Fig. 3J–L) and dorsal (Fig. 3M–O) parts are almost free of anterograde labeling.

The BMAp sends fibers rostromedially to provide an input to the medial nucleus. The anterodorsal (Fig. 3H–L) part of the medial nucleus receives a moderate plexus of fibers, while only a small number of fibers coursing ventromedially, and displaying a few terminal boutons, provide a light input to the posteroventral part (Fig. 3M). The anteroventral (Fig. 3K–L) and posterodorsal (Fig. 3M,N) parts of the medial nucleus, except for occasional sparse fibers, are avoided by PHAL-labeled axons from the BMAp.

Labeled fibers from the injection site also could be traced rostrally into the BMAa (Fig. 3G–M), where they provide a light input that becomes slightly denser at more caudal levels (Fig. 3K,L). Some fibers continue farther rostrally to reach the nucleus of the lateral olfactory tract ventrally, and the anterior amygdaloid area dorsally. The nucleus of the lateral olfactory tract is sparsely innervated except for the most medial part of layer 3 (Fig. 3G–I), which receives a light input. A dorsomedial and caudal region of the anterior amygdaloid area (Fig. 3I) receives a light input, whereas more sparse fibers could be traced throughout the entire nucleus (Fig. 3F–J).

A group of fibers extending ventrally from the injection site provides a moderate input to the piriform-amygdaloid area and a light input to lateral and medial parts of the posterior cortical nucleus. Layer 3 of the piriform-amygdaloid area receives a moderate input (Fig. 3M–O) and some fibers enter layers 1 and 2. Interestingly, only layer 3 of the lateral (Fig. 3O,P), and layer 1 of the medial (Fig. 3Q), part of the posterior cortical nucleus receive a moderate to light input; the rest of the nucleus is sparsely innervated (Fig. 3L–Q).

Although many fibers course through the posterior part of the basolateral nucleus, they do not branch and only display occasional boutons-of-passage, thus appearing more like fibers-of-passage. At more caudal levels, however, fibers show occasional branching with boutons, thus clearly providing a light input (Fig. 3P,Q).

Finally, only occasional boutons-of-passage are observed on scattered fibers in the COAa (Fig. 3G–M), intercalated nuclei (Fig. 3E–M), and anterior part of the basolateral nucleus (Fig. 3I–M).

Ascending projections

The BMAp provides an extraordinary pattern of extra-amygdalar projections that may be divided into an ascending pathway that innervates a number of telencephalic targets and a descending pathway that provides an input primarily to the hypothalamus.

Ascending projections from the BMAp follow three major routes to various telencephalic targets: the longitudinal amygdalo-pyriform association bundle of Johnston (1923), stria terminalis, and ansa peduncularis.

Longitudinal association bundle. Most fibers ascending from the BMAp to the cerebral cortex appear to travel through the longitudinal association bundle, and lateral and medial branches of this bundle were recognized in our material.

The lateral part of the longitudinal association bundle is a diffuse, fan-shaped group of fibers (Fig. 3N,O), extending laterally to innervate cortical areas located both rostral and caudal to the injection site. Dorsally, labeled fibers provide an input to the agranular insular, perirhinal, and ectorhinal areas. Immediately after leaving the nucleus, a number of labeled fibers course dorsally through the posterior part of the basolateral nucleus, and continue through ventral then dorsal regions of the endopiriform nucleus and deep layers of the piriform area to end mainly in the superficial cortical layers (1–3). In addition, some fibers course through the external capsule and claustrum to end in the deeper cortical layers (5 and 6). Although a significant number of fibers travel through the claustrum, they do not seem to branch or display terminal boutons. Rostrally, these fibers provide a light input to the caudal (Fig. 3D–M), dorsal, and ventral (Fig. 3A–D) agranular insular areas. Cortical layer 5 is innervated lightly by some fibers that display occasional branching, while other layers of the agranular insular area receive an even sparser input. Interestingly, labeled fibers could be traced to more dorsal cortical areas, including a few in all layers (except 4) of the visceral area (Fig. 3F–M), as well as layers 1, 5, and 6 of the somatosensory area (Fig. 3H–M, not illustrated).

Caudally, fibers traveling through the longitudinal association bundle innervate densely the perirhinal and ectorhinal areas. This is one of the most striking projections of the BMAp. A remarkable plexus of anterogradely labeled axons could be traced throughout the entire rostrocaudal length of the perirhinal area (Fig. 3M–T). The labeling was particularly dense in layers 2, 3, and 5 where many fibers display moderate branching with boutons. The ectorhinal area receives a similar pattern of labeling, although somewhat lighter, with the densest input going to layer 2 and deeper parts of layer 5 (Fig. 3N–T). Curiously, some fibers continue farther dorsally to innervate lightly the ventral temporal association area and sparse fibers are observed even more dorsally in layers 1, 5, and 6 of the primary, ventral, and dorsal auditory areas, as well as in the posterior parietal association area (Fig. 3N–T).

A group of fibers that extends ventrally through the piriform-amygdaloid and piriform areas ends in the olfactory tubercle rostrally, and in the postpiriform transition

and entorhinal areas caudally. The olfactory tubercle (Fig. 3A–F) appears to receive a light input to all three layers. Axons coursing through the piriform area tend to display few branches and terminal boutons, thus appearing more like fibers-of-passage, except ventrally (Fig. 3E–P) where some branching with terminal boutons occurs, thus providing a light input. From the injection site, fibers traveling caudally through the piriform-amygdaloid area innervate the postpiriform transition and lateral entorhinal areas. The BMAp sends a very light input to all three layers of the postpiriform transition area (Fig. 3P–R). Fibers from the BMAp reach mainly ventral regions of the lateral entorhinal area, where they provide a moderately dense input to the deep part of layer 3, and layer 5 (Fig. 3S,T). Distinctly fewer axons were found in the superficial layers, and layer 6.

The BMAp sends fibers caudally through the medial part of the longitudinal association bundle to innervate the ventral subiculum, ventral field CA1, and parasubiculum. From the injection site, labeled fibers course medially and ventrally through the lateral and medial parts of the posterior cortical nucleus and posterior nucleus of the amygdala (Fig. 3N–Q) to reach the hippocampal formation. These fibers appear to enter the hippocampal formation by two routes. One group of fibers travels ventrally to enter the ventral subiculum (Fig. 3P–R), whereas the other extends dorsally through the alveus to reach field CA1 (Fig. 3P,Q). At the rostral pole of the ventral hippocampus, fibers appear to travel through the pyramidal and molecular (stratum oriens and stratum lucidum) layers of field CA1, and the pyramidal and molecular (stratum oriens and stratum radiatum) layers of field CA3 (Fig. 3P,Q). Although these fibers have numerous varicosities, they branch little if at all and only very occasional boutons-of-passage were seen in the stratum radiatum at these levels. However, these fibers provide a significant input to ventral and caudal regions of field CA1 (Fig. 3R,S). The stratum lacunosum-moleculare and stratum radiatum receive a moderate input from a large number of fibers that show moderate branching with boutons, while the stratum oriens and the entire pyramidal layer show lighter labeling.

Farther caudally, fibers from the BMAp provide a moderate input to the ventral subiculum (Fig. 3S,T). The pyramidal layer receives the densest input, the stratum radiatum receives a lighter input, and the molecular layer is only lightly innervated (Fig. 3S,T). The labeling becomes lighter at the caudal pole of the ventral subiculum, where fibers remain mainly in the pyramidal layer with only an occasional fiber in the stratum radiatum. Finally, some fibers traveling medially and ventrally through the medial entorhinal area (Fig. 3S,T) provide a discrete, moderate input to the molecular layer and superficial cells in layer 2 of the parasubiculum (Fig. 3T).

Stria terminalis. Many axons from the BMAp course rostrally and dorsally through the stria terminalis (Fig. 3F–O) to end in various parts of telencephalon, including the septum, striatum, medial prefrontal cortex, and anterior olfactory nucleus. Within the most caudal pole of the bed nuclei of the stria terminalis (BST) (Fig. 3G,H), the transverse nucleus contains a moderately dense plexus of fibers displaying branches with terminal boutons, whereas only occasional branching was observed in fibers traveling through the interfascicular and ventral nuclei. At this level (Fig. 3G,H), axons arriving through the ansa peduncularis merge with fibers from the stria terminalis, and most likely contribute to the innervation of more rostral telencephalic targets. The magnocellular nucleus of the BST (Fig. 3F) receives a dense plexus of fibers with a large number of boutons, whereas the anterolateral area and dorsal part of the ventral nucleus receive a moderately dense input, and the rhomboid and dorsolateral nuclei receive a sparse input. The principal nucleus (Fig. 3F–H) is completely avoided by PHAL-labeled axons from the BMAp, except for the most posterior region that contains an occasional fiber-of-passage. In the rostral division of the BST (Fig. 3D,E) the anterodorsal area, subcommissural zone, and dorsomedial nucleus are filled with a dense plexus of highly branched axons displaying many boutons. It is important to note that, in spite of massive inputs to nearby areas, the oval and juxtacapsular nuclei, as well as the anterolateral area, show only sparse anterograde labeling, while the fusiform nucleus is virtually free of such labeling.

At the rostral pole of the BST, fibers coursing through the stria terminalis split into two components. One group of fibers extends dorsally to end in the lateral septal nucleus, infralimbic and prelimbic areas, and anterior olfactory nucleus. The other group curves ventrally, just rostral to the anterior commissure, and continues rostrally to innervate mainly the nucleus accumbens, although some fibers reach the olfactory tubercle and striatal fundus as well. The BMAp provides a light input to the ventral part of the lateral septal nucleus (Fig. 3B–D), and some fibers-of-passage travel through the intermediate and dorsal parts of this nucleus to end in the infralimbic and prelimbic areas, and farther rostrally, in the anterior olfactory nucleus as well. Layers 2, 3, and 5 of the infralimbic area (Fig. 3A) receive a moderate input, and layers 1 and 6 a light input. The prelimbic area receives only a very light input, mainly in layer 5 (Fig. 3A). The anterior olfactory nucleus is also lightly innervated. Most fibers are confined to the posteroventral part (Fig. 3A), although some fibers could also be traced to the medial part, more rostrally (not shown).

The BMAp provides a dense plexus of fibers (which display a highly branched pattern and generate a fairly large number of terminal boutons) to caudal regions of the nucleus accumbens (Fig. 3C). Interestingly, the rostral pole of the nucleus accumbens (Fig. 3A,B) is only lightly innervated by a few axons with very little branching.

Ansa peduncularis. Two distinct bundles in the ansa peduncularis were labeled: a rostral bundle extending through the substantia innominata and providing ascending and descending projections, and a caudal bundle descending directly to and through the lateral hypothalamic area.

Many labeled axons could be traced dorsomedially from the injection site; they extend through rostral regions of the central nucleus and dorsal regions of the anterodorsal medial nucleus to enter the ansa peduncularis. These fibers could be followed through the substantia innominata (Fig. 3G–K) to the caudal pole of the BST, where they split into two components, one continuing rostrally through ventral regions of the substantia innominata (Fig. 3B–G) and the other merging with fibers from the stria terminalis (Fig. 3G,H) and probably contributing to the innervation of various telencephalic targets (see above). Because many fibers were labeled with PHAL, it is not possible in our material to determine whether one axon branches to enter both bundles of the pathway, and for that matter whether one axon sends branches to different pathways.

Axons transversing the substantia innominata display few branches, although they show numerous boutons-of-

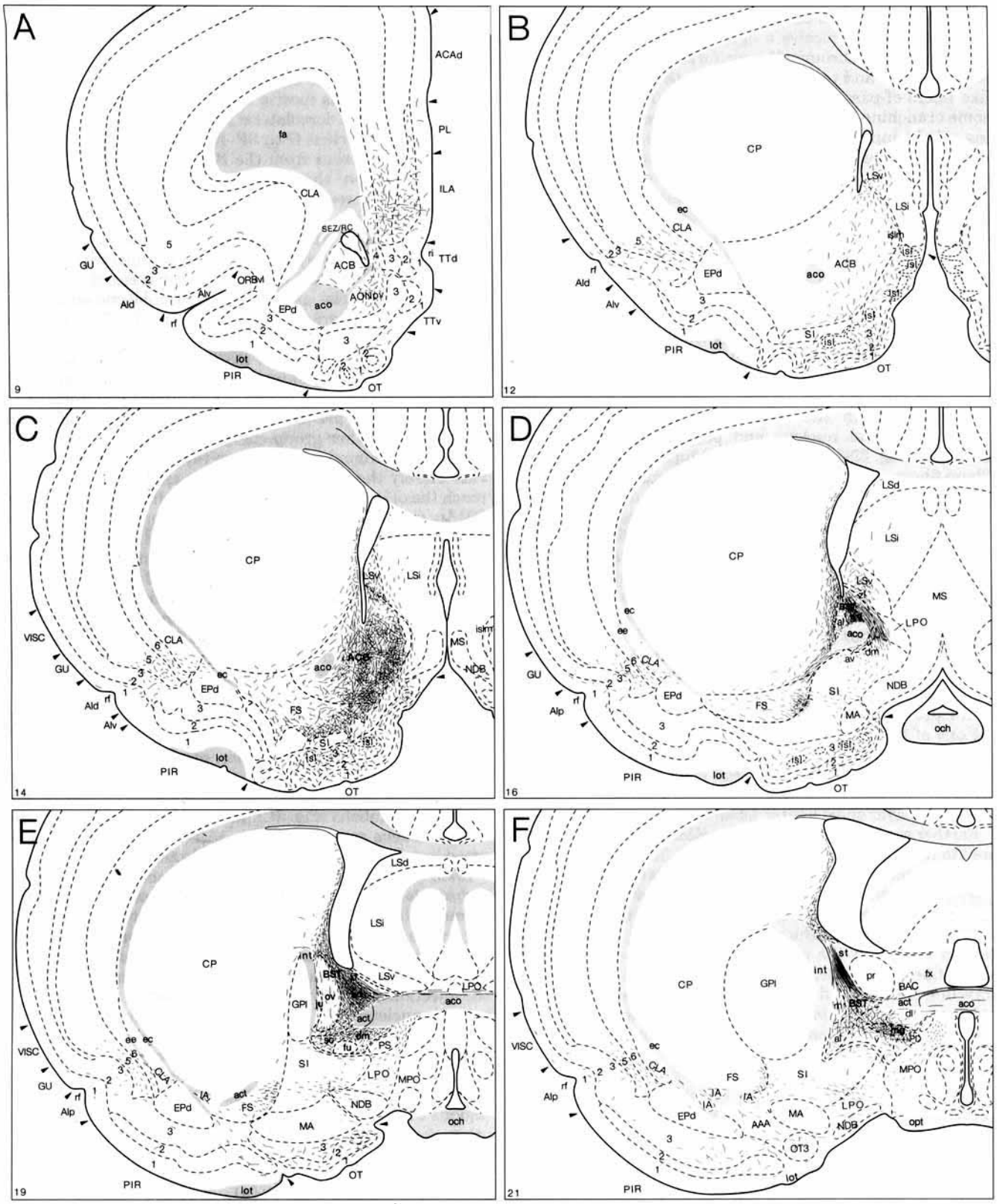
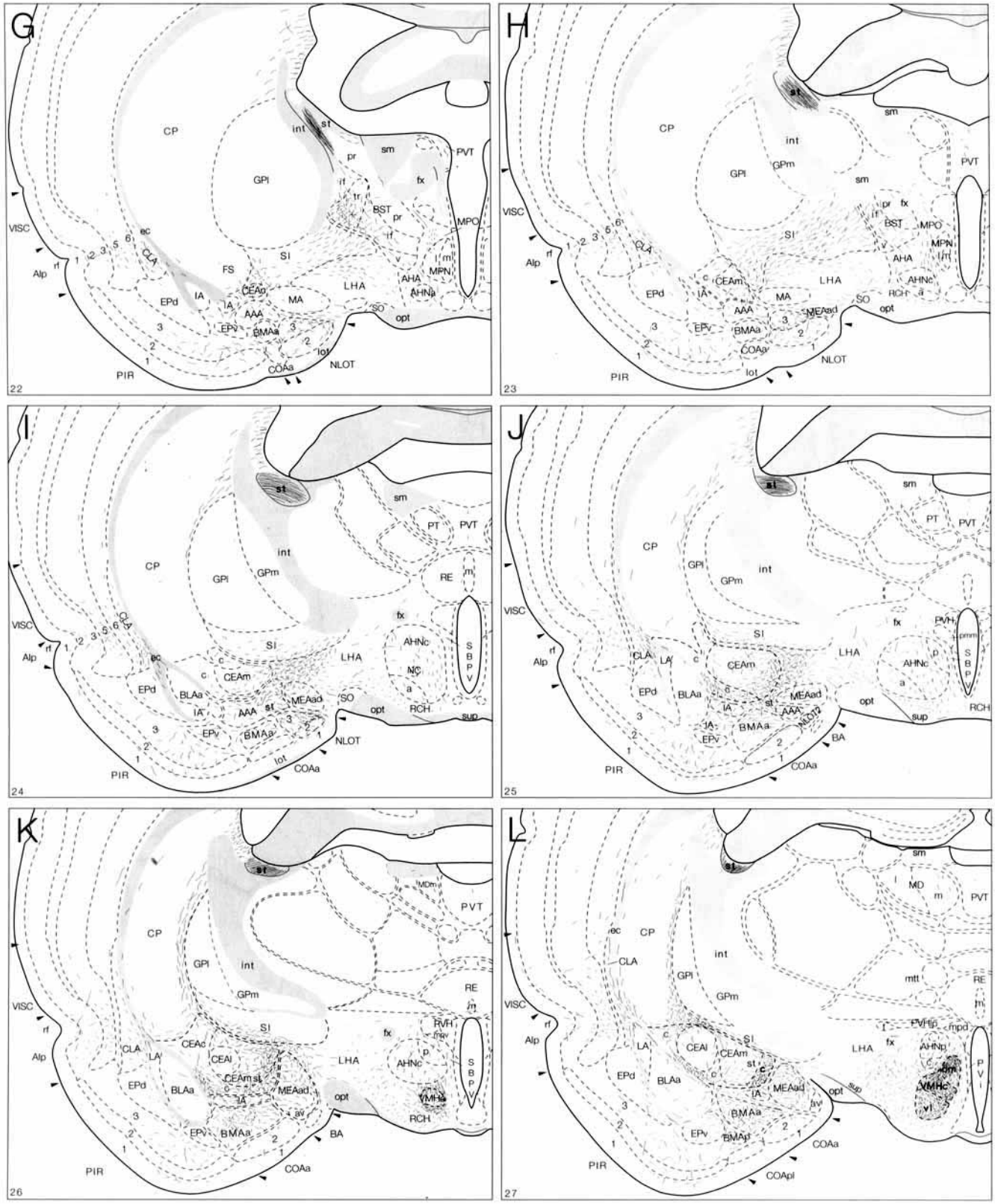


Fig. 3. **A-T:** The projections of the BMAp. The distribution of PHAL-labeled axons in experiment number 28 was plotted onto a series of standard drawings of the rat brain derived from an atlas (Swanson, 1992), arranged from rostral (A) to caudal (T). The dark gray area in N and O indicates the injection site (see Figs. 1 and 2). The number in the lower left corner of each drawing refers to the corresponding rostrocaudal level of the atlas (as in Figs. 4 and 5).



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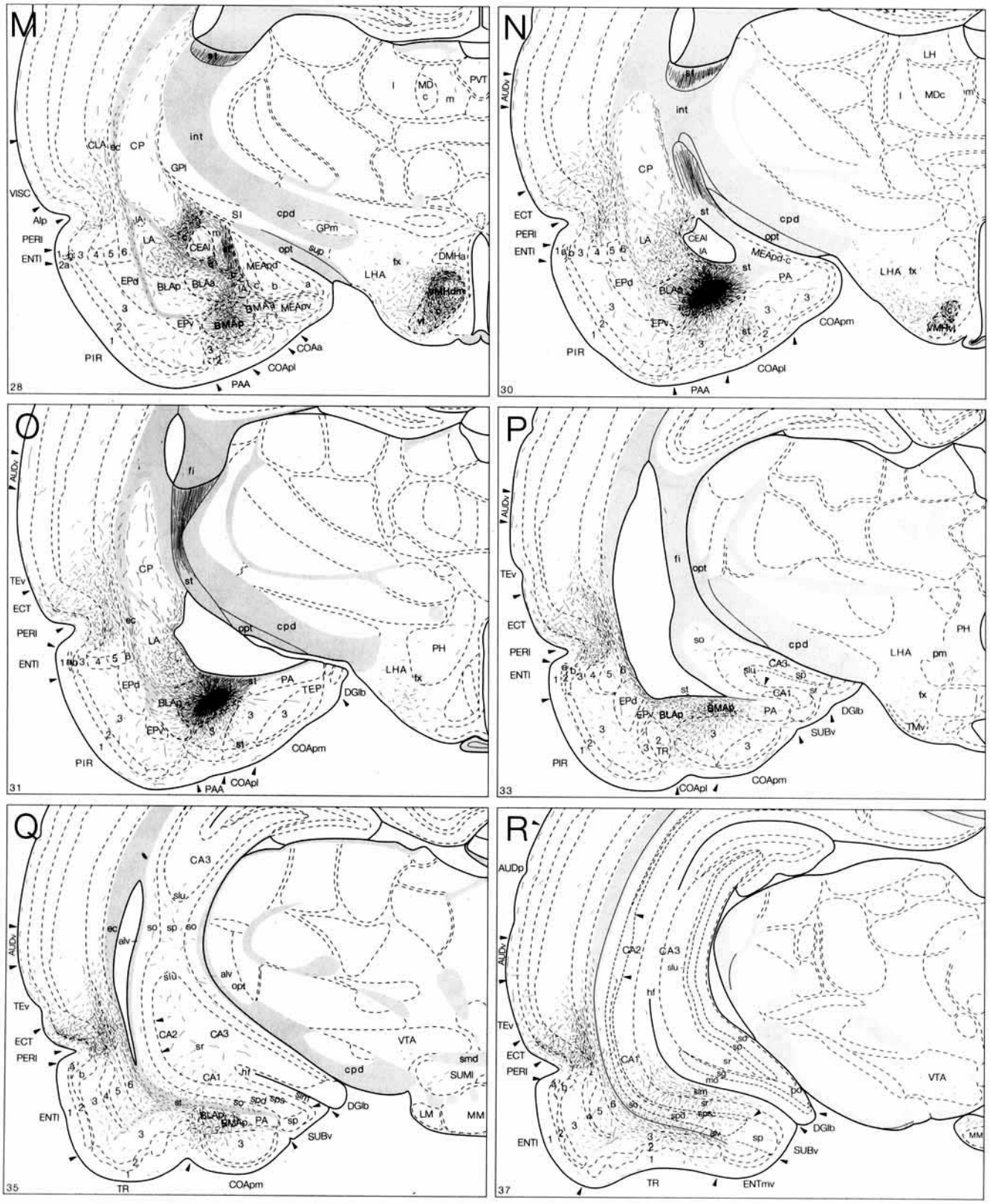

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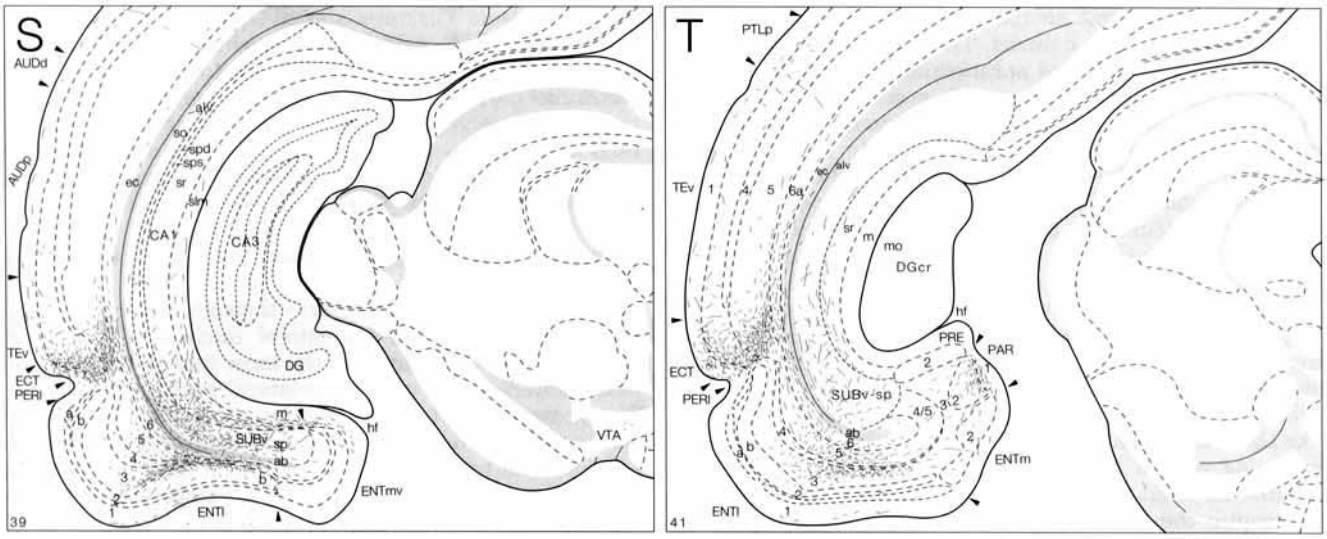


Figure 3 (Continued.)

passage along the pathway, thus providing a significant input.

Fibers ascending through the rostral bundle of the ansa peduncularis innervate the fundus of the striatum and caudoputamen. One group of fibers transversing the rostral central nucleus of the amygdala continues dorsally to innervate ventral regions of the striatal fundus (Fig. 3C–G). These fibers occasionally branch to provide a very light input that becomes somewhat more dense rostrally (Fig. 3C). Within the caudoputamen, a significant plexus of fibers could be traced in a distinct, thin, most medial band (Fig. 3C–O) throughout its entire rostrocaudal length, as well as in a ventral region bordering the central nucleus of the amygdala more caudally (Fig. 3M–O). Most fibers appear to reach the caudoputamen by extending laterally through the lateral nucleus of the amygdala, external capsule, and dorsal region of the capsular part of the central nucleus (Fig. 3N,O). It is also possible that some fibers reach the caudoputamen (particularly rostrally) through the stria terminalis. Although some fibers appear to continue dorsally from the stria terminalis (Fig. 3F), their direction is difficult to confirm with certainty.

Descending projections

The BMAp sends descending projections through both the stria terminalis and ansa peduncularis to innervate the hypothalamus and, to a much lesser extent, the thalamus.

Stria terminalis. Two descending components of the stria terminalis were labeled: the rostral-precommisural and caudal-postcommisural bundles (Heimer and Nauta, 1969). These correspond to the supracommissural and hypothalamic bundles, respectively, of Johnston (1923), and the supracommissural and preoptic bundles, respectively, of Gurdjian (1928). The precommissural bundle curves just rostral to the anterior commissure (Fig. 3D) and descends through the hypothalamic medial zone to innervate specifically the hypothalamic ventromedial nucleus. After leaving the stria terminalis, the postcommisural bundle continues ventrally through the caudal pole of the BST (Fig. 3G,H) to end in various hypothalamic nuclei.

Fibers in the precommisural bundle travel caudally through the lateral (Fig. 3E) and medial (Fig. 3F–H) preoptic areas, following an essentially sagittal orientation, that is, appearing short in the transverse plane of section, without branching or displaying boutons. Extending caudally, these fibers show occasional branching with boutons, providing a very light input to the anterior, central, and posterior parts of the anterior hypothalamic nucleus (Fig. 3I–K). Finally, these fibers reach the hypothalamic ventromedial nucleus where they generate an exceptionally dense input. The cellular core of the ventromedial nucleus (Fig. 3K–N), particularly centrally, is filled with an extraordinary dense plexus of highly branched axons displaying numerous boutons. Interestingly, labeling density is lower in the anterior (Fig. 3K) and ventrolateral parts of the nucleus (Fig. 3L–N), and some patches that are almost free of labeling were seen in the dorsomedial part (Fig. 3L,M). Ventral and lateral regions of the cell-sparse capsule of the ventromedial nucleus, and the adjacent tuberal nucleus, receive a light input.

The postcommissural bundle enters the hypothalamus by way of the caudal pole of the BST and the anterior hypothalamic area (Fig. 3G,H), where it merges with axons from the ansa peduncularis (see below), and more caudally axons from these two pathways could not be distinguished. The BMAp provides a light input to various parts of the lateral hypothalamic area (Fig. 3I–P), tuberal nucleus (Fig. 3K–N), and retrochiasmatic area (Fig. 3H–K), and it sends a few axons to the subparaventricular zone (Fig. 3I–K). Some scattered fibers-of-passage were also traced into the dorsomedial (Fig. 3M) and paraventricular (Fig. 3J) nuclei.

Ansa peduncularis. Two labeled descending bundles course through the ansa peduncularis. One extends rostromedially through the substantia innominata to end in the thalamus and hypothalamus (Fig. 3H–K), while the other extends caudoventrally through the lateral hypothalamic area to innervate mainly the caudal hypothalamus (Fig. 3L–P).

A very few fibers traveling rostrally eventually curve medially through a dorsal region of the lateral hypotha-

lamic (Fig. 3I,J) and medial preoptic (Fig. 3H) areas to reach midline thalamic nuclei. These fibers travel through the nucleus reuniens and parataenial nucleus, where only apparent fibers-of-passage were observed, to provide a very light input to the thalamic paraventricular nucleus and medial part of the mediodorsal nucleus (Fig. 3G–M).

Within the caudal hypothalamus, some fibers were seen in caudal regions of the lateral hypothalamic area and in the posterior nucleus (Fig. 3O,P), and sparse fibers were also noted in the lateral part of the supramammillary nucleus (Fig. 3Q). Interestingly, a few fibers could also be traced into the capsule of the medial mammillary nucleus (Fig. 3Q,R). No anterograde labeling was found caudal to the hypothalamus, except for an occasional smooth fiber in the ventral tegmental area (Fig. 3Q,R).

Finally, it is important to note that BMAp projections, like those from other amygdalar nuclei, are mainly ipsilateral, and only a very small number of axons cross the midline through the anterior commissure (Fig. 3E,F) and supraoptic commisures (Fig. 3J). These fibers appear to innervate very lightly only those regions that receive a dense ipsilateral input, including the BST, nucleus accumbens, and hypothalamic ventromedial nucleus. Sparse fibers were also noted in the lateral hypothalamic area, the lateral, central, and medial amygdalar nuclei, and the BMAp itself.

Projections from the BMAa

In 15 experiments the PHAL injection labeled many neurons within the BMAa, and of these 10 were confined almost entirely to this nucleus. Two injections labeled cells mainly dorsally, one injection was medial, two were lateral, and two were ventral. In addition, one injection was centered rostrally and two were centered in the caudal half of the nucleus. The projections labeled in experiment number 60 (Figs. 1,2), with a large injection confined almost entirely to the BMAa, were typical of those labeled in other experiments and are described in detail because no obvious topographic organization of projections from different parts of the cell group was found.

Intra-amygdalar projections

Within the amygdala, the BMAa provides dense terminal fields to the central, medial, and anterior cortical nuclei, and moderate terminal fields to the anterior amygdaloid area, piriform-amygdaloid area, and lateral and medial parts of the posterior cortical nucleus. The bed nucleus of the accessory olfactory tract, lateral nucleus, anterior and posterior parts of the basolateral nucleus, and BMAp show light anterograde labeling, while the nucleus of the lateral olfactory tract and intercalated nuclei are very sparsely innervated.

The central nucleus of the amygdala contains by far the densest labeled terminal field after PHAL injections in the BMAa. The medial part, and ventral and anterior regions of the capsular part, of the central nucleus are filled with an overwhelming number of axons that display spectacular branching with terminal boutons (Fig. 4G–N). The density of terminals is clearly less in the lateral part of the central nucleus (Fig. 4K–N), and the dorsal region of the capsular part receives only sparse fibers (Fig. 4I–M).

Many labeled axons were observed throughout all parts of the medial nucleus, including both neuronal and molecular layers. Unlike the BMAp, axons from the BMAa innervate heavily the anteroventral part (Fig. 4K,L) of the medial nucleus. The anterodorsal (Fig. 4H–L) and posteroventral (Fig. 4M) parts of the medial nucleus receive a moderate number of fibers with boutons, while the posterodorsal part (Fig. 4M,N) is lightly innervated.

Anterogradely-labeled axons from the injection site extend ventrally to provide a dense input to the anterior cortical nucleus (Fig. 4H–M), particularly layer 2, and more medially to innervate lightly the bed nucleus of the accessory olfactory tract. Anteriorly and dorsally, the BMAa provides a moderate plexus of fibers to the anterior amygdaloid area (Fig. 4F–I).

Many fibers-of-passage course through the anterior and posterior parts of the basolateral nucleus. These fibers provide a very light input to the most ventrolateral region of the anterior part of the basolateral nucleus (Fig. 4K,L). The posterior part of the basolateral nucleus receives a moderate input to its ventrolateral region (Fig. 4M,N), and a dense input to its most caudal part (Fig. 4O,P). Numerous fibers also travel through the BMAp, and provide a moderate input to its caudal region (Fig. 4N–P).

Labeled fibers were observed throughout the entire length of the lateral nucleus (Fig. 4J–O), providing a very light input, although ventrocaudally (Fig. 4N) this input appeared somewhat more dense.

Caudal to the injection site, many fibers traveling ventrolaterally provide a moderate input to layer 3 and a very light input to layers 1 and 2 of the piriform-amygdaloid area (Fig. 4M–O). A group of fibers coursing medially innervates very lightly lateral (Fig. 4L–P) and medial (Fig. 4N–Q) parts of the posterior cortical nucleus. Interestingly, dorsal regions of layer 3 and the molecular layer of the lateral (Fig. 4O–P) part (and a very small caudal region of the medial part, Fig. 4O) of the posterior cortical nucleus receive a notably denser input.

Many fibers travel through the intercalated nuclei (Fig. 4F–M), particularly caudally (Fig. 4J–M), although they apparently provide only a sparse input by way of scattered boutons-of-passage. The nucleus of the lateral olfactory tract (Fig. 4G–J) receives a sparse input that becomes somewhat denser caudally in ventral region of layer 3 (Fig. 4I). Finally, occasional smooth fibers could be traced through the posterior nucleus of the amygdala (Fig. 4N–P), and they never show branching or boutons.

Ascending projections

As with the BMAp, fibers from the BMAa ascend through the longitudinal association bundle, stria terminalis, and ansa peduncularis.

Longitudinal association bundle. Numerous fibers from the BMAa traverse the lateral part of the longitudinal association bundle, whereas only a few fibers could be traced through the medial part.

Labeled fibers from the BMAa travel through the lateral part of the longitudinal association bundle (Fig. 4L–P) to reach the agranular insular and perirhinal areas dorsally, as well as the olfactory tubercle, piriform, postpiriform transition, and entorhinal areas, ventrally. They follow the same route (Fig. 4L–P) described for axons from the BMAp, extending through the anterior and posterior basolateral nucleus, ventral and dorsal endopiriform nucleus, deep layer 3 of the piriform area, and external capsule to reach these cortical areas. Although a particularly large number of fibers travel through the endopiriform nucleus, especially ventrally, they seem to provide only a sparse input by way of occasional boutons-of-passage. In contrast to what

was described for the BMAp, axons from the BMAa mainly innervate the superficial cortical layers, and accordingly more fibers travel through the piriform area than through the external capsule. The posterior agranular insular area (Fig. 4C–M) receives a moderate to light input to layers 1–3, and scattered fibers could be traced to layers 5 and 6, as well as more anteriorly to the dorsal and ventral (Fig. 4A,B) agranular insular areas. Unlike the BMAp, fibers from the BMAa provide a very light input to the perirhinal area (Fig. 4M–S), and only rare fibers could be traced to more dorsal cortical areas, the visceral area (Fig. 4F–M) rostrally, and the ectorhinal (Fig. 4N–T) caudally.

Anterogradely-labeled fibers traveling through the ventral component of the longitudinal association bundle provide a light input to the olfactory tubercle, piriform area (rostrally), and postpiriform transition and entorhinal areas (caudally). Although these fibers provide a very light input through the entire rostrocaudal length of the piriform area (Fig. 4A–O), they tend to be more concentrated caudally. From this pathway, fibers could be followed into the olfactory tubercle, where they appear to innervate mainly layer 3 (Fig. 4E,F), although some fibers could be seen in all three layers (Fig. 4A–F).

Many fibers extending ventrally and caudally through the piriform and piriform-amygdaloid areas, end in the postpiriform transition (Fig. 4O-R) and entorhinal (Fig. 4S,T) areas. Interestingly, the BMAa provides a rather dense input to a deep region of the molecular layer and a moderate to light input to layers 2 and 3 of the postpiriform transition area (Fig. 4Q,R). Ventral and rostral regions of the lateral entorhinal area (Fig. 4P–R) receive a significant number of fibers that occasionally branch, while dorsal (Fig. 4M–T) and caudal (Fig. 4S–T) regions receive only sparse fibers. The medial entorhinal area (Fig. 4Q–T) is, however, completely avoided, except for an occasional fiber-of-passage.

Few axons from the BMAa extend through medial parts of the longitudinal association bundle to reach the hippocampal formation. As with the BMAp, axons from the BMAa could be followed medially through the posteroventral part of the medial nucleus, lateral and medial parts of the posterior cortical nucleus, and posterior nucleus of the amygdala (Fig. 4M–P) to end in field CA1 and the ventral subiculum. Nevertheless, unlike inputs from the BMAp, the BMAa only very sparsely innervates the most caudal region of ventral field CA1 and the ventral subiculum. Scattered fibers were detected in the molecular and pyramidal layers of field CA1 (Fig. 4P–S) and the ventral subiculum (Fig. 4Q–T).

Stria terminalis. From the injection site, a large group of fibers extends dorsally and then caudally to enter the stria terminalis (Fig. 4M,N) and then caudal levels of the BST (Fig. 4G,H) where they provide a heavy input to the transverse nucleus, a light input to the interfascicular nucleus, and a sparse input to the ventral and principal nuclei. More rostrally (Fig. 4F), labeled fibers from the BMAa provide a dense plexus of terminals to the rhomboid nucleus, anterolateral area, and dorsal regions of the ventral and dorsolateral nuclei. Interestingly, the magnocellular nucleus of the BST, which is densely innervated by axons from the BMAp, receives only a light input from the BMAa. Within the anterior division of the BST (Fig. 4D,E), the BMAa provides a remarkable plexus of PHAL-labeled axons to the anterodorsal and anteroventral areas, as well as to the subcommissural zone and dorsomedial nucleus. The oval nucleus is very lightly innervated, while the anterolateral area and fusiform nucleus are almost free of anterograde labeling. Similar to what was described for the BMAp, two groups of fibers could be traced rostrally. Some of these fibers curve dorsally through the ventral and intermediate parts of the lateral septal nucleus, where they provide a very light input, and continue rostrally to innervate very lightly layers 2–3 (and even less layer 1) of the infralimbic area (not shown), and few axons were also noted in the posteroventral part of the anterior olfactory nucleus (not shown). Another group of fibers continues ventrally to innervate the nucleus accumbens. Dorsocaudal regions of the nucleus accumbens (Fig. 4C) receive a dense plexus of fibers, whereas ventrally only the most medial cells, bordering the substantia innominata, receive a moderate input (Fig. 4A,B).

Ansa peduncularis. Many fibers extend dorsally and medially from the injection site to enter the ansa peduncularis. As described for the BMAp such fibers extend through the substantia innominata (Fig. 4G–K) to the caudal pole of the BST, where one group of fibers merges with axons from the stria terminalis (Fig. 4G,H), and the other group continues rostrally, extending ventrally through the rostral substantia innominata (Fig. 4A–G). Numerous boutons-of-passage were detected in all parts of the substania innominata along the pathway, providing a moderate input.

As described for the BMAp, a group of fibers branches from the ansa peduncularis to innervate the fundus of the striatum. The BMAa provides a dense input to caudal regions of the fundus (Fig. 4A-G), whereas the BMAp provides a dense input to rostral regions of the fundus.

Descending projections

Labeled axons from the BMAa reach the thalamus, hypothalamus, and brainstem via the stria terminalis and ansa peduncularis.

Thalamus. As described for the BMAp, the thalamus appears to be innervated by fibers that arrive almost exclusively by way of the ansa peduncularis, traveling through the substantia innominata and dorsal regions of the lateral hypothalamic area (Fig. 4G–K). Very light anterograde labeling could be traced into the nucleus reuniens and medial part of the mediodorsal nucleus, and sparse fibers were also noted in the paraventricular, parataenial, parvicellular part of the subparafascicular, and central medial nuclei (Fig. 4G–O). A very few axons may reach the thalamus through the stria medullaris (Fig. 4H–I) as well.

Hypothalamus. Fibers descending to the hypothalamus traverse the ansa peduncularis and stria terminalis.

As described for the BMAp, two fiber bundles (pre- and post-commisural) descend from the stria terminalis. Unlike the BMAp, only a few axons could be traced through the precommisural bundle to innervate the cellular core of the hypothalamic ventromedial nucleus. Most of the fibers travel through the lateral and medial preoptic areas and some fibers were also detected in the median preoptic nucleus (Fig. 4D,E). Within more caudal regions of the medial preoptic area (Fig. 4G,H) labeled fibers display some branching, and generate a very light terminal field. Farther caudally, these fibers provide a sparse input to the anterior (Fig. 4H–J), preoptic (Fig. 4F,G), and intermediate (Fig. 4K–N) parts of the periventricular nucleus, as well as the medial preoptic nucleus (Fig. 4F–H) and subparaventricular zone of the hypothalamus (Fig. 4I–K). While sparse fibers could be seen throughout the hypothalamic ventrome-

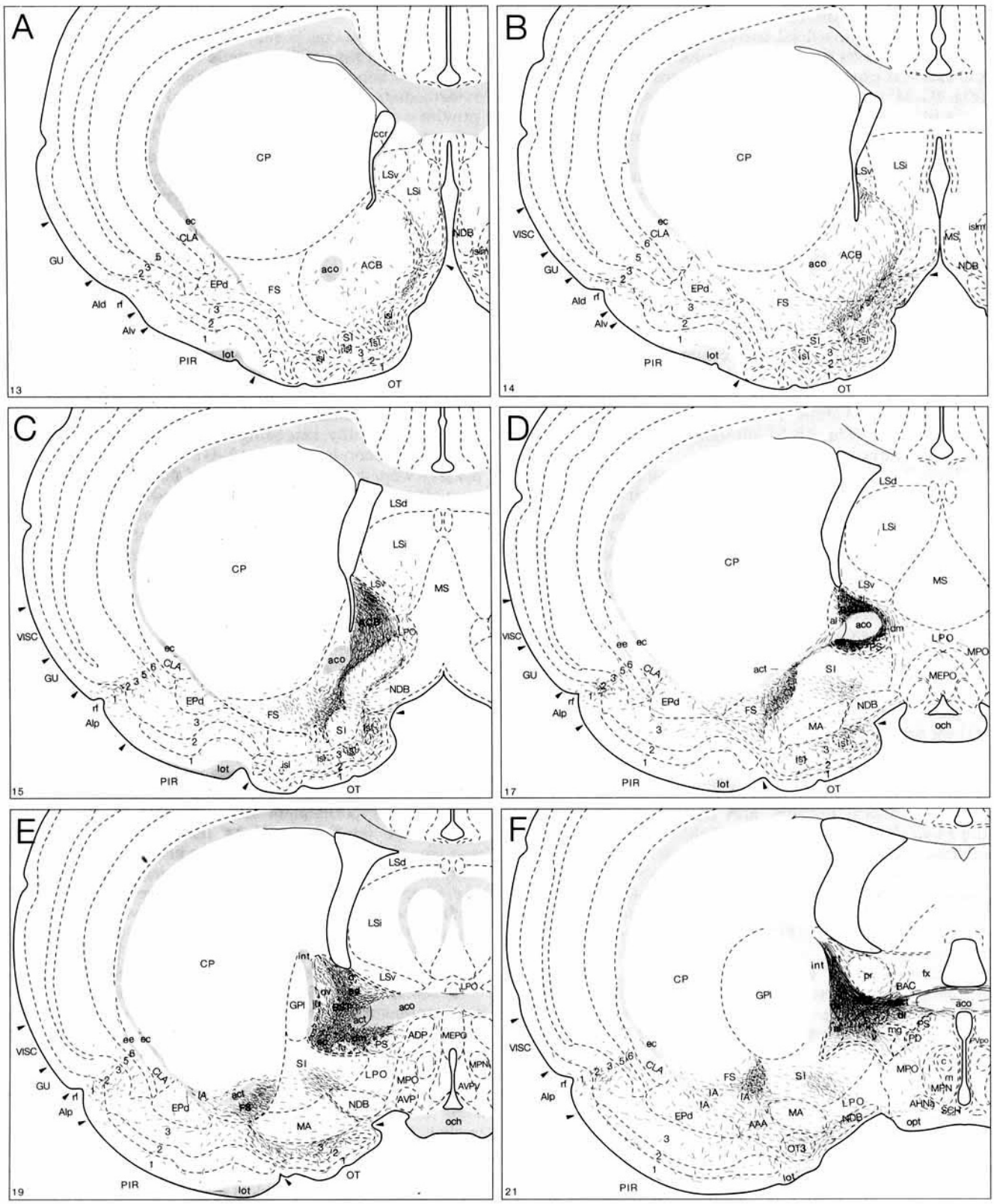
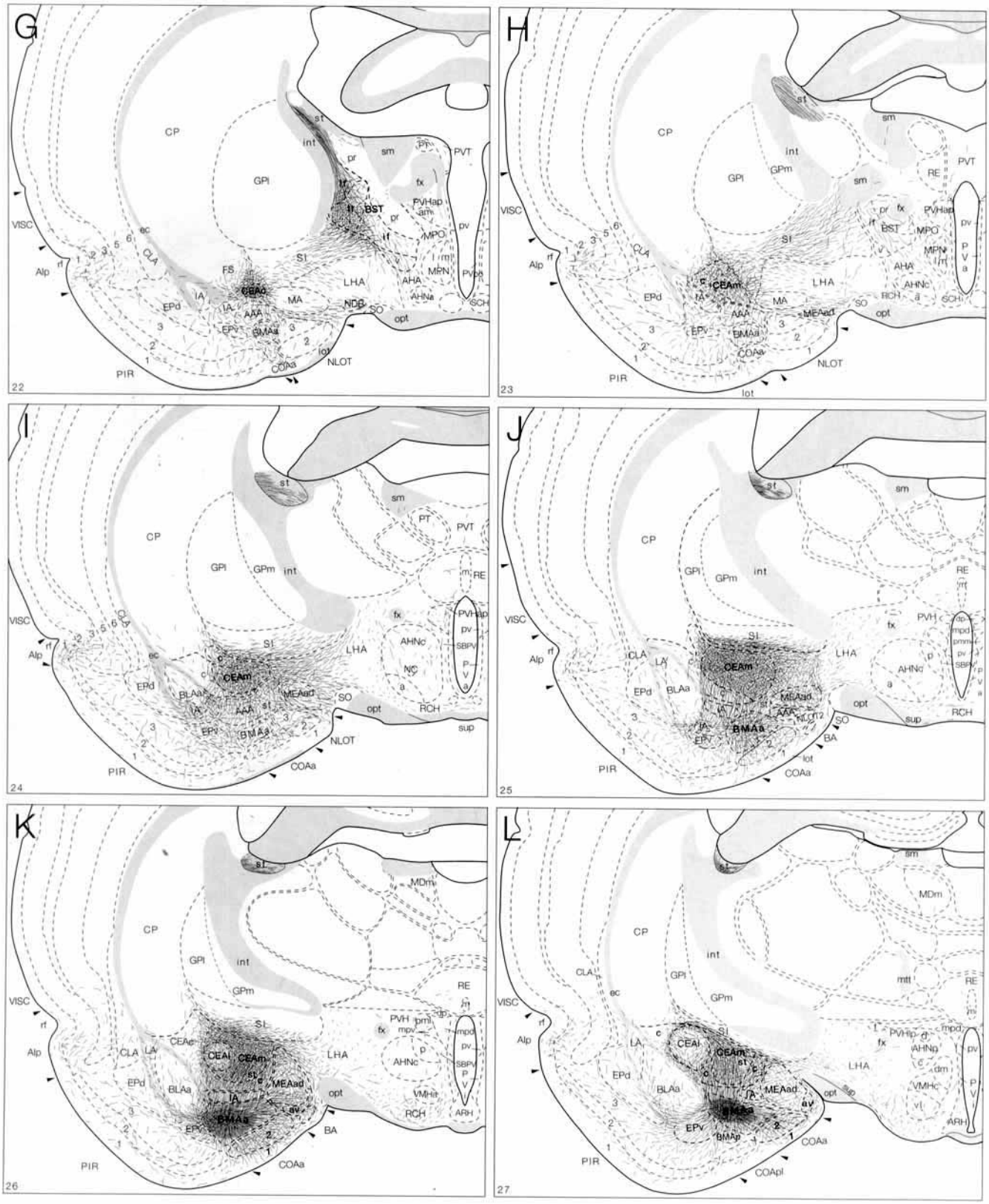


Fig. 4. **A-T:** The projections of the BMAa. The distribution of PHAL-labeled axons in experiment #60 was plotted onto a series of standard drawings of the rat brain, arranged from rostral (A) to caudal (T). The dark gray area in K and L indicates the injection site (see Figs. 1 and 2).



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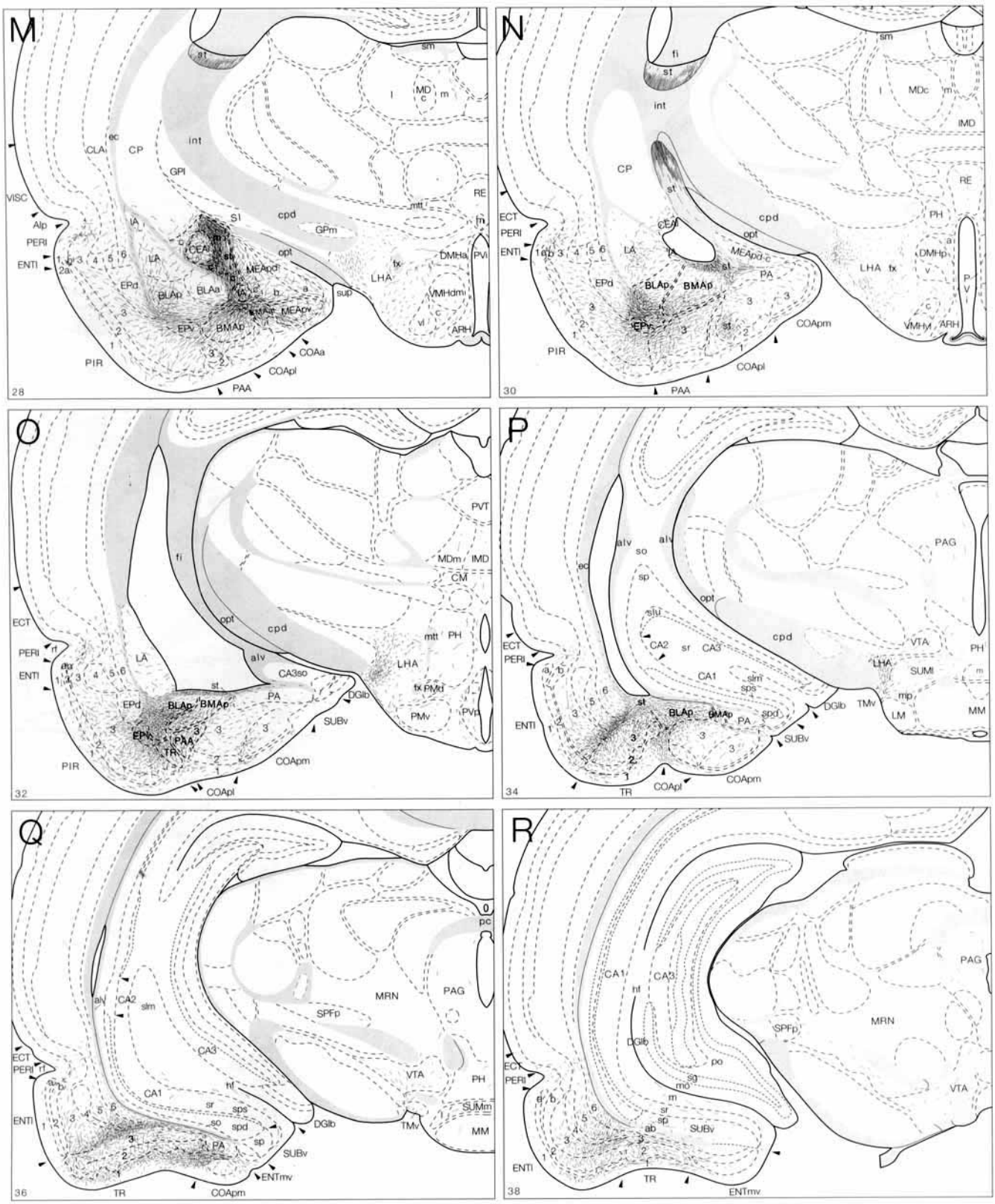

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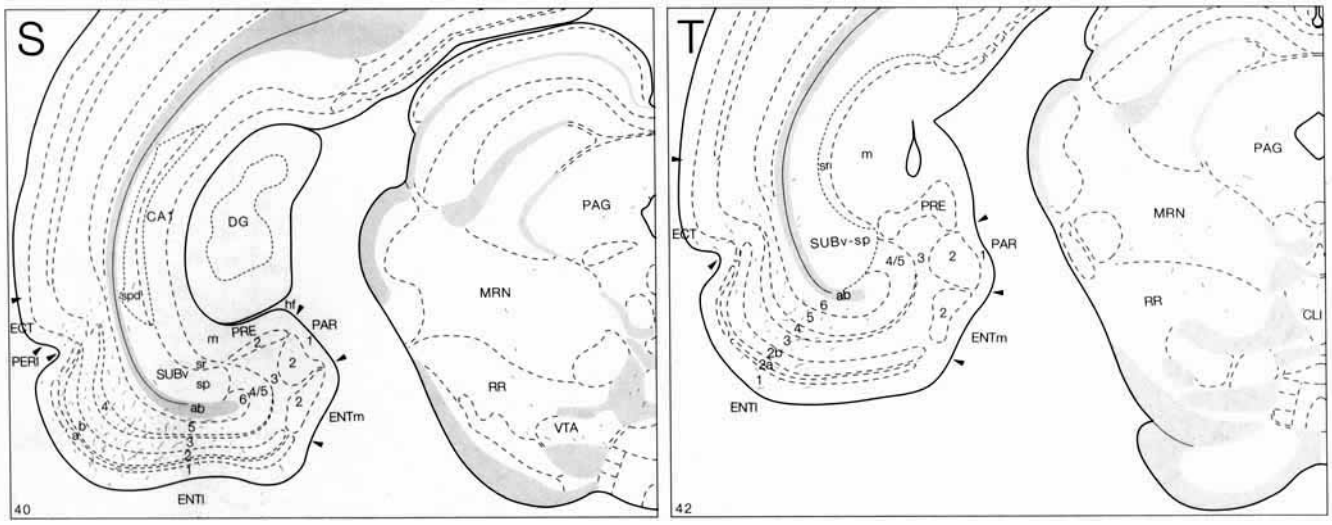

Figure 4 (Continued.)

dial nucleus (Fig. 4K–N), its ventrolateral part shows somewhat denser, although still very light, labeling.

The postcommissural bundle descends ventrally through the caudal pole of the BST. Fibers from a descending branch of the ansa peduncularis merge at this level and contribute to the hypothalamic innervation. Labeled axons extending caudally branch occasionally in the anterior hypothalamic area and central part of the anterior hypothalamic nucleus, providing a very light input (Fig. 4F–L). Sparse fibers could also be detected in the anterior and posterior parts of the anterior hypothalamic nucleus. Although sparse fibers occur in all parts of the paraventricular nucleus (Fig. 4G–L), only fibers in the anterior parvicellular part (Fig. 4G–I) display occasional terminal boutons, providing a very light input. The BMAa sends a moderate to dense input to the lateral hypothalamic area (Fig. 4G–K), a light input to the retrochiasmatic area (Fig. 4H–K) and tuberal nucleus (Fig. 4L–N), and a few sparse fibers to the dorsomedial (Fig. 4M,N) and arcuate (Fig. 4K–N) nuclei.

Unlike the BMAp, a significant number of axons from the BMAa descend to and through the caudal lateral hypothalamic area. These fibers travel through a very distinct caudolateral region of the lateral hypothalamic area (Fig. 4L–P), where they generate collaterals with boutons, thus providing a moderate to dense input. Within the caudal hypothalamus, these fibers innervate lightly the lateral supramammillary nucleus and sparsely the posterior nucleus, posterior periventricular nucleus, ventral and dorsal premammillary nuclei, and medial supramammillary nucleus (Fig. 4O–Q). In addition, a few axons extend caudally through the ventral tegmental area (Fig. 4P–S) and central linear nucleus of the raphe (Fig. 4T) to innervate sparsely rostral regions of the periaqueductal gray. A very few axons could be traced laterally through the mesencephalic reticular nucleus (Fig. 4S,T) to innervate sparsely the caudal periaqueductal gray, and scattered fibers were also detected in a medial and "waist" region of the parabrachial nucleus (not shown).

As with the BMAp, some axons from the BMAa cross the midline in the anterior commissure (Fig. 4E,F) and supraoptic commissures (Fig. 4J). On the contralateral side, the BMAa sends a moderate input to the BST, and lightly innervates the fundus of the striatum and nucleus accumbens. Sparse fibers were also observed in the agranular insular area, central amygdalar nucleus, and BMAa itself.

Analysis of control injections

A number of injections were placed in regions surrounding the BMA, including the anterior amygdaloid area, the basolateral and central amygdalar nuclei, and the endopiriform nucleus. Projections from the posterior, posterior cortical, and medial amygdalar nuclei have been previously described on the basis of PHAL experiments (Canteras et al., 1992). Projections from neighboring regions were compared with those from the BMA, for control purposes, and will not be analyzed here because the results were characteristically different. However, projections from the COA will be described in some detail because this cell group appears to be closely related to the BMAa, and as mentioned earlier the latter is sometimes included within the former.

Projections of the COAa

In eight experiments the PHAL injection labeled many neurons within the COAa, and of these, two injections were confined almost entirely to this nucleus. The projections in experiment number 73 will be described in detail because the injection site was confined almost entirely to the COAa (Fig. 2), and the projections were typical of other injections including the COAa.

Labeled axons from the COAa follow the same pathways described above for the BMA.

Intra-amygdalar projections

Before describing intra-amygdalar projections, it is important to note that many labeled fibers were observed in both layers of the COAa itself, extending rostral (Fig. 5B–F) and caudal to the injection site (Fig. 5F,G).

Within the amygdala, the COAa provides a heavy input to the anterior basomedial and medial nuclei. The central nucleus and anterior amygdaloid area receive a moderately dense input, whereas the medial and lateral parts of the posterior cortical nucleus and the piriform-amygdaloid area are lightly innervated by the COAa.

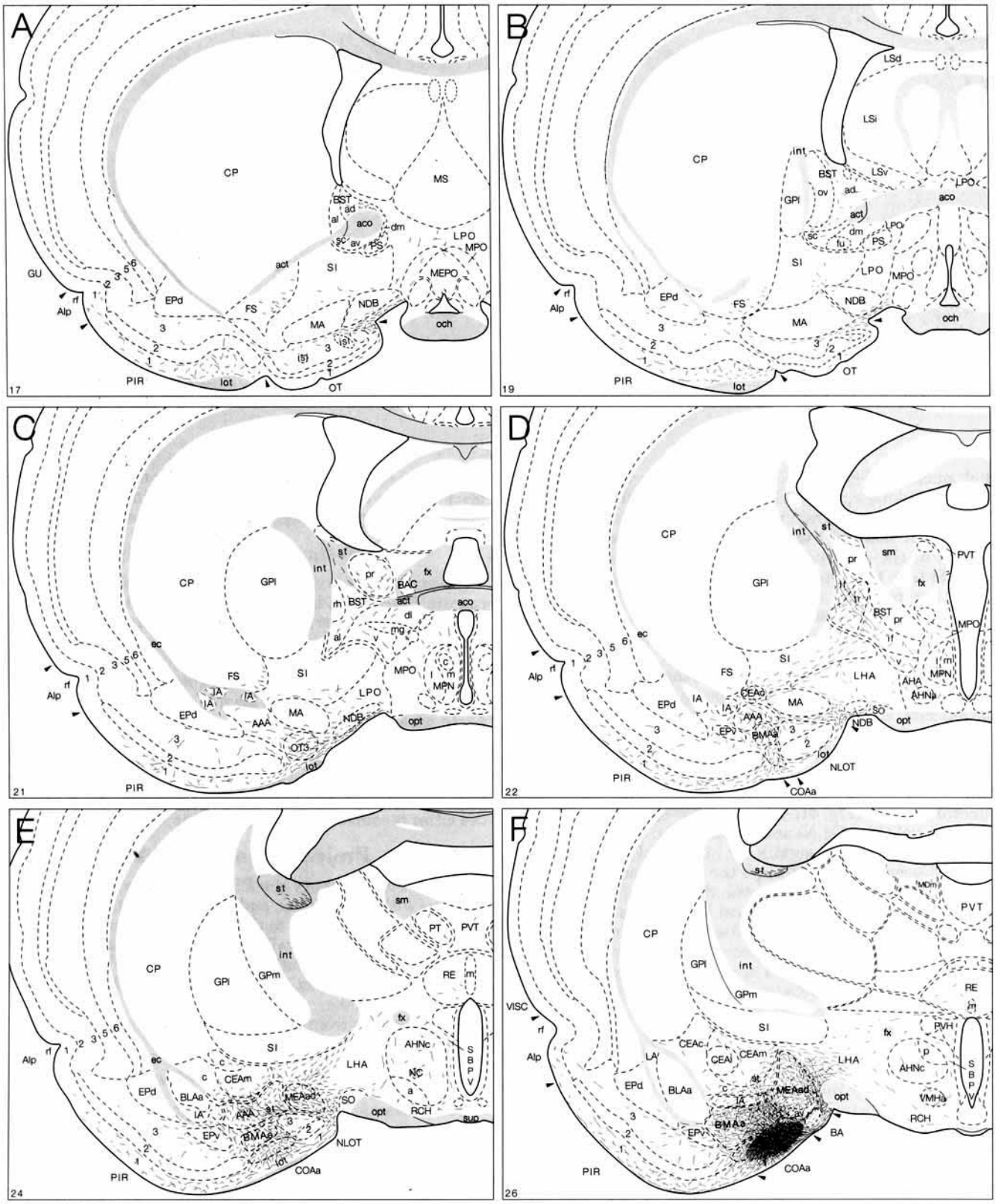

Fig. 5. **A-L:** The projections of the COAa. The distribution of PHAL-labeled axons in experiment number 73 was plotted onto a series of standard drawings of the rat brain, arranged from rostral (A) to caudal (L). The dark gray area in F indicates the injection site (see Figs. 1 and 2).

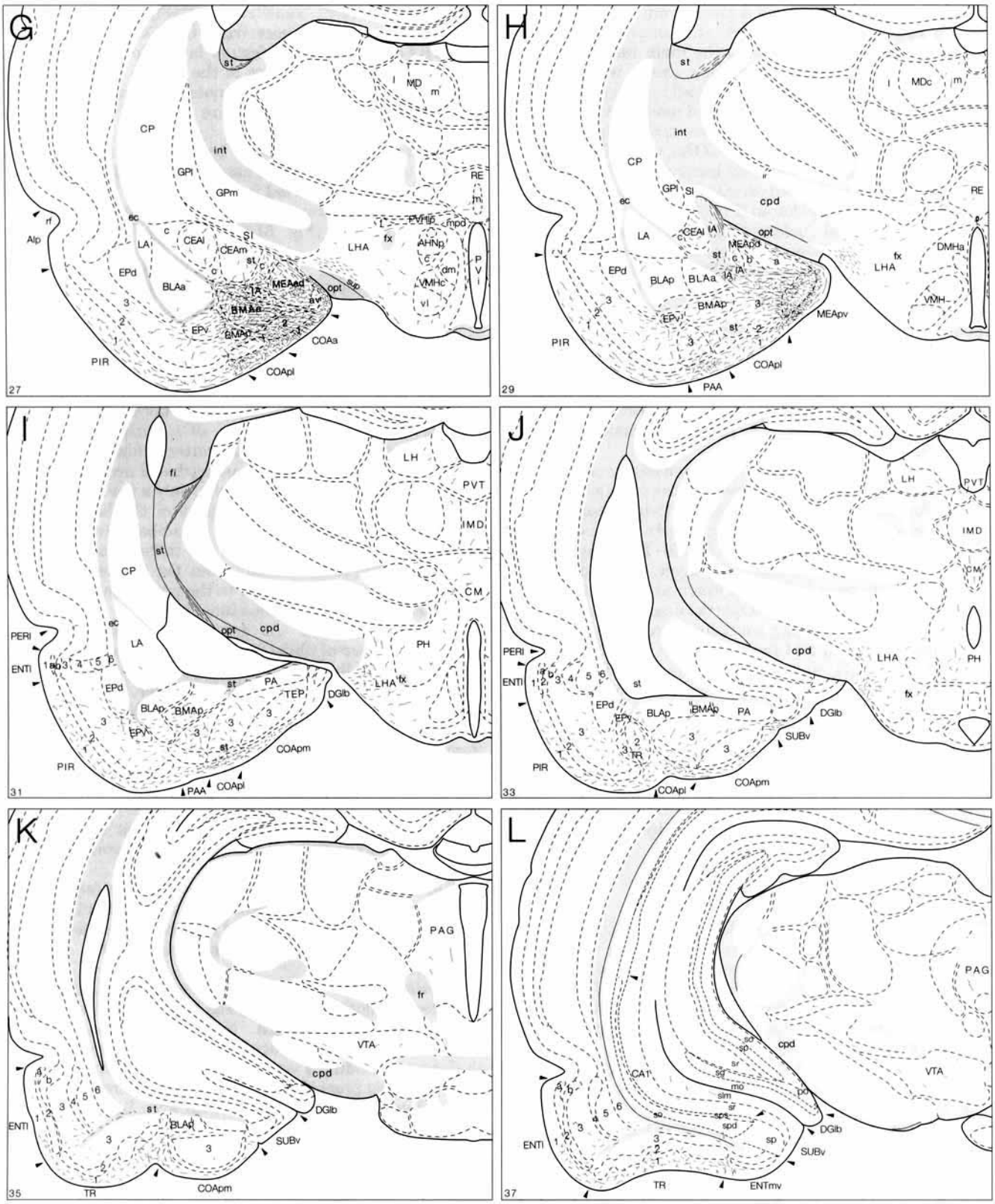

Figure 5 (Continued.)

Labeled fibers also extend dorsally from the COAa to end in the BMAa, central nucleus, and anterior amygdaloid area. The BMAa appears to be the main target for axons from the COAa. Thus, numerous axons with terminal boutons could be traced throughout all regions of the BMAa (Fig. 5D–G). Ventral (Fig. 5F,G) and most rostral (Fig. 5D) regions of the capsular part of the central nucleus receive a moderate to light input from the COAa, while the rest of the central nucleus is only sparsely innervated (Fig. 5D–H). A number of fibers continue rostrally to innervate moderately the anterior amygdaloid area (Fig. 5C–E).

Within the medial nucleus, COAa projections end densely in the cellular and molecular layers of the anterodorsal (Fig. 5E–G) and posteroventral (Fig. 5H) parts. The cellular part of the anteroventral medial nucleus (Fig. 5F,G) appears to be avoided by projections from the COAa, whereas its molecular layer receives a dense input. Both the molecular and cellular layers of the posterodorsal part (Fig. 5H) receive a light input. Interestingly, although a number of fibers from the COAa run through the molecular layer of the bed nucleus of the accessory tract to provide a terminal field in surrounding areas, the bed nucleus itself appears to be avoided (Fig. 5F).

Labeled axons from the COAa densely innervate the molecular layer, and lightly innervate the neuronal layer, of the piriform-amygdaloid area (Fig. 5H,I) and lateral part of the posterior cortical nucleus (Fig. 5G–J). The medial part of the posterior cortical nucleus (Fig. 5I–K) receives a very light input, mainly to its molecular layer. It is important to note that fibers from the COAa innervate the entire depth of the molecular layer (both superficial and deep parts).

Labeled fibers extending caudally from the injection site occasionally branch, and provide a very light input to the BMAp (Fig. 5H,I), and a sparse input to the posterior basolateral nucleus (Fig. 5H–K). Apparent fibers-of-passage were traced through the molecular layer of the nucleus of the lateral olfactory tract (Fig. 5D,E), where some fibers with occasional branching were seen in layer 3.

Finally, an occasional fiber-of-passage could be traced through the intercalated nuclei (Fig. 5C–G), and the lateral (Fig. 5F–I) and anterior basolateral (Fig. 5E–H) nuclei seem to be almost completely avoided by axons from the COAa.

Ascending projections

Longitudinal association bundle. Anterogradely-labeled fibers from the COAa course through the lateral branch of the longitudinal association bundle to end in the piriform area, olfactory tubercle, and nucleus of the diagonal band rostrally, and the post-piriform transition and entorhinal areas caudally. The molecular layer of the piriform area (Fig. 5A–J) receives a moderate input, and layer 3 receives a very light input. Some fibers in this pathway extend ventrally to innervate sparsely layers 1 and 3 of the olfactory tubercle (Fig. 5A–C). Interestingly, a distinct group of fibers traveling rostroventrally near the ventromedial surface of the brain generate many boutons in the molecular layer of the nucleus of the diagonal band (Fig. 5A–D), just superficial to neuronal cell bodies.

Unlike the BMAp and BMAa, axons from the COAa do not seem to innervate cortical areas dorsal to the piriform area, except for very sparse fibers in the molecular layer of the posterior agranular insular (Fig. 5A,F) and perirhinal (Fig. 5H,I) areas.

The postpiriform transition area (Fig. 5K,L) receives a moderate plexus of fibers from the COAa, with a vast majority ending in the molecular layer. Sparse fibers could be traced through all layers of the lateral entorhinal area (Fig. 5K,L). It is important to note that the COAa, unlike the BMAa, innervates the entire depth of the molecular layer in olfactory cortical areas.

Although no axons could be traced through medial regions of the longitudinal association bundle, a few scattered fibers were detected in the molecular layer (stratum lacunosum-moleculare and stratum radiatum) of the caudoventral field CA1 (Fig. 5L) and ventral subiculum (not shown).

Stria terminalis. A significant number of fibers from the COAa extend through the stria terminalis (Fig. 5C-I) to reach the BST. In the posterior division of the BST the transverse nucleus receives a moderately dense plexus of fibers, and the interfascicular nucleus is lightly innervated (Fig. 5D). Very few axons could be traced into the principal nucleus (Fig. 5C,D), and occasional scattered fibers were seen in the anterolateral area, and the dorsolateral, magnocellular, and ventral nuclei (Fig. 5C). Within the anterior division of the BST, occasional scattered fibers were noted in the subcommissural zone, anterodorsal area, and dorsomedial nucleus (Fig. 5A,B). Finally, only a few sparse fibers could be traced to the ventral part of the lateral septal nucleus (Fig. 5B) and nucleus accumbens (not shown), whereas layers 1, 2, and 3 of the infralimbic area (not shown) receive a light input from the COAa and a few smooth fibers were also noted in the posteroventral part of the anterior olfactory nucleus (not shown).

Ansa peduncularis. As described for the BMAp and BMAa, one group of fibers from the ansa peduncularis joins axons arriving by way of the stria terminalis, near the caudal pole of the BST (Fig. 5D). The other, smaller, bundle continues rostrally through the rostral substantia innominata (Fig. 5A–D), where they provide a light although clear input by way of boutons-of-passage.

Descending projections

The COAa sends descending projections through the stria terminalis and ansa peduncularis along routes already described for the BMAp and BMAa.

Thalamus. The COAa provides a very light input to the nucleus reuniens, medial part of the mediodorsal nucleus, and central medial nucleus, and an even more sparse input to the parataenial and paraventricular nuclei, and the lateral habenula.

Hypothalamus. The COAa appears mainly to innervate the lateral hypothalamic area (Fig. 5D–J), where it provides a moderately dense input. Nevertheless, some PHAL-labeled fibers could be traced throughout the entire hypothalamus, including a very light input to the anterior (Fig. 5D–F), medial preoptic (Fig. 5C,D), and ventromedial (Fig. 5F–H) hypothalamic nuclei; and an even lighter input to the lateral (Fig. 5A,B) and medial (Fig. 5A–C) preoptic, anterior hypothalamic (Fig. 5D), and retrochiasmatic (Fig. 5E,F) areas.

Interestingly, some axons from the COAa descend through the caudal hypothalamus to provide a moderate input to a distinct far lateral and caudal region of the lateral hypothalamic area (Fig. 5G–J), and a sparse input to the posterior hypothalamic nucleus (Fig. 5I–J). A very few axons continue farther caudally through the ventral tegmental area

to reach the periaqueductal gray (Fig. 5K–L), where they provide a rather sparse input.

Finally, only very few sparse fibers were observed to cross the midline through the anterior commissure from the COAa (Fig. 5C). On the contralateral side, sparse labeled fibers were observed in the caudal BST, thalamic nucleus reuniens, and lateral hypothalamic area.

DISCUSSION

The main conclusion to be drawn from the experimental results presented here is that the two cell groups previously recognized on cytoarchitectonic grounds in the BMA (the BMAa and BMAp) differ significantly in both the topography and extent of their axonal projections, and also differ from the adjacent COAa.

Projections from the BMA

In general, the BMAa and BMAp give rise to different sets of projections although their axons appear to follow the same general pathways. Ascending fibers take three basic routes—the longitudinal association bundle, stria terminalis, and ansa peduncularis—to reach various telencephalic regions, and descending fibers travel through the stria terminalis and ansa peduncularis to reach the thalamus, hypothalamus, and brainstem (for summary, see Fig. 7).

Intra-amygdalar projections

Both the BMAa and BMAp innervate other amygdalar nuclei. The BMAa most heavily projects to the central, medial, and cortical nuclei, whereas the BMAp sends much more restricted projections to the lateral nucleus and to parts of the central and medial nuclei.

Based on the results of HRP retrograde transport experiments in the rat, Ottersen (1982) suggested a projection from the basomedial nucleus (corresponding to our BMAp) to the central nucleus. We demonstrated an extraordinarily heavy input from the BMAa to almost all parts of the central nucleus, whereas in contrast the BMAp specifically innervates only restricted quite ventral and caudodorsal regions of the central nucleus (see Fig. 7). The central nucleus is a complex cell group that contains at least three (medial, lateral, and capsular) morphologically, immunohistochemically, and hodologicallly distinct parts (McDonald, 1982; Cassell et al., 1986). Although the exact contribution of these different parts to the overall function of the central nucleus is not presently clear, the striking difference in innervation patterns from the BMAa and BMAp implies that they differentially influence central nucleus function.

In their classic study of amygdalar efferents, Krettek and Price (1978b) described autoradiographically a projection from the basomedial nucleus (corresponding to our BMAp) to the medial nucleus in the cat. Previous retrograde tracer studies in the rat also suggested a projection from the posterior part of the BMAp to the anterodorsal part of the medial nucleus (Ottersen, 1982). Here, PHAL-labeled axons from the BMAp were found mainly in the anterodorsal and posteroventral parts of the medial nucleus, while axons from the BMAa innervate all parts of the medial nucleus, but especially the anteroventral part. Unlike the BMAp, the BMAa sends fibers to the molecular layer of the medial nucleus, and innervates the adjacent bed nucleus of the accessory olfactory tract.

The COAa and BMAa are linked by very dense bidirectional connections, whereas the COAa receives only scattered fibers from the BMAp. The lateral amygdalar nucleus, which provides an especially dense input to the BMAp (Krettek and Price, 1978b; Aggleton, 1985; Smith and Pare, 1994; Pitkanen et al., 1995), also receives a dense input from the BMAp. The dorsolateral part of the lateral nucleus is thought to receive input from early sensory association areas (Mascagni et al., 1993; Romanski and LeDoux, 1993) and its neurons respond to sensory stimuli with short latencies (Bordi and LeDoux, 1992), while the ventromedial part receives inputs from higher order association areas and no responses to sensory stimuli have yet been identified. Interestingly, the BMAp receives input from both parts of the lateral nucleus (Pitkanen et al., 1995), but in return only innervates its ventromedial region. The BMAa also sends fibers to caudoventral regions of the lateral nucleus.

Both the BMAa and BMAp project to the anterior amygdaloid area, to different parts of the lateral and medial posterior cortical nucleus, to the posterior basolateral nucleus, and to the piriform-amygdaloid area. Finally, the BMAp sends a few axons to the BMAa, which in turn sends an even lighter input to caudal regions of the BMAp.

Interestingly, a projection from the BMA (corresponding to our BMAp) to the amygdalo-hippocampal area (corresponding to our posterior nucleus) was suggested in the cat by Krettek and Price (1978b). However, we did not observe such a projection in any of our experiments, confirming a recent retrograde tracer study (Canteras et al., 1992). Nevertheless, some labeled fibers do travel through the posterior nucleus to reach the hippocampal formation. While these fibers do not branch and appear not to generate boutons (and are thus presumably fibers-of-passage), they could explain the autoradiographic labeling reported by Krettek and Price. Species differences are also possible.

Pare et al. (1995) reported PHAL-labeled intra-amygdalar projections from the cat basomedial nucleus (corresponding to the rat BMAp) to the lateral nucleus, parts of the central nucleus, periamygdalar areas, and nucleus of the lateral olfactory tract, similar to our results. However, they also found projections to the COAa but not to the medial nucleus. In the rat, both the BMAa and BMAp project to the medial nucleus, whereas only the BMAa projects heavily to the COAa.

Ascending projections

Longitudinal association bundle. Fibers from the BMA ascend to the cerebral cortex mainly through the longitudinal association bundle and stria terminalis (for the infralimbic and prelimbic areas) (see Results for details).

The BMAa innervates the agranular insular area and olfactory areas including the olfactory tubercle, piriform, postpiriform transition, and entorhinal areas. More widespread cortical projections originate in the BMAp, which sends fibers to all regions innervated by the BMAa, and to the perirhinal, ectorhinal, infralimbic, and prelimbic areas, and hippocampal formation.

Innervation of the agranular insular area by the BMA has been observed with retrograde tracer methods (McDonald and Jackson, 1987). Our results suggest that the BMAa projects mainly to superficial layers, while the BMAp projects to deep (mainly 5) layers of the agranular insular area.

A projection to the olfactory tubercle has been shown on the basis of anterograde (Krettek and Price 1978a) and retrograde (Haberly and Price, 1978; McDonald, 1991b)

tracer studies in the rat, cat, and monkey (Aggleton et al., 1987). Our results demonstrate that all three layers of the olfactory tubercle receive a light input from the BMA. Axons from the BMAp tend to be more concentrated in medial and caudal regions, while axons from the BMAa are concentrated caudally in layer 3 of the olfactory tubercle. Furthermore, the BMAp, but not the BMAa, sends a light input to the anterior olfactory nucleus.

The piriform area is traversed by fibers en route to other cortical areas, although some of them display branches with terminal boutons. After injections into the BMAp, PHAL-labeled fibers seem to innervate lightly only ventral regions of the piriform area, whereas the BMAa sends a light input to the entire piriform area, although it is somewhat more dense caudally.

The heaviest cortical projection field of the BMAa was found in the postpiriform transition area, especially in the deep half of the molecular layer (Fig. 6G). This area (area TR) lies between the piriform area rostrally and the entorhinal area caudally, and was originally defined by Haug (1976). Like the piriform and entorhinal areas, it receives a direct input from the main olfactory bulb (Kosel et. al., 1981), and it substantially projects to the BMAa (our unpublished observations using PHAL). The BMAp also projects lightly to all three layers of the postpiriform transition area.

The heaviest cortical projections from the BMAp are to the perirhinal and ectorhinal areas (Fig. 6H), which have been described for the rat (McDonald and Jackson, 1987), cat (Room and Groenewegen, 1986), and monkey (Saunders and Rosene, 1988).

Within the rat hippocampal formation, the BMAp projects significantly to the ventral subiculum, ventral field CA1, and parasubiculum (Fig. 6H); in contrast, axons from the BMAa only sparsely innervate the ventral subiculum and ventral field CA1. The monkey accessory basal nucleus reportedly innervates fields CA1, CA2, and CA3, and the adjacent subiculum (Aggleton, 1986; Saunders et al., 1988), and the medial basal nucleus (homologues with the parvicellular part of the basal nucleus, Amaral et al., 1992) was found by Saunders et al. (1988) to project only to the subiculum, although Aggleton (1986) also noted projections to fields CA1-3. Previous evidence suggested that the BMAp in the rat corresponds to the accessory basal (Price, 1981; Price et al., 1987) and parvicellular basal (Canteras and Swanson, 1992) nuclei of the monkey. As in the rat BMAp, the accessory basal nucleus in monkey receives a heavy input from the lateral amygdalar nucleus, and projects to the hypothalamic ventromedial nucleus and perirhinal area (see Price et al., 1987). On the other hand, monkey parvicellular basal nucleus connections with the hippocampal formation are similar to those of the BMAp (Canteras and Swanson, 1992). More work is needed to clarify which part(s) of the monkey amygdala is homologous to the rat BMAp, and because the basolateral nuclear group (including lateral, basolateral, and basomedial nuclei) is significantly more differentiated in primates (Crosby and Humphrey, 1941), it is possible that the rat BMAp corresponds to more than one nuclear group in the monkey.

Projections from the BMAp to the parasubiculum (to the deep part of layer 1 and to layer 2) observed here are strikingly similar to a projection from the basolateral nucleus reported by Krettek and Price in the rat and cat (1977b). However, their injection sites may have spread to include some neurons in the BMAp because we found few labeled axons in the parasubiculum after PHAL injections in the basolateral nucleus (unpublished observations). Our results also indicate that both the BMAa and BMAp project selectively to the lateral rather than medial part of the entorhinal area, and that the BMAa sends fibers rostroventrally, whereas the BMAp sends many fibers to deep layers caudally. Krettek and Price (1977a) did not report cortical projections from the BMA in the rat or cat. However, more recent work in the cat (Room and Groenewegen, 1986) and monkey (Insausti et al., 1987; Saunders and Rosene 1988) also suggest projections to the entorhinal area.

Finally, some axons from the BMAp provide a moderate input to the infralimbic and prelimbic areas, whereas the BMAa only sparsely innervates these areas. Projections from the BMA to prefrontal cortical areas have been previously detected in the rat (McDonald, 1991a) and monkey (Barbas and De Olmos, 1990).

In summary, the cerebral cortex appears to be the major target of ascending projections from the BMA. The BMAa innervates primarily olfactory and agranular insular areas, while the BMAp also sends fibers to the infralimbic, prelimbic, perirhinal, and ectorhinal areas, and to the hippocampal formation.

Stria terminalis and ansa peduncularis. Fibers traveling through the stria terminalis generate major terminal fields in the septal region and striatum, and lighter inputs to the medial prefrontal region and anterior olfactory nucleus.

Within the septum, the BST is the region most heavily innervated by axons from the BMA. In addition, the BMAp projects to the ventral, while the BMAa projects to the intermediate, part of the lateral septal nucleus. Krettek and Price (1978a) observed a projection from the basomedial nucleus to the "central zone" of the BST, and retrograde labeling was observed in the BMA after HRP injections in the BST (Weller and Smith, 1981). Recently, a number of cyto- (Ju and Swanson, 1989; Moga et al., 1989) and chemo-architectonic (Ju et al., 1989; Moga et al., 1989) divisions of the BST have been recognized. Our study reveals an extensive, topographically organized projection to the BST from the BMAa and BMAp (Fig. 6C,D). The anterior division of the BST, including the anterodorsal, anteroventral, subcommisural, and dorsomedial nuclei, and the posterior division of the BST including the transitional, intrafasicular, and ventral nuclei, receive massive inputs from both the BMAa and BMAp. In addition, the BMAp sends a dense input specifically to the magnocellular nucleus, whereas the BMAa projects lightly to the magnocellular, rhomboid, and oval nuclei.

The BMA also innervates the ventral striatum, including the nucleus accumbens, striatal fundus, and a specific region of the caudoputamen. The most striking projection within the striatum is to the nucleus accumbens via axons from the BMAp (Fig. 6B). Although these projections have been demonstrated previously in the rat, cat, and monkey (Krettek and Price, 1978a; Kelley et al., 1982; Russchen and Price, 1984; Russchen et al., 1985; McDonald, 1991a,b), it was generally concluded that the BMA sends only a light projection to the nucleus accumbens. Recently, Johnson et al. (1995) showed, in agreement with our results, extensive labeling in the rat nucleus accumbens after a biocytin injection centered in the BMA. Our results suggest that the BMAp specifically innervates the caudomedial nucleus accumbens, whereas the BMAa sends fibers to the most dorsocaudal (septal) nucleus accumbens, and to the most

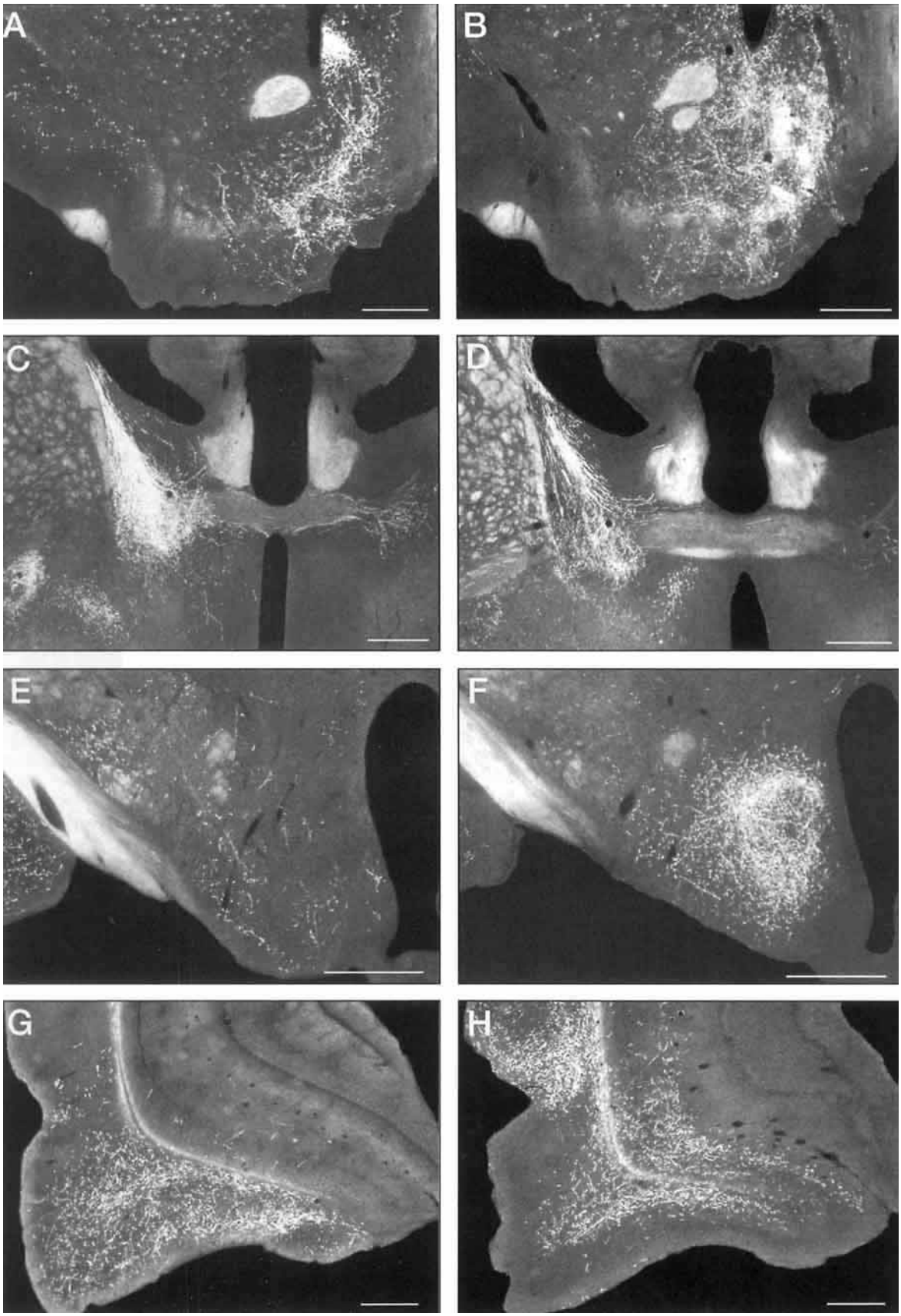

Fig. 6. Darkfield photomicrographs showing the distribution of PHAL-labeled axons in the nucleus accumbens (**A,B**), BST (**C,D**), hypothalamus (**E,F**), postpiriform transition area (**G**), and perirhinal and ectorhinal areas (**H**) after injections centered in the BMAa (A,C,E, and G) and BMAp (B,D,F, and H). All scale bars = 500 μm. For identification of major structures in B, D, F, and H see approximately corresponding levels in Figure 3C,F,M, and S; and for A, C, E, and G see Figure 4B,F,M, and Q, respectively.

medial edge of the nucleus accumbens bordering the rostral substantia innominata (Fig. 6A). This general topography was also suggested by fluorogold injections in the "medial shell" and "septal pole" of the nucleus accumbens that retrogradely labeled cells in the BMAp and BMAa, respectively (Brog et al., 1993).

At least some projections to the nucleus accumbens from the BMA are thought on anatomical (Fuller et al., 1987) and electrophysiological (Yim and Mogenson, 1982 in the rat; DeFrance et al., 1980 in the rabbit) grounds to be excitatory. Furthermore, recent anatomical evidence (Johnson et al., 1995) demonstrates that at least some axons from the BMAp converge with dopaminergic inputs on individual neurons in the nucleus accumbens. Excitatory responses in nucleus accumbens neurons (produced by BMA stimulation) were significantly attenuated by dopamine, either applied iontophoreticaly, or released by stimulation of the ventral tegmental area (Yim and Mogenson, 1982). Electrophysiological work in the rat (Callaway et al., 1991) and rabbit (DeFrance et al., 1980) also suggests that amygdalar inputs (presumably including projections from the BMAp) converge with hippocampal inputs on projection neurons in the nucleus accumbens. Thus, the BMAp, together with at least dopaminergic and hippocampus inputs, may influence locomotor behavior mediated by the nucleus accumbens.

The striatal fundus receives a major input from the BMA. Although labeled axons from the BMA were detected throughout most of the fundus, its rostral pole appears to receive a denser input from the BMAp, whereas more caudal regions are preferentially innervated by the BMAa. Anterograde tracer studies in the rat, cat, and monkey (Krettek and Price, 1978a; Aggleton et al., 1987), and retrograde tracer studies in the rat (McDonald, 1991a,b), have previously demonstrated these projections. Anatomical results suggest that at least a part of these projections are excitatory (Fuller et al., 1987).

The BMAp, but not the BMAa, clearly innervates the caudoputamen. In agreement with the topography of amygdalar projections suggested by Kelley et al. (1982), the BMAp sends fibers specifically to the most medial and caudoventral region (bordering the amygdala), and avoids dorsolateral parts of the caudoputamen, which receive inputs from sensorimotor cortical areas. Earlier retrograde (Kelly et al., 1982) and anterograde (Russchen and Price, 1984) tracer studies suggested this projection pattern, although observed projections were considerably lighter than those noted here.

Axons from the BMAa and BMAp ascend through the ansa peduncularis to innervate the substantia innominata, as observed earlier with both anterograde (Krettek and Price, 1978a; Grove, 1988) and retrograde (Fuller et al., 1987; Grove, 1988) tracer methods. Importantly, some PHAL-labeled axons in the ansa peduncularis join those arriving through the stria terminalis at caudal levels of the BST, and most likely contribute to the innervation of endbrain targets. Lehman and Winans (1983) found that stria terminalis interruption with electrolytic lesions or knife cuts decreases but does not eliminate retrograde labeling of cells in the amygdala after HRP injections in the BST in the golden hamster, suggesting a "ventral nonstrial pathway" (presumably corresponding to the rostral ansa peduncularis pathway labeled here).

In summary, projections from both the BMAa and BMAp ascend to the septum and striatum, mainly through the stria terminalis, and to the substantia innominata, by way of the ansa peduncularis. The BMAa innervates the BST, striatal fundus, and limited regions of the nucleus accumbens. The BMAp also projects to the BST, striatal fundus, and substantia innominata, but also sends a major input to the nucleus accumbens and caudoputamen. Finally, our results strongly imply that in addition to known projections from the basolateral amygdalar nucleus, projections from the BMA (and especially from the BMAp) contribute greatly to amygdalostriatal projections.

Descending projections

Axons from the BMA descend mainly to the hypothalamus, with a much lighter input to the thalamus.

Thalamus. The BMA sends a weak input to the thalamus. The medial part of the mediodorsal nucleus receives a very light input from both parts of the BMA, as reported earlier (McDonald, 1987). The nucleus reuniens and paraventricular nucleus are also very lightly innervated by the BMAa and BMAp, respectively. The thalamic paraventricular nucleus projects back to the BMAp (Moga et al., 1995).

Hypothalamus. Axons from the BMAp and BMAa provide topographically organized inputs to the hypothalamus. The heaviest projection from the BMAp ends in the cellular core of the hypothalamic ventromedial nucleus (Fig. 6F), whereas the BMAa most heavily innervates the lateral hypothalamic area (Fig. 6E), confirming in general previous anterograde (Krettek and Price, 1978a) and retrograde (Berk and Finkelstein, 1981) tracer studies. Electrophysiological evidence suggests that stimulation of the "basolateral amygdalar nucleus," corresponding at least in part to our BMAp, produces responses (excitatory, inhibitory, and disinhibitory) in the hypothalamic ventromedial nucleus (Ono and Oomura, 1975). In contrast, the BMAa sends a light input to the ventrolateral ventromedial nucleus, innervating instead the ventral capsular region of the nucleus, and the adjacent tuberal nucleus. After selective injections of HRP into different parts of the ventromedial nucleus, Luiten et al. (1983) suggested that the most medial part of the "basolateral nucleus" (containing at least a part of our BMAp) projects to all parts of the ventromedial nucleus, while the BMAa only projects to restricted parts of it.

The BMAa projects substantially to the lateral hypothalamic area, specifically to a far lateral, caudal part, and injections of HRP into this region retrogradely label neurons in the BMAa (Ono et al., 1985).

The BMAp also lightly innervates the anterior hypothalamic nucleus and retrochiasmatic and lateral hypothalamic areas. In contrast, the BMAa sends a light input to the anterior hypothalamic and medial preoptic nuclei, and to the medial preoptic and retrochiasmatic areas. Furthermore, within the caudal hypothalamus, the posterior and supramammillary nuclei are lightly innervated by both the BMAa and BMAp; and some fibers were also noted in the capsule of the medial mammillary nucleus and premammillary nuclei from the BMAp and the BMAa, respectively.

Only a few axons from the BMAa could be followed to the periaqueductal gray and parabrachial nucleus.

Krettek and Price (1978a) described a projection to the ventral premammillary nucleus from the basomedial nucleus (corresponding to our BMAp). Here, only the BMAa was observed to send a few sparse axons to the ventral premammillary nucleus. Because the posterior amygdalar nucleus and lateral posterior cortical nucleus (just medial and ventral to the BMAp, respectively) send heavy inputs to the

ventral premammillary nucleus, injection sites analyzed by Krettek and Price may have spread slightly to include these regions.

Projections from the COAa

Injections of the COAa yielded a unique projection pattern that is considerably more restricted than that generated by the adjacent BMAa (Fig. 7). The COAa mainly generates ascending fibers to the amygdala and olfactory cortical areas, and descending fibers to the thalamus and hypothalamus. Its overall projection pattern is distinct from that of the BMAa, although part of its projection field is similar, and the two cell groups are massively interconnected.

Intra-amygdalar projections

Within the amygdala, the COAa innervates the corticomedial group and adjacent ventral regions of the central nucleus, but completely avoids the basolateral group (including the basolateral and lateral nuclei). Luskin and Price (1983a) described a moderate projection to the lateral nucleus from the COAa, although their injection sites undoubtedly included neurons in the BMAa, which they included in the COAa. Within the corticomedial group, the COAa projects to all groups related to the main and accessory olfactory systems, and to the BMAa; the latter appears to be the densest projection from the COAa.

The COAa receives a direct input from the main olfactory bulb, in mammals (Powell et al., 1965; Price, 1973; Broadwell, 1975; Scalia and Winans, 1975), and sends a projection to amygdalar nuclei receiving direct (the piriform-amygdaloid area and lateral part of the posterior cortical nucleus: Price, 1973; Scalia and Winans, 1975) and indirect (the anterior amygdaloid area: Luskin and Price, 1983a) olfactory inputs. However, the nucleus of the lateral olfactory tract is only sparsely innervated by the COAa.

The COAa also sends a major input to the "accessory olfactory amygdala." Projections to the medial amygdalar nucleus have been reported in the rat (Ottersen, 1982) and golden hamster (Kevetter and Winans, 1981), and our results confirm their existence. We also showed that the COAa innervates the medial posterior cortical nucleus, which, like the medial nucleus, receives a direct input from the accessory olfactory bulb (Scalia and Winans, 1975). Thus, the main and vomeronasal olfactory systems converge at early stages of information processing.

To summarize, the COAa, unlike the BMAa, specifically innervates the corticomedial group, and a restricted part of the central nucleus, within the amygdala.

Ascending projections

Ascending PHAL-labeled axons from the COAa travel through essentially the same pathways as those from the BMA.

The COAa, like other olfactory cortical areas, sends association fibers to most olfactory areas, including the olfactory tubercle, and the piriform, postpiriform transition, and entorhinal areas. Most of these projections have already been shown with anterograde (Luskin and Price, 1983a,b; Krettek and Price, 1977a) and retrograde (Haberly and Price, 1978) tracer methods. The anterior olfactory nucleus and taenia tecta appear to be the only olfactory areas (outside the olfactory bulb itself) not innervated by the COAa. The olfactory tubercle receives a light input from the COAa, and accordingly, Fuller et al. (1987) indicated that only a few cells in the COAa were retrogradely labeled after injections of WGA-HRP into the olfactory tubercle. Correspondingly, the olfactory tubercle, anterior olfactory nucleus, and taenia tecta appear to be the only olfactory areas that do not project to the COAa (Luskin and Price, 1983a).

Axons from the COAa, unlike other olfactory association fibers that end specifically in the deep zone of the plexiform layer, layer 1b (Luskin and Price, 1983a), innervate both the superficial (1a) and deep zones of the plexiform layer. This unique feature of the COAa, which distinguishes it from other olfactory cortical areas, had been noted previously (Luskin and Price, 1983b). Thus, COAa projections may converge with information arriving directly from the main olfactory bulb (innervating zone 1a; Price, 1973) and with information arriving indirectly from association fibers generated in olfactory areas receiving main olfactory bulb input (innervating zone 1b; Price, 1973; Luskin and Price, 1983a). Information received by the COAa may well undergo further processing within the nucleus itself before relay, because extensive intranuclear connections were observed after our PHAL injections.

No projections from the COAa back to the olfactory bulb were labeled in our material, in agreement with previous anterograde (Luskin and Price, 1983a) and retrograde (De Olmos et al., 1978) tracer studies in the rat, and work in the hamster (Kevetter and Winans, 1981).

Previous retrograde (Haberly and Price, 1978) and anterograde tracer studies (Krettek and Price, 1977a; Luskin and Price, 1983a) have suggested a projection to the infralimbic and agranular insular areas, and to the taenia tecta, from the COAa. Furthermore, Krettek and Price (1977a) also found a projection to the perirhinal area. We observed a light input to the infralimbic area, only very sparse fibers in the posterior agranular insular and rostral perirhinal areas, and no labeled fibers in the taenia tecta. However, the BMAa does project to the agranular insular area (this study), and the medial amygdalar nucleus projects to the taenia tecta (Canteras et al., 1995). Thus, injections in previous studies may have spread to involve the medial nucleus and/or BMAa.

A projection from the COAa to the molecular layer of the subiculum has been reported in the golden hamster (Kevetter and Winans, 1981). Only very sparse fibers were detected in the molecular layer of the ventral subiculum and adjacent field CA1 in our material. The discrepancy may be due to species differences or to major differences in injection site size.

Krettek and Price (1978a) did not report subcortical projections from the COAa in the rat or the cat. In our material, clear projections from the COAa to the septum and striatum were labeled. The main septal input is to the transverse, interfascicular, and ventral nuclei of the posterior division of the BST, although some scattered fibers were detected in the anterior division of the BST. Interestingly, the COAa projects lightly to the principal nucleus of the BST, which receives a direct, though small, input from the accessory olfactory bulb (Scalia and Winans, 1975). Thus, with the exception of the bed nucleus of the accessory olfactory tract, the COAa sends fibers to all olfactory cortical areas in receipt of olfactory bulb projections, a feature previously noted in the golden hamster (Kevetter and Winans, 1981). Finally, within the basal ganglia, axons from the COAa provide an input to the substantia innominata and striatal fundus.

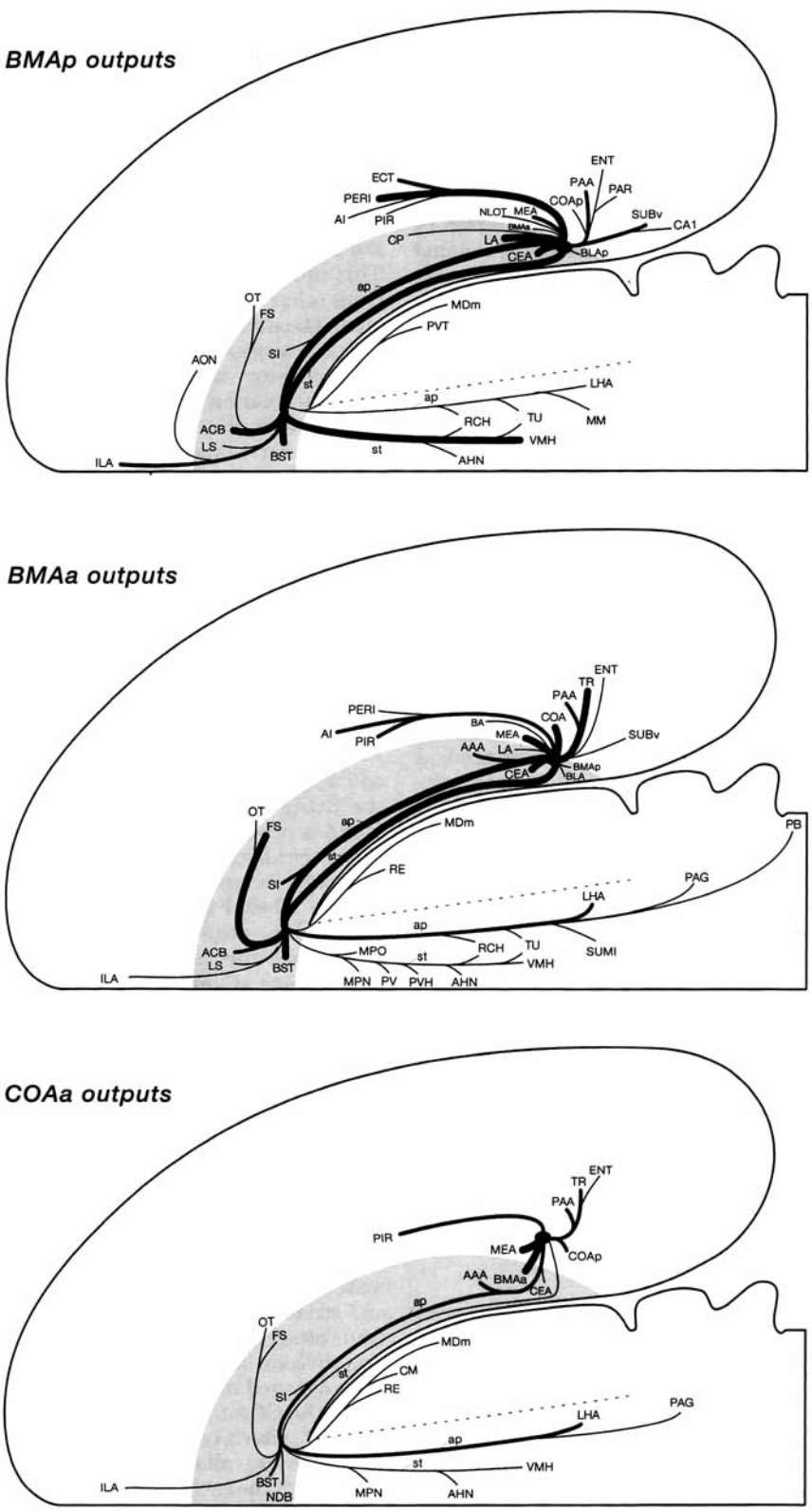

Fig. 7. Summary diagrams to indicate the general organization of projections from the BMAa, COAa, and BMAp. The relative size of each pathway is roughly proportional to the thickness of the line representing it.

In summary, the COAa mainly projects to olfactory cortical areas. However, it also sends a major input to subcortical regions including the BST, striatal fundus, and substantia innominata.

Descending projections

Although the COAa sends only a light input to the thalamus, it appears to be somewhat more dense than that from the BMA. In agreement with previous work (McDonald, 1987; Price et al., 1991), we observed light inputs to the medial mediodorsal nucleus, nucleus reuniens, and central medial nucleus.

Within the hypothalamus, the COAa projects mainly to caudolateral regions of the lateral hypothalamic area. This projection has been suggested previously, based on selective retrograde tracer injections into the lateral hypothalamic area (Ono et al., 1985). Furthermore, this part of the lateral hypothalamic area has been shown to receive a major olfactory input from most olfactory cortical areas, including the COAa (Price et al., 1991). HRP injections into this region of the lateral hypothalamic area retrogradely label more neurons in the COAa than in any other olfactory cortical area, and most if not all cells from the COAa contribute to this projection (Price, 1985).

After PHAL injections in the COAa we observed some labeled fibers in other parts of the hypothalamus including the medial preoptic nucleus (previously shown with retrograde methods; Simerly and Swanson, 1986) and the anterior, ventromedial, tuberal, and posterior hypothalamic nuclei.

Kevetter and Winans (1981) described autoradiographically in the golden hamster a projection from the COAa to the hypothalamic ventromedial nucleus but not to the lateral hypothalamic area. Because all of their injections included cells in the BMAa, and the larger injections included some of the medial nucleus as well, it is not surprising that a dense projection to the ventromedial nucleus was labeled. However, their failure to label a projection to the lateral hypothalamic area is not easy to explain but could reflect species differences.

Finally, a few sparse axons from the COAa were traced to the periaqueductal gray.

In summary, the COAa, like the BMA, sends a descending projection that in the diencephalon is restricted mainly to the hypothalamus, where it provides a substantial input to a specific, olfactory-related, region of the lateral hypothalamic area that also receives an input from the BMAa. The COAa also sends more fibers to the thalamus than does the BMAa or BMAp.

Functional considerations

The amygdala as a whole has been linked to a wide variety of functions ranging from sexual and other social behaviors to emotion and associative learning. The structural organization of the amygdala appears to mimic its functional complexity. Broadly speaking, this part of the medial temporal lobe has been divided into a number of distinct nuclear groups that seem to play different roles. In the following discussion, an attempt is made to clarify the basic input-output relationships of the BMA and associated COAa and thus to clarify basic organizing principles of amygdalar circuitry.

Almost 75 years ago, Johnston divided the amygdala into corticomedial (cortical, medial, and central nuclei) and basolateral (basolateral and lateral nuclei) groups, based on phylogenetic and ontogenetic considerations (Johnston, 1923). Relatively minor variations on this scheme have been used in most later descriptions of the amygdala and have been adopted by physiologists. Thus, a large body of evidence suggesting major functional differences between these two groups has accrued. For example, the corticomedial group (without the central nucleus) can be further subdivided into "main olfactory" (rostrolateral) and "accessory olfactory" (caudomedial) components that receive direct olfactory and pheromonal inputs from the main and accessory olfactory bulbs, respectively (Scalia and Winans, 1975). Neurons in this component send descending projections to the hypothalamic medial zone nuclei (Krettek and Price, 1978a; Canteras et al., 1992, 1995) and are thought to be involved in feeding and various aspects of sexual and agonistic behaviors (e.g., Kaada, 1972; Lehman et al., 1980; Luiten et al., 1985; Schulkin et al., 1989).

In contrast, the basolateral group, which receives most other classes of sensory information, and has widespread striatal, isocortical, and hippocampal connections, is generally thought to be important for emotional responses and amygdalar influences on mnemonic processes (Krettek and Price, 1977a,b; Ottersen 1982; LeDoux et al., 1990; Campeau and Davis, 1995).

Finally, the central nucleus, originally included in the corticomedial group, has emerged as a separate group involved in visceral functions (e.g., Applegate et al., 1983; Iwata et al., 1987; LeDoux et al., 1988). It receives major viscerosensory inputs including a direct projection from the nucleus of the solitary tract (e.g., Ricardo and Koh, 1978; Ottersen, 1981), an indirect input from the parabrachial nucleus (Fulwiler and Saper, 1984; Bernard et al., 1993), and an input from the insular region (Ottersen, 1982; McDonald and Jackson, 1987); it also receives intrinsic projections from most parts of the amygdala. Furthermore, its descending projections end in visceromotor areas including the BST, hypothalamus, and dorsal vagal complex (e.g., Hopkins and Holstege, 1978; Krettek and Price, 1978a; Veening et al., 1984; Danielsen et al., 1989).

Where does the BMA fit in this scheme? What little has been done in the past is inconclusive. It was included in the corticomedial group by Kaada (1972) and considered part of the basolateral and medial groups by De Olmos et al. (1985). Our results suggest that the BMAa shares certain features with the corticomedial group whereas the BMAp shares certain features with the basolateral group. However, the situation is more complex because they also share certain features with the central and accessory corticomedial groups, respectively.

A strong input from olfactory cortical areas, including a very heavy input from the COAa, suggests that the BMAa is part of the main olfactory corticomedial group. However, the BMAa also shares connections with the central group. Its major output is to the central nucleus, and like the central group, it receives inputs from the parabrachial nucleus and insular cortex and projects to the hypothalamic lateral zone. Thus, at the very least, the BMAa shares features with both the corticomedial and central groups of the amygdala.

In contrast, the BMAp is heavily innervated by the lateral amygdalar nucleus, and like the basolateral group has widespread striatal, isocortical, and hippocampal connections. However, it also shares bidirectional connections with the accessory olfactory corticomedial group (the medial nucleus and medial part of the posterior cortical

nucleus), and like the corticomedial group, projects to the hypothalamic medial zone (the ventromedial nucleus). Thus, the BMAp shares features with the basolateral and accessory olfactory corticomedial groups.

These considerations suggest that earlier schemes for grouping amygdalar nuclei are incomplete. To help clarify this problem, we shall now briefly consider the organization of inputs to the BMAa, BMAp, and COAa, along with unique input-output relationships of these three cell groups (see Fig. 8).

Organization of BMAa circuitry

Unfortunately, very little is known in detail about neural inputs to the BMAa. Nevertheless, it does receive association fibers from several main olfactory areas, including the COAa (this study), piriform area (Ottersen, 1982; Luskin and Price, 1983a), and postpiriform transition area (our unpublished observations using PHAL); Luskin and Price (1983a) also found an input from the entorhinal area, which receives a direct input from the olfactory bulb. The BMAa most likely does not receive a direct input from the olfactory bulb, although it is possible that some of its neurons extend dendrites into the deep molecular layer (McDonald, 1992) where olfactory association fibers are abundant (Price, 1973; Price and Luskin, 1983a).

Recently, Bernard et al. (1993) used PHAL to demonstrate a massive input to the BMAa from regions of the parabrachial nucleus (medial and "waist") involved at least partly in the relay of gustatory sensory information. These regions of the parabrachial nucleus receive inputs from the rostral zone of the medial nucleus of the solitary tract (Herbert et al., 1990), which receives gustatory inputs (Hamilton and Norgren, 1984; Travers and Norgren, 1995) and contains neurons responding to gustatory stimuli (Ogawa et al., 1987). The insular cortex also projects heavily to the BMAa and the part involved (rostral half of the posterior agranular and ventral dysgranular areas) has visceromotor functions (Yasui et al., 1991).

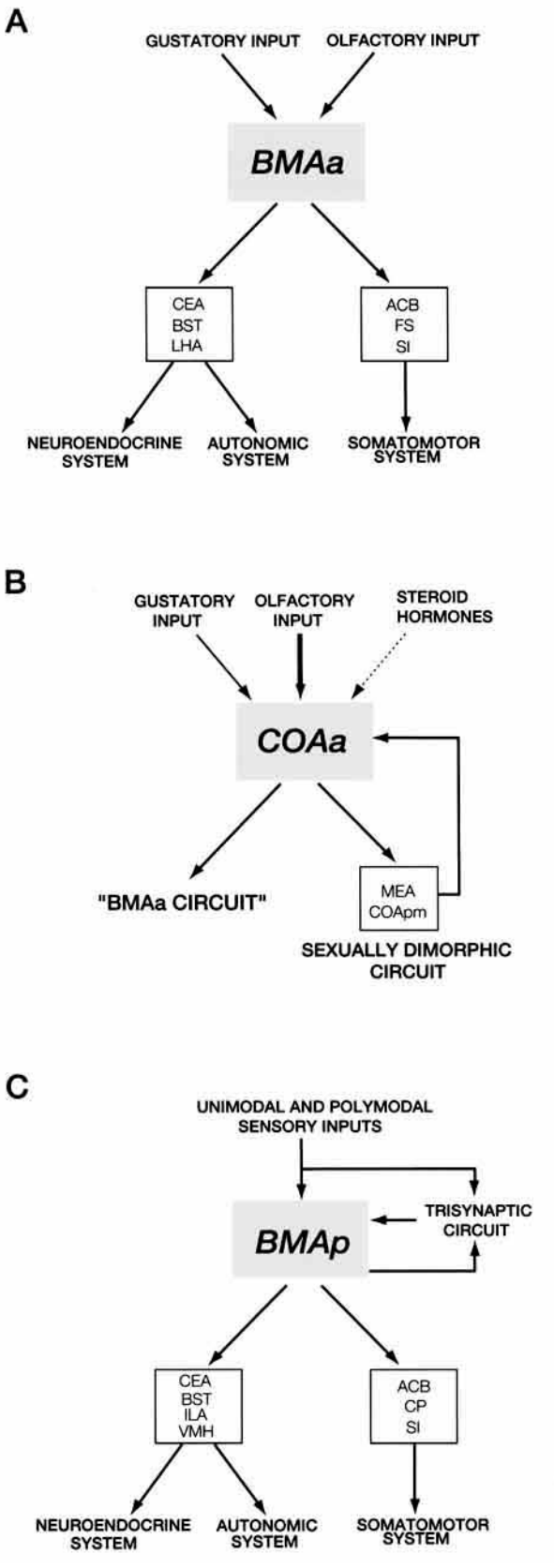

Fig. 8. A summary of the major connections of the BMAa (A), COAa (B), and BMAp (C). **A:** Major inputs to the BMAa are associated with the relay of olfactory (by inputs from the COAa, piriform, postpiriform transition, and entorhinal areas) and gustatory (by inputs from the parabrachial nucleus and insular area) information. The BMAa massively innervates areas projecting to neuroendocrine, autonomic, and somatomotor (behavioral) effector systems, probably involved in the expression of some aspects of feeding behavior. **B:** The COAa receives a major olfactory input (including direct input from the main olfactory bulb) as well as inputs from areas relaying gustatory information (parabrachial nucleus and insular region). In addition to neuronal inputs, the COAa also receives major hormonal inputs: high levels of gonadal steroid and mineralocorticoid receptors are expressed in the COAa. Outputs from the COAa suggest its participation in two separate circuits. The COAa sends massive projections to the BMAa and most parts of the "BMAa circuit" (Fig. 8A) (e.g., the amygdalar central nucleus, BST, striatal fundus, substantia innominata, and lateral hypothalamic area), and also innervates parts of the sexually dimorphic circuit (amygdalar medial nucleus, and medial part of the posterior cortical amygdalar nucleus), most likely mediating behaviors related to reproduction and agonistic behavior. **C:** The BMAp receives inputs from most sensory modalities by way of unimodal and polymodal sensory relays (e.g., lateral amygdalar nucleus, perirhinal area) and information associated with the hippocampal trisynaptic circuit (by way of the ventral subiculum). Widespread BMAp outputs strongly suggest that it may influence neuroendocrine, autonomic, and somatomotor (behavioral) systems and also information processing within the hippocampal formation (by outputs to the entorhinal area and ventral subiculum).

The BMAa in turn projects back to all of the olfactory cortical areas that it receives input from, and it also projects to the agranular insular area (Cechetto and Saper, 1987), a region that may receive convergent olfactory, gustatory, and visceral sensory information (Shipley and Geinsman, 1984 in mouse; Krushel and van der Kooy, 1988 in rat). Furthermore, the BMAa innervates the striatal fundus, a region of the ventral striatum that receives olfactory inputs from the piriform, piriform-amygdaloid, and entorhinal areas (Fuller et al., 1987; Luskin and Price, 1983a), and an input from the same regions of the parabrachial nucleus (Bernard et al., 1993) and insular cortex (Yasui et al., 1991) that also project to the BMAa. Within the hypothalamus, the BMAa innervates a distinct region of the lateral hypothalamic area that also receives a major olfactory input (Price et al., 1991). Finally, the most dense BMAa projection observed here is to the central amygdalar nucleus and adjacent substantia innominata. This terminal field also receives an input from the same regions of the insular cortex (Yasui et al., 1991) and parabrachial nucleus (Bernard et al., 1993) that project to the BMAa. The only other amygdalar nuclei that are innervated by the same regions of the parabrachial nucleus are the COAa and a distinct part of the posterior basolateral nucleus (Bernard et al., 1993), which also receive inputs from the insular cortex (Yasui et al., 1991) and BMAa. Based on its anatomical connections, the BMAa thus appears to form part of a circuit involved in processing olfactory, gustatory, and visceral information.

Functional studies involving the BMAa specifically have not yet been performed, although Kaada (1972) included the BMAa in the corticomedial amygdala, suggesting its involvement in feeding and sexual behaviors. As just mentioned, the anatomical evidence strongly suggests convergence of olfactory and gustatory information within the BMAa, and taste-responsive neurons have been recorded in the BMAa (Azuma et al., 1984). Taste and olfaction together make flavor, and convergence of the two is important for conditioned taste aversion (Lasiter, 1985). Olfaction seems to be important as an alternative conditioned stimulus in conditioned taste aversion paradigms, when taste information is not available (Lasiter, 1985). Furthermore, the amygdala plays a role in taste-potentiated odor aversion learning (e.g., Bermudez-Rattoni et al., 1983; Hatfield et al., 1992), where convergence of gustatory and olfactory modalities is important.

It is thus tempting to suggest that the BMAa is involved in taste and olfactory convergence related to feeding behavior. After processing in the BMAa such information would be relayed to viscerosensory (in the insular region), visceromotor (in the insular region, central amygdalar nucleus, BST, and lateral hypothalamic area), and somatomotor (in the striatal fundus and substantia innominata) parts of the circuitry (Fig. 8A). Interestingly, the infralimbic area (Brittain 1988; Hurley et al., 1991) projection to the BMAa and its efferent targets (the central amygdalar nucleus and lateral hypothalamic area) could be viewed as feedback from "motor" to "sensory" parts of the circuitry, because the infralimbic area is at least in part visceromotor cortex.

Organization of COAa circuitry

The COAa lies immediately superficial to the BMAa and its major sensory input is undoubtedly olfactory. It receives a direct input from the main olfactory bulb (Price, 1973; Scalia and Winans, 1975; Broadwell, 1975), as well as inputs from most other pars of the olfactory cortex (Luskin and Price, 1983a). Accordingly, olfactory-responsive cells have been recorded in the COAa (Cain and Bindra, 1972). However, it also receives other sensory information, including inputs from the parabrachial nucleus (Bernard et al., 1993) and insular region (Ottersen, 1982; Yasui et al., 1991), which most likely relay gustatory and visceral sensory information (see above). Furthermore, the COAa is innervated by the medial amygdalar nucleus (Canteras et al., 1995) and medial part of the posterior cortical nucleus of the amygdala (Canteras et al., 1992), which receive direct inputs from the accessory bulb (Scalia and Winans, 1975) and thus relay pheromonal information.

The COAa (see summary diagram in Fig. 7) in turn projects to all of the olfactory areas it receives input from (except the olfactory bulb) and to parts of the amygdala receiving accessory olfactory inputs. However, it appears to innervate only sparsely the agranular insular area and does not seem to innervate the parabrachial nucleus.

The exact function of the COAa is not known at this time, although its connections suggest participation in at least two distinct anatomical circuits (Fig. 8B).

First, the COAa, together with the BMAa, seems to participate in a circuit involved in feeding behavior (see above). The COAa and BMAa share dense bidirectional connections, and both send ascending projections to the same olfactory cortical areas and descending projections to the same part of the lateral hypothalamic area (see Results). The COAa most likely provides olfactory information to the BMAa, where it converges with at least gustatory sensory information. However, regions of the insular area and parabrachial nucleus that project to the BMAa also send a light input to the COAa. Thus, at least some convergence of these different sensory modalities probably occurs even at the level of the COAa, especially in light of the fact that taste-responsive neurons have been detected there (Azuma et al., 1984). Nevertheless, neurons in the COAa are distinct from those in the rest of the amygdala in their inhibitory response to NaCl stimulation (Azuma et al., 1984). Thus, information is processed differently within the BMAa and COAa. Finally, high levels of mineralocorticoid receptors are expressed in the COAa (Arriza et al., 1988), suggesting that the COAa, in addition to neuronal inputs, may be under the influence of this steroid hormone.

Second, the COAa like the medial amygdalar nucleus, appears to be a site of convergence for the main and accessory olfactory systems (see above). Such convergence may be important for the expression of sexual (Winans and Powers, 1977; Powers et al., 1979; Johnston and Rasmussen, 1984; Williams et al., 1992) and social (e.g., agonistic) (Edwards et al., 1993) behaviors.

Both main and vomeronasal systems appear to be important for the expression of reproductive behaviors (e.g., Winans and Powers, 1977; Powers et al., 1979). Mating behavior of inexperienced, but not experienced, male hamsters is abolished by removal of the vomeronasal organ (Meredith, 1986), and lesions of the vomeronasal amygdala produce serious deficits in both inexperienced and experienced male hamsters (Lehman and Winans, 1982). Thus, as previously suggested (Canteras et al., 1992), main olfactory input through the "accessory olfactory amygdala" might be sufficient for mating behavior, when pheromonal inputs are not available. The COAa constitutes one pathway for main olfactory information to reach the accessory olfactory amygdala. Accordingly, the COAa expresses high levels of both

androgen and estrogen receptor mRNAs (Simerly et al., 1990).

Olfactory bulb removal eliminates intermale aggression in rodents (Rowe and Edwards, 1971), and it has been suggested that multisynaptic pathways link chemosensory systems of the olfactory bulbs with the hypothalamus (Edwards et al., 1993). The COAa projection to the medial amygdalar nucleus, which in turn projects to the hypothalamic medial zone nuclei (Canteras et al., 1995), may provide olfactory information required for the expression of agonistic behavior.

Organization of BMAp circuitry

Based on neural inputs, the BMAp appears to receive a wide variety of sensory information at various stages of processing. It may thus receive unimodal and polymodal sensory information from the lateral nucleus of the amygdala (Krettek and Price, 1978b; Aggleton, 1985; Smith and Pare, 1994; Pitkanen et al., 1995), polymodal sensory information from the perirhinal area (McDonald and Jackson, 1987; Romanski and LeDoux, 1993), and polymodal sensory information from the hippocampal formation (Canteras and Swanson, 1992). The lateral amygdalar nucleus has limited intra-amygdalar projections, but it does innervate significantly the BMAp (Krettek and Price, 1978b; Aggleton, 1985; Smith and Pare, 1994; Pitkanen et al., 1995). Recently, a dense projection to the BMAp from the ventral subiculum has also been identified (Canteras and Swanson, 1992). Interestingly, the ventral subiculum sends heavy inputs that are remarkably confined within the morphological borders of the BMAp and sends only light projections to other parts of the amygdala. Thus, these two inputs alone distinguish the BMAp from the rest of the amygdala and imply a unique role in the function of the amygdala.

The BMAp has widespread extra-amygdalar projections and relatively few and restricted intra-amygdalar projections. In general it sends projections back to the sensory areas that it receives input from, and it sends heavy projections to visceromotor (the central amygdalar nucleus and BST) and somatomotor (the nucleus accumbens, caudoputamen, and substantia innominata) brain areas, and to the hippocampal formation (Fig. 8C).

Unfortunately, the BMAp has never been subjected to functional analysis in the rat. Work in the monkey suggests that the accessory basal nucleus (which corresponds at least in part to the rat BMAp) contains highly selective neurons that respond to complex sensory stimulation (Nishijo et al., 1988) and also neurons that respond specifically to faces, particularly those with emotional expressions (Leonard et al., 1985). This is particularly interesting in view of recent evidence suggesting involvement of the human amygdala in the recognition of emotion in facial expression (Adolphs et al., 1994, 1995).

Thus, the primate accessory basal nucleus (most likely the rat BMAp) is involved in the complex processing of highly convergent sensory information that may involve associative sensory learning. The BMAp may thus be part of amygdalar circuitry involved in "assigning emotional significance to sensory input," a proposed function of the amygdala (e.g., Weiskrantz, 1956; Aggleton and Mishkin, 1986) and more generally the inferior temporal lobe, since the classical work of Brown and Schäfer (1888) and Klüver and Bucy (1937). It may also be important for amygdalar involvement in emotion-related learning and memory (e.g., for reviews, see Davis, 1992; Kapp et al., 1992; LeDoux, 1992), and emotional influence on memory (for review, see McGaugh et al., 1992). While the mechanisms for these possible functions are not known, the anatomical connections of the BMAp support a general notion that the amygdala, after processing information, generates responses by projecting to other brain areas more directly involved in one aspect of behavior or another. For example, extensive and diverse projections enable the BMAp to influence somatomotor and autonomic brain areas, as well as information processing in the hippocampal formation. Based on the topography of its projections to medial regions of the nucleus accumbens and medial prefrontal cortex, and its inputs from the thalamic anterior paraventricular nucleus (Ottersen and Ben-Ari, 1979; Moga et al., 1995) and ventral subiculum (Canteras and Swanson, 1992), the BMAp would be a part of the circuit (the "prelimbic circuit") suggested by Groenewegen et al. (1990) to play a role in the integration of locomotor activity and visceral functions associated with motivated behavior and the expression of affect.

Through its massive projections to the hypothalamic ventromedial nucleus, the BMAp is in a unique position to influence a wide range of hypothalamic mechanisms including reproductive and agonistic behaviors (Canteras et al., 1994). Furthermore, its projections to specific parts of the BST and central amygdalar nucleus suggest an influence on visceral mechanisms. Direct innervation of the nucleus accumbens and substantia innominata by the BMAp may represent an important pathway for amygdalar influences on somatomotor behavior (Swanson et al., 1984). Thus, neurons in the BMA have the lowest reported thresholds in the amygdala for eliciting a response in the nucleus accumbens (Yim and Mogenson, 1982).

Although other amygdalar nuclei share connections with the hippocampal formation (e.g., Krettek and Price, 1978b; Ottersen, 1982; Canteras et al., 1992, 1995), the BMAp appears to be in a unique position to influence both the input and the output of the trisynaptic circuit by way of projections to the entorhinal area and ventral subiculum, respectively. Furthermore, the BMAp, unlike the rest of the amygdala, receives a particularly dense input from the ventral subiculum, and the parvicellular basal nucleus in the monkey (which may be homologous with the rat BMAp) displays the highest percentage of responses, and shortest mean latencies, after hippocampal stimulation (Morrison and Poletti, 1980).

A large body of evidence suggests a modulatory role for the amygdala on memory formation (for review, see McGaugh et al., 1992). For example, it has been reported that the amygdala may modulate both striatal- and hippocampal-dependent memory processes (Packard et al., 1995). Because the BMAp sends major projections to the striatum (including the caudoputamen, nucleus accumbens, and fundus) and hippocampal formation, it is probably involved in such modulations.

The BMAp may also be an important link in circuitry mediating conditioned fear. The amygdalar lateral nucleus is a sensory interface in the conditioned fear circuitry, at least when auditory or visual stimuli are used as conditioned stimuli (LeDoux et al., 1990; Campeau and Davis, 1995). A large body of evidence has demonstrated that the central nucleus is the amygdalar output of the conditioned fear circuitry (e.g., LeDoux et al., 1988; Rosen et al., 1991; Campeau and Davis, 1995). The lateral nucleus, however,

has very limited direct projections to the central nucleus (Krettek and Price, 1978b; Smith and Pare, 1994; our unpublished observation with PHAL) and seems not to innervate neurons in the medial central nucleus projecting to hypothalamic and brainstem autonomic areas (Hopkins and Holstege, 1978; Kapp et al., 1982; Veening et al., 1984). Alternative pathways appear to involve relays in the basolateral nucleus and BMAp, which receive inputs from the lateral nucleus (Pitkanen et al., 1995) and in turn project to the medial part of the central nucleus (Krettek and Price, 1978b; this study; our unpublished observation with PHAL). Interestingly, the BMAp receives the heaviest intra-amygdalar output of the lateral nucleus (Pitkanen et al., 1995), suggesting that it may be a stronger link with the central nucleus. Finally, the dense projection from the ventral subiculum specifically to the BMAp may be the critical link for hippocampal contributions to conditioned fear circuitry. The hippocampus appears to be essential in fear conditioning when a contextual cue is used as a conditioned stimulus (Selden et al., 1991; Kim and Fanselow, 1992; Phillips and LeDoux, 1992), whereas the amygdala may be necessary for the expression of conditioned fear when either a simple sensory or a contextual cue is used as a conditioned stimulus.

The overall conclusion to be drawn from this work is that cytoarchitectonically distinct parts of the BMA, the BMAa and BMAp, have distinct projection patterns and also form parts of different anatomical circuits. The BMAa appears to be a part of a circuit involved in feeding and social behaviors, whereas the BMAp may be part of circuitry involved in emotion-related learning and memory. The COAa, like the BMAa, also seems to participate in feeding behavior, and in addition may contribute to circuitry mediating reproductive and other social behaviors.

Clearly, these three cell groups contribute differentially to the functional organization of the amygdala. More work is needed to clarify mechanisms whereby they, together with their parent circuitry, generate or modulate goal-oriented behavior.

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LITERATURE CITED

Adolphs, R., D. Tranel, H. Damasio, and A. Damasio (1994) Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature *372*:669–672.

Adolphs, R., D. Tranel, H. Damasio, and A. Damasio (1995) Fear and the human amygdala. J. Neurosci. *15*:5879–5891.

Aggleton, J.P. (1985) A description of intra-amygdaloid connections in old world monkeys. Exp. Brain Res. *57*:390–399.

Aggleton, J.P. (1986) A description of the amygdalo-hippocampal interconnections in the macaque monkey. Exp. Brain Res. *64*:515–526.

Aggleton, J.P., and M. Mishkin (1986) The amygdala: Sensory gateway to the emotions. In Emotion: Theory, Research, and Experience. New York: Academic Press, Inc., pp. 281–299.

Aggleton, J.P., D.P. Friedman, and M. Mishkin (1987) A comparison between the connections of the amygdala and hippocampus with the basal forebrain in the macaque. Exp. Brain Res. *67*:556–568.

Amaral, D.G., J.L. Price, A. Pitkanen, and S.T. Carmichael (1992) Anatomical organization of the primate amygdaloid complex. In J.P. Aggleton (eds): The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. New York: Wiley-Liss, Inc., pp. 1–66.

Applegate, C.D., B.S. Kapp, M.D. Underwood, and C.L. McNall (1983) Autonomic and somatomotor effects of amygdala central n. stimulation in awake rabbits. Physiol. Behav. *31*:353–360.

Arriza, J.L., R.B. Simerly, L.W. Swanson, and R.M. Evans (1988) The neuronal mineralocorticoid receptor as a mediator of glucocorticoid response. Neuron *1*:887–900.

Azuma, S., T. Yamamoto, and Y. Kawamura (1984) Studies on gustatory responses of amygdaloid neurons in rats. Exp. Brain Res. *56*:12–22.

Barbas, H., and J. De Olmos (1990) Projections from the amygdala to basoventral and mediodorsal prefrontal regions in the rhesus monkey. J. Comp. Neurol. *300*:549–571.

Berk, M.L., and J.A. Finkelstein (1981) Afferent projections to the preoptic area and hypothalamic regions in the rat brain. Neuroscience *6*:1601–1624.

Bermudez-Rattoni, F., F.K. Rusiniak, and J. Garcia (1983) Flavor-illness aversions potentiated of odor by taste is disrupted by application of novocaine into amygdala. Behav. Neurol. Biol. *37*:61–75.

Bernard, J.F., M. Alden, and J.M. Besson (1993) The organization of the efferent projections from the pontine parabrachial area to the amygdaloid complex: A *Phaseolus vulgaris* leucoagglutinin (PHA-L) study in the rat. J. Comp. Neurol. *329*:201–229.

Bordi, F., and J.E. LeDoux (1992) Sensory tuning beyond the sensory system: an initial analysis of auditory response properties of neurons in the lateral amygdaloid nucleus and overlying areas of the striatum. J. Neurosci. *12*:2493–2503.

Brittain, D.A. (1988) The Efferent Connections of the Infralimbic Area in the Rat. PhD thesis, Department of Neurosciences, University of California San Diego.

Broadwell, R.D. (1975) Olfactory relationships of the telencephalon and diencephalon in the rabbit. J. Comp. Neurol. *163*:329–346.

Brodal, A. (1947) The amygdaloid nucleus in the rat. J. Comp. Neurol. *87*:1–16.

Brog, J.S., A. Salyapongse, A.Y. Deutch, and D.S. Zahm (1993) The patterns of afferent innervation of the core and shell in the "accumbens" part of the rat ventral striatum: Immunohistochemical detection of retrogradely transported fluoro-gold. J. Comp. Neurol. *338*:255–278.

Brown, S., and E.A. Schäfer (1888) An investigation into the functions of the occipital and temporal lobes of the monkey's brain. Phil. Trans. R. Soc. London. *179B*:303–327.

Cain, D.P., and D. Bindra (1972) Responses of amygdala single units to odors in the rat. Exp. Neurol. *35*:98–110.

Callaway, C.W., R.L. Hakan, and S.J. Henriksen (1991) Distribution of amygdala input to the nucleus accumbens septi: An electrophysiological investigation. J. Neural Transm. *83*:215–225.

Campeau, S., and M. Davis (1995) Involvement of the central nucleus and basolateral complex of the amygdala in fear conditioning measured with fear-potentiated startle in rats trained concurrently with auditory and visual conditioned stimuli. J. Neurosci. *15*:2301–2311.

Canteras, N.S., and L.W. Swanson (1992) Projection of the ventral subiculum to the amygdala, septum and hypothalamus: A PHAL anterograde tract-tracing study in the rat. J. Comp. Neurol. *324*:180–194.

Canteras, N.S., R.B. Simerly, and L.W. Swanson (1992) Connections of the posterior nucleus of the amygdala. J. Comp. Neurol. *324*:143–179.

Canteras, N.S., R.B. Simerly, and L.W. Swanson (1994) Organization of projections from the ventromedial nucleus of the hypothalamus: A *Phaseolus vulgaris*-leucoagglutinin study in the rat. J. Comp. Neurol. *348*:41–79.

Canteras, N.S., R.B. Simerly, and L.W. Swanson (1995) Organization of projections from the medial nucleus of the amygdala: A PHAL study in the rat. J. Comp. Neurol. *360*:213–245.

Cassell, M.D., T.S. Gray, and J.Z. Kiss (1986) Neuronal architecture in the rat central nucleus of the amygdala: A cytological, hodological, and immunocytochemical study. J. Comp. Neurol. *246*:478–499.

Cechetto, D.F., and C.B. Saper (1987) Evidence for a viscerotopic sensory representation in the cortex and thalamus in the rat. J. Comp. Neurol. *262*:27–45.

Crosby, E.C., and T. Humphrey (1941) Studies of the vertebrate telencephalon. J. Comp. Neurol. *74*:309–352

Danielsen, E.H., D.J. Magnuson, and T.S. Gray (1989) The central amygdaloid nucleus innervation of the dorsal vagal complex in rat: A *Phaseolus vulgaris* leucoagglutinin lectin anterograde tracing study. Brain Res. Bull. *22*:705-715.

Davis, M. (1992) The role of the amygdala in fear and anxiety. Annu. Rev. Neurosci. *15*:353–357.

DeFrance, J.F., J.E. Marchand, J.C. Stanley, R.W. Sikes, and R.B. Chronister (1980) Convergence of excitatory amygdaloid and hippocampal input in the nucleus accumbens septi. Brain Res. *185*:183–186.

De Olmos, J., G.F. Alheid, and C.A. Beltramino (1985) Amygdala. In G. Paxinos (ed): The Rat Nervous System. Sydney: Academic Press., pp. 223–334.

De Olmos, J., H. Hardy, and L. Heimer (1978) The afferent connections of the main and accessory olfactory bulb formations in the rat: An experimental HRP-study. J. Comp. Neurol. *181*:213–244.

Edwards, D.A., F.R. Nahai, and P. Wright (1993) Pathways linking the olfactory bulbs with the medial preoptic anterior hypothalamus are important for intermale aggression in mice. Physiol. Behav. *53*:611–615.

Fuller, T.A., F.T. Russchen, and J.L. Price (1987) Source of presumptive glutamergic/aspartergic afferents to the rat ventral striatopallidal region. J. Comp. Neurol. *258*:317–338.

Fulwiler, C.E., and C.B. Saper (1984) Subnuclear organization of the efferent connections of the parabrachial nucleus in the rat. Brain Res. *319*:229–259.

Gerfen, C.R., and P.E. Sawchenko (1984) An anterograde neuroanatomical tracing method that shows the detailed morphology of neurons, their axons and terminals: Immunohistochemical localization of an axonally transported plant lectin, *Phaseolus vulgaris* leucoagglutinin (PHA-L). Brain Res. *290*:219–238.

Groenewegen, H.J., H.W. Berendse, J.G. Wolters, and A.H.M. Lohman (1990) The anatomical relationship of the prefrontal cortex with the striatopallidal system, the thalamus and the amygdala: Evidence for a parallel organization. Prog. Brain Res. *85*:95–118.

Grove, E.A. (1988) Neural association of the substantia innominata in the rat: Afferent connections. J. Comp. Neurol. *277*:315–346.

Gurdjian, E.S. (1928) The corpus striatum of the rat. J. Comp. Neurol. *45*:249–281.

Haberly, L.B., and J.L. Price (1978) Association and commissural fiber systems of the olfactory cortex of the rat. J. Comp. Neurol. *178*:711–740.

Hamilton, R.B., and R. Norgren (1984) Central projections of gustatory nerves in the rat. J. Comp. Neurol. 222:560–577.

Hatfield, T., P.W. Graham, and M. Gallagher (1992) Taste-potentiated odor aversion learning: Role of the amygdaloid basolateral complex and central nucleus. Behav. Neurosci. *106*:286–293.

Haug, F.M.S. (1976) Sulphide silver pattern and cytoarchitectonics of parahippocampal areas in the rat: Special reference to the subdivision of area entorhinalis (area 28) and its demarcation from pyriform cortex. Adv. Anat. Embryol. Cell. Biol. *52*:1–73.

Heimer, L., and W.J.H. Nauta (1969) The hypothalamic distribution of the stria terminalis in the rat. Brain Res. *13*:284–297.

Herbert, H., M.M. Moga, and C.B. Saper (1990) Connections of the parabrachial nucleus with the nucleus of the solitary tract and the medullary reticular formation in the rat. J. Comp. Neurol. *293*:540–580.

Hopkins, D.A., and G. Holstege (1978) Amygdaloid projections to the mesencephalon, pons and medulla oblongata in the cat. Exp. Brain Res. *32*:529–547.

Hurley, K.M., H. Herbert, M.M. Moga, and C.B. Saper (1991) Efferent projections of the infralimbic cortex of the rat. J. Comp. Neurol. *308*:249–276.

Insausti, R., D.G. Amaral, and W.M. Cowan (1987) The entorhinal cortex of the monkey: III. Subcortical afferents. J. Comp. Neurol. *264*:396–408.

Iwata, J., K. Chida, and J.E. LeDoux (1987) Cardiovascular responses elicited by stimulation of neurons in the central amygdala nucleus in awake but not anesthetized rats resemble conditioned emotional responses. Brain Res. *418*:183–188.

Johnson, L.R., R.L.M. Aylward, Z. Hussain, and S. Totterdell (1995) Input from the amygdala to the rat nucleus accumbens: Its relationship with tyrosine hydroxylase immunoreactivity and identified neurons. Neuroscience *61*:851–865.

Johnston, J.B. (1923) Further contributions to the study of the evolution of the forebrain. J. Comp. Neurol. *35*:337–482.

Johnston, R.E., and K. Rasmussen (1984) Individual recognition of female hamsters by males: Role of chemical cues and of the olfactory and vomeronasal systems. Physiol. Behav. *33*:95–104.

Ju, G., and L.W. Swanson (1989) Studies on the cellular architecture of the bed nuclei of the stria terminalis in the rat: I. Cytoarchitecture. J. Comp. Neurol. *280*:587–602.

Ju, G., L.W. Swanson, and R.B. Simerly (1989) Studies on the cellular architecture of the bed nuclei of the stria terminalis in the rat: II. Chemoarchitecture. J. Comp. Neurol. *280*:603–621.

Kaada, B.R. (1972) Stimulation and regional ablation of the amygdaloid complex with reference to functional representations. In B.E. Eleftheriou (ed): The Neurobiology of the Amygdala. New York: Plenum Press, pp. 205–283.

Kapp, B.S., M. Gallagher, M.D. Underwood, C.L. McNall, and D. Whitehorn (1982) Cardiovascular responses elicited by electrical stimulation of the amygdala central nucleus in the rabbit. Brain Res. *234*:251–262.

Kapp, B. S., P. J. Whalen, W. F. Supple, and J. P. Pascoe (1992) Amygdaloid contributions to conditioned arousal and sensory information processing. In J.P. Aggleton (ed): The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. New York: Wiley-Liss, Inc., pp. 431-451.

Kelley, A.E., V.B. Domesick, and W.J.H. Nauta (1982) The amygdalostriatal projections in the rat: An anatomical study by anterograde and retrograde tracing methods. Neuroscience 7:615–630.

Kevetter, G.A., and S.S. Winans (1981) Connections of the corticomedial amygdala in the golden hamster. II. Efferents of the "olfactory amygdala." J. Comp. Neurol. *197*:99–111.

Kim, J.J., and M.S. Fanselow (1992) Modality-specific retrograde amnesia of fear. Science *256*:675–677.

Klüver, H., and P.C. Bucy (1939) Preliminary analysis of functions of the temporal lobes in monkeys. Arch. Neurol. Psychiatr. *42*:979–1000.

Kosel, K.C., G.W. Van Hoesen, and J.R. West (1981) Olfactory bulb projections to the parahippocampal area of the rat. J. Comp. Neurol. *198*:467–482.

Krettek, J.E., and J.L. Price (1977a) Projections from the amygdaloid complex to the cerebral cortex and thalamus in the rat and cat. J. Comp. Neurol. *172*:687–722.

Krettek, J.E., and J.L. Price (1977b) Projections from the amygdaloid complex and adjacent olfactory structures to the entorhinal cortex and the subiculum in the rat and cat. J. Comp. Neurol. *172*:723–752.

Krettek, J.E., and J.L. Price (1978a) Amygdaloid projections to subcortical structures within the basal forebrain and brainstem in the rat and cat. J. Comp. Neurol. *178*:225–254.

Krettek, J.E., and J.L. Price (1978b) A description of the amygd id complex in the rat and cat with observation on intra-amygdaloid a al connections. J. Comp. Neurol. *178*:255–280.

Krushel, L.A., and D. van der Kooy (1988) Visceral cortex: Integration of the mucosal senses with information in the rat agranular insular cortex. J. Comp. Neurol. *270*:39–54.

Lasiter, P.S. (1985) Thalamocortical relations in taste aversion learning. II. Involvement of the medial ventrobasal thalamic complex in taste aversion learning. Behav. Neurosci. *99*:477–495.

Lauer, E.W. (1945) The nuclear patter and fiber connections of certain basal telencephalic centers in the macaque. J. Comp. Neurol. *183*:785–816.

LeDoux, J. E. (1992) Emotion and the amygdala. In J.P. Aggleton (ed): The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. New York: Wiley-Liss,Inc., pp. 431–451.

LeDoux, J.E., P. Cicchetti, A. Xagoraris, and L.M. Romanski (1990) The lateral amygdaloid nucleus: Sensory interface of the amygdala in fear conditioning. J. Neurosci. *10*:1062–1069.

LeDoux, J.E., J. Iwata, P. Cicchetti, and D.J. Reis (1988) Different projections of the central amygdaloid nucleus mediate autonomic and behavioral correlates of conditioned fear. J. Neurosci. *8*:2517–2529.

Lehman, M.N., S.S. Winans, and J. B. Powers (1980) Medial nucleus of the amygdala mediates chemosensory control of male hamster sexual behavior. Science *210*:557–560.

Lehman, M.N., and S.S. Winans (1982) Vomeronasal and olfactory pathways to the amygdala controlling male hamster sexual behavior: Autoradiographic and behavioral analyses. Brain Res. *240*:27–41.

Lehman, M.N., and S.S. Winans (1983) Evidence for ventral non-strial pathway from the amygdala to the bed nucleus of the stria terminalis in the male golden hamster. Brain Res. *268*:139–146.

Leonard, C.M., E.T. Rolls, F.A.W. Wilson, and G.C. Baylis (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav. Brain Res. *15*:159–176.

Luiten, P.G.M., T. Ono, H. Nishijo, and M. Fukuda (1983) Differential input from the amygdaloid body to the ventromedial hypothalamic nucleus in the rat. Neurosci. Lett. *35*:253–258.

Luiten, P.G.M., J.M. Koolhaas, S. De Boer, and S.J. Koopmans (1985) The cortico-medial amygdala in the central nervous system organization of agonistic behavior. Brain Res. *332*:283–297.

Luskin, M.B., and J.L. Price (1983a) The topographic organization of associational fibers of the olfactory system in the rat, including centrifugal fibers to the olfactory bulb. J. Comp. Neurol. *216*:264–291.

Luskin, M.B., and J.L. Price (1983b) The laminar distribution of intracortical fibers originating in the olfactory cortex of the rat. J. Comp. Neurol. *216*:292–302.

Mascagni, F., A.J. McDonald, and J.R. Coleman, J.R. (1993) Corticoamygdaloid and corticocortical projections of the rat temporal cortex: A *Phaseolus vulgaris* leucoagglutinin study. Neuroscience *57*:697–715.

McDonald, A.J. (1982) Cytoarchitecture of the central amygdaloid nucleus of the rat. J. Comp. Neurol. *208*:401–418.

McDonald, A.J. (1987) Organization of amygdaloid projections to the mediodorsal thalamus and prefrontal cortex: A fluorescence retrograde transport study in the rat. J. Comp. Neurol. *262*:46–58.

McDonald, A.J. (1991a) Organization of amygdaloid projections to the prefrontal cortex and associated striatum in the rat. Neuroscience *44*:1–14.

McDonald, A.J. (1991b) Topographical organization of amygdaloid projections to the caudatoputamen, nucleus accumbens and related striatal-like areas of the rat brain. Neuroscience *44*:15–33.

McDonald, A.J. (1992) Cell types and intrinsic connections of the amygdala. In J.P. Aggleton (eds): The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. New York: Wiley-Liss, Inc., pp. 67–96.

McDonald, A.J., and T.R. Jackson (1987) Amygdaloid connections with posterior insular and temporal cortical areas in the rat. J. Comp. Neurol. *262*:59–77.

McGaugh, J.L., I.B. Introini-Collison, L. Cahill, M. Kim, and K.C. Liang (1992) Involvement of the amygdala in neuromodulatory influences on memory storage. In J.P. Aggleton (ed): The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. New York: Wiley-Liss, Inc., pp. 431–451.

Meredith, M. (1986) Vomeronasal organ removal before sexual experience impairs male hamster mating behavior. Physiol. Behav. *36*:737–743.

Moga, M.M., C.B. Saper, and T.S. Gray (1989) Bed nucleus of the stria terminalis: Cytoarchitecture, immunohistochemistry, and projection to the parabrachial nucleus in the rat. J. Comp. Neurol. *283*:315–332.

Moga, M.M., R.P. Weis, and R.Y. Moore (1995) Efferent projections of the paraventricular thalamic nucleus in the rat. J. Comp. Neurol. *359*:221–238.

Morrison, F., and C.E. Poletti (1980) Hippocampal influence on amygdala unit activity in awake squirrel monkeys. Brain Res. *192*:353–369.

Nishijo, H., T. Ono, and H. Nishino (1988) Single neuron responses in amygdala of alert monkey during complex sensory stimulation with affective significance. J. Neurosci. *8*:3570–3583.

Ogawa, H., T. Hayama, and S. Ito (1987) Response properties of the parabrachio-thalamic taste and mechanoreceptive neurons in rats. Exp. Brain Res. *68*:449–457.

Ono, T., P.G.M. Luiten, H. Nishijo, M. Fukuda, and H. Nishino (1985) Topographic organization of projections from the amygdala to the hypothalamus of the rat. Neurosci. Res. *2*:221–239.

Ono, T., and Y. Oomura (1975) Excitatory control of hypothalamic ventromedial nucleus by basolateral amygdala in rats. Pharmacol. Biochem. Behav. *3*:37–47.

Ottersen, O.P. (1981) Afferent connections to the amygdaloid complex of the rat with some observations in the cat. III. Afferents from the lower brain stem. J.Comp.Neurol. *202*:335–356.

Ottersen, O.P. (1982) Connections of the amygdala of the rat. IV. Corticoamygdaloid and intraamygdaloid connections as studied with axonal transport of horseradish peroxidase. J. Comp. Neurol. *205*:30–48.

Ottersen, O.P., and Y. Ben-Ari (1979) Afferent connections to the amygdaloid complex of the rat and cat. J. Comp. Neurol. *187*:401–424.

Packard, M.G., L. Cahill, and J.L. McGaugh (1995) Amygdala modulation of hippocampal-dependent and caudate nucleus-dependent memory processes. Proc. Natl. Acad. Sci. U.S.A. *91*:8477–8481.

Pare, D., Y. Smith, and J.-F. Pare (1995) Intra-amygdaloid projections of the basolateral and basomedial nuclei in the cat: *Phaseolus vulgaris*-leucoagglutinin anterograde tracing at the light and electron microscopic level. Neuroscience *69*:567–583.

Phillips, R. G., and J. E. LeDoux (1992) Differential contribution of amygdala and hippocampus to cued and contextual fear conditioning. Behav. Neurosci. *106*:274–285.

Pitkanen, A., L. Stefanacci, C.R. Farb, G. Go, J.E. LeDoux, and D.G. Amaral (1995) Intrinsic connections of the rat amygdaloid complex: projections originating in the lateral nucleus. J. Comp. Neurol. *356*:288–310.

Powell, T.P.S., W.M. Cowan, and G. Raisman (1965) The central olfactory connexions. J. Anat. *99*:791–813.

Powers, J.B., R.B. Fields, and S.S. Winans (1979) Olfactory and vomeronasal system participation in male hamsters' attraction to female vaginal secretions. Physiol. Behav. *22*:77–84.

Price, J.L. (1973) An autoradiographic study of complementary laminar patterns of termination of afferent fibers to the olfactory cortex. J. Comp. Neurol. *150*:87–108.

Price, J.L. (1981) Toward a consistent terminology for the amygdaloid complex. In Y. Ben-Ari (ed): The amygdaloid complex. Amsterdam: Elsevier, pp. 13–19.

Price, J.L. (1985) Beyond the primary olfactory cortex: Olfactory-related areas in the neocortex, thalamus and hypothalamus. Chem. Senses *10*:239–258.

Price, J.L., F.T. Russchen, and D.G. Amaral (1987) The amygdaloid complex. In A. Bjorklund, T. Hokfelt, and L.W. Swanson (eds): Handbook of Chemical Neuroanatomy, Vol. 5, Integrated Systems of the CNS, Part I. Amsterdam: Elsevier, pp. 279–377.

Price, J.L., B.M. Slotnick, and M.F. Revial (1991) Olfactory projections to the hypothalamus. J. Comp. Neurol. *306*:447–461.

Ricardo, J.A., and E.T. Koh (1978) Anatomical evidence of direct projections from the nucleus of the solitary tract to the hypothalamus, amygdala, and other forebrain structures in the rat. Brain Res. *153*:1–26.

Risold, P.Y., N.S. Canteras, and L.W. Swanson (1994) Organization of projections from the anterior hypothalamic nucleus: A *Phaseolus vulgaris*-leucoagglutinin study in the rat. J. Comp. Neurol. *348*:1–40.

Romanski, L.M., and J.E. LeDoux (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.

Room, P., and H.J. Groenewegen (1986) Connections of the parahippocampal cortex in the cat. II. Subcortical afferents. J. Comp. Neurol. *251*:451–473.

Romanski, L.M., and J.E. LeDoux (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.

Rosen, J.B., J.M. Hitchcock, C.B. Sananes, M.J. Miserendino, and M. Davis (1991) A direct projection from the central nucleus of the amygdala to the acoustic startle pathway: Anterograde and retrograde tracing studies. Behav. Neurosci. *105*:817–825.

Rowe, F.A., and D.A. Edwards (1971) Olfactory bulb removal: Influences on the aggressive behaviors of male mice. Physiol. Behav. *7*:889–892.

Russchen, F.T., and J.L. Price (1984) Amygdalostriatal projections in the rat: Topographical organization and fiber morphology shown using the lectin PHA-L as an anterograde tracer. Neurosci. Lett. *47*:15–22.

Russchen, F.T., I. Bakst, D.G. Amaral and J.L. Price (1985) The amygdalostriatal projections in the monkey: An anterograde tracing study. Brain Res. *329*:241–257.

Saunders, R.C., and D.L. Rosene (1988) A comparison of the efferents of the amygdala and the hippocampal formation in the rhesus monkey. I. Convergence in the entorhinal, prorhinal, and perirhinal cortices. J. Comp. Neurol. *271*:153–184.

Saunders, R.C., D.L. Rosene, and G.W. Van Hoesen (1988) Comparison of the efferents of the amygdala and the hippocampal formation in the rhesus monkey. II. Reciprocal and non-reciprocal connections. J. Comp. Neurol. *271*:185–207.

Scalia, F., and S.S. Winans (1975) The differential projections of the olfactory bulb and accessory olfactory bulb in mammals. J. Comp. Neurol. *161*:31–56.

Schulkin, J., J. Marini, and A.N. Epstein (1989) A role of the medial region of the amygdala in mineralocorticoid-induced salt hunger. Behav. Neurosci. *103*:178–185.

Selden, N. R., B. J. Everitt, L. E. Jarrard, and T. W. Robbins (1991) Complementary roles for the amygdala and hippocampus in aversive conditioning to explicit and contexual cues. Neuroscience *42*:335–350

Shipley, M.T., and Y. Geinisman (1984) Anatomical evidence for convergence of olfactory, gustatory, and visceral afferent pathways in mouse cerebral cortex. Brain Res. Bull. *12*:221–226.

Simerly, R.B., C. Chang, M. Muramatsu, and L.W. Swanson (1990) Distribution of androgen and estrogen receptors mRNA-containing cells in the rat brain: An in situ hybridization study. J. Comp. Neurol. *294*:76–95.

Simerly, R.B., and L.W. Swanson (1986) The organization of neural inputs to the medial preoptic nucleus of the rat. J. Comp. Neurol. *246*:312–342.

Smith, Y., and D. Pare (1994) Intra-amygdaloid projections of the lateral nucleus in the cat: PHA-L anterograde labeling combined with postembedding GABA and glutamate immunocytochemistry. J. Comp. Neurol. *342*:232–248.

Swanson, L.W. (1992) Brain Maps: Structure of the Rat Brain. Amsterdam: Elsevier.

Swanson, L.W., G.J. Mogenson, C.R. Gerfen, and P. Robinson (1984) Evidence for a projection from the lateral preoptic area and substantia innominata to the "mesencephalic locomotor region" in the Rat. Brain Res. *295*:161–178.

Travers, S.P., and R. Norgren (1995) Organization of orosensory responses in the nucleus of the solitary tract of the rat. J. Neurophysiol. *73*:2144–2162.

Turner, B.H., and J. Zimmer (1984) The architecture and some of the interconnections of the rat's amygdala and lateral periallocortex. J. Comp. Neurol. 227:540–557.

Veening, J.G., L.W. Swanson, and P.E. Sawchenko (1984) The organization *of projections from* the central nucleus of the amygdala to brainstem sites involved in central autonomic regulation: a combined retrograde transport-immunohistochemical study. Brain Res. *303*:337–357.

Weiskrantz, L. (1956) Behavioral changes associated with the ablation of the amygdaloid complex in monkeys. J. Comp. Physiol. Psychol. *49*:381–391.

Weller, K.L., and D.A. Smith (1982) Afferent connections to the bed nucleus of the stria terminalis. Brain Res. *232*:255–270.

Williams, J.R., B.M. Slotnick, B.W. Kirkpatrick, and C.S. Carter (1992) Olfactory bulb removal affects partner preference development and estrus induction in female prairie voles. Physiol. Behav. *52*:635–639.

Winans, S.S., and J.B. Powers (1977) Olfactory and vomeronasal deafferentation of male hamsters: Histological and behavioral analysis. Brain Res. *126*:325–344.

Yasui, Y., C.D. Breder, C.B. Saper, and D.F. Cechetto (1991) Autonomic responses and efferent pathways from the insular cortex in the rat. J. Comp. Neurol. *303*:355–374.

Yim, C.Y., and G.J. Mogenson (1982) Responses of nucleus accumbens neurons to amygdala stimulation and its modification by dopamine. Brain Res. *239*:401–415.