

## TEGMENTAL AFFERENTS OF THE AMYGDALOID BODY IN THE RAT

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*Abstract.* Horseradish peroxidase (HRP) was injected to various parts of the amygdala in 50 rats. Retrograde axonal transport revealed that tegmental areas containing biogenic amines: dorsal and median raphe nuclei, locus coeruleus and ventral tegmental area, project diffusely to various amygdaloid areas. Moreover, HRP labeled cells were found in the parabrachial nucleus (following injection of the lateral amygdaloid nucleus) and in tegmental dorsolateral nucleus (after injection of the central nucleus of amygdala).

### INTRODUCTION

Tegmental nuclei of the cerebral peduncle and the upper part of the pons are the source of numerous systems of ascending fibers terminating in various areas of the brain. Some of these nuclei contain neurons rich in serotonin, norepinephrine, or dopamine. Biochemical characteristics of others are still unknown. They are of significance for various functions, such as control of wakefulness and sleep, control of endocrine glands, modulation of pain perception etc. (2, 18, 19, 37, 38). Connections of these nuclei with the amygdala, one of the main limbic regions, have been studied only recently (1, 5, 9-11, 20, 26, 27, 31). Ottersen and Ben-Ari (31) made a more detailed study on the localization of tegmental neurons projecting to the central nucleus of the amygdala. However, the afferent tegmental connections to other amygdaloid nuclei have not yet been studied.

## MATERIALS AND METHOD

Brains of 50 Wistar rats of both sexes, weighting 200–250 g were investigated. Injections of horseradish peroxidase (0.05 to 0.5  $\mu$ l 30% solution Sigma VI) were made to the amygdala by means of a micropipette within 5–10 min. Postoperative survival time was 24–48 h. The brains were perfused with a solution of 0.4% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer of pH—7.2. After removal the brains were fixed for 24 h in the solution used for perfusion. Next they were kept for 24 h in 0.1 M phosphate buffer of pH—7.2 containing 5% sucrose. The brains were cut on a freezing microtome in 50  $\mu$ m sections. Incubation was carried out in a 0.05% solution of 3,3'-diaminobenzidine, then in the same solution plus 3%  $H_2O_2$  (0.3 ml/100 ml incubation solution).

HRP was injected to amygdaloid nuclei by two stereotactic approaches. The micropipette with HRP solution was inserted either through the cortex covering the upper surface of the brain and through striatum, or through the piriform cortex. A detailed description of histological and surgical procedures was given in an another publication (27).

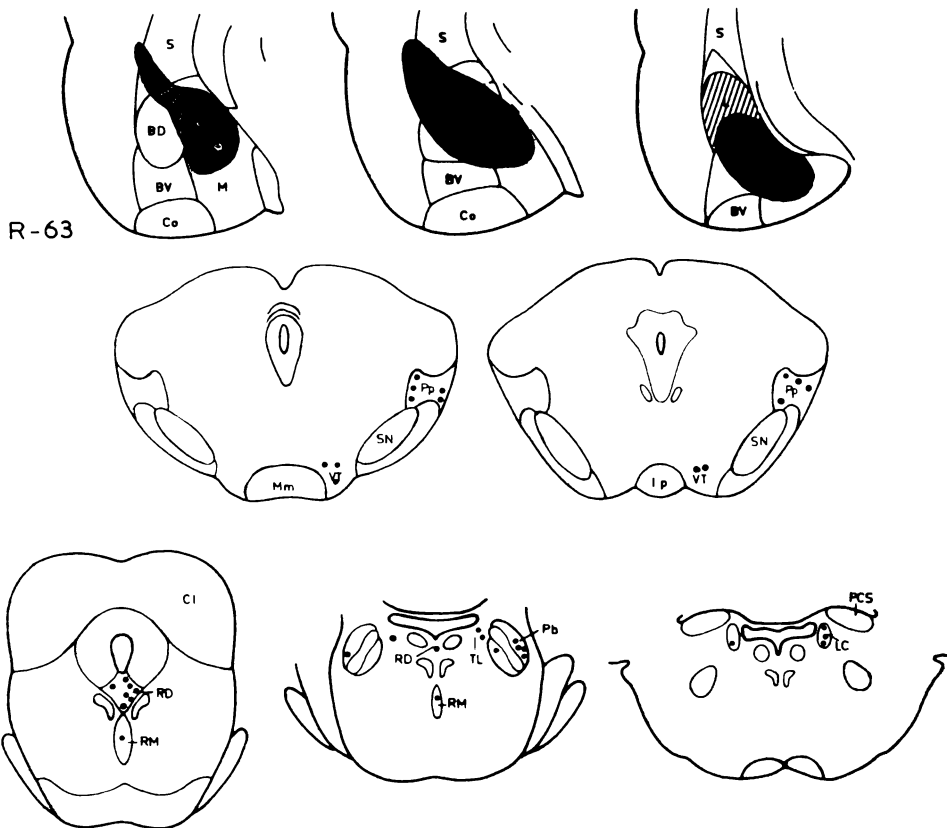
## RESULTS

*The localization of labeled neurons in the tegmental nuclei following injections of HRP involving most of the amygdaloid nuclei (Rat 63; Figs. 1 and 2).* The HRP injection involved, although in various degrees, all nuclei of the amygdala with the exception of the basal ventral nucleus. In the lateral nucleus the injection was localized mainly anteriorly. Moreover, injection involved the entire central nucleus, the dorsal part of medial nucleus, the medial part of basal dorsal nucleus and the dorsal area of posterior part of cortical nucleus. As a result of this injection, neurons with labeled granules were found in various tegmental nuclei:

1. Parabrachial nucleus ipsilaterally; a small number of labeled cells occurred contralaterally. They were located mainly in its inferolateral part. Some labeled cells were also observed in the medial part. Granules of labeled cells of the parabrachial nucleus were moderately or lightly stained.

2. Dorsal raphe nucleus: here the labeled neurons were located mainly in its rostral part, whereas only few were found in the caudal part. In the dorsal raphe nucleus two kinds of neurons containing HRP granules were observed. Some fusiform, relatively small neurons, were

located medially and ventrally; other oval neurons, much larger, were found in the entire area, sometimes contralaterally. These neurons were labeled rather intensively.



**Fig. 1.** Distribution of HRP labeled cells in the tegmental nuclei following injection involving most of the amygdaloid nuclei (Rat 63). Black areas, injection site; hatched areas, slight diffusion of the enzyme; Dots represent labeled cells. Frontal sections.

3. **Peripeduncular nucleus:** all labeled cells were located ipsilaterally to the injection side. The neurons were moderately labeled.

4. **Median raphe nucleus:** the labeled neurons were not particularly numerous neither in its rostral nor caudal part. These were comparatively large intensively labeled cells.

5. **Locus coeruleus:** intensively labeled neurons were located both in its dorsal and ventral part; not infrequently single labeled cells appeared contralaterally.

6. **Tegmental dorsolateral nucleus.** Small number of round medium

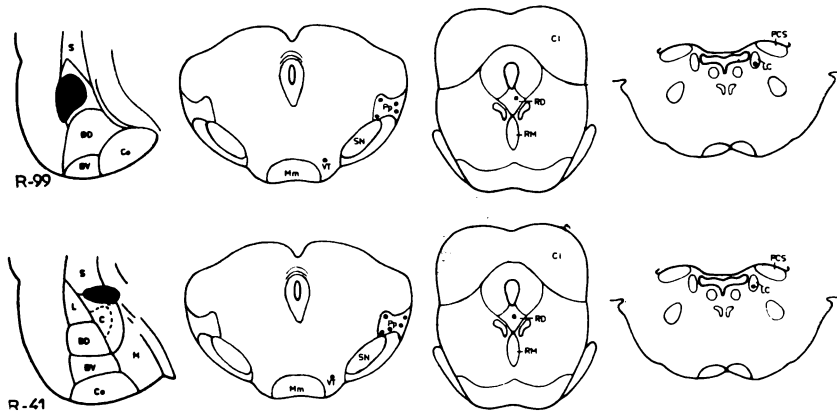


Fig. 3. Distribution of labeled cells in the tegmental nuclei following injections into lateral nucleus of the amygdala (Rat 99) and injection into lateral part of central nucleus (Rat 41). In these cases similar localization of labeled cells in the tegmental nuclei was found. Denotations as in Fig. 1.

sized, intensively labeled neurons were observed in this nucleus; a few labeled neurons also occurred contralaterally.

7. Ventral tegmental area (Tsai); the greatest number were found in the anterior part of the ventral tegmental area. These were rather large neurons with varying intensity of labeling, in general lightly labeled. In the posterior part of the ventral tegmental area we found merely a few neurons quite intensively labeled.

*Localization of labeled neurons in tegmental nuclei following small injections of HRP involving individual nuclei of amygdala. Rat 99 (Fig. 3).* The HRP injection was exclusively confined to the posterior part of the lateral nucleus of the amygdala. Many labeled cells were observed in the peripeduncular nucleus like in Rat 41. They occurred sporadically in the dorsal raphe nucleus, in locus coeruleus and in posterior part of the ventral tegmental area (Tsai).

Rat 41 (Fig. 3). HRP injection involved almost exclusively the lateral part of the central nucleus and, to a slight degree, the dorsal area of the intermediate part.

Many labeled cells were found in the peripeduncular nucleus. There were single labeled neurons in the rostral part of the dorsal raphe nucleus, in the locus coeruleus and in rostral part of the ventral tegmental area (Tsai).

Rat 60 (Fig. 4). HRP injection involved all the parts of the central nucleus: lateral, intermediate and medial. Many labeled cells were found in the peripeduncular nucleus, in the parabrachial nucleus, and

in the rostral segment of dorsal raphe nucleus; fewer in the tegmental dorsolateral nucleus and in the locus coeruleus. In the ventral tegmental area the labeled neurons, few in number, were localized primarily in

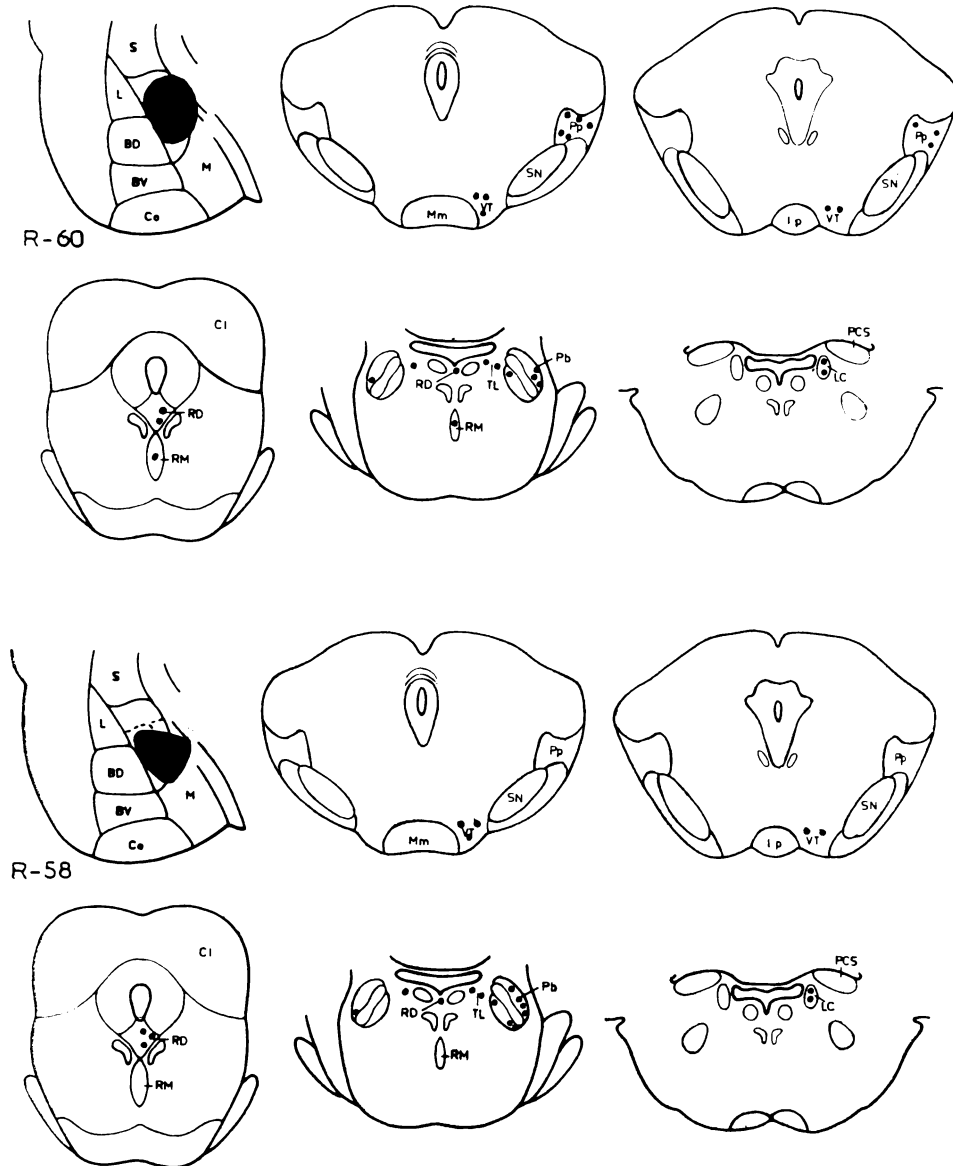


Fig. 4. Distribution of labeled cells in the tegmental nuclei following injections involving various parts of the central nucleus of amygdala in Rat 60 and Rat 58. Denotations as in Fig. 1.

its posterior part. Labeled neurons of the posterior part of the ventral tegmental area were filled with HRP granules, although in other cases of HRP injections to the amygdala the granularity of labeled cells in this area was, on the whole, much less marked. Single labeled cells were seen in the median raphe nucleus and in the caudal part of the dorsal raphe nucleus. Sometimes they were found contralaterally in locus coeruleus, in the parabrachial, in the tegmental dorsolateral, and in the dorsal raphe nucleus.

Rat 58 (Fig. 4). The injection covered primarily the intermediate and medial parts of the central nucleus as well as a small dorsal area of the medial nucleus. There were many labeled cells in the parabrachial nucleus, in the rostral part of dorsal raphe nucleus, fewer in the tegmental dorsolateral nucleus, in locus coeruleus and in the caudal segment of dorsal raphe nucleus; few cells were observed in the median raphe nucleus. None appeared in the peripeduncular nucleus.

Rat 95 (Fig. 5). HRP injection was exclusively confined to basal

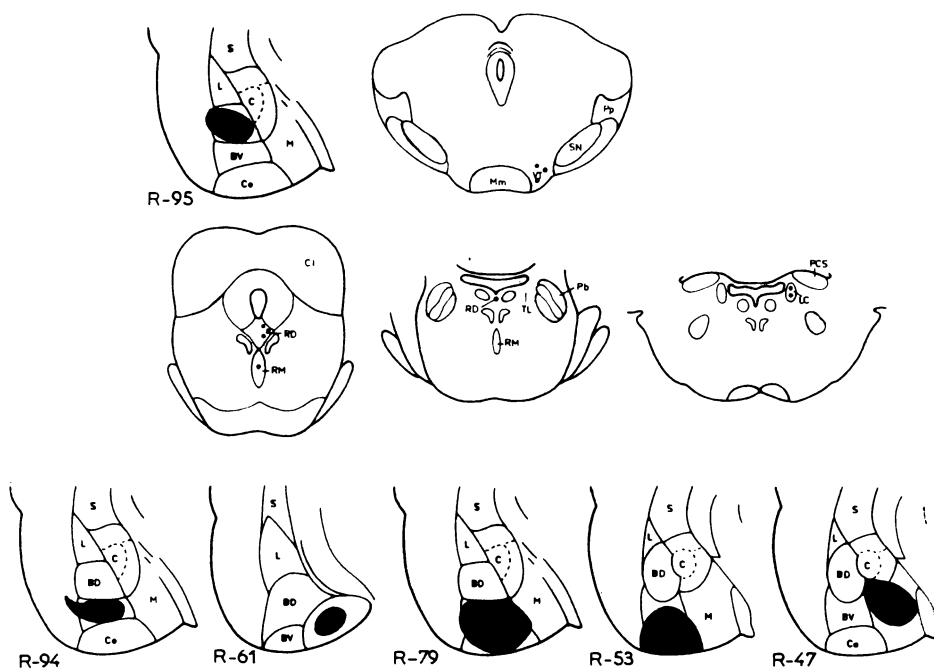


Fig. 5. Distribution of labeled cells in the tegmental nuclei following injection into the basal dorsal nucleus (Rat 95). In two lower rows injections followed by similar localization of labeled cells in the tegmental nuclei was found. Denotations as in Fig. 1.

dorsal nucleus. Labeled cells were found in locus coeruleus, in both rostral and caudal part of dorsal raphe nucleus, and in the ventral tegmental area; in the latter the labeled cells were found on frontal cross-sections through the posterior segment of mammillary bodies. Single cells were seen in median raphe nucleus.

Rat 94 (Fig. 5). The injection was confined to the basal ventral nucleus. Labeled cells were seen in the rostral segment of dorsal raphe nucleus; single cells in the locus coeruleus and the anterior segment of ventral tegmental area.

Rat 61 (Fig. 5). The injection covered a small area of cortical nucleus in its posterior part. Single labeled neurons were observed in locus coeruleus, in dorsal raphe nucleus and in anterior part of ventral tegmental area.

Rat 79 (Fig. 5). HRP injection covered primarily the posterior part of basal ventral nucleus and the cortical nucleus, as well as a small area of adjacent cortex. HRP labeled cells were found in the dorsal and median raphe nuclei, in locus coeruleus and in the anterior part of ventral tegmental area. In comparison to Rat 95 and Rat 61, in which the injection was limited respectively to basal ventral and cortical nucleus, in Rat 79 we found a relatively larger number of labeled neurons in the tegmental nuclei.

Rat 53 (Fig. 5). The injection involved the anterior part of cortical nucleus and basal ventral nucleus. Labeled cells were seen in the locus coeruleus, in dorsal raphe nucleus; additionally single cells were labeled in the anterior part of the ventral tegmental area.

Rat 47 (Fig. 5). The injection involved a small area of the anterior pole of basal dorsal nucleus, almost all of medial nucleus; slightly touched the medial part of central nucleus. A considerable number of labeled cells appeared in the dorsal raphe nucleus, in locus coeruleus and in the anterior part of ventral tegmental area; single cells in the median raphe nucleus. No labeled cells were found in the parabrachial or in tegmental dorsolateral nucleus.

*The localization of labeled neurons in tegmental nuclei following control injections into the neighbourhood of the amygdala.* Rat 98 (Fig. 6). The injection involved the lateral portion of piriform cortex. Labeled cells occurred in dorsal raphe nucleus, in locus coeruleus, few were visible in the anterior part of ventral tegmental area. Relatively many labeled cells were seen in the median raphe nucleus.

Rat 59 (Fig. 7). The injection covered a small anteroventral part of the striatum and globus pallidus. A great number of labeled cells were seen in the posterior part of ventral tegmental area and in lateral area of substantia nigra (pars compacta).

Rat 22 (Fig. 7). The injection involved a large area of anterior striatum and, to a small degree, the lateral nucleus and lateral part of the central nucleus. Labeled cells were observed in the lateral area of substantia nigra (pars compacta), in the peripeduncular nucleus, a small number in locus coeruleus. The presence of labeled cells in the last two nuclei is probably due to a slight leakage of HRP to the amygdaloid nuclei mentioned above.

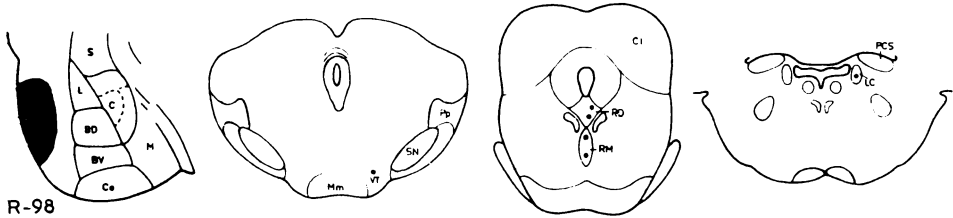


Fig. 6. Distribution of labeled cells in tegmental nuclei following injection involving piriform cortex—Rat 98. Denotations as in Fig. 1.

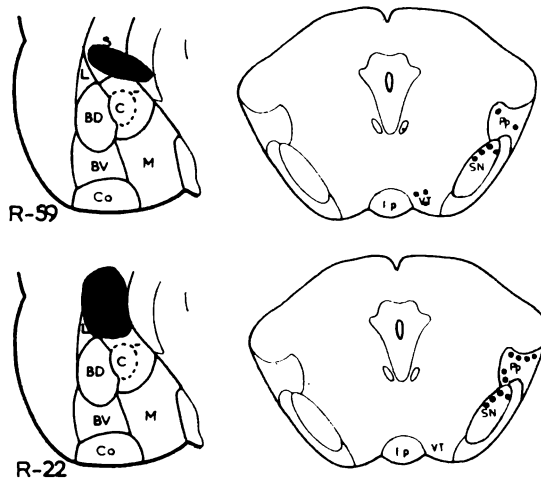


Fig. 7. Distribution of labeled neurons in tegmental nuclei following injections involving various regions of striatum—Rat 59 and Rat 22. Denotations as in Fig. 1.

#### DISCUSSION

As a result of our observations of retrograde axonal transport from the amygdala we may distinguish in the tementum: 1. nuclei where HRP granules in cells occur following injection to various areas of the amyg-



dala and, 2. nuclei in which labeled cells are found only after HRP is injected to a strictly definite amygdaloid nucleus.

1. The following nuclei seem to have amygdalopetal projection spreading over the entire or almost entire amygdala: dorsal raphe nucleus, median raphe nucleus, locus coeruleus and ventral tegmental area (Tsai). As is well known from biochemical and histochemical investigations, these are nuclei in which a considerable part of the cells contains biogenic amines: serotonin (raphe nuclei), norepinephrine (locus coeruleus), and dopamine (ventral tegmental area) (7, 10, 15, 25). The fact that they project to many nuclei of the amygdaloid body agrees with the results of studies according to which they innervate large areas of the forebrain in a diffuse manner (5, 6, 8, 10-12, 16, 21, 22, 24, 30, 32, 33, 41).

*Nuclei containing cells rich in serotonin.* The greatest number of HRP labeled cells, after injection to the amygdala, were found in the rostral part of the dorsal raphe nucleus, while relatively few in its caudal part and in the median raphe nucleus. None, were observed in the lateral raphe nucleus. The above results lead to the assumption that the largest serotonergic projection from the tegmentum to amygdala comes from the dorsal raphe nucleus, which, according to biochemical and histochemical fluorescent studies, is the largest serotonin-containing nucleus (15, 25, 32).

According to Jacobs et al. (16) labeled cells occur in various areas of the dorsal raphe nucleus, depending on the localization of HRP injection, but the differences in localization are not sharply marked. In our material after HRP injections to the amygdala, neurons with HRP containing granules were observed bilaterally in the rostral part of dorsal raphe nucleus; more abundantly, however, on the ipsilateral side. Much fewer labeled neurons were found in the caudal part of the dorsal raphe nucleus and in the median raphe nucleus, where they were localized mostly in the vicinity of the midline. There were no essential differences in localization of labeled neurons in raphe nuclei between various injection sites within the amygdala. Thus it would seem that connections of the dorsal raphe nucleus with the amygdala consist of a rather homogenous, diffuse projection system. On the basis of the investigations of Saavedra et al. (36) the serotonin level in various nuclei of amygdala is similar (15.9-23.0 ng/mg protein). This may suggest a uniform distribution of boutons terminaux of axons originating in the serotonin-containing raphe nuclei.

On the basis of investigations carried out by degeneration and autoradiographic methods Conrad et al. (9) noted that fibers arising in

raphe nuclei approach the amygdala along the medial border of stria terminalis and that most of them probably project to the medial and cortical nuclei. Other fibers from raphe nuclei supposedly approach through the anterior and lateral part of the median forebrain bundle. Projections from the dorsal raphe nucleus to the amygdala were observed also by Aghajanian (1) and Babilier et al. (5).

Moreover, Palkovits et al. (32) by means of electron microscope noted a degeneration of nerve terminals in the lateral nucleus of the amygdala after lesions in the dorsal raphe nucleus. All the above data seem to provide a convincing evidence of the diffuse character of projection from the raphe nuclei to the entire amygdaloid body.

The role of these connections is not clear, because diverse functions are ascribed to the ascending serotonin—containing neurons. They are supposed to regulate sleep and wakefulness (18, 19), to effect sexual behavior and aggressiveness (38), as well as endocrine functions, regulation of temperature (2) and perception of pain (37).

*Nuclei containing cells rich in dopamine.* Most of the perikarya of neurons containing dopamine and sending their axons to the forebrain are located in the pars compacta of the substantia nigra (A9) and in the ventral tegmental area of Tsai (A10). It was generally accepted that neurons of substantia nigra project, mainly to the striatum, while in neurons of the ventral tegmental area axons of the dopaminergic mesolimbic system (13, 35) are supposed to arise. But the delineation of these two dopaminergic systems is not wholly clearcut. Ungerstedt (41) assumed that the dopaminergic afferentation of the central nucleus of amygdala arises in the substantia nigra. Carter and Fibiger (8) after injecting HRP to the amygdala, and Ottersen and Ben-Ari (31) following injection to the amygdaloid central nucleus, found the presence of labeled cells not only in the ventral tegmental area but also in the substantia nigra. Results of Fallon et al. (10) and Fallon and Moore (11) seem to prove that dopamine-containing fibers reaching amygdala arise both in ventral tegmental area and in the most medial part of the substantia nigra. However, in our material, after HRP injections confined exclusively to the central nucleus of the amygdala, accomplished when the needle was inserted diagonally by passing the striatum, no HRP labeled cells were found in the substantia nigra. But they did appear when the injection involved additionally, however slightly, the striatum.

In our material HRP labeled cells appeared in the anterior part of the ventral tegmental area after most amygdaloid injections. If injection involved the central nucleus of the amygdala, HRP labeled cells were found additionally in the posterior part.

In interpreting these results it should be kept in mind that not all the cells located in the ventral tegmental area contain dopamine (10), although the experiments of Ljungdahl et al. (23) and Beckstedt (3) suggest that at least a large number of neurons of this area, projecting to various areas of the telencephalon, are dopaminergic. The fact that HRP labeled cells in the posterior part of the ventral tegmental area were observed only after injections to the central nucleus (more precisely to its intermediate and medial part), may be particularly interesting in confrontation with biochemical and histochemical data. Ben-Ari et al. (4) noted the highest concentration of dopamine in the central and basal dorsal (basal lateral) nucleus of the amygdala (five times higher than in its cortico-medial part). Brownstein et al. (7) also consider the concentration of dopamine to be the highest in the central nucleus and moreover, in the lateral nucleus. According to Fallon et al. (10) fibers containing dopamine are concentrated mainly in the central and basolateral nucleus. At any rate the influence of the ventral tegmental area on the level of dopamine in the amygdala seems to be evident in the light of investigations of Fuxe et al. (12). They noted, following lesions in the lateral part of this area, a decrease in dopamine fluorescence in the amygdala. Recently Fallon et al. (10) found, following lesion of the lateral part of the ventral tegmental area, a 35% decrease of dopamine in the amygdala. The role of dopaminergic connections passing from ventral tegmental area to the amygdala seems to be important in the light of studies of the dopaminergic mesolimbic system.

*Nuclei containing cells rich in norepinephrine.* After HRP injection to the nuclei of the amygdala we found HRP labeled cells in various parts of the locus coeruleus. Connections from the locus coeruleus to the amygdala were studied by histofluorescence and autoradiography (10, 33, 41). According to Brownstein et al. (7) and Ben-Ari et al. (4), regional differences in the distribution of norepinephrine are, on the whole, much smaller than in the distribution of dopamine. According to Fallon et al. (10) norepinephrine — containing fibers are widely distributed, moderately densely in the central and basal lateral nuclei; on the other hand, Swanson and Hartman (39), who investigated the localization of the noradrenergic system using dopamine-3-hydroxylase as a marker, suggest that the only structures in the amygdala to be reached by a considerable number of axons are the central nucleus and the adjacent part of the basal lateral (basal dorsal) nucleus and anterior amygdaloid area. Our experiments show that in locus coeruleus, cells containing HRP labeled granules are also

found after injections into the other nuclei of the amygdala, including medial and cortical.

Probably most of the catecholamine-containing amygdalopetal fibers penetrate the amygdala passing through its central nucleus, a fact which must be linked with their much greater concentration in the central nucleus than in the remaining nuclei of the amygdala. However, it is not possible to exclude entirely that HRP is also taken up by damaged passing nerve fibers and not only by fiber terminals. For this reason a large number of HRP labeled cells in catecholamine-containing tegmental nuclei after injections to the central nucleus of the amygdala cannot be interpreted univocally as the result of the occurrence of an exceptionally large number of amygdalopetal connections from the tegmental nuclei to that particular nucleus of the amygdaloid body.

2. Parabrachial nucleus. According to Tokyama et al. (40) the parabrachial nucleus projects to the hypothalamus, but HRP labeled granules do not accumulate in its cells after injections of the enzyme to the cerebral cortex, cerebellum, posterior thalamus and spinal cord. Moreover the parabrachial nucleus is supposed to receive connections from the nucleus of the tractus solitarius (34) and from the central nucleus of the amygdala (20, 31). HRP labeled granules appearing in the neurons of the amygdaloid central nucleus after injections to the lateral tegmentum (14) may be to a significant degree caused by amygdaloparabrachial connections. Thus, our finding of direct connections from the parabrachial nucleus to the intermediate and medial part of the central nucleus of the amygdala supplements the above data, which taken together suggest that there is a closely related system, to which nucleus of the tractus solitarius, parabrachial nucleus and central nucleus of the amygdala belong. Moreover, some thalamic and hypothalamic nuclei, those of preoptic area and bed nucleus of stria terminalis seem also to be related to this system (34). It has been suggested that the parabrachial nucleus is the gustatory center of the pons, receiving gustatory impulses from the nucleus of the tractus solitarius (28, 29). However, primarily it seems to be an area of reticular formation involved in mediating visceral reflexes, the effects of which are: neuroendocrine functions, functions of the autonomic system and complex mechanisms of behavior connected with drives and emotions.

3. Dorsolateral tegmental nucleus. After injections to the amygdala HRP labeled cells were observed in the dorsolateral tegmental nucleus; none were found in the nuclei of Gudden (ventral tegmental nucleus

and dorsal tegmental nucleus). The connections of the tegmental dorsolateral nucleus have not been much studied. Tokyama et al. (40) found numerous medium-sized labeled granules in its cells following administration of HRP to the hypothalamus. According to Ricardo and Koh (34), fibres from the nucleus of the tractus solitarius project to the lateral part of the dorsolateral tegmental nucleus.

4. Peripeduncular nucleus. It sends an amygdalopetal projection confined to a definite part of the amygdala. Peripeduncular nucleus in principle, is considered as a part of either the tegmentum or the thalamus. It shows a considerable number of HRP labeled cells after injection to the lateral nucleus of the amygdala and (or) to the lateral part of the central nucleus. This agrees with the results of our experiments carried out by degenerative methods on rats (26). Jones et al. (17) using autoradiography, reported in the monkey a similar projection, from peripeduncular nucleus to the lateral and partly to medial nucleus of amygdala.

The present studies show that the nuclei of the amygdala receive afferent connections from several areas of the upper part of the brain stem. On the one hand, nuclei containing a large amount of biogenic amines send axons which, having diffuse projection to the amygdala, may evoke a rather general effect on functions of all the amygdaloid nuclei. On the other hand, the central and lateral nucleus of the amygdala receive additional connections from other tegmental nuclei (central—from parabrachial, and dorsolateral tegmental lateral—from peripeduncular) which seem to have some specific influence on their function.

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#### LIST OF ABBREVIATIONS

BD	nucleus basalis dorsalis corporis amygdaloidei
BV	nucleus basalis ventralis corporis amygdaloidei
C	nucleus centralis corporis amygdaloidei
CI	colliculus inferior
Co	nucleus corticalis corporis amygdaloidei
Ip	nucleus interpeduncularis
L	nucleus lateralis corporis amygdaloidei
LC	locus coeruleus
M	nucleus medialis corporis amygdaloidei
Mm	corpora mamillaria
Pb	nucleus parabrachialis
PCS	pedunculus cerebellaris superior
Pp	nucleus peripeduncularis
RD	nucleus dorsalis raphes
RM	nucleus medianus raphes
S	striatum
SN	substantia nigra
TL	nucleus dorsolateralis tegmenti
VT	area ventralis tegmenti (Tsai)