CONNECTIONS OF THE HYPOTHALAMUS AND PREOPTIC AREA WITH NUCLEI OF THE AMYGDALOID BODY IN THE RAT; HRP RETROGRADE TRANSPORT STUDY

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Abstract. Horseradish peroxidase (HRP) was injected into various nuclei of the amygdala in 50 rats. The retrograde axonal transport of HRP showed various connections arising from the hypothalamic nuclei and the basal forebrain. Neurons of the magnocellular preoptic nucleus send out amygdalopetal axons to all amygdaloid nuclei except the lateral nucleus. The amygdalopetal projections emerge from the large neurons situated dorsally in the most lateral preoptic area (probably substantia innominata) and terminate in the basal dorsal and the central amygdaloid nuclei. Neurons in the lateral division of the hypothalamus (the lateral hypothalamic area proper and the perifornical region) send out axons which terminate in the medial and central nuclei and in the posterior part of the cortical amygdaloid nucleus. Axons emerging from the ventromedial hypothalamic nucleus end mainly in the medial nucleus and in the central amygdaloid nucleus. Amygdalopetal fibers arising from neurons of the ventral premamillary and dorsal hypothalamic nuclei reach the medial amygdaloid nucleus and perhaps a few of them end in the posterior part of the cortical amygdaloid nucleus. Neurons of the bed nucleus of the stria terminalis project to the medial, the posterior part of the cortical and probably to the basal dorsal amygdaloid nuclei.
INTRODUCTION

Experimental results and clinical observations indicate that both the hypothalamus and the amygdaloid body control many autonomic functions, influence the endocrine glands and also affect the emotional behavior and drives (11, 12, 15).

Neuroanatomical observations showed that the nuclei of the amygdaloid body receive projections from and send out axons to the hypothalamus and to some prosencephalic structures (4–6, 8, 9, 16, 18, 19, 20, 26, 27, 33–36, 38, 39). The distribution of amygdalopetal pathways which arise from the hypothalamus and preoptic area has been partly established in some experimental animals (4–6, 19, 20, 26, 27, 33–36, 38, 39). However, few data are available concerning the exact distribution of hypothalamic neurons sending amygdalopetal axons in the rat (33, 38). This is due partly to the fact that the hypothalamic nuclei in the rat are relatively small. It is difficult, therefore, to make selective lesions or to inject labeled aminoacids strictly limited to a single nucleus. Moreover, various pathways run through the lateral hypothalamus (37) and their damage affects the results. It seems that experiments carried out by the HRP retrograde transport method should be helpful in establishing the precise location of the hypothalamic neurons projecting to various amygdaloid nuclei in the rat brain.

Our investigation was an attempt to find the precise origin of amygdalopetal axons in the hypothalamic and preoptic neurons by means of the HRP retrograde transport method. The observations presented below include the distribution of neurons sending amygdalopetal axons not only in the hypothalamus and preoptic area but also in the bed nucleus of the stria terminalis. This seemed useful because the hypothalamus, the preoptic area and the bed nucleus of stria terminalis — structures derived according to Broadwell and Bleier (3) from a common embriological anlage — are functionally interrelated and form an important link of the limbic system. The nomenclature of the amygdaloid nuclei is based on the results of our investigation on the cytoarchitectonics and acetylcholinesterase (AChE) activity in the amygdaloid nuclei of the rat and other experimental animals (22, 28).

The nomenclature of the hypothalamic and preoptic nuclei is based mainly on the results of cytoarchitectonical and embriological studies by Bleier (2), Broadwell and Bleier (3), Gurdijan (13) and Swanson (36).

MATERIAL AND METHODS

Our material consists of the brains of 50 Wistar rats of both sexes, weigh 200–250 g. Injections of 0.05–0.5 μl of 30% solution of horseradish
peroxidase (Sigma VI) were made in the nuclei of the amygdala through a glass micropipette within 5–10 min. The postoperative survival time was 24–48 h. The brains were subsequently perfused through the heart with a 0.4% solution of paraformaldehyde and a 1.25% glutaraldehyde in the 0.1 M phosphate buffer of pH 7.2. After removal from the skulls the brains were fixed for 24 h in the perfusion solution. They were kept for another 24 more hours in a 5% solution of sucrose in the 0.1 M phosphate buffer of pH 7.2. The brains were cut on a freezing microtome into 50 μm slices. Incubation was then carried out in 0.05% solution of 3.3' — diaminobenzidine and afterwards, in the same solution plus 3% H₂O₂ (0.3 ml/100 ml incubation solution).

The HRP was injected into the amygdaloid nuclei by two stereotactic approaches; the micropipette with the HRP solution was inserted either (i) through the dorsal cerebral cortex and the striatum, or (ii) through the piriform cortex. A detailed description of the histological and surgical procedures was given in an earlier publications (24, 25).

RESULTS

Cells containing HRP labeled granules were found in various nuclei and areas of the hypothalamus. The examples of the results obtained following HRP injections into the amygdaloid nuclei presented below are chosen as the most characteristic ones.

*Distribution of the HRP labeled neurons in the lateral division of the hypothalamus and preoptic area*

The HRP labeled cells were numerous here. They were found in the most laterally situated parts of the lateral preoptic area and in the lateral hypothalamic area proper (Fig. 2).

In the most lateral preoptic area of rat numerous, large cells may be seen. Their derivation is still controversial. Divac (10) defined them as magnocellular nuclei of the basal forebrain. According to our own observations and the results of cytoarchitectonic studies by Swanson (36) in this most lateral region of the preoptic area two structures may be differentiated: (i) magnocellular preoptic nucleus situated ventrally and (ii) a dorsally situated area containing loosely scattered large cells probably corresponding in some respect to the substantia innominata of other animals.

The anterior pole of the magnocellular preoptic nucleus is found in the frontal sections through the posterior portion of nucleus accumbens, while its posterior pole reaches the anterior hypothalamus. This nucleus for the most part corresponds to Gurdijan’s “nucleus intersti-
tialis septo-hypothalamicus" as well as Price and Powell's "nucleus of the horizontal limb of the diagonal band" (13, 31, 32).

The substantia innominata cells are seen anteriorly at the level of the posterior part of the nucleus accumbens; they are clearly visible in all frontal sections through the preoptic area and the anterior pole of the hypothalamus up to the level of the optic chiasma.

The HRP labeled cells in the ventral part of the most lateral region of the preoptic area — magnocellular preoptic nucleus. In rat R-30 the HRP injection involved nearly all the nuclei of the amygdala (Fig. 1).

Fig. 1. Localization of large HRP injection into the amygdala of the rat R30. The injection site is marked in black. Slight diffusion of the enzyme is indicated by hatches. 1-3: Frontal sections in the rostro-caudal order. Distribution of the HRP labeled cells following injection is shown in Fig. 2.

Rather numerous HRP labeled cells were observed in the preoptic magnocellular nucleus (NPM; Fig. 2). They contained generally relatively few HRP labeled granules.

In almost all cases where the HRP injections involved a single amygdaloid nucleus (Fig. 4) (the basal dorsal nucleus — rat R95, the basal ventral nucleus — rat R94, the anterior parts of the basal ventral and cortical nuclei — rat R45, posterior part of the cortical nucleus — rat R76, the central nucleus — rat R60, the medial nucleus — rat R57) the HRP labeled cells were observed in the preoptic magnocellular nucleus. Only after injections involving the lateral nucleus of the amygdala — rat R20, no HRP labeled cells were found in the preoptic magnocellular nucleus (Fig. 5). Certain differences could be seen in the topographical distribution of the labeled cells in the magnocellular preoptic nucleus following injections of particular nuclei of the amygdaloid body. After injections of the cortical nucleus and basal ventral nucleus labeled cells appeared mainly in the vicinity of the anterior pole of the preoptic magnocellular nucleus (Fig. 4, rat R45). In the remaining cases the distribution of the labeled cells was more uniform. The magnocellular preoptic nucleus in its rostral part abuts medially on the nucleus of
the horizontal limb of the diagonal band. Following the HRP injection into various amygdaloid nuclei, single labeled cells in the nucleus of the horizontal limb of the diagonal band were sometimes observed.

Fig. 2. Distribution of the HRP labeled cells in the hypothalamus and preoptic area in rat R30 following the injection shown in Fig. 1. Dots represent labeled cells. 1–11: Frontal sections in the rostro-caudal order.

The HRP labeled cells in the dorsal part of the most lateral region of the preoptic area-substantia innominata. Following a large injection into the amygdaloid nuclei (Figs. 1 and 2, rat R30) the HRP labeled cells were observed in the whole dorsal part of the most lateral preoptic area (SI, Figs. 2 and 3A). They were comparatively more numerous than in the magnocellular preoptic nucleus. The labeled neurons were often clustered in the form of small islands consisting of several average five cells. These were generally cells characte-
ristically round in shape. The labeled cells were comparatively most numerous in the frontal sections passing through the anterior commissure. They were situated mainly inferolaterally to the bed nucleus of the stria terminalis.

A similar localization of the HRP labeled cells was found in rats R95 and R60 following the HRP injections into the basal dorsal nucleus and into the medial and intermediate parts of the central nucleus (Fig. 4, rats R95 and R60). In cases where the HRP injections involved other nuclei of the amygdala (lateral, basal ventral, medial or cortical nuclei) cells containing HRP labeled granules were not observed in the substantia innominata.

The HRP labeled neurons in the lateral hypothalamic area proper. Following large injection into the amygdala HRP labeled cells were observed in two regions of the proper lateral hypothalamic area: (HL, Fig. 2) inferolaterally to the medial forebrain bundle and in the perifornical region. They appeared in the intermediate and posterior parts of the hypothalamus; and predominantly in the frontal sections passing through the ventromedial hypothalamic nucleus. Cells located inferolaterally to medial forebrain bundle were most often of medium size and contained many HRP labeled granules. There were a few of them in one section.

In the perifornical region the HRP labeled cells were found in various positions in relation to the column of fornix, sometimes above and often below or medially. These were mostly quite large oval cells; however, sometimes they were very elongated and fusiform. Generally these neurons contained few HRP labeled granules. The number of labeled neurons were slightly smaller here than in the immediate vicinity of the medial forebrain bundle.

Similarly situated HRP labeled cells were observed following small injections of the HRP into the posterior part of the cortical nucleus (Fig. 4, rat R76) or the posterior portion of the medial nucleus (Fig. 4, rat R57). In cases where injections involved other single amygdaloid nuclei (the basal dorsal, basal ventral or the anterior part of the cortical nucleus) the labeled cells appeared rather sporadically (Fig. 4, rats R95, R94 and R45) and they were regularly observed after injections involving selectively the central nucleus (Fig. 4, rat R60). The labeled cells were not observed in the lateral hypothalamic area following injections into the lateral nucleus (Fig. 5, rat R20). In addition the HRP labeled cells were found in the ventral tegmental area which is sometimes considered as belonging to the lateral hypothalamus. Data concerning the location of labeled cells in this area were presented in another publication (25).
Distribution of the HRP labeled neurons in the medial division of the hypothalamus and preoptic area

After large injections of the HRP involving most of the amygdaloid nuclei, labeled cells appeared in many structures of the medial hypothalamus, mainly in the ventromedial, ventral premammillary and the posterior nuclei (Figs. 1 and 2, rat R30). Besides, labeled neurons appeared sporadically, in the supramammillary, the dorsal premammillary nuclei, and also in other areas of the tuber cinereum.

The HRP labeled neurons in the ventromedial hypothalamic nucleus. In rat R30 following a large injection of the HRP to the amygdaloid nuclei labeled cells were primarily found in the ventrolateral portion of ventromedial nucleus (VM, Fig. 2). There were several of them in each section. In the central and the dorsomedial portion of the nucleus — they appeared less frequently. Labeled cells were located primarily in the peripheral part of the nucleus, more rarely appearing in its central part. The labeled cells found here were small, oval, containing comparatively few HRP labeled granules.

Similarly located labeled cells in the ventromedial hypothalamic nucleus were found following injections selectively involving the medial nucleus, and mainly its posterior part (Fig. 4, R57). The HRP labeled cells in the ventromedial hypothalamic nucleus were clearly visible, although much less numerous, after injections into the central nucleus. The labeled cells were not observed in the ventromedial nucleus following injections involving other amygdaloid nuclei: basal dorsal, basal ventral, cortical or lateral (Fig. 4, rats R95, R94, R45, R76 and Fig. 5, rat R20).

After large injections into the amygdala and smaller ones involving only the medial nucleus the HRP labeled neurons were sometimes seen in various areas of the tuber cinereum (Figs. 1, 2 and 3). They appeared here in small numbers, rather sporadically and were located anteriorly in the area of tuber cinereum, lying above the ventromedial hypothalamic nucleus.

The HRP labeled cells in the ventral premammillary nucleus. In the rat R30 following a large injection of the HRP into the amygdala, significant numbers of labeled neurons were observed in the ventral premammillary nucleus (PV, Figs. 1 and 2). They were situated in the central part of the nucleus, which contain tightly packed medium size cells. Labeled cells of the ventral premammillary nucleus were numerous and contained many distinct HRP labeled granules.

A similar location and distribution of the labeled cells in the ventral
Premammillary nucleus was observed after injections involving only the medial nucleus (Fig. 4, R57). Single labeled cells appeared here following selective injections into the posterior part of the cortical nucleus (Fig. 4, R76). After injections into other amygdaloid nuclei no HRP labeled cells were seen in the ventral premammillary nucleus (Fig. 4, R95, R94, R60 and Fig. 5, R20).

The HRP labeled cells in the posterior hypothalamic nucleus. In the posterior hypothalamic nucleus only single HRP labeled cells were found, 1–2 in respective sections. They appeared after large injections of HRP to the amygdala (NP, Fig. 2, rat R30) and also in cases of small injections involving the medial nucleus (Fig. 4, R57).

Moreover, after large injections of HRP to the amygdala (Figs. 1 and 2, R30) labeled cells appeared sporadically in the dorsal premammillary nucleus and in the supramammillary nucleus. Labeled neurons of the latter contained many granules. In cases of small injections single labeled cells in the dorsal premammillary nucleus were observed after injections limited to the medial nucleus while in the supramammillary nucleus after injections, selectively involving the medial nucleus or posterior part of cortical nucleus, and sometimes after injections into the rostral part of the cortical nucleus.

_Distribution of HRP labeled neurons in the bed nucleus of the stria terminalis_

The HRP labeled cells following injections into the majority of nuclei of the amygdala (Fig. 1, rat R30) were seen primarily in the inferoposterior portion of the bed nucleus of the stria terminalis. They were visible in frontal sections through the posterior region of the preoptic area and anterior hypothalamus; in the part of the nucleus which lies just above the lateral and medial portion of the preoptic area and anterior hypothalamus (NST, Fig. 2). This area of the bed nucleus of the stria terminalis corresponds to “medial preoptic hypothalamic junction area” according to de Olmos and Ingren (9). The labeled cells here were of medium size and oval shape, they contained many HRP labeled granules. Besides, several HRP labeled cells appeared in the anterolateral area of the bed nucleus of stria terminalis; all of them were located along the lateral edge of the nucleus.

Following small injections involving the medial nucleus (Fig. 4, R57) or the posterior part of the cortical nucleus (Fig. 4, R76) HRP labeled cells appeared in the above described posteroinferior portion of the bed nucleus of the stria terminalis; whereas in the anterolateral portion of this nucleus labeled cells were seen following injection involving basal dorsal nucleus (Fig. 4, R95).
Fig. 3. Dark field microphotographs of labeled cells from the substantia innominata (A) and ventral premammillary nucleus (B) in rat R30.

Fig. 4. Localization of small HRP injections into single amygdaloid nuclei. Injections involve mainly: basal dorsal nucleus (rat — R95), basal ventral nucleus (rat — R94), anterior parts of the cortical and basal ventral nuclei (rat — R45), posterior part of the cortical nucleus (rat — R76), central nucleus (rat — R60), and medial nucleus (rat — R57). Denotations as in Fig. 1.
Fig. 5. Localization of a small HRP injection into the lateral amygdaloid nucleus (rat-R20). No labeled cells in the preoptic-hypothalamic area following this injection were observed.

Fig. 6. Diagram showing the origin and termination of the amygdalopetal axons arising from the ventral part of the most lateral region of the preoptic area (preoptic magnocellular nucleus). Amygdaloid nuclei supplied by these axons are indicated by hatches.

Fig. 7. Diagram of the origin and termination of the amygdalopetal axons arising from the dorsal part of the most lateral region of the preoptic area (probably substantia innominata). Denotations as in Fig. 6.

Fig. 8. Diagram of the origin and termination of amygdalopetal axons arising from the lateral hypothalamus (lateral hypothalamic area and perifornical region). Denotations as in Fig. 6.
CONCLUSIONS AND DISCUSSION

The experimental results lead to the conclusion that all nuclei of the amygdaloid body — excluding the lateral nucleus receive direct afferent connections from the hypothalamus or from neurons of the basal forebrain: the preoptic area and the bed nucleus of the stria terminalis.

These connections either terminate in a dispersed manner in most of the nuclei of the amygdaloid body or end in one or more of its.

Amygdalopetal axons emerging from neurons of the magnocellular preoptic nucleus seem to extend to most of the amygdaloid nuclei (Fig. 6). The only exception is the lateral nucleus of the amygdala, which probably also receive no afferent connections from the hypothalamus and other preoptic areas. The neurons of the magnocellular preoptic nucleus seem to be the only source of the preoptic and hypothalamic projections running to the cortical and basal ventral nuclei. The investigations by Beckstead (1) indicate that the magnocellular preoptic nucleus sends also projections to the entorhinal cortex as well.

According to results of Price and Powell (31, 32) and Swanson (36), the magnocellular preoptic nucleus has reciprocal connections with the olfactory bulb, and projects to various areas of the limbic system, including the amygdala. It may thus be supposed that the magnocellular preoptic nucleus transmits impulses from the olfactory bulb to the amygdaloid nuclei while receiving reciprocal projections from the amygdala.

Among the amygdalopetal axons which arise in the preoptic-hypothalamic area and project to particular amygdaloid nuclei, we may distinguish connections which emerge from: (i) dorsal area of most lateral region of the preoptic area, (ii) the proper lateral hypothalamic area, (iii) the medial hypothalamus.

The neurons located in the dorsal part of most lateral region of the preoptic area seem to correspond well to the substantia innominata, although according to Divac (10) no substantia innominata is present in the rat's brain.

Amygdalopetal connections which arise from neurons situated in the extreme dorso-lateral preoptic area end in the basal dorsal nucleus and in the medial and intermediate parts of the central nucleus (Fig. 7). The presence of these amygdalopetal connections in the brain of the rat was suggested by earlier experimental results carried out by silver degeneration methods and autoradiography (26, 27, 36).

Amygdalofugal axons arising from the basal dorsal and central nuclei of the amygdala have been found to terminate in the substantia
innominata (16, 36). Experimental data indicate that some projections from the brainstem, among others from the taste and auditory areas, also terminate in the substantia innominata of the primates (14, 29, 30). Moreover, large neurons of substantia innominata, like the neurons of other magnocellular nuclei of the basal forebrain, project abundantly to various cortical areas (10). It is possible that the neocortex sends out axons to the substantia innominata, from which, in turn, it receives projections. In this way, the neocortex may directly influence the amygdala. The data on the function of the substantia innominata are scanty, but some authors (7, 14) suggest that it may exert an effect on the emotional behavior and feeding activities. This would explain the role of the amygdalopetal projections arising from this area.

The axons of the amygdalopetal projection from the substantia innominata terminate mainly in the basal dorsal nucleus and the medial part of the central nucleus. The basal dorsal nucleus according to our data, in turn, send out short axonal projections to almost all the remaining nuclei of the amygdala (23).

The neurons located in the lateral hypothalamic area proper project mainly to the medial amygdaloid nucleus and to the posterior part of the cortical nucleus; and, to a lesser degree to the central nucleus and may be to other nuclei of the amygdala (Fig. 8).

These connections have not been previously reported. They were not apparent in our studies carried out by silver degeneration methods (26, 27). The amygdalofugal connections running to the lateral hypothalamus were described by Krettek and Price (16). According to these investigators, these paths begin in the medial, cortical and central amygdaloid nuclei.

Studies on the lateral hypothalamus indicate that its function is related to the control of some drives, and, predominantly, the control of feeding activities and flight and defense responses (11, 12, 15). It is considered that the medial and cortical and perhaps the also basal ventral amygdaloid nuclei, are functionally related to the lateral hypothalamus (15). Stimulation of these nuclei may induce hyperphagia, and hypophagia may result from their injury. Opposite alimentary reactions are obtained from the basal dorsal amygdaloid nucleus. There is no evidence that the basal dorsal amygdaloid nucleus is directly connected to the lateral hypothalamus. It may, however, exert its effect on the lateral hypothalamus by acting through the medial amygdaloid nucleus to which it projects by short intraamygdaloid connections (23).

An amygdalopetal projection, similar to that originating in the neurons of the lateral hypothalamus, seems to arise from the cells located in the infero-posterior portion of the bed nucleus of the stria
terminalis. The fibers beginning here terminate in the medial nucleus and the posterior part of the cortical nucleus.

Amygdalopetal connections emerging from the medial hypothalamus. Several structures of the medial hypothalamus seem to send out projections to amygdala. They arise mainly from the ventromedial, ventral premammillary and the posterior nuclei. Some axons may also originate in other areas of the tuber cinereum, in the dorsal premammillary and the supramammillary nuclei. They terminate primarily in the medial nucleus, and also in the central and the posterior part of the cortical amygdaloid nuclei (Fig. 9). With regard to the cortical amygdaloid nucleus we may assume that impulses from the medial hypothalamus are conducted there mainly indirectly via the medial nucleus, which sends out a large intraamygdaloid projection to the cortical nucleus (8, 17, 23).

The amygdalopetal projections arising from the ventromedial hypothalamic nucleus, as established in this report, are in agreement with autoradiographic studies by other authors (5, 34). Renaud and Hopkins (33) who injected the HRP into the amygdala, also found labeled cells in the ventromedial hypothalamic nucleus of the rat. The results of the present report, however, do not fully agree with those of the above authors.

Our observations together with those of other investigators (8, 16) show that connections between the amygdala, on one side, and the

Fig. 9. Diagram of the origin and termination of amygdalopetal axons arising from the nuclei of the medial hypothalamus. Amygdaloid nuclei supplied by these axons are indicated by hatches; broken hatches indicate nuclei with probable projections from the medial hypothalamus. Denotations as in Fig. 6.
ventromedial nucleus and the premammillary area, on other, are reciprocal.

The interconnected areas of the medial hypothalamus (the area of tuber cinereum including the ventromedial nucleus) and the amygdala (the medial and cortical nuclei) have, according to Kaada (15) an activating effect on the sexual behavior, e.g. they induce ovulation, release of gonadotropins and uterine movements.

As mentioned before the amygdaloid lateral nucleus is the only part of the amygdala which probably neither sends out nor receives projections to or from the hypothalamus and the basal forebrain nuclei. Nevertheless, the lateral, amygdaloid nucleus receives direct projections from the posterior-thalamic region and the peripeduncular nucleus (14, 21). The pulvinar-posterior system of the thalamus, as a whole is involved in the integration of a variety of sensory inputs. This permits an assumption that the impulses conducted by these projections are related to sensory perception.

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REFERENCES

10. DIVAC, J. 1975. Magnocellular nuclei of the basal forebrain project to neo-


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ABBREVIATIONS

Ac  nucleus accumbens
ALH  lateral hypothalamic area
BD  basal dorsal nucleus of the amygdala
BV  basal ventral nucleus of the amygdala
C  central nucleus of the amygdala
Ca  anterior commissure
CM  mammillary body
Co  cortical nucleus of the amygdala
Coa  cortical nucleus of the amygdala (anterior part)
Cop  cortical nucleus of the amygdala (posterior part)
DM  dorsomedial nucleus of the hypothalamus
F  fornix
FPM  medial forebrain bundle
HA  anterior hypothalamic area
HL  lateral part of the hypothalamus
L  lateral nucleus of the amygdala
LM  lemniscus medialis
M  medial nucleus of the amygdala
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<th>Abbreviation</th>
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<tr>
<td>NP</td>
<td>posterior nucleus of the hypothalamus</td>
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<td>NPM</td>
<td>preoptic magnocellular nucleus</td>
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<td>NST</td>
<td>bed nucleus of the stria terminalis</td>
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<td>NTOL</td>
<td>nucleus of the lateral olfactory tract</td>
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<td>PD</td>
<td>dorsal premammillary nucleus</td>
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<td>PL</td>
<td>lateral preoptic area</td>
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<td>PM</td>
<td>medial preoptic area</td>
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<td>PV</td>
<td>ventral premammillary nucleus</td>
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<td>RP</td>
<td>perifornical region</td>
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<td>SI</td>
<td>substantia innominata</td>
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<td>supramammillary nucleus</td>
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<td>ventromedial nucleus of the hypothalamus</td>
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