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The dorsal premammillary nucleus: An unusual component of the mammillary body

(hypothalamus/anterior thalamus/periaqueductal gray/limbic circuitry/motivated behavior)

N. S. CANTERAS* AND L. W. SWANSON†

Department of Biological Sciences, University of Southern California, Los Angeles, CA 90089-2520

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ABSTRACT **The results of anterograde and retrograde axonal transport experiments in the rat indicate that the dorsal premammillary nucleus (PMd) gives rise to a branched pathway ending in the anterior thalamic group and brainstem, like the medial and lateral mammillary nuclei. However, unlike these nuclei, the ascending PMd projection courses through and to the anterior hypothalamic nucleus, and the descending PMd projection ends in the periaqueductal gray, superior colliculus, and adjacent parts of the reticular formation. Also unlike the traditional mammillary nuclei, the PMd does not receive a direct input from the columns of the fornix; instead, it receives a bilateral input from the anterior hypothalamic nucleus, which in turn receives inputs from areas related to the prefrontal cortex, amygdala, and hippocampus. The results provide interesting perspectives on the organization of medial hypothalamic circuits underlying the goal-oriented behaviors associated with hunger, thirst, and reproduction.**

The medial zone of the hypothalamus contains a longitudinally arranged series of well-defined nuclei that play a critical role in expression of goal-oriented behaviors, ensuring survival of the individual (homeostasis) as well as the species (reproduction) (1). And while the input/output relationships of the medial zone are complex, the nuclei are dominated by afferents from limbic regions of the telencephalon that clearly divide them into two groups: caudal (mammillary) and rostral. The mammillary group receives a major input from the postcommissural fornix, which arises in the subicular complex of the hippocampal formation (2–5) and is a major component of the classical "Papez circuit" (6), which is now thought to play a role in learning and memory (7–10). In contrast, the rostral group of medial zone nuclei receives massive inputs from the amygdala (11), ventral subiculum (3, 11), and lateral septal nucleus (12) that are dominated by olfactory information and play a role in expression of ingestive and reproductive behaviors (1). The separation of medial hypothalamic nuclei into rostral and caudal groups is also strengthened by evidence that few pathways appear to interconnect the two, and most ascending inputs from the brainstem end in one or the other (1). Thus, the neuroanatomical evidence indicates that information processed in the rostral nuclei of the medial hypothalamus has no major direct access to the Papez circuit.

While reexamining the projections of the medial hypothalamic nuclei by the *Phaseolus vulgaris* agglutinin L (leukoagglutinin) subunit (PHA-L) method (13), we found that a previously unexplored cell group, the dorsal premammillary nucleus (PMd), projects to the anterior thalamic nuclei and to the upper brainstem, much like the medial and lateral mammillary nuclei, but appears to receive its major input from the anterior hypothalamic nucleus (in the rostral medial group) rather than from the postcommissural fornix (4, 14). These observations form the basis of the work reported here, which suggests that the PMd provides a link between the rostral and caudal groups of the medial hypothalamus.

MATERIALS AND METHODS

Adult male Sprague–Dawley rats (275–330 g) were used in all experiments.

Anterograde Tracing Experiments. Ten animals received an injection of PHA-L (Vector Laboratories) aimed at the PMd, according to methods described in detail elsewhere (13, 15).

Retrograde Tracing Experiments. Five animals received a unilateral iontophoretic deposit of a 2% solution of fluorogold (Fluorochrome, Englewood, CA; see ref. 16) in 0.9% saline placed stereotaxically into the region of the anteromedial nucleus of the thalamus. After the animals were anesthetized with tribromoethanol, deposits were made through a glass micropipette (tip diameter, 40 μm), with a positive current of 5 μA applied every other 7 sec for 15 min. Two of these rats also received a deposit of 0.2 μl of a concentrated solution of rhodamine-labeled fluorescent latex microspheres (Luma-Fluor, New York) in the region of the periaqueductal gray, delivered by slow-pressure injection from a stereotaxically positioned 26-gauge needle attached to a 1-μl Hamilton syringe. After a survival time of 1 week, the animals were deeply anesthetized and perfused transcardially with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). The brains were then removed and postfixed overnight in the perfusate with 10% (wt/vol) sucrose added. Two series of 30-μm-thick sections were cut on a sliding microtome in the frontal plane and collected at the level of the injection sites and through the region of the PMd. In one series, the sections were mounted onto gelatin-coated slides and coverslipped with methyl salicylate. The adjacent series was always stained with thionin for cytoarchitectonic purposes. A Leitz Dialux 20 microscope equipped with epifluorescence was used for observation of the fluorescent material. Fluorogold was visualized with Leitz filter system A (which provides wide-band UV excitation wavelengths) and the rhodamine-labeled fluorescent latex microspheres were visualized with Leitz filter system N2, which provides narrow-band green excitation, thus allowing detection of doubly labeled cells.

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Abbreviations: PMd, dorsal premammillary nucleus; PHA-L, *Phaseolus vulgaris* agglutinin L subunit.

*Present address: Department of Physiology and Biophysics, Institute of Biomedical Sciences, University of São Paulo, São Paulo 05508, Brazil.

†To whom reprint requests should be addressed at: Hedco Neuroscience Building, mc 2520, Department of Biological Sciences, University of Southern California, University Park Campus, Los Angeles, CA 90089-2520.

RESULTS

Neuronal Output of the PMd. In 3 of 10 experiments, the PHA-L injection labeled a large number of neurons in the PMd. In one experiment (PMd-8), labeled neurons were entirely confined within the nucleus, which stretches <400 μm rostrocaudally (Fig. 1), whereas in the other two experiments, the injection also labeled a few neurons in the adjacent ventral premammillary and posterior hypothalamic nuclei. In all three experiments, the injection site did not involve any part of the medial mammillary nucleus lying immediately caudal to the PMd. The overall pattern of labeled projections in experiment PMd-8 was confirmed in the other experiments. The following description is based on experiment PMd-8, which is illustrated in detail in Fig. 2.

The vast majority of labeled fibers arising from the injection site travel dorsally through the posterior hypothalamic nucleus and then follow an ascending and/or a descending course. Although fibers coursing through the posterior hypothalamic nucleus tend to be poorly branched, many labeled terminal boutons were found in more rostral parts of this nucleus and in the immediately adjacent magnocellular part of the subparafascicular nucleus (Fig. 2 *G* and *H*). The ascending group of fibers initially courses dorsal to the dorsomedial nucleus, just medial to the mammillothalamic tract, providing a significant input to the A13 dopaminergic group and adjacent medial regions of the rostral zona incerta (Fig. 2*F*). At caudal levels of the hypothalamic paraventricular nucleus, many of these fibers enter the anterior hypothalamic area, whereas another group of labeled axons continues dorsally to end primarily in a clearly defined ventral part of the anteromedial nucleus of the thalamus (Fig. 2*E*). The anterior hypothalamic nucleus constitutes by far the densest hypothalamic terminal field for axons from the PMd, and labeled fibers and terminal boutons were particularly abundant in the posterior and central parts of the nucleus (Figs. 2 *B–E* and 3). At this level, we also observed a moderate plexus of fibers and terminal boutons surrounding the fornix and a much sparser plexus of fibers in more ventral regions of the lateral hypothalamic area (Figs. 2 *B–D* and 3). At more rostral levels, a moderate number of fibers coursing through the anterior hypothalamic area appear to veer dorsally toward rostral parts of the thalamus (Fig. 2*C*). In addition, a few fibers from the PMd may continue rostral to the anterior hypothalamic area to provide a very sparse input to the medial preoptic area and septal region (Fig. 2 *A* and *B*). In addition to this massive bundle of fibers ascending from the PMd, a much smaller number of labeled axons also takes a ventral route from the nucleus, providing a sparse input to the basal lateral hypothalamic area adjacent to the ventromedial nucleus (Fig. 2 *E–H*).

Within the thalamus, the PMd supplies a dense plexus of highly branched axons with an overwhelming number of terminal boutons that tend to be circumscribed to a ventral part of the anteromedial nucleus of the thalamus that can be distinguished cytoarchitectonically by its larger, more deeply stained, and more densely packed neurons (Figs. 2 *C–E* and 3). Only a few scattered labeled fibers were observed in other parts of the anterior thalamic group. The PMd also provides a moderate innervation to the thalamic paraventricular nucleus and especially the nucleus reuniens, where a dense plexus of fibers was observed in rostral parts of the nucleus adjacent to the anteromedial nucleus (Fig. 2*C*). Other thalamic nuclei, including the parataenial, interanterodorsal, interanteromedial, rhomboid, central lateral, lateral posterior, and medial zone of the ventral lateral geniculate nucleus (data not shown) appear to receive a very sparse input from the PMd. Although the ascending projections of the PMd are mostly ipsilateral, at rostral levels of the thalamus a number of fibers cross the midline to provide a moderately dense terminal field to the ventral part of the anteromedial nucleus on the opposite side of the brain.

A vast majority of descending fibers from the PMd course initially through the posterior hypothalamic nucleus to enter the periaqueductal gray (Fig. 2 *H* and *I*), whereas only a few labeled fibers extend caudally to end in the supramammillary nucleus and cell-free zone around the medial mammillary nucleus (Fig. 2 *I* and *J*). Labeled fibers in the rostral periaqueductal gray form a dense terminal field immediately lateral to the subcommissural organ and in a region just dorsal to the posterior commissure (Fig. 2 *I* and *J*). At this level, some fibers course laterally to provide a sparse input to parvicellular parts of the subparafascicular nucleus (Fig. 2*I*), and a larger group of labeled axons enters the pretectal region and then apparently courses rostrally to end in the paraventricular, central lateral, and lateral posterior nuclei of the thalamus (Fig. 2 *G–I*). More caudally, axons from the PMd generate a strikingly dense terminal field centered in the dorsolateral sector of the periaqueductal gray, whereas a much smaller number of fibers appear to end in its dorsal and ventrolateral parts (see ref. 17 for parcellation of the central gray) (Fig. 2 *K* and *L*). A moderate number of fibers coursing through the central gray enter the deep and intermediate layers of the superior colliculus and, to a lesser extent, caudal regions of the mesencephalic reticular formation (Fig. 2 *J* and *K*). At caudal levels of the periaqueductal gray, a moderate number of fibers reach the cuneiform nucleus, which seems to be the caudalmost region innervated to any extent by the PMd (Fig. 2*L*); only a very few axons continue into the

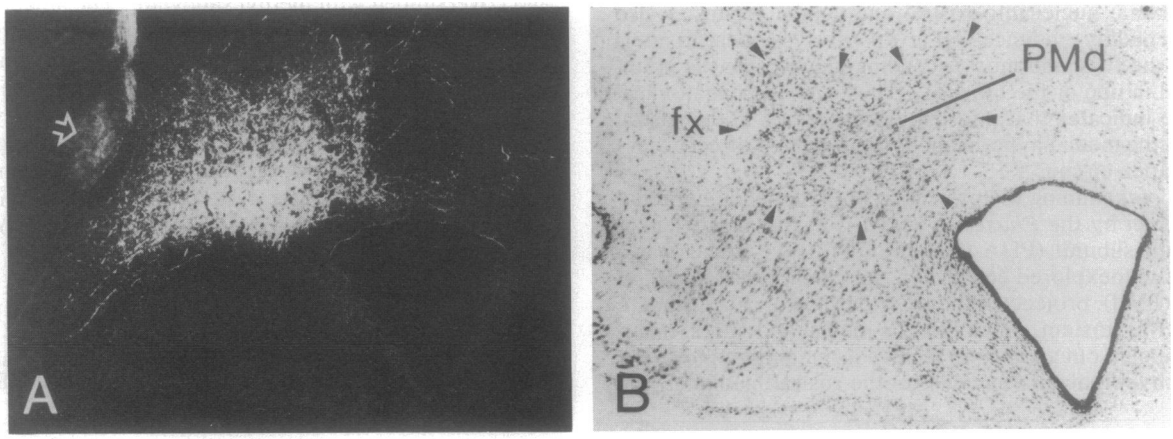

FIG. 1. (*A*) Dark-field photomicrograph illustrating the PHA-L injection site in experiment PMd-8; arrow, fornix (fx). (*B*) Bright-field photomicrograph of adjacent thionin-stained section; arrowheads, border of the PMd. (×45.)

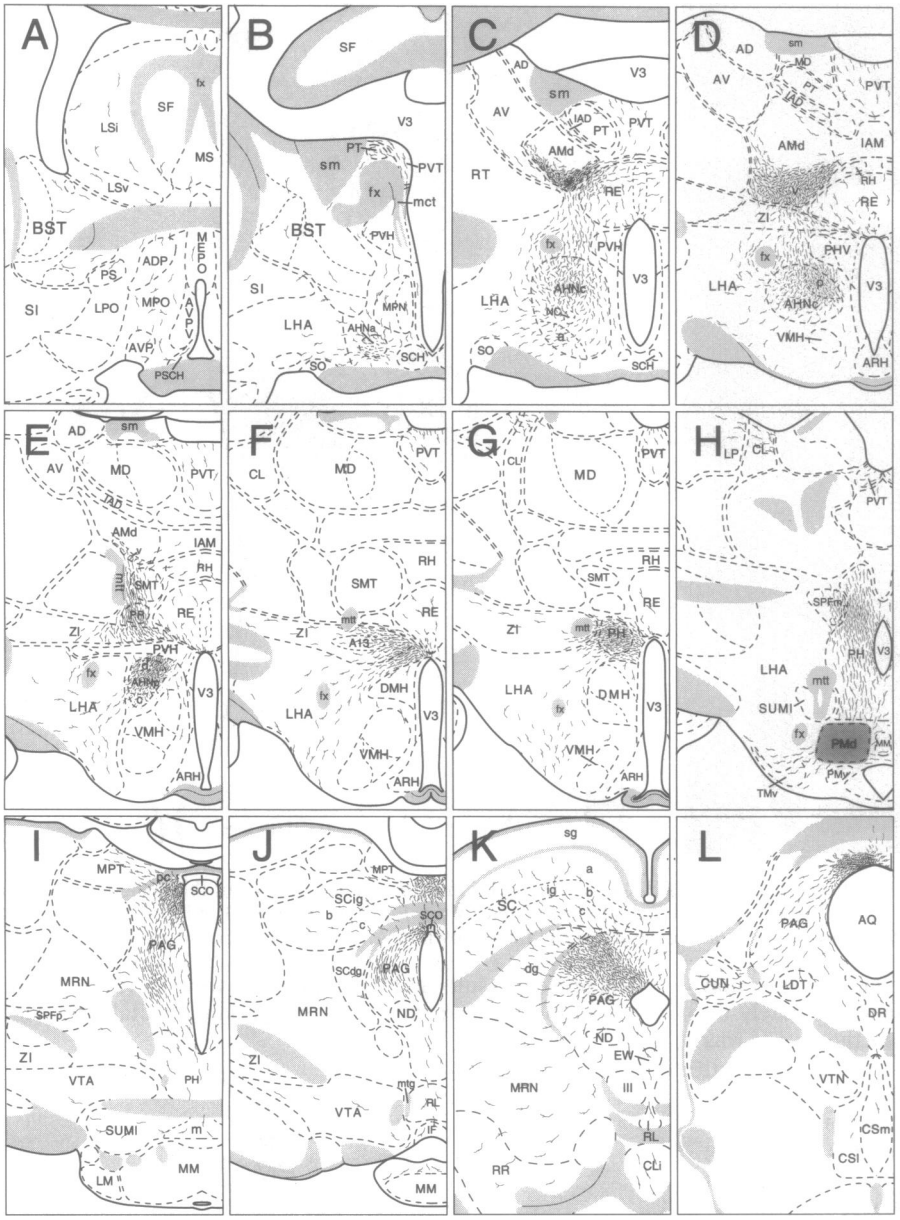

FIG. 2. PHA-L-labeled projections of the PMd (experiment PMd-8). A13, dopaminergic group A13; AD, anterodorsal nucleus (n.); ADP, anterodorsal preoptic n.; AHNa, -c, -d, -p, anterior hypothalamic n., anterior, central, dorsal, posterior parts; AMd, -v, anteromedial n., dorsal, ventral parts; AQ, cerebral aqueduct; ARH, arcuate n.; AV, anteroventral n.; AVP, anteroventral preoptic n.; AVPV, anteroventral periventricular n.; BST, bed nuclei stria terminalis; CL, central lateral n.; CLi, central linear n.; CSl, -m, superior central n., lateral, medial parts; CUN, cuneiform n.; DMH, dorsomedial n.; DR, dorsal n.; EW, Edinger–Westphal n.; fx, fornix; IAD, interanterodorsal n.; IAM, interanteromedial n.; IF, interfascicular n.; III, oculomotor n.; LDT, laterodorsal tegmental n.; LHA, lateral hypothalamic area (a.); LM, lateral mammillary n.; LP, lateral posterior n.; LPO, lateral preoptic a.; LSi, -v, lateral septal n., intermediate, ventral parts; mct, medial corticohypothalamic tract (tr.); MD, mediodorsal n.; MEPO, median preoptic n.; MM, medial mammillary n.; MPN, medial preoptic n.; MPO, medial preoptic a.; MPT, medial pretectal a.; MRN, mesencephalic reticular n.; MS, medial septal n.; mtg, mammillotegmental tr.; mtt, mammillothalamic tr.; NC, n. circularis; ND, n. Darkschewitsch; PAG, periaqueductal gray; pc, posterior commissure; PH, posterior n.; PHV, paraventricular n. hypothalamus; PMd, -v, dorsal, ventral premammillary n.; PR, perireuniens n.; PS, parastrial n.; PSCH, suprachiasmatic preoptic n.; PT, parataenial n.; PVT, paraventricular thalamic n.; RE, n. reuniens; RH, rhomboid n.; RL, rostral linear n.; RR, retrorubral a.; RT, reticular n.; SCdg, -ig, -sg, superior colliculus, deep, inner, superficial gray layers; SCH, suprachiasmatic n.; SCO, subcommissural organ; SF, septofimbrial n.; SI, substantia innominata; sm, stria medullaris; SMT, submedial n.; SO, supraoptic n.; SPFm, -p, subparafascicular n., magnocellular, parvicellular parts; SUMl, -m, supramammillary n., lateral, medial parts; TMv, tuberomammillary n., ventral part; V3, third ventricle; VMH, ventromedial n.; VTA, ventral tegmental a.; VTN, ventral tegmental n.; ZI, zona incerta.

pontine central gray. Throughout the length of the periaqueductal gray, some fibers were also observed to course ventrally where they appear to innervate sparsely the rostral linear and central linear nuclei, the dorsal raphe, and the superior central nucleus. Finally, the contralateral projections from the PMd to the brainstem are basically a mirror image of the ipsilateral projection, although much less dense.

Retrograde Tracing Experiments. To confirm a projection from the PMd to the anterior thalamic group, five animals received an iontophoretic deposit of fluorogold in this part of the thalamus. In all experiments, the injection site was centered in the anteromedial nucleus and involved both the dorsal and ventral parts as well as immediately adjacent parts of the thalamus. In agreement with the results of our anterograde experiments, many retrogradely labeled cells were observed bilaterally within the PMd, where labeled neurons on the side of the fluorogold deposit outnumbered those on the contralateral side. In these experiments, we also confirmed that the projection from the medial mammillary nucleus to the thalamus is almost entirely ipsilateral, in contrast to the projection described here for the PMd, which is bilateral.

Two of the five animals with a fluorogold injection in the thalamus also received a deposit of rhodamine-labeled latex beads in the region of the central gray on the same side of the brain (approximately at level *K* in Fig. 2). In these experiments, we observed a number of doubly labeled neurons in the PMd, demonstrating that at least some neurons in this cell group send collateral branches to the anterior thalamus and to the midbrain, like neurons in the medial and lateral mammillary nuclei.

DISCUSSION

The major conclusion that emerges from our results is that the PMd gives rise to a branched output to the thalamus and brainstem reminiscent of projections from the medial and lateral mammillary nuclei (Fig. 4). Before considering the evidence in detail, and discussing its functional implications, it is important to comment on the methods used to establish these pathways. The major problems we faced were the very small size of the PMd and the possibility of a branched pathway. The first problem was approached by using the highly sensitive and reliable anterograde tracer PHA-L,

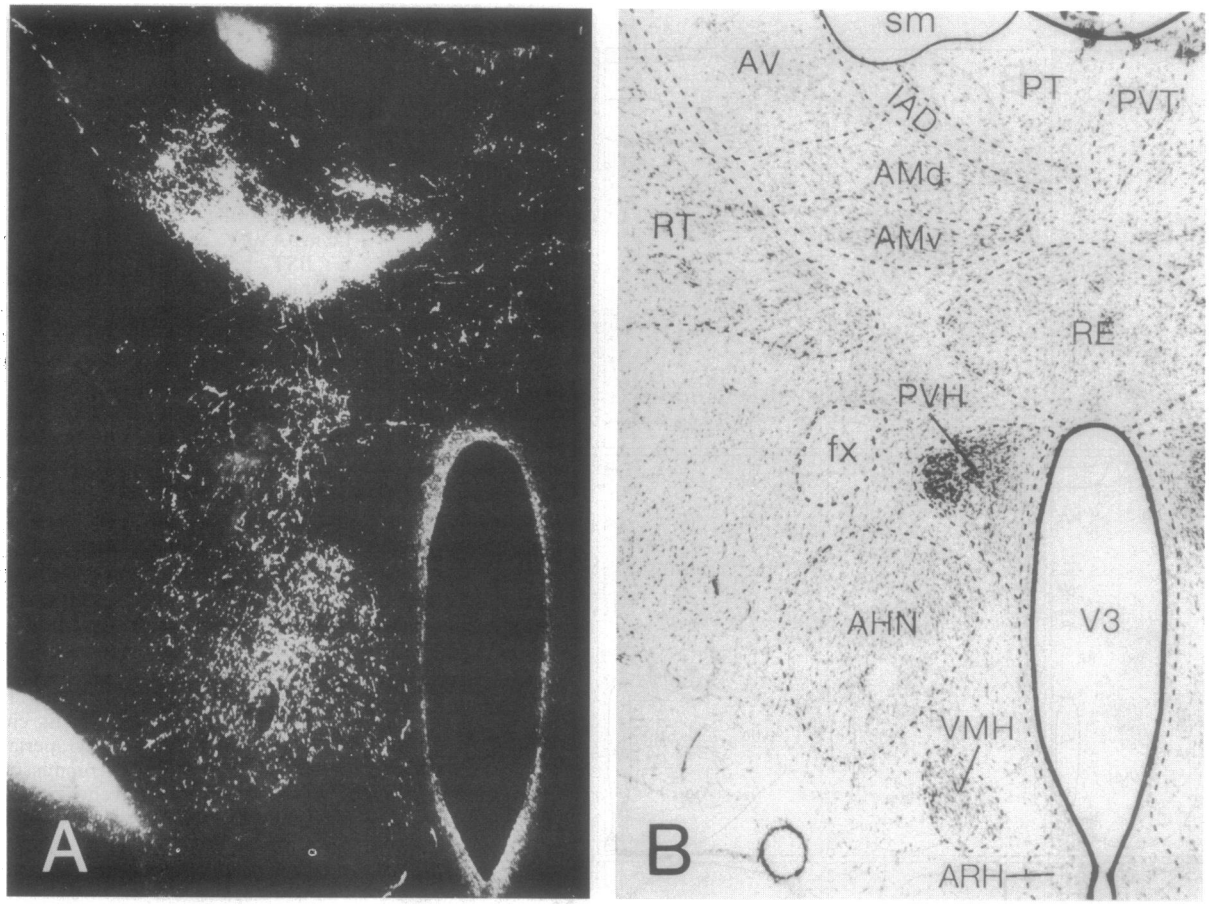

FIG. 3. (*A*) Dark-field photomicrograph to show the distribution of PHA-L-labeled axons in anteromedial nucleus of the thalamus, anterior hypothalamic nucleus, and perifornical region after PHA-L injection virtually restricted to the PMd (experiment PMd-8). (*B*) Bright-field photomicrograph of adjacent thionin-stained section to show cytoarchitecture of the field shown in *A*. For abbreviations, see Fig. 2. (×40.)

which has the great advantage of producing tiny injection sites with boundaries that can be determined accurately by the distribution of labeled cell bodies (13), and the second was approached by using a multiple retrograde tracing method, which also showed independently that neurons throughout the PMd project to the anterior thalamus and/or midbrain.

The PHA-L experiments indicate that the ascending branch of the PMd projection does not course through the mammillothalamic tract but does end massively in the ventral anteromedial nucleus of the thalamus and anterior hypothalamic nucleus; this branch also provides moderate inputs to rostral parts of the zona incerta and nucleus reuniens, and to perifornical areas of the lateral hypothalamic area at the level of the anterior hypothalamic area, as well as sparse inputs to several other diencephalic cell groups. The descending branch of the PMd projection courses to and through the posterior hypothalamic nucleus and ends in specific parts of the periaqueductal gray, deep and intermediate gray layers of the superior colliculus, and caudal parts of the midbrain reticular formation (including the cuneiform nucleus).

The output of the PMd has not been examined previously by anterograde tracing methods; and of all the projections described here, only that to the central gray has been reported in retrograde tracing experiments (18–21). The latter indicate that the PMd contains the highest density of retrograde labeling in the hypothalamus following tracer injections in the central gray. Our work indicates that the PMd densely innervates a region of the periaqueductal gray adjacent to the subcommissural organ, as well as the dorsolateral sector more caudally. Based on previous anterograde tracing studies of other hypothalamic regions (14, 15, 22–25), the PMd supplies the densest known input to the dorsolateral sector. The present results add to a rapidly growing literature on the topographic organization of the periaqueductal gray and

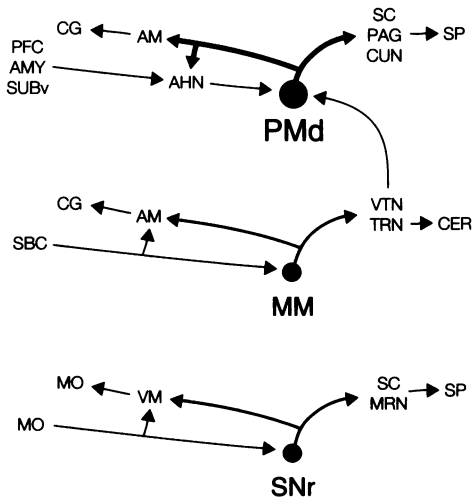

FIG. 4. Major input/output relations of the PMd, medial mammillary nucleus (MM), and reticular part of substantia nigra (SNr). Hypothetical pathway from the periaqueductal gray (PAG) to the spinal cord (SP) may be direct or indirect. AHN, anterior hypothalamic nucleus (n.); AM, anteromedial n. thalamus; AMY, amygdala; CER, cerebellum; CG, cingulate gyrus; CUN, cuneiform n.; MO, motor cortex; MRN, mesencephalic reticular n.; PAG, periaqueductal gray; PFC, prefrontal cortex; SBC, subicular complex; SC, superior colliculus; SP, spinal cord; SUBv, ventral subiculum; TRN, tegmental reticular n.; VM, ventral medial n. thalamus; VTN, ventral tegmental n.

underscore the importance of further work to determine the connections of specific parts of this region, like the dorsolateral sector.

A particularly interesting result of our anterograde tracing experiments was the dense bilateral projection from the PMd to the ventral part of the anteromedial nucleus of the thalamus, a pathway that was confirmed with the retrograde tracer fluorogold. Previous retrograde tracer studies indicate that the ventral part of the anteromedial nucleus, as delineated here, sends fibers to or through the anterior cingulate and retrosplenial areas of the cingulate gyrus as well, perhaps, as to adjacent motor and visual areas of the isocortex (26). The anteromedial nucleus also receives a dense input from the medial mammillary nucleus, which is almost exclusively ipsilateral (27–29), although it is not known whether it extends to the ventral part receiving a bilateral input from the PMd. It is also known that neurons in the medial mammillary nucleus give rise to a bifurcating axon with one branch to the anteromedial nucleus and another to the brainstem, including the ventral tegmental nucleus of Gudden and medial parts of the tegmental reticular nucleus (30). Although neither of these pontine targets receives a projection from the PMd, our retrograde double-labeling experiments indicate that at least some PMd axons bifurcate, sending an ascending branch to the thalamus and a descending branch to the brainstem.

Both the PMd and medial mammillary nucleus receive a dense input from the ventral tegmental nucleus (31), which may thus provide feedback information to the medial mammillary nucleus (31), as well as feedforward information from the medial mammillary nucleus to the PMd, since there is no direct link from the medial mammillary nucleus to the PMd. In view of similarities between the connections of the PMd and medial mammillary nucleus, and the fact that they are immediately adjacent, it is tempting to suggest that the PMd is a rostral component of the mammillary body with unique features.

Unlike other mammillary nuclei, the PMd does not receive a direct input from subicular regions of the hippocampal formation but instead receives a massive input from the anterior hypothalamic nucleus. Previous autoradiographic work suggests that the PMd is a target of the anterior hypothalamic nucleus (4, 14), and we found (unpublished observations) that PHA-L injections here label an exceedingly dense bilateral terminal field in the PMd, similar to that described for inputs to the medial and lateral mammillary nuclei from the subicular complex (2–5). The dense input described here to the anterior hypothalamic nucleus from the PMd may thus represent a feedback loop between these two nuclei.

The anterior hypothalamic nucleus in turn receives heavy direct projections from ventral parts of the lateral septum (12), which themselves convey information from ventral parts of Ammon's horn and the subiculum (3); from the ventral subiculum itself, via the medial corticohypothalamic tract (unpublished observations); and from the infralimbic area of the prefrontal cortex (32). In addition, our unpublished observations with the PHA-L method show that the anterior hypothalamic nucleus is one of the main recipients of fibers arising throughout the ventromedial nucleus. The latter is in turn heavily innervated by the corticomedial nuclei of the amygdala (11) and by other nuclei in the medial zone of the hypothalamus related to the sexually dimorphic circuit, including the medial preoptic nucleus (15) and ventral premammillary nucleus (unpublished observations). Thus, the anatomical evidence as a whole suggests that the massive direct projection from the anterior hypothalamic nucleus integrates and transmits (either directly or indirectly) information from the prefrontal cortex, amygdala, hippocampus, and septal region to the PMd, and that the only other major input to the nucleus is from the ventral tegmental nucleus.

In summary, the PMd may integrate information both from the mammillary part of the medial zone (which receives inputs primarily from the hippocampal formation) and from rostral parts of the medial zone that play an important role in mediating the goal-oriented behaviors associated with maintaining homeostasis and ensuring reproduction of the species. As such, it may provide an important interface between the two major components of the medial zone. The PMd then sends this information back to one of its two major sources of input (the anterior hypothalamic nucleus), to the hippocampal trisynaptic circuit (by way of the anteromedial nucleus and its outputs), and to motor-related regions of the brainstem, including the superior colliculus and periaqueductal gray. And in an even broader context, the results suggest that caudal nuclei of the medial hypothalamic zone give rise to a bifurcated output similar in many ways to that arising in the caudally adjacent reticular zone of the substantia nigra. It will be of interest to determine whether other cell groups in the medial hypothalamic zone and midbrain form part of a larger complex sharing this fundamental design feature.

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