Thalamic Afferents from the Dorsal Column Nuclei

AN EXPERIMENTAL ANATOMICAL STUDY IN THE RAT

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ABSTRACT The distribution of axons originating in the dorsal column nuclei has been studied using the Nauta technique on brains with lesions restricted to small parts of the gracile and cuneate nuclei. The caudal area of each nucleus projects contralaterally to the ventrobasal complex in a topographical manner and in small amount to the pars medialis of the medial geniculate body. In addition, the rostral part of each nucleus sends axons to the contralateral zona incerta, anterior pretectal nucleus and posterolateral complex within the diencephalon as well as to the collicular plate and pontine protuberance of the brain stem. There is no clear evidence of a projection to the area comparable to the posterior thalamic complex of the cat.

This work establishes the identity of some of the cytoarchitectonic divisions of the rat diencephalon, and indicates that the rostro-caudal differences shown for the dorsal column nuclei are reflected in their ascending projections.

The role of the thalamus in the transmission of somatosensory information to the cortex has been studied in some detail in the monkey and cat. Although the ventrobasal complex is known to play an important part in this activity (e.g. Mountcastle and Henneman, '52; Rose and Mountcastle, '52), it has become obvious that several other thalamic regions are also involved, particularly a posterior region between the ventrobasal and medial geniculate complexes (Whitlock and Perl, '59; Poggio and Mountcastle, '60) and the intralaminar system (Kruger and Albe-Fessard, '60; Whitlock and Perl, '61). The dorsal column nuclei of the cat are now known to be organised in a rostro-caudal sequence with respect to the evoked response following peripheral stimulation (Gordon and Jukes, '64), and there is some evidence that the efferents from these different regions have a differential distribution in the thalamus (Kuypers and Tuerk, '64; Hand and Liu, '66).

Work on the rat thalamus has produced some confusing results, partly because the identity of the thalamic nuclei concerned has not been clearly established; the studies of Le Gros Clark ('32) and of Krieg ('47) are not sufficiently precise to give more than a general indication of the organisation of the ventral thalamic nuclei. Davidson ('65), using the evoked potential method, found responses from the contralateral body surface in a region corresponding to Gurdjian's ('27) nuclei ventralis and ventralis pars dorsomedialis, whilst Emmers ('65) found responses in the nucleus ventralis but in only a very restricted part of the nucleus ventralis pars dorsomedialis. This author also describes a localised second somatic sensory (SII) representation in the nucleus ventralis following peripheral stimulation. Angel and Dawson ('63) found that the dorsal column nuclei (but not, presumably, the trigeminal nuclei) project to virtually the whole of the nucleus ventralis. This is contradicted by Emmers' ('65) work but partially supported by that of Davidson ('65). The present work forms the first part of a study carried out in order to attempt some clarification of these reports and to compare them with the results obtained from other species.

MATERIALS AND METHODS

Twenty adult albino rats were used with lesions restricted to the cytological limits of the dorsal column nuclei. Normal control animals were also studied. All operative procedures were carried out under ether anesthesia with aseptic conditions. A postoperative course of chloramphenicol was used to combat possible

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infection. Cautery and aspiration were tried as methods for making lesions in the gracile and cuneate nuclei, but from the point of view of restriction of necrosis to the nuclei the most satisfactory results were obtained by pricking with a fine suture needle. The dorsal surface of the medulla was approached through the atlanto-occipital membrane and then, immediately before making the lesion, the head of the animal was flexed. By this means the whole length of the gracile and cuneate nuclei could be exposed without retracting or touching the cerebellum or any other neural structure. The lesions themselves were made with virtually no hemorrhage. The head of the animal was returned to the normal position as quickly as possible to avoid kinking of the trachea. Postoperative recovery was usually uneventful.

After 5–8 days' survival the rats were perfused with 10% neutral formol-saline or with buffered formalin (Pease, '64). Fifteen of the brains were subesquently sectioned by the freezing method: in each case a series of one in every five sections cut at 30 μ was stained by the method of Nauta and Gygax ('54) and each adjacent section was cut at 60 μ and stained with cresyl violet acetate. Two of the brains were cut in the horizontal plane, the remainder in the frontal plane. Serial order of frozen sections was maintained by collecting them in divided perspex trays, and staining them in trays similar to those described by Wilson and Cragg ('67). The remaining five brains were embedded in paraffin wax and sectioned frontally at 15 μ. One series of every tenth section from each brain was stained by the modified Nauta method of Guillery, Shirra and Webster ('61), and an adjacent series with cresyl violet acetate. Some further series were stained with the suppressing agent omitted from the first silver bath. Lesions and areas of degeneration were plotted by using a Zeiss microscope projector attachment. The presence of all degeneration was checked against control material. The degeneration plots were finally transferred to a series of standard drawings.

RESULTS

Nomenclature of thalamic nuclei. The scheme to be given by Webster and Lund (in preparation) will be used throughout. This description has the advantage of using a terminology basically similar to that employed in the cat and monkey. The numbers on each section refer to the above atlas in which consecutive numbers indicate separation by approximately 180 μ.

Lesions in the caudal half of the dorsal column nuclei. In all the animals with

Abbreviations

B, nucleus of Bischoff
c, Nucleus cuneatus
cbt, cerebello-thalamic tract
Cl, nucleus centralis lateralis
Cp, cerebral peduncle
DM, nucleus medialis dorsalis
ecn, nucleus cuneatus externus
ep, nucleus entopeduncularis
Fx, fornix
g, nucleus gracilis
hl, nucleus habenularis lateralis
hm, nucleus habenularis medialis
HPt, habenulo-peduncular tract
LD, nucleus lateralis dorsalis
LGd, lateral geniculate complex pars dorsalis
LGvl, lateral geniculate complex pars ventralis lateralis
LGvm, lateral geniculate complex pars ventralis medialis
LPp, posterolateral complex pars paralaminaris
mtt, mammillo-thalamic tract
ML, medial lemniscus
MGm, medial geniculate complex pars medialis
MGp, medial geniculate complex pars principalis
NS, nucleus subthalamicus
Ot, optic tract
Pa, nucleus pulvinaris anterior
Pg, nucleus pulvinaris pars geniculata
Pp, nucleus posterior parabrachialis
Ptad, nucleus pretectalis anterior pars ventralis
R, nucleus reticularis
r, nucleus rhomboidalis
Re, nucleus reuniens
SG, medial geniculate complex pars supragenic-ulata
SM, nucleus submedius
SN, substantia nigra
VB, ventrobasal complex
VL1, nucleus ventralis lateralis pars medialis
VL2, nucleus ventralis lateralis pars lateralis
Vm, nucleus ventralis medialis
Vmp, nucleus ventralis medialis posterior
ZI, zona incerta
5, nucleus trigeminalis spinalis pars caudalis

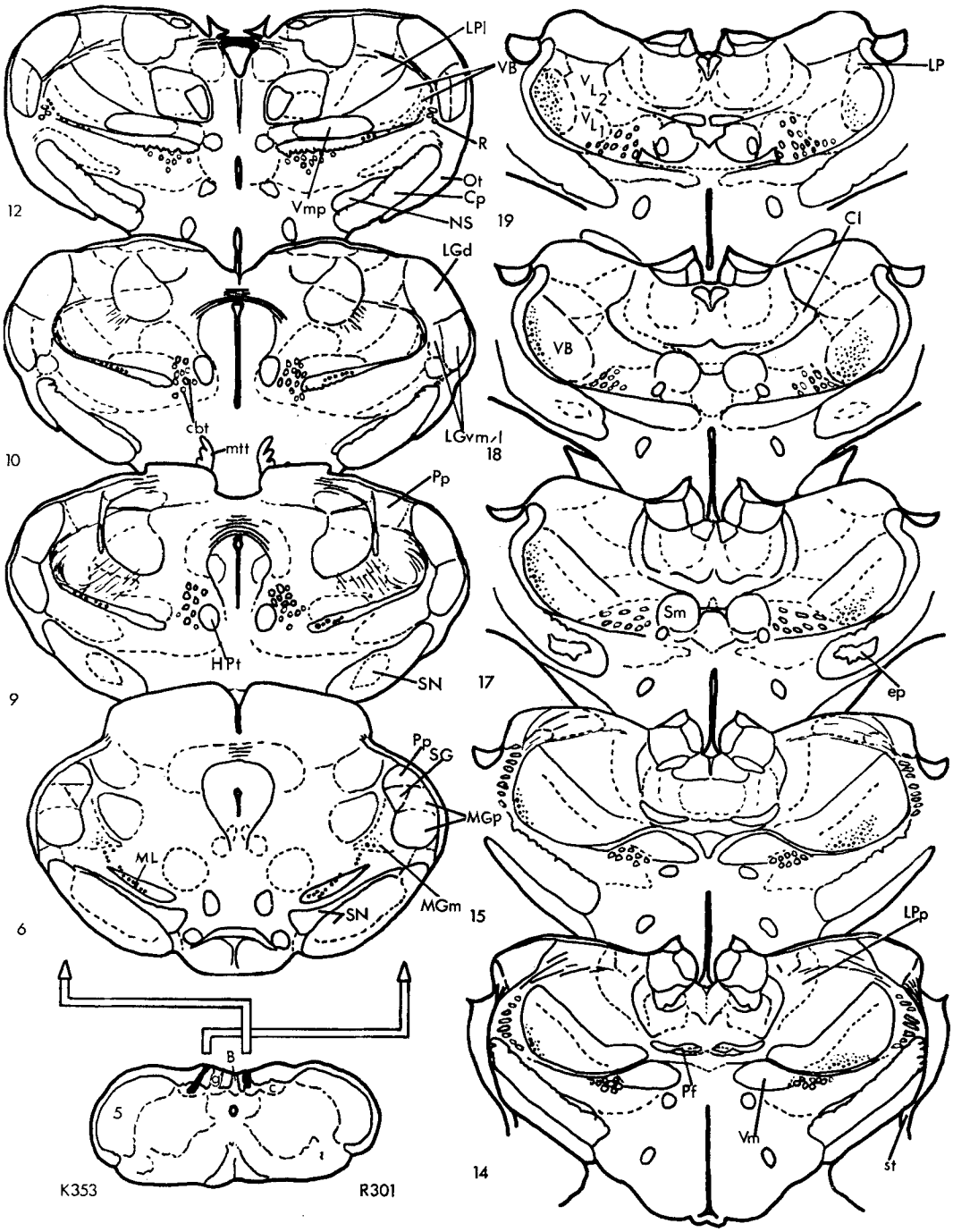

Fig. 1 Degeneration produced by lesions in the caudal part of the nuclei cuneatus and gracilis. The lesions are drawn at approximately their maximum depth and at the center of their rostro-caudal extent. The degeneration is plotted contralateral to the lesion in each case. Coarse dots indicate passage fibers, and fine, scattered dots represent terminal plexuses. For explanation of section numbers see text.

such lesions the classical course and distribution pattern of the medial lemniscus was found. Two typical examples will be described in detail.

Rat R301 (fig. 1). A very small lesion (rostro-caudal extent about 500 μ) in the caudal nucleus gracilis produced degenerating fibers in the internal arcuate bundles close to the lesion. There is no evidence that any significant number of fibers run into the more rostral parts of the nuclei before decussating. The degeneration crosses the mid-line and ascends in the medial lemniscus. In the rostral mid-brain a few fibers appear to terminate in the caudal part of the contralateral medial geniculate complex pars medialis (MGm, fig. 1/6). The lemniscal fibers continue rostrally to reach the ventrobasal complex (VB), and terminate in the pars externa. The most caudal parts of the complex contain no degenerating pericellular plexuses but in its rostral two thirds signs of termination appear immediately adjacent to its ventrolateral boundary (fig. 1/14). This plexus extends to the rostral part of the complex becoming more dense as it does so and also apparently expanding medially (fig. 1/15–19). The increased density is due to the pericellular ramification of fibers travelling rostrally close to the external medullary lamina. Horizontal sections reveal that the medio-lateral broadening of the band of degeneration is illusory: the lamina of degeneration is concentric with the outer boundary of the ventrobasal complex and more rostrally the lamina curves medially so that in frontal section it appears to widen. In unsuppressed sections (i. e. stained with a "neurofibrillar" method) degenerating endfeet were seen in the ventrobasal complex and some appeared to establish axosomatic relationships with ventrobasal cells, but degeneration in the surrounding neuropil makes it impossible to exclude the existence of axodendritic contacts.

Rat K353 (fig. 1). In this animal a lesion of roughly the same size as that above, but confined to the caudal part of the cuneate nucleus, produced a degeneration similar to that described above. Within the ventrobasal complex the expected topographical pattern is evident: termination occurs more posteriorly (fig. 1/12), more medially (fig. 1/14), and is more sparse in the most rostral part of the complex (fig. 1/19). The apparent medial expansion of the degeneration field rostrally may be explained in exactly the same way as in rat R301. The degeneration patterns strongly suggest the presence of concentric laminae that are somatopic, and are related to the "onion-skin" arrangement of cells in the external portion of the ventrobasal complex (Scheibel and Scheibel, '66; Webster and Lund, '67). The results afford no evidence of a topographical organisation in the distribution to the medial geniculate complex pars medialis.

Lesions in the rostral half of the dorsal column nuclei. This material produced evidence of connections outside the usually described thalamic areas. As previously, only two examples will be described. All other animals in this category confirm the observations.

Rat K362 (fig. 2). A small lesion confined within the boundaries of the gracile nucleus. Its rostro-caudal extent is less than 1 mm. As with caudal lesions a small amount of pericellular degeneration was found in the contralateral medial geniculate complex pars medialis (fig. 2/6). At the level of the mesencephalo-diencephalic transition more degenerating fibers leave the lemniscus: one group swings ventrolaterally through, and ends in, the zona incerta (ZI) predominantly in its lateral region close to the dorsal surface of the cerebral peduncle (fig. 2/9–12 and fig. 6). A second group of degenerating axons moves dorsomedially through the posterior thalamic radiations to end partly in the nucleus pretectalis anterior pars ventralis (Ptav, fig. 2/9–10 and fig. 5). Some of these fibers run rostrally to be joined by others which have swept laterally through the radiations, skirting the medial geniculate complex pars suprageniculata (SG, fig. 2/9–12), and terminate in the dorsal part of the posterolateral complex pars lateralis (LPl, fig. 2/14–15 and fig. 4). There is no sign of termination in either the nucleus posterior parabrachialis (Pp) or in the bulk of the pars suprageniculata. In the most rostral extent of the pars supragenicula (fig. 2/10) the fibrous nature of the region makes inter-

pretation very difficult; if a projection to this nucleus exists it is very small indeed and localised to this most rostral area. Within the ventrobasal complex the pattern of degeneration is much the same as that found with caudal lesions; there is no consistent evidence that the projection from the more rostral parts of the nucleus is more diffusely organised than that from the caudal parts, and its density is apparently the same (fig. 3)

Rat R320 (fig. 2). A lesion in the rostral part of the nucleus cuneatus of comparable size to that in rat K362. The degeneration pattern outside the ventrobasal complex is much the same as in rat K362. Within the complex the expected topographical arrangement is evident, but outside it no consistent topographical pattern emerged.

DISCUSSION

The distribution of the medial lemniscus within the ventrobasal complex of the rat appears to be identical with that generally accepted for other animals (e. g. Walker, '38), but apart from the brief report of Hand and Liu ('66) on the projections from the gracile nucleus of the cat, we are not aware of any previous specific evidence that all parts of the dorsal column nuclei project to the ventrobasal complex. In our investigation, no animal has failed to give evidence of such a projection. There is now much evidence that the gracile and cuneate nuclei of both cat and rat have a rostro-caudal organisation with respect to the properties of those cells which respond to peripheral stimulation (Gordon and Paine, '60; Gordon and Jukes, '64; Perl, Whitlock and Gentry, '62; McComas, '63; Winter, '65). The nuclei also exhibit rostro-caudal differences in their anatomical organisation (Kuypers and Tuerk, '64; Hand, '66). Gordon and Seed ('61) on the basis of recording antidromic impulses after systematically stimulating loci in the rostral midbrain concluded that in the rostral and caudal thirds of the dorsal column nuclei a smaller fraction of the cell population contributes axons to the lemniscus than in the middle one-third. The observations of Kuypers and Tuerk ('64) on retrograde cell degeneration in dorsal column nuclei after lemniscal section in the midbrain indicate that any projection from the rostral half of the nuclei must be very small or of the "sustaining" type.[2] Our failure to find any obvious difference in the density of ventrobasal degeneration from the rostral or caudal parts of the nuclei may be due to the poor quantitative sensitivity of methods for demonstrating preterminal and terminal degeneration, but it remains possible that lesions in rostral parts of the nuclei interrupt projection fibers from the more caudal regions, which run into the more rostral parts of the nuclei before decussating to enter the medial lemniscus. In this case "pure" lesions of the rostral parts of the dorsal column nuclei would be impossible to make. Our observations on the pattern of degeneration within the dorsal column nuclei and internal arcuate bundles after caudal lesions do not support this hypothesis.

The fact that all regions of the gracile and cuneate nuclei—which are not functionally homogeneous—project upon the ventrobasal complex is of interest because the functional properties of ventrobasal cells activated by cutaneous stimuli approximate most closely to those of the cells of the middle third of the dorsal column nuclei, with the notable difference that the phenomenon of surround inhibition is rare in the ventrobasal complex whilst it is usually the rule in this region of the medullary relay nuclei (Poggio and Mountcastle, '63). Poggio and Mountcastle suggest that one possible explanation of this difference is that many of the ventrobasal cells from which they were recording are activated by fibers arising from cells outside the middle one-third of the relay nuclei. The discrepancy is, however, as they point out, so large as to make this explanation improbable and they suggest that limitations of their adopted experimental procedure are more likely to explain the results. We have no evidence that the

[2] If the collateral hypothesis is used in the latter explanation, the collaterals must be within the nuclei themselves because caudal to the diencephalon the only offshoots we have seen from lemniscal fibers arising in the rostral parts of the dorsal column nuclei are a projection to the inferior parts of the contralateral inferior colliculus together with a very small distribution to the caudal part of the contralateral superior colliculus — see also Hand and Liu ('66) — and a rather larger input to the pontine nuclei. This latter projection has also been described by Nauta and Kuypers, '58.

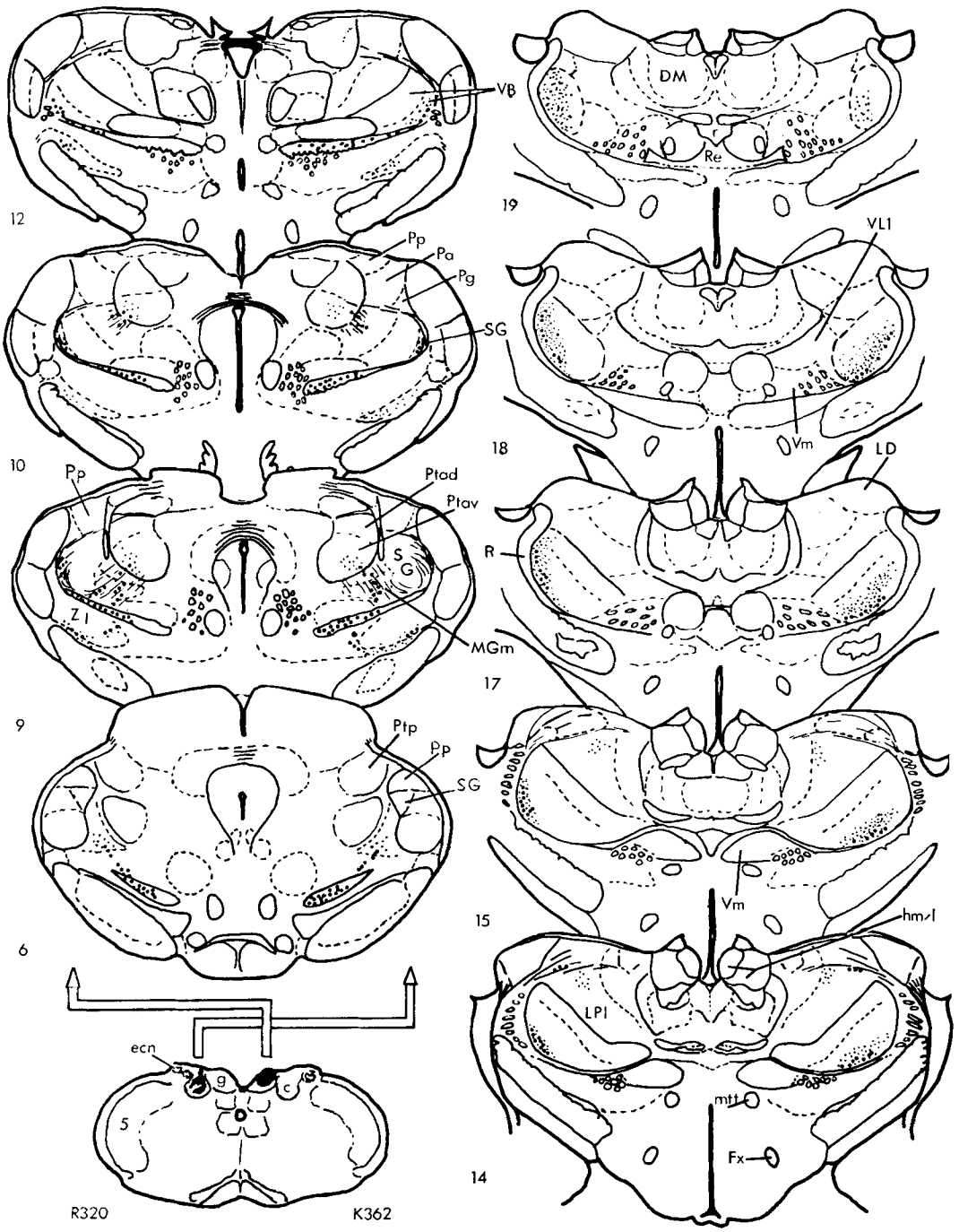

Fig. 2 Degeneration produced by lesions in the rostral part of the nuclei cuneatus and gracilis. See figure 1 for key.

functionally different parts of the relay nuclei project onto different cell populations within the ventrobasal complex and the lack of any physiological description of such populations with properties corresponding to the regional variations in the dorsal column nuclei would make it unlikely that such groupings exist. Nevertheless the apparent "disappearance" of certain functional characteristics (particularly inhibition and facilitation) between the gracile and cuneate nuclei and the ventrobasal complex remains to be explained; the problem cannot be dismissed by assuming that lemniscal axons to the ventrobasal complex arise only from certain regions (and thus from cells with certain properties) of the dorsal column nuclei.

The topographical distribution of the medial lemniscus within the ventrobasal complex in the rat is compatible with the results of the evoked response studies of Davidson ('65) and Emmers ('65). The latter author described a thalamic second somatic sensory area in the ventrobasal complex. Our results indicate that this second area lies within the region of termination of afferents from the nucleus gracilis and afford no explanation of Emmers' findings. There is reason to believe that Emmers' results are related to the distribution of afferents from the dorsal horn of the spinal cord (Webster and Lund, '67; Lund and Webster, '67).

Of the other thalamic regions concerned with somatosensory activity, most attention has been paid to that region lying at the confluence of the medial geniculate complex, ventrobasal complex, and the posterolateral complex and pulvinar. The cytoarchitecture of this part of the thalamus has proved especially difficult to analyse in all the species so far studied. Details of our own analysis of the configuration in the rat and a discussion of the nomenclature are to be published elsewhere, but a brief summary is essential at this point. Our "medial geniculate complex pars suprageniculata" probably corresponds to the "posterior group" (PO) of Rose and Woolsey ('58) and to at least part of "PO lateralis" of Moore and Goldberg ('63) as defined in the cat. The posterior group as defined in the rabbit by Tarlov and Moore ('66) corresponds to our nucleus posterior parabrachialis plus our pulvinar. It is not altogether clear whether our nucleus posterior parabrachialis should be included in the posterior group, and as it receives no fibers from the medial lemniscus (or spinothalamic tract) it will be omitted from further discussion here. The posterior-pulvinar complex of Rose and Woolsey ('58) appears to correspond to our "posterolateral complex" and "pulvinar" combined, and the rostral part of "PO medialis" of Moore and Goldberg ('63) to our "posterolateral complex." Our "medial geniculate complex pars medialis" corresponds to the magnocellular division of the medial geniculate body as usually defined in the cat, but not as defined by Tarlov and Moore ('66) in the rabbit.

That the rostral but not the caudal half of the gracile and cuneate nuclei of the cat projects to the pars medialis of the medial geniculate complex has been suggested by Kuypers and Tuerk ('64). Although we have detected some difference of this nature in the rat the contrast is not an absolute one—an observation supported by Hand and Liu ('66) working on the cat. We have never found degeneration with an appearance even remotely suggesting termination in the greater part of the medial geniculate complex pars suprageniculata. There may be a projection from the rostral parts of the dorsal column nuclei to the most rostral part of the pars suprageniculata where it adjoins the ventrobasal complex, but, as we have pointed out, this depends upon the interpretation of very sparse degeneration in a very fibrous area. If such a projection exists it is extremely small. Bowsher ('61) maintains that in the monkey the medial lemniscus distributes to the suprageniculate nucleus. Kuypers and Tuerk ('64) describe a projection from the rostral part of the dorsal column nuclei to the suprageniculate nucleus of the cat but in preliminary observations on this species we have not been able to confirm this (Webster and Lund, unpublished data).

We are not aware of any previous descriptions of a projection from the dorsal column nuclei (rostral parts only) to the dorsal (large celled) part of the postero-

lateral complex, although Walker ('38) describes in the monkey a few lemniscal fibers terminating in "the anterior portion of the pulvinar near its junction with the ventral nucleus." The observation by Hand and Liu ('66) of a dorsal column nuclear projection to the "posterior thalamic complex" may be compatible with our findings if by this term the authors mean the whole posterior group of Moore and Goldberg ('63) i. e. to include the posterolateral nucleus, or even the posterior group plus the pretectum. It appears that Davidson's ('65) report of evoked responses (all of latency approximating to that of ventrobasal responses) in the rat posterior thalamus following peripheral stimulation may be explained on a similar basis. The loci of these responses lie almost entirely within the pretectum, with which, as we have shown, the rostral parts of the gracile and cuneate nuclei establish a direct connection. Collaterals from "Reil's ribbon" to the pretectum have been described by Cajal ('11). Libouban ('60) has described short latency evoked responses in the rat pretectum produced by hair displacement and light pressure on the skin. Davidson ('65) also described a distribution of short latency responses in the posterolateral complex (his nucleus ventralis pars dorsomedialis). Although we have noted a direct lemniscal input to this complex, the distribution is to a more restricted region than might be suggested by Davidson's electrophysiological results.

In the cat the properties of neurons on the posterior group proper (i. e. our medial geniculate complex pars supragenicula ta) responding to somatic stimuli are very different from those of the ventrobasal complex neurons. In general posterior group neurons show long latency, although a few have latencies approximating to those of ventrobasal cells (Poggio and Mountcastle, '60). It seems reasonable to consider these short latency responses to be mediated via the dorsal column-medial lemniscus system, but our failure to find conclusive evidence of direct afferents to any part of this thalamic area outside the medial part of the medial geniculate complex is difficult to reconcile with this assumption. (It may be argued that the spino-thalamic tract is responsible for the short latency responses but our observations on this system are similar, with regard to the posterior group, to those described above). The observation that most of the responses are of long latency is, however, compatible with our findings and suggests that the chief source of ascending somatic afferents to this thalamic region may be the reticular formation.

Afferents from the rostral part of the dorsal column nuclei to the zona incerta have been described by Hand and Liu ('66). These authors also mention a projection to the field Hl of Forel, but in our material the degeneration is always ventral and lateral to this field. Few physiological studies report evoked potentials in the zona incerta following somatic stimulation, but those workers who do usually describe these responses following stimulation of the skin of the face (Darian-Smith, '64; Pubols and Pubols, '66). Some of the evoked potentials described by Davidson ('65) in the rat appear to lie in the zona incerta, and to result from limb stimulation. We are unable to explain why incertal responses have been recorded only rarely, subsequent to stimulation of the trunk and limbs.

With the exception of the pretectum and zona incerta the thalamic regions discussed above are all known to have projections to the neocortex. The dorsal column-medial lemniscus system is generally thought of as a recent phylogenetic acquisition, largely because of its ultimate, oligosynaptic relationship with the neocortex. Within the anterolateral system it is customary to discern a division considered to be phylogenetically old (and not related directly to the neocortex), as well as a more recent division related to the neocortex in the same way as the medial lemniscus. The present results show that the medial lemniscus also has a component which lacks a direct route to the neocortex, distributing to the collicular plate, the pons, the pretectum and the subthalamus. The dorsal column afferents to these regions originate in those parts of the nuclei which appear to be functionally the least precisely organised; it is tempting to speculate that this represents the dorsal column-medial lemniscus pathway in those vertebrates which pos-

sess dorsal columns and associated nuclei but lack neocortex. This remains to be investigated in detail, but it may be that theories of somatic sensibility associated with the concepts of "neo-" and "palaeo-" projection systems have placed too great a stress on the apparent dichotomy of the anterolateral system in contrast to the supposed unity of the dorsal column pathway.

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PLATE 1

EXPLANATION OF FIGURES

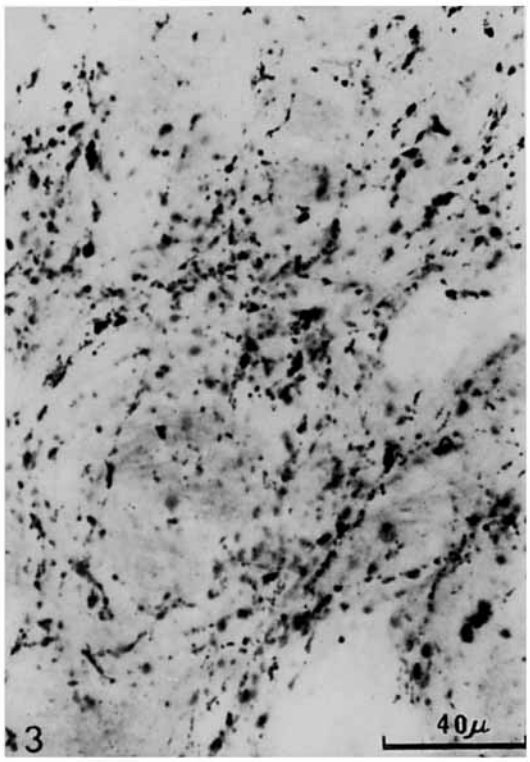
All sections are stained by the Nauta method.

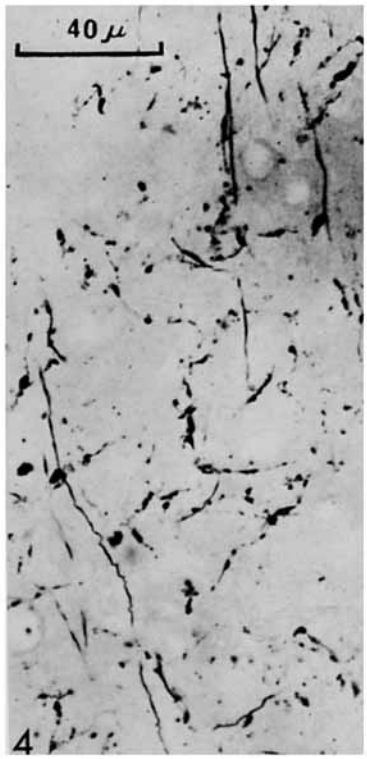
3 Degeneration in the ventrobasal complex after a lesion in the rostral part of the cuneate nucleus (rat K188). Paraffin section at 15 μ.

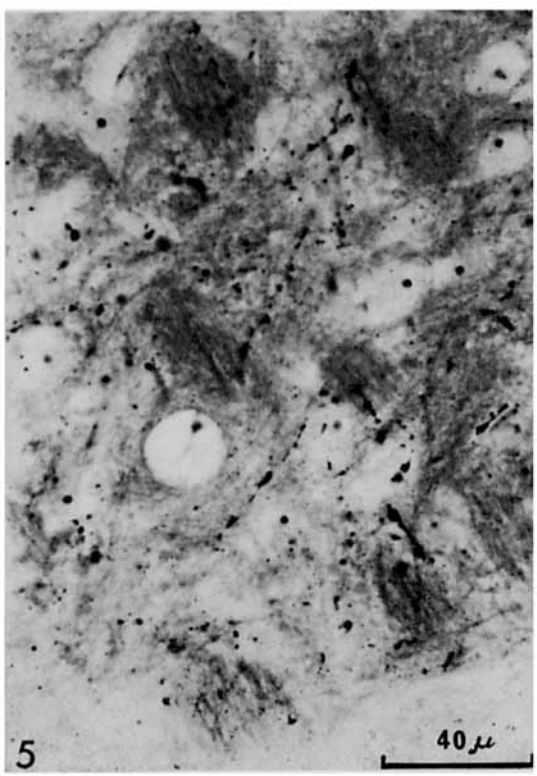
4 Degeneration in the posterolateral complex pars lateralis after a lesion in the rostral part of the cuneate nucleus (rat R320). Frozen section at 30 μ.

5 Degeneration in the nucleus pretectalis anterior pars ventralis after a rostral cuneate nucleus lesion (rat K188). Paraffin section at 15 μ.

6 Degeneration in the zona incerta in rat K188. Paraffin section at 15 μ.


3
40μ


40μ
4


5
40μ


40μ
6