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VISUAL CORTICOPONTINE AND TECTOPONTINE PROJECTIONS IN THE MACACQUE

M. GLICKSTEIN, J. MAY* AND B. MERCIER

Department of Anatomy and Developmental Biology, University College London, London, England

INTRODUCTION

Lesions of the cerebellum produce deficits in movement. A fundamental problem in neurobiology has been to understand the anatomical and physiological basis for such deficits. In the early part of the 19th century Flourens (8) recognized that the motor deficits caused by cerebellar lesions were not the same as those produced by direct damage to the muscles or motor nerves, since individual movements were still present after he made cerebellar lesions in mammals or birds. Flourens argued that it was the loss of coordination of movement that was caused by cerebellar damage.

The demonstrated role for the cerebellum in the organization and coordination of movement led naturally to the question of whether sensory afferents to the cerebellum might play a role in such coordination. On the basis of anatomical evidence the first sensory inputs to the cerebellum to be recognized were those from the vestibular system and the spinal cord. Sherrington (23) reviewed this evidence in his discussion of the functions of the cerebellum. He noted that the cerebellum receives information about head position from the vestibular system and proprioceptive information via the spino-cerebellar tracts. He proposed that the cerebellum uses such sensory information to regulate organized movement like walking or running. The cerebellum, Sherrington suggested, is the head ganglion of the proprioceptive system.

Sherrington's conclusions were limited by the amount of anatomical evidence which was available to him. Further progress towards understanding the function of the cerebellum was dependent on a clearer understanding of its anatomical circuitry.

An important contribution to our understanding of the nature of sensory input to the cerebellum was the discovery by Snider & Stowell (24) that visual and auditory stimuli evoke electrical responses on the cortex of the cerebellar vermis of anaesthetized cats. They suggested that the visual response is probably relayed via the superior colliculus since removal of the entire cerebral cortex failed to abolish the flash evoked response in the cerebellum.

Following Snider and Stowell's discovery of visual evoked potentials it became

* Present Address: Department of Psychology, State University of New York, Stony Brook, Long Island, USA.

clear that, in addition to visual responses on the cerebellar vermis, visually evoked potentials can also be recorded on the cerebellar hemispheres (7). It seemed likely that, in addition to the superior colliculus, visual information may be relayed by way of other structures. It is now clear that, in addition to an input from the superior colliculus (e.g. 3, 13, 15, 26, 28) visual areas of the cerebral cortex also project to the cerebellum. Both inputs relay by way of the pontine nuclei (2, 9, 10, 19, 25, 29), and pontine cells which receive a collicular (19), or cortical (1) input respond vigorously to appropriate visual targets. In addition to its cortical and collicular inputs there is also anatomical evidence that the pretectal area (19, 27) and the ventral lateral geniculate body (6, 12) provide a possible source of visual information to the cerebellar cortex by way of a relay in the pontine nuclei. All of these inputs are relayed to the cerebellum by way of mossy fibers. There are also climbing fiber pathways relayed via projections from the accessory optic nuclei (16, 17) or superior colliculus (26) to the dorsal cap of Kooy or other subdivisions of the olivary complex. The unravelling of the many pathways whereby sensory information may reach the cerebellum has been a continuous process over the last few decades. The studies of Professor Brodal and his colleagues have been in the forefront of the contributions to our understanding of those circuits.

The present report is concerned with the pathways which relay visual information to the cerebellum of monkeys. We began these experiments after Kawamura and Brodal (15) had described the tectal input to the pontine nuclei of cats, and the questions asked and the methods used in our study were influenced by their approach to the problem. The experiments were done in order to compare the input to the pontine nuclei from the superior colliculus with the input from the extrastriate visual cortical areas. We asked the following questions:

1) To which areas of the pontine nuclei of monkeys does the superior colliculus project? Harting's (13) and Weber and Harting's (26) autoradiographic evidence showed that there is a projection from the superior colliculus to the dorsolateral region of the pontine nuclei and to the nucleus reticularis tegmenti pontis (NRTP). Harting's experiment (13) dealt with all of the subcortical targets of the superior colliculus, hence he had space to present only limited data on the extent of the projections to the pontine nuclei. The present study amplifies that description. The studies of Weber and Harting (26, 27) focused principally on the inputs to the inferior olivary nucleus from the colliculus and pretectum. The olive is the source of climbing fiber afferents to the cerebellum. In the present report we deal only with pathways for visual mossy fiber activation, all of which are relayed to the cerebellum by way of the pontine nuclei.

2) How does the tectopontine projection in monkeys compare to that from the cortical visual areas? There is a large projection to the pontine nuclei from extrastriate visual areas of the monkey cerebral cortex (9, 10). These projections arise from both banks of the superior temporal sulcus, (areas MT and MST; V5 and V5a of Zeki), from adjacent visual regions of the parietal lobe including the cortex within the intraparietal sulcus and from the rostral bank of the parietal-occipital sulcus and the cortex adjacent to it rostrally on the medial face of the

hemispheres. In cats tectopontine and visual corticopontine projections are largely non-overlapping (15, 19, 21). In rats there appears to be at least a partial overlap (3). Do the superior colliculus and the extrastriate visual areas project to overlapping or distinct areas within the pontine nuclei of monkeys? How extensive is the distribution of corticopontine and tectopontine visual fibers within the pontine nuclei? If one of these two inputs distributes over a wider region of the pontine nuclei, then it should be capable of influencing a larger territory on the surface of the cerebellar cortex.

3) A final question which these experiments address is that of the cellular origin of the tectopontine projections. Which collicular cells project to the pontine nuclei and which to the nucleus reticularis tegmenti pontis (NRTP)? Kawamura and Brodal (15) suggested that in cats "some (tectopontine) fibers come even from layers superficial to the stratum griseum intermediale". We confirmed this finding in cats (19) by injecting horseradish peroxidase amongst visually activated cells in the dorsolateral pontine nuclei. In addition to labelled cells in the deeper collicular layers, there were labelled cells throughout the entire stratum opticum of the superior colliculus. Cells in the dorsolateral pontine nuclei of cats which receive collicular terminals have visual receptive fields which are consistent with their activation from the purely visual cells found in the superficial layers of the colliculus (19).

In the present series we made lesions, or injected ^{3}H leucine or wheatgerm agglutinin horseradish peroxidase (WGA-HRP), into the superior colliculus or cortical visual areas of the dorsolateral visual area of the pontine nuclei of monkeys to study the nature and extent of the visual input to the pontine nuclei.

A word of explanation and apology is necessary at the outset. These experiments were started at Brown University in Providence, Rhode Island, U.S.A. About one year after the experiments were begun, the laboratory moved to University College London. In the move some data files and histological slides were lost. The only important loss, however, is that we cannot be certain of the exact survival time after ^{3}H leucine injection (or lesion in one case). Where necessary these data are approximated on the basis of our usual practise and these approximations are clearly indicated in the text.

METHODS

Six monkeys (Macaca fascicularis) were studied. In five of these we used degeneration staining and/or autoradiographic labelling to plot the distribution of fibers from visual cortex and/or the superior colliculus to the pontine nuclei. In the sixth we used the retrograde transport of WGA-HRP to identify the cells of origin of the tectopontine projection. In three of the animals two tracing methods were used together. In two of these a lesion was placed in the visual cortical areas of one hemisphere and ^{3}H leucine/proline was injected into the superior colliculus of the opposite side. In the third case ^{3}H leucine was injected into the extrastriate cortex and a lesion was placed in the opposite superior colliculus. We were also able to refer to a set of autoradiographically labelled sections from monkeys in which the superior colliculus had been injected with ^{3}H leucine and

proline kindly lent to us by Dr Harting. These sections were used to confirm our own findings of tectopontine projections but are not reported here. The procedures are summarised in Table I.

Table 1.

Animal no.	*Surgical details*	*Day*	*Perfusion day*
DLM 1	Unilateral occipital lobectomy 15μCi ^{3}H leucine contralateral superior colliculus	1 2	5
DLM 2	Unilateral occipital lobectomy 40μCi ^{3}H leucine/proline contralateral superior colliculus	1 7	10
DLM 4	Superior colliculus lesions 14×31.6μCi ^{3}H leucine contralateral extra striate cortex	1 [7]	10
MSC 2	Superior colliculus lesion 2×1 mA/1 minute	1	8
MSC 3	Superior colliculus lesion 3×1 mA/1 minute	1	8
P10	50 nl 4% WGA-HRP dorsolateral pontine nuclei	1	3

Double labelled cases.

In two of the animals a lesion was made to include the entire occipital lobe and some or all of the surrounding extrastriate areas which are known to project to the pontine nuclei (9, 10). In both cases the superior colliculus was subsequently injected with ^{3}H leucine. The animals were perfused three days after the ^{3}H leucine injection. In the third double-labelled case a lesion was made first in the superior colliculus. Subsequently, ^{3}H leucine was injected within the extrastriate visual areas on the bans of the superior temporal and intraparietal sulci.

Operative procedure: Cortical lesions (DLM 1 and DLM 2).

The animals were deeply anaesthetized and operated under strict aseptic precautions. A large skull opening was made to expose the cerebral cortex from the level of the central sulcus to the occipital pole. The entire occipital lobe was removed as a single block and the lesion was extended rostrally by suction. In one case (DLM 2) the lesion was extended to include the cortex on both banks of the superior temporal sulcus medial to its confluence with the lateral fissure, both banks of the parieto-occipital notch and both banks of the parieto-occipital sulcus on the medial face of the hemispheres. In the other case (DLM 1) the lesion was somewhat less extensive and spared the rostral bank of the superior temporal fissure and the anterior bank of the parieto-occipital fissure. The animals were sutured in anatomical layers and post-operative recovery was uneventful.

^{3}H Leucine/Proline injection (DLM 1 and DLM 2).

The animals were re-anaesthetized one or six days after the first operation and mounted in a stereotaxic instrument. A small skull opening was made on the side contralateral to the occipital lesion at the level of the central sulcus. A micro-electrode was lowered

toward the superior colliculus and neural activity was recorded until we located the characteristic flash evoked response in the superior colliculus. When the colliculus was located the micro-electrode was withdrawn and a cannula was placed at the same stereotaxic locus within the superior colliculus. In one case (DLM 1) a single injection of 15μCi [.3 μl of a 50 μCi/μl solution] of ^{3}H leucine in saline was made slowly over a 10 minute period, the cannula left in place for 10 minutes and withdrawn. In the other (DLM 2), 40μCi of ^{3}H leucine/proline was injected. The animals were perfused three days after the amino acid injection and the brains blocked in the following way. The brainstem was first separated from the remainder of the brain by a transverse cut just rostral to the superior colliculus. The cerebral hemispheres were divided at the corpus callosum and parasagittal sections were prepared through the cortex on the side of the lesion. The brainstem was sectioned transversely, and the extent of the injection in the superior colliculus was plotted from these sections. Alternate transverse sections were prepared to reveal degenerating nerve fibers and terminals or autoradiographically labelled fibers and terminals within the pontine nuclei and NRTP.

The cortical sections were traced and the brain reconstructed to illustrate the location of lesions in relation to the major fissures. The collicular sections were traced and the extent of the primary injection site plotted. The pontine sections were read to plot degenerating preterminal fibers as revealed by the Nauta method and ^{3}H labelled fibers and terminals as revealed by autoradiography.

DLM 4.

The animal was placed in the stereotaxic apparatus under barbiturate anaesthesia and the superior colliculus was located by recording evoked response to flash. Three adjacent lesions were placed within the colliculus at successive depths within the colliculus. The distance between the centre of the most superficial and the deepest lesions was 2.3mm. Recovery was uneventful. Six days later the animal was re-anaesthetized and a series of injections of ^{3}H leucine was made on the banks of the superior temporal sulcus, the intraparietal sulcus and the parieto-occipital sulcus. A total of 14 injections was made, each over a time course of 10 minutes. Each injection was .2μl containing 31.6 μCi/injection.

P10.

The animal was placed in the stereotaxic apparatus under barbiturate anaesthesia. The dorsolateral region of the pontine nuclei was injected with 50nl of 4% WGA-HRP via a Hamilton microsyringe. Two days later the animal was perfused under deep barbiturate anaesthesia. The brain was removed and frozen sections cut at 50 μm in the parasagittal plane through the cortex and transverse plane through the brainstem. The sections were reacted with TMB to reveal retrogradely labelled cells or with DAB to delineate the injection site.

Superior colliculus lesions.

In two cases we made lesions only in the superior colliculus and did no ^{3}H leucine injections. The colliculus was first located by recording evoked potentials to flash. In one of these cases, (MSC 2), the lesion was made from the contralateral side. Two electrolytic lesions, each of 1 milliamp for 1 minute were made. In the second case the colliculus was approached from above in the stereotaxic plane.

In all cases but one, sections through the pontine nuclei were cut transversely. In MSC 3 the entire brainstem was cut in a parasagittal plane in order to provide a supplementary picture of the extent of the tectopontine terminals.

RESULTS

DLM 1.

This animal received a large right occipital lobectomy followed by ^{3}H leucine injection into the superior colliculus (Fig. 1). Postmortem reconstruction of the cortical lesion shows that it included all of area 17 including the cortex on the banks and depths of the calcarine fissure, all of the surrounding cortex on the banks and depths of the inferior occipital and lunate fissures, including the annectant gyrus, the cortex rostral to the lunate fissure up to and including the posterior

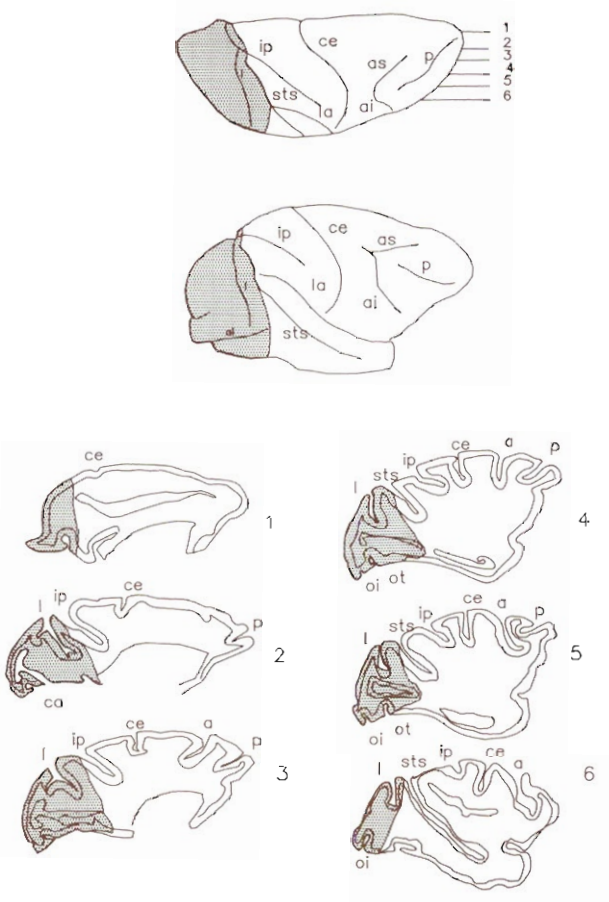

Fig. 1A. – *DLM 1.* The upper part of the figure shows a reconstruction of cortical lesion (shown as stippling). The lower part of the figure shows the extent of the lesion in parasagittal sections.

bank of the superior temporal sulcus medial to its confluence with the lateral fissure. The lesion also included the tissue on both banks of the parieto-occipital notch and extended along the medial face of the hemisphere to include the cortex on the caudal but not rostral bank of the parieto-occipital fissure.

Thus, although the lesion included nearly all of areas 17 and 18, it spared some cortical visual areas now known to project to the pontine nuclei (10). The spared areas included the rostral bank of the superior temporal sulcus (area MST) and adjacent parietal lobe (area 7a) and medially, the rostral bank of the parieto-occipital fissure.

Degenerating fibers were found terminating extensively in the pontine nuclei. The extent of the degenerating fiber terminals was greatest rostrally but degenerating fibers and terminals were present throughout almost the entire anterior-posterior extent of the pontine nuclei. Nearly all of the degenerating fibers were confined to the side of the pontine nuclei ipsilateral to the cortical lesion. A few degenerating fibers were found contralaterally, some of which probably resulted from damage to overlyng cortex and white matter caused by the microelectrode and cannula

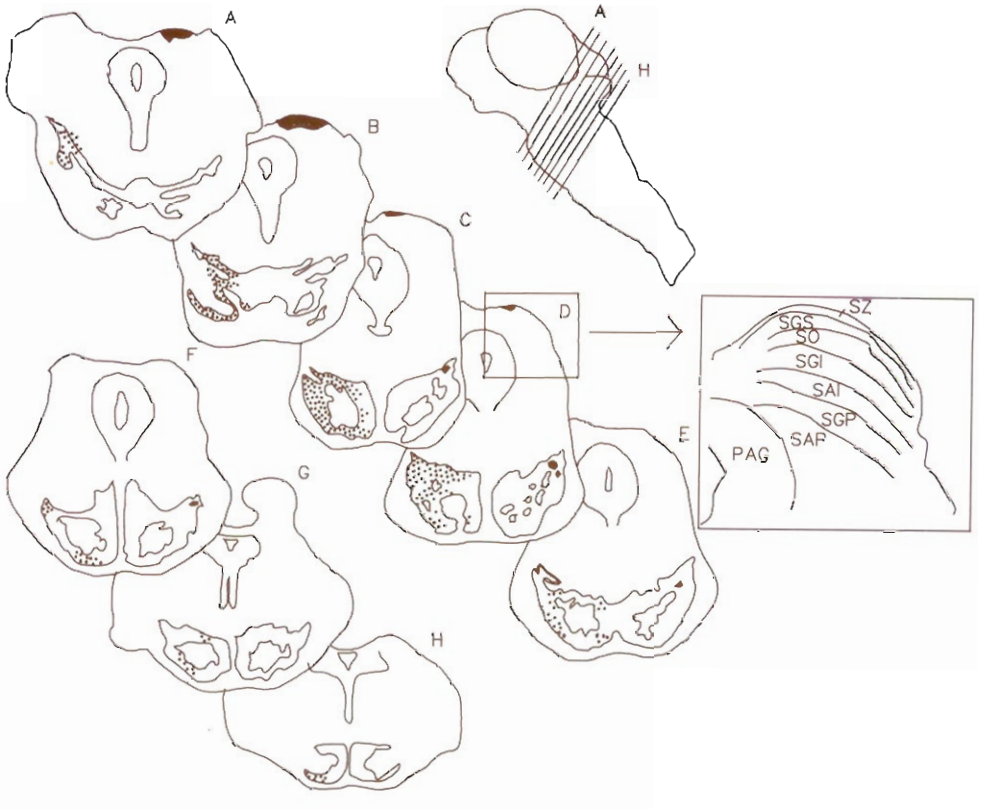

Fig. 1B. – *DLM 1. The extent of the primary injection site following an injection of* ^{3}H leucine into the superior colliculus and the location of resulting tectopontine terminal label (solid black areas). Areas of pontine degeneration resulting from the cortical lesion are shown as stippling.

tracks overlying the colliculus. For clarity, these fibers are not shown in the figures, since they represent a negligible contribution to the total number of degenerating terminals.

As expected, in addition to the projection to the pontine nuclei there were projections to other subcortical structures. For example, there was dense degeneration in the ipsilateral superior colliculus. Since the aim of this study was to locate and compare visual inputs to the pontine nuclei, these other targets of the cortical visual areas will not be presented here.

Autoradiography.

The injection site was confined to the most superficial layers of the superior colliculus and extended only to the depth of lamina 3, the stratum opticum, as illustrated by the photomicrograph (Fig. 1C). The injection was centred in the medial half of the superior colliculus and extended from its anterior border to include roughly the anterior two thirds of the colliculus. Labelled fibers were seen coursing ventrally and laterally from the injection site enroute to the lateral edge of the brainstem. Many of these fibers terminated in discrete small patches within the dorsolateral region of the ipsilateral pontine nuclei.

In summary, following lesions in the striate and extrastriate cortical visual areas there was a massive projection which extended throughout the dorsolateral region of the ipsilateral pontine nuclei. On the oposite side of the brain in which an injection of ^{3}H leucine was placed in the most superficial layers of the superior colliculus, small restricted patches of terminal labelling were found within the pontine nuclei. The cortical projection extended over a much larger area of the pontine nuclei than that seen after the colliculus injection. Although we cannot say from these results alone whether cortical and collicular terminals converge onto the same individual pontine cells, there is overlap in the territory of the

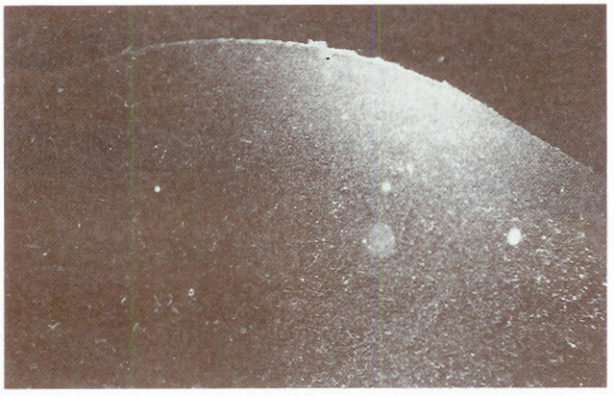

Fig. 1C. – *DLM 1.* A photomicrograph illustrating the center of the collicular injection site. × 30.

projections from the two sources. The collicular terminals are contained within the much larger region of the terminal field of corticopontine fibers.

Although the autoradiographic labelling showed good transport to the dorsolateral pontine nuclei, in this case there was no evidence for a projection to the nucleus reticularis tegmenti pontis (NRTP). This lack of projection to NRTP stands in sharp contrast to the results seen in the next case, DLM 2.

DLM 2.

The lesion of extrastriate cortex was larger than that in the previous case (Fig. 2A); it included all of the cortex removed in DLM 1 and, in addition, the cortex on the rostral bank of the superior temporal sulcus and the anterior bank of

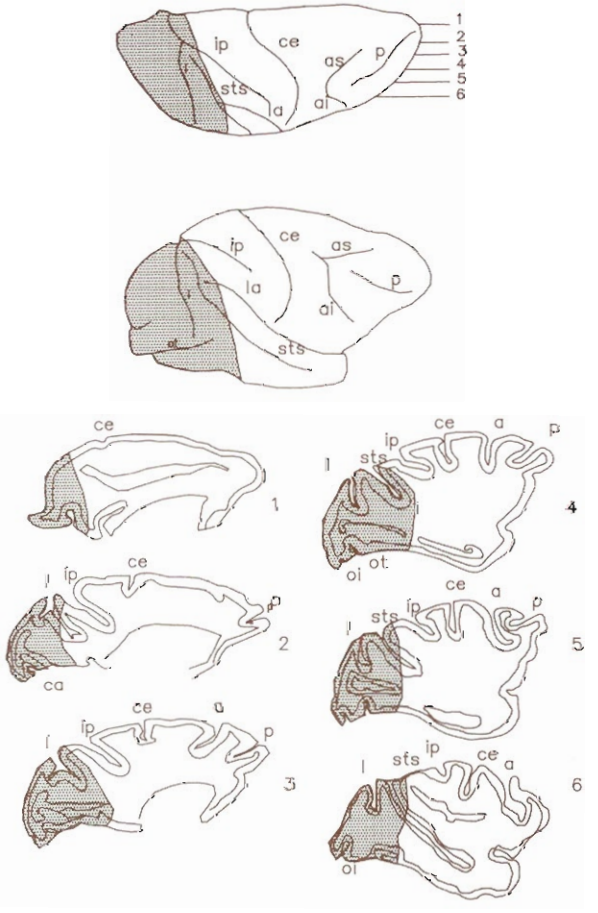

Fig. 2A. – *DLM 2.* Convention as for Fig. 1A.

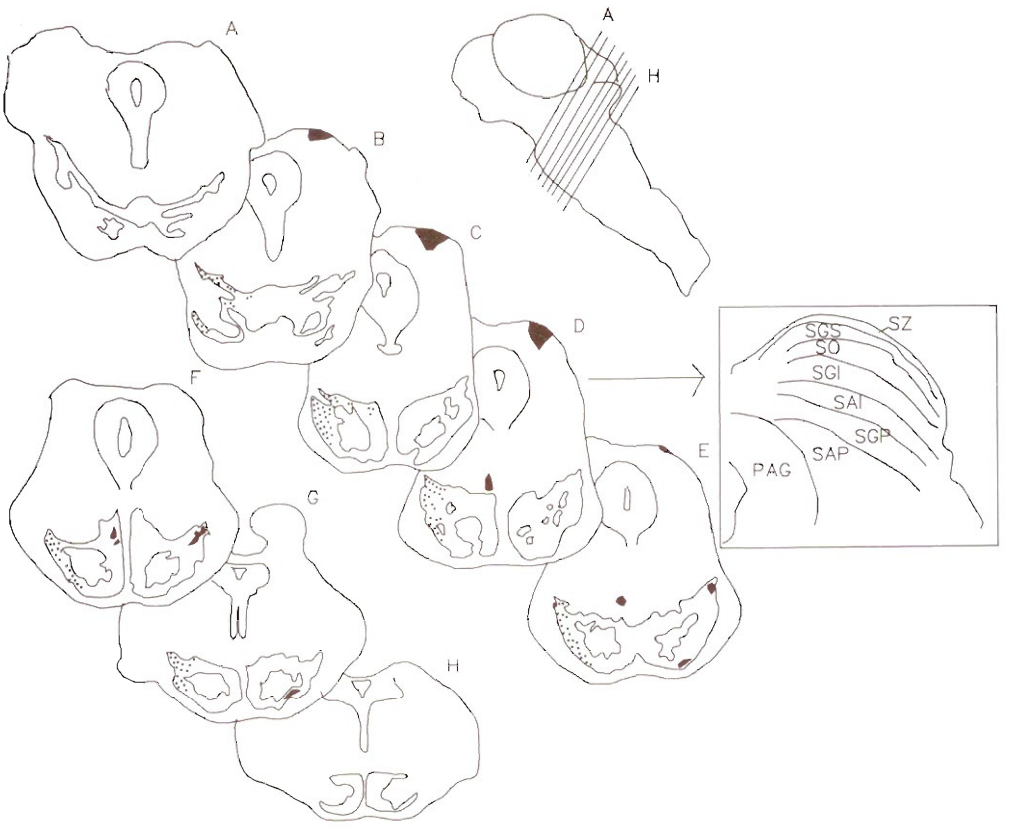

Fig. 2B. – *DLM 2.* Convention as for Fig. 1B.

the parieto-occipital fissure on the medial face of the hemispheres. Thus nearly all of the extrastriate cortical visual areas which are known to project to the pons (10) were included in the lesion. The center of the injection site within the superior colliculus was similar to that of the previous case. However, in this case the injection site extended more deeply and included the stratum griseum intermediale and the stratum album intermediale as well as the more superficial layers. The injection was centered at the same medio-lateral position but the rostro-caudal extent of the injection was slightly more restricted than in DLM 1 (Figs. 2B and 2C).

As was the case for DLM 1, we saw fibers leaving the injection site coursing ventro-laterally, many of which terminated in small patches in the dorsolateral region of the pontine nuclei. These tectopontine terminals were distributed more widely within the ipsilateral pontine nuclei than in DLM 1. In addition to terminals in the extreme angle of the dorsolateral pons, patches of labelled terminals were found more medially and more ventrally than in DLM 1. Unlike the results found in DLM 1, in this case, in which the injection extended to include deeper layers of the superior colliculus, there were also labelled terminals in the contralateral NRTP.

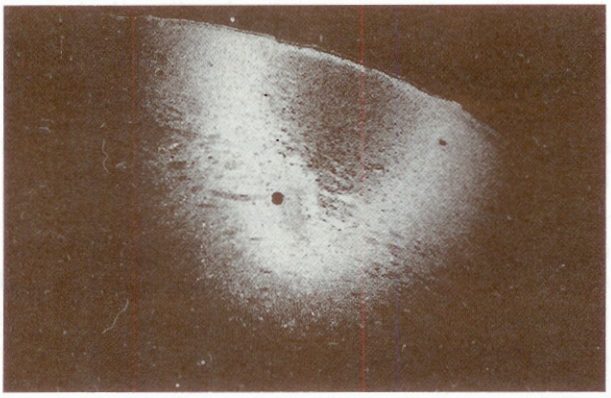

Fig. 2C. – *DLM 2.* A photomicrograph illustrating the center of the collicular injection site. × 25.

DLM 1 and DLM 2, provide a comparable set of injections in the superior colliculus which differ principally in the depth of the injected label. We conclude that the superficial collicular layers project to the dorsolateral pons but not to NRTP. The deep cells project to NRTP and possibly to dorsolateral pons as well.

In both DLM 1 and DLM 2 the projection from the superior colliculus covered a much smaller territory within the pontine nuclei than the projection from the extrastriate visual areas (Fig. 2B). The degenerating fibers and terminals within the pontine nuclei following cortical lesion were more extensively distributed. Very few degenerating fibers were found in the contralateral pontine nuclei, and most of these were probably caused by damage to the white matter and colliculus from the injection canulae and electrode track overlying the superior colliculus.

One possible explanation for the difference between the extent of cortical and collicular terminals might be due to the fact that the colliculus injections were subtotal and included only a part of the collicular representation of the visual field, whilst the cortical lesions encompassed the entire visual field in striate and extrastriate areas. This may account for some of the differences in the extent of the terminal field, but it cannot be a complete explanation. In both DLM 1 and DLM 2 a sizable portion of the visual field representation was involved. These data suggest that the visual cortical projection extends over a much larger territory of the pontine nuclei than does the colliculus. There is, however, the possibility that there might be a difference in the sensitivity of the autoradiographic and degeneration tracing methods.

DLM 4.

In order to control for differential sensitivity we did a reverse experiment (DLM 4), making a unilateral lesion in the superior colliculus to trace degenerating fibers

and injecting ^{3}H leucine into the extrastriate visual cortical areas on the opposite side (Fig. 3A).

The autoradiographic injections resulted in a massive projection to the dorsolateral region of the pontine nuclei. The labelled fibers were distributed within an area of the pontine nuclei which was almost identical to that seen using degeneration following lesions of striate and adjacent prestriate cortex. Thus the extent of the corticopontine projection is not related to the particular tracing method by which it is studied.

This case, however, was inappropriate for detailed study of collicular terminals. In addition to the projections to the ipsilateral dorsolateral pons and the contralateral NRTP, which were related to the collicular lesions, there were also a great number of degenerating fibers and terminals on the side of the cortical injection in the pontine nuclei. It seems very likely that this degeneration was

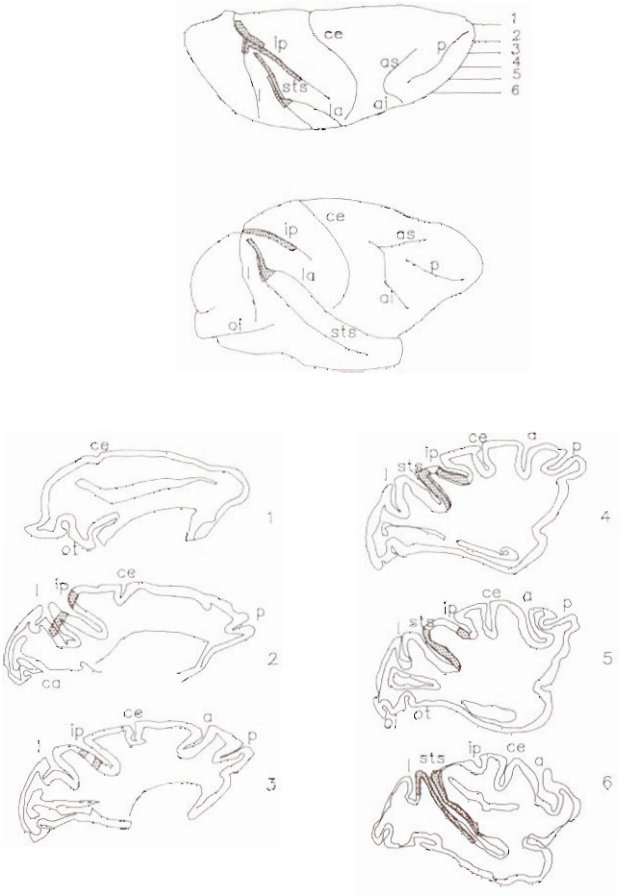

Fig. 3A. – *DLM 4.* The upper part of the figure illustrates a reconstruction of the primary site (shown as stippling), following cortical injections of ^{3}H leucine. The lower part of the figure illustrates the extent of the injection site in parasagittal sections.

due to cortical and white matter damage from the ^{3}H leucine injections and it was more extensive than the modest focus of terminals attributable to the collicular lesion. On the side of the collicular lesion, we did find a small region of degenerating fibers and terminals in the dorsolateral corner of the pontine nuclei. This distribution was similar in its location to that seen after the autoradiographic injections in the previous case. In addition, there were also degenerated fibers in the NRTP contralateral to the collicular lesion.

Because the degenerating fibers attributable to the collicular lesion in this case were masked by the large amount of preterminal Nauta degeneration caused by the injection tracks, only the cortical projections as determined autoradiographically are shown in the figure (Fig. 3B).

In summary, this case clearly shows that the extent of the corticopontine projection from the extrastriate visual areas is independent of the technique used to study it. Autoradiographic injections reveal the same distribution within the dorsolateral region of the pontine nuclei as did the Nauta method for staining degenerating fibers. The use of degeneration staining techniques for the study of the

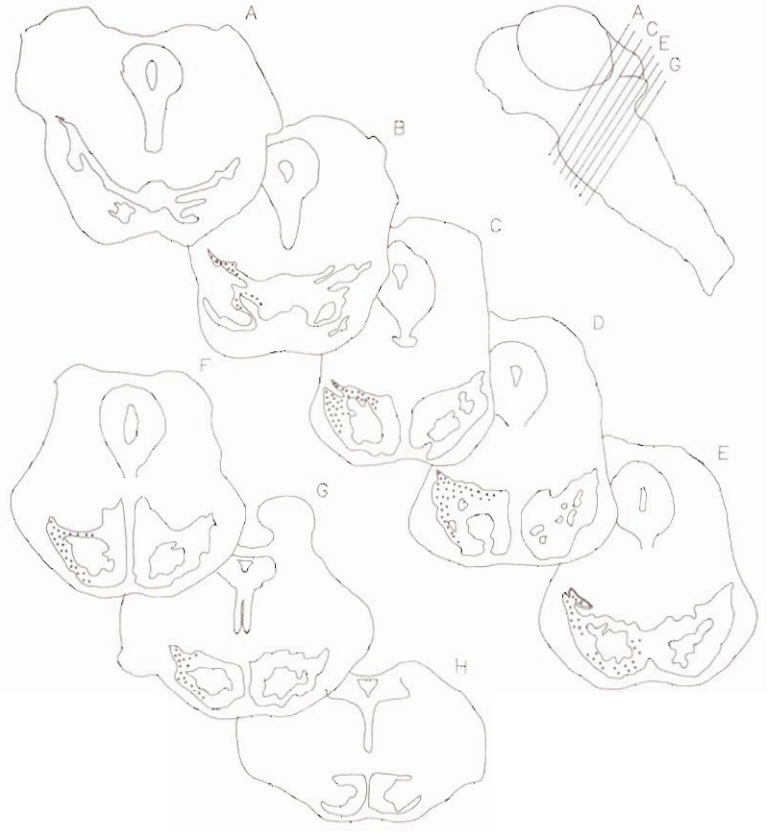

Fig. 3B. – *DLM 4*. The location of terminal label within the pontine nuclei resulting from the cortical injections.

collicular efferents is clearly less appropriate than it is for cortex since it necessarily involved bilateral damage to overlying cortex and white matter caused by recording tracks and injection cannulae. Nevertheless, the degeneration caused by the collicular lesion is consistent with findings using the more precise autoradiographic methods. A small focus of degenerating fibers is found in the dorsolateral pontine nuclei ipsilateral to the collicular lesion and also a projection to the contralateral NRTP.

MSC 2.

In this case, MSC 2, we made a lesion in the superior colliculus by way of an electrode angled toward the colliculus from the contralateral side. This experiment was an attempt to study the projection from the superior colliculus to the pons with less contamination attributable to the electrode tracks than in cases in which the colliculus is approached directly through ipsilateral cortex and white matter.

The colliculus was approached as illustrated in Fig. 4A. When the contralateral superior colliculus was located electrophysiologically we placed a lesion in it. Fig. 4B is a photomicrograph through that superior colliculus. As can be seen, there was a small, circular lesion which was centered entirely within the superior colliculus and extended to the depth of the stratum griseum intermediale and the stratum album intermediale. There was no overlying damage to the cerebral cortex or white matter on the ipsilateral side.

On the side of the colliculus lesion degenerating fibers and terminals were seen in the dorsolateral region of the pontine nuclei, as illustrated in Fig. 5. On the

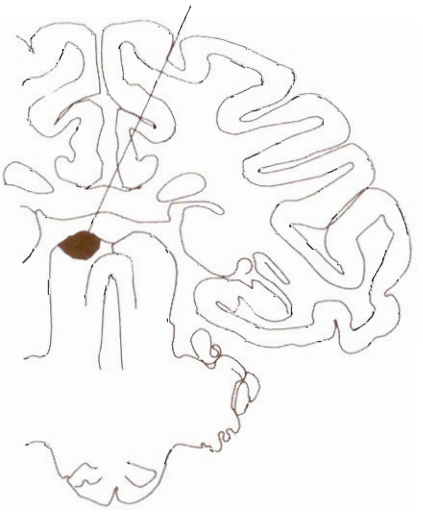

Fig. 4A. – *MSC 2.* The angle of the electrode used to place a lesion in the superior colliculus from the contralateral side.

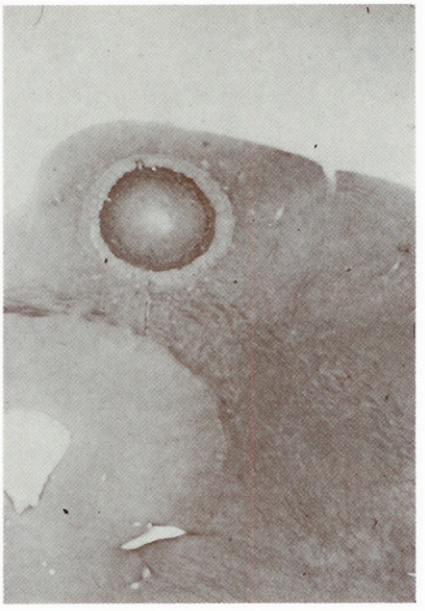

Fig. 4B. – *MSC 2.* A photomicrograph illustrating the center of the collicular lesion. × 18.

contralateral side there was a focus of degenerating fiber terminals in NRTP. In addition to the NRTP projection contralaterally, there were a few additional degenerating fibers scattered within the pontine nuclei, probably attributable to the passage of the needle track.

In summary, this case replicates and confirms the results from autoradiographic study demonstrating the location of collicular terminals. There was a restricted terminal field of collicular projections in the dorsolateral pons extending over a much smaller territory than that seen after lesions of extrastriate cortical visual areas.

MSC 3.

In all of the previous cases we plotted the location of tectopontine fibers and terminals in trasverse sections. In this case, MSC 3, we made a lesion in the superior colliculus after first recording evoked potentials to flash. However, in MSC 3 the entire brainstem was sectioned, including the superior colliculus and pontine nuclei in a parasagittal plane. The results show that the great majority of ipsilateral collicular projections are confined to a single parasagittal plane and ipsilateral to the NRTP on the contralateral side. The results help to complete a picture of the dorso-ventral and anterior-posterior extent of collicular terminals.

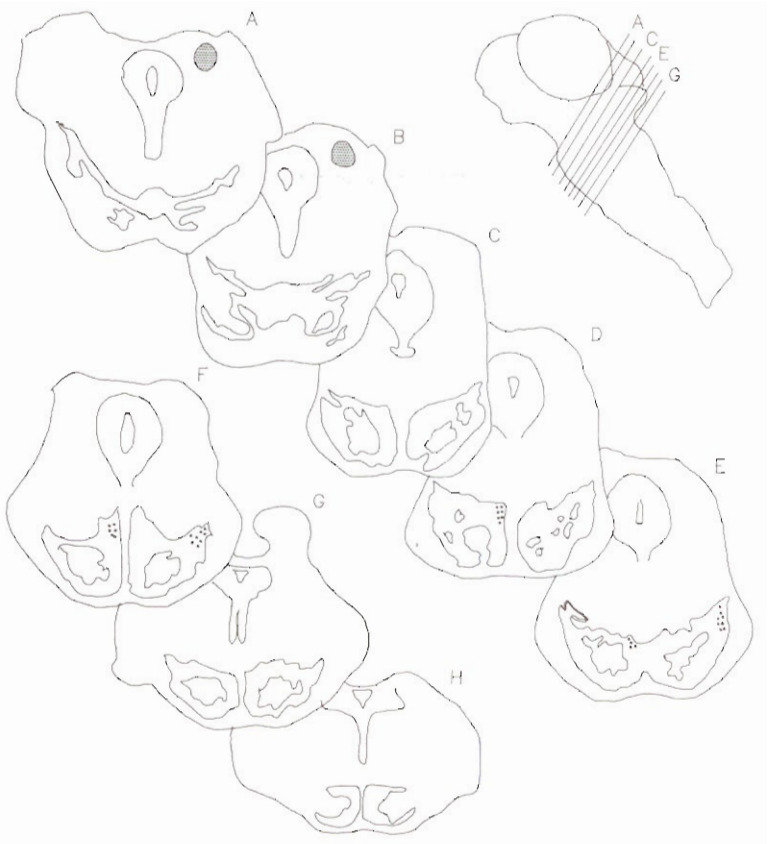

Fig. 5. – *MSC 2.* Transverse sections through the brainstem illustrating the extent of the collicular lesion and the location of the resulting sites of degeneration in the pontine nuclei (shown as stippling).

Laminar depth of the tectopontine efferents.

Previous studies in cats showed that the pontine nuclei receive a projection from superficial as well as deep layers of the superior colliculus (19).

We know that the superficial colliculus projects to dorsolateral pons and the deep colliculus to NRTP. It cannot be established from the data presented so far whether cells of the deeper layers of the superior colliculus also project to the dorsolateral pons. Accordingly, we report here one case (P10) in which we first recorded from visually activated cells in the dorsolateral area of the pontine nuclei. When the pontine visual area was thus located by the response to bright flash, we injected this area with WGA-HRP (Fig. 6A and 6B) and traced retrogradely filled cells and orthogradely labelled fibers. We confirmed the pattern of cortical projection to this region seen in previous studies (10). We also analysed the laminar depth within the superior colliculus of tectopontine cells. We found that there was a rich projection both from superficial and deep collicular cells,

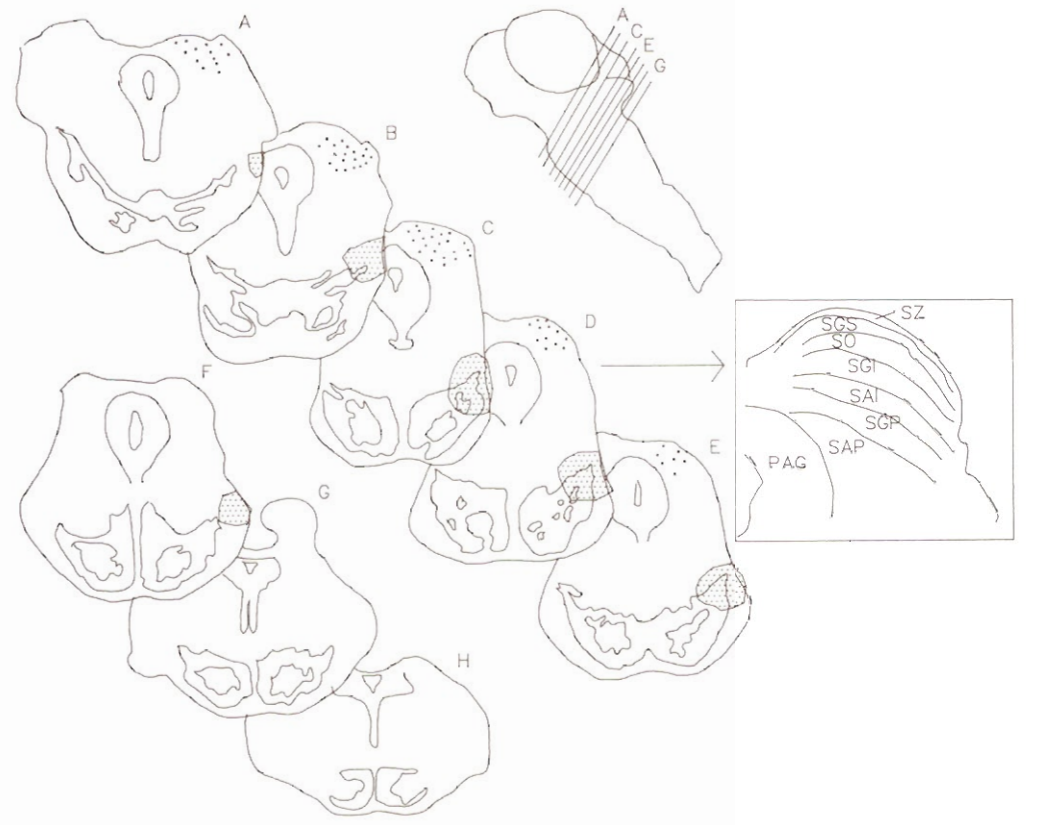

Fig. 6A. – *P10.* Transverse sections through the brainstem illustrating the extent of the primary site following an injection of WGA-HRP into the pontine nuclei and the resulting retrogradely labelled cells in the superior colliculus (shown as stippling).

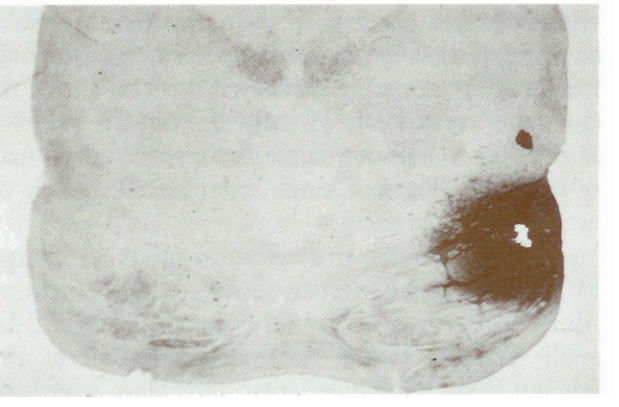

Fig. 6B. – *P10.* A photomicrograph illustrating the center of the primary injection site. × 12.

suggesting that both the lamina 3 stratum opticum cells, as well as the deeper cells, project to the same region of the pontine nuclei.

DISCUSSION

This study had three purposes. The first was to confirm and extend the findings of Harting (13) and his colleague (26) on the projections of the superior colliculus to the pontine nuclei and NRTP. The second was to compare directly the extent of pontine projections of visual areas of the cerebral cortex with those from the superior colliculus. Finally, we hoped to determine the cells of origin within the colliculus of the projections to the dorsolateral pontine nuclei and to the NRTP.

We confirmed the reports of Harting (13) and Weber and Harting (26) of a projection to the dorsolateral region of the pontine nuclei from the superior colliculus. This projection arises from superficially located cells in the stratum opticum as well as from cells in deeper layers of the colliculus.

The NRTP projection arises solely from deeper layers of the colliculus. In our case DML 1, which had an injection of ^{3}H leucine restricted to superficial layers, there was a projection to the dorsolateral region of the ipsilateral pontine nuclei, but not to the NRTP of either side. In case DLM 2, the injection was centered in the same region of the superior colliculus but penetrated more deeply to include the deeper collicular layers. In addition to fibers in the ipsilateral dorsolateral pons there was also a clear projection to the contralateral NRTP in this animal. Thus we confirmed the results of Weber and Harting's case in which tritiated amino acids were injected bilaterally into the superior colliculus of a monkey. On one side the injection was restricted to superficial layers of the colliculus and the projection was restricted to the ipsilateral pontine nuclei. On the opposite side in which the label included deeper collicular layers, fibers were traced both to ipsilateral dorsolateral pontine nuclei and to the NRTP contralateral to the injection.

Thus, in monkeys, as in cats (15, 19), there is a projection to the dorsolateral pons from superficial as well as deeper tectal layers. In cats, the tectopontine and corticopontine terminals are largely non-overlapping. Dorsolateral pontine cells which receive input from the superior colliculus have receptive fields which resemble those of cells in the superficial, visually dominated layers of the colliculus. The most obvious difference between these collicular and pontine receptive fields is the much larger receptive fields of single pontine cells when compared to those within the colliculus.

How extensive is the tectopontine projection in monkeys compared to that from the cortical visual areas? In the present series and in Harting's cases (13), the projection to the dorsolateral pontine nuclei from the colliculus is largely restricted to a relatively small territory in the dorsolateral region of the pontine nuclei. The extrastriate visual areas distribute their terminals over a very much wider area within the pontine nuclei.

However, in monkeys, unlike cats, collicular and cortical terminals may overlap.

Although the terminals from the superior colliculus are entirely contained within the much larger region of the pontine nuclei which receives visual cortical input, we cannot say whether there is convergence onto individual pontine cells of tectopontine and corticopontine terminals.

The third question which we raised is about the cells of origin of the tectopontine projection in monkeys. In the case presented here in which we filled the dorsolateral region of the pontine nuclei with WGA-HRP, retrogradely labelled cells were found both in the superficial and deep collicular laminae. In addition, in this case the same pattern of retrograde labelling of the extrastriate cortical visual areas replicated those presented in our earlier reports (10). The combined retrograde and orthograde studies thus show that cells in both the superficial and deep tectal laminae project to dorsolateral pms but that only the deeper tectal laminae project to the NRTP. Further studies, using double-labelling procedures, would be needed to see if the same tectal cells which project to the NRTP send a branch to the pontine nuclei.

In their report of visual responses on the cat cerebellar cortex, Snider and Stowell (24), recorded visual potentials to flash which were distributed principally on lobules 6 and 7 of the vermis. Snider & Stowell argued that these visual-evoked potentials were probably activated by way of the superior colliculus since the responses survived bilateral ablation of the cerebral hemispheres. Since Snider & Stowell's first report it has become increasingly clear that visual information is distributed far more widely on the cerebellar cortex of mammals than to lobules 6 and 7 alone. For example, Burne *et al.*, demonstrated that there is a rich projection of visual information to the paraflocculus of rats (3) and we found a powerful relay of cortical visual information to the paraflocculus of cats (20, 21). Our own preliminary evidence (11) fully confirms that, in addition to projections to the vermis, there is also a powerful projection to the paraflocculus and adjacent hemispheric cerebellar cortex of monkeys. It is not yet clear, however, how the tectopontine and corticopontine visual projections differ in their projections to the cerebellar cortex.

A final comment is needed on the input to the NRTP. Although it must be considered as a possible source of visual information to the cerebellum, NRTP can not yet be thought of in the same way as dorsolateral pons as a route for relaying specifically visual information to the cerebellar cortex. Only the deeper tectal laminae of monkeys project to NRTP. It is now well established that there is a difference in the anatomical circuitry and response properties of cells in the superficial and deep strata of the superior colliculus (5). Cells in the superficial colliculus are dominated by their visual input from the optic tract and visual cortex and respond briskly to appropriate visual targets (14, 22, 30). Deep collicular cells may also respond to visual inputs but they also can be activated by auditory and somatosensory stimuli (4). As Edwards (5) argued convincingly, the deep layers in the colliculus are, in many ways, more similar in their response properties and connections to the adjacent reticular areas of the midbrain than they are to the superficial tectal laminae.

SUMMARY

We studied projections from extrastriate visual areas and the superior colliculus to the pontine nuclei of monkeys using degeneration staining and transport of wheatgerm agglutinin horseradish peroxidase, and ^3H amino acids.

The superior colliculus and the extrastriate cortical visual areas both project to the ipsilateral dorsolateral region of the pontine nuclei. The projections from extrastriate visual cortex occupy a much larger territory within the pontine nuclei than those from the superior colliculus. The superficial laminae of the superior colliculus project only to the ipsilateral pontine nuclei. The projection to the contralateral nucleus reticularis tegmenti pontis arises from cells in deeper laminae within the superior colliculus.

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