

A QUANTITATIVE STUDY OF THE MAMILLARY BODIES AND THEIR CONNEXIONS

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INTRODUCTION

The mamillary bodies are comparatively small and clearly defined groups of cells where the impulses from a number of widely separated parts of the brain meet and presumably interact. They form a part of the hypothalamus, and they are linked by their afferent and efferent tracts to the anterior thalamus, the hippocampus and the midbrain tegmentum. Following Gudden's description of the mamillary tracts (Gudden, 1889) a number of detailed studies of the mamillary bodies and their fibre connexions have appeared, but the functional role of the mamillary bodies is not known. The majority of authors have described either the topographical relations of the mamillary tracts, or the size, shape, staining reaction and distribution of the mamillary cells. Quantitative studies have only appeared recently. Rose (1939-40) published some volume measurements of the mamillary nuclei, and Simpson (1952) and Daitz (1953) have counted the number of fibres in the fornix of the macaque and man. Although these quantitative studies have drawn attention to certain inter-species differences in the mamillary system of connexions, they are not sufficient to form any coherent picture of the quantitative aspect of the comparative anatomy of this system. Nor do they show the relative size of each of the mamillary components within any one species. The present counts were planned to give a numerical criterion for assessing the relative importance of the parts of the mamillary system of connexions and to form a basis for a quantitative study of mamillary organization. The cells in the medial and lateral mamillary nuclei and the fibres in the fornix, the mamillary peduncle, the principal mamillary tract† and the mamillo-thalamic tract of the cat and the rabbit have been counted.

MATERIALS AND METHODS

All the brains that have been used in the present investigation were fixed by perfusion with formol saline and were cut in paraffin. The cells were stained with a 0.25% aqueous solution of thionin buffered at pH 4.6 with an acetic acid:acetate buffer. The fibres were stained by the Holmes silver method‡ (Holmes, 1947). Some of the series were stained by both the silver and the Nissl method. In these, regularly spaced pairs of adjacent sections were selected and one of each pair was silver stained, the other Nissl stained.

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† The principal mamillary tract is the common origin of the mamillo-thalamic and mamillo-tegmental tracts from the mamillary nuclei (Koelliker, 1896).

‡ In stage 2 of the procedure 3 ml. of 1% aqueous silver nitrate and 5 ml. of pure pyridine were used. In stage 6 the reducer was heated to 50° C.

It has not been possible to obtain a complete set of cell and fibre counts from individual animals. Certain thicknesses and planes of section have been found particularly suitable for each of the counts. Table 1 gives details of sectioning and also shows the animal from which each of the counts has been taken.

Table 1. *The series that have been used for the cell and fibre counts.*

(‘Oblique’ is the plane perpendicular to the direction of the post-commissural fornix (see Text-figs. 1–4). *F*, fornix counts; *LMN*, lateral mamillary cell counts; *MMN*, medial mamillary cell counts; *MP*, mamillary peduncle counts; *PMT*, principal mamillary tract counts; *MT*, mamillo-thalamic tract counts.)

Animal no.	Plane of section	Thickness of section (μ)	Staining method	Observations
Cat 1	Frontal	18	Nissl and silver	<i>LMN, MP</i>
Cat 2	Frontal	12	Nissl and silver	<i>LMN, MP</i>
Cat 3 <i>a</i>	Oblique	5	Silver	<i>F</i>
Cat 3 <i>b</i>	Horizontal	15	Nissl and silver	<i>PMT, MT</i>
Cat 4	Oblique	7	Silver	<i>F</i>
Cat 5	Frontal	17	Nissl and silver	<i>MMN, MP</i>
Cat 6	Horizontal	11	Silver	<i>PMT, MT</i>
Cat 7	Parasagittal	15	Nissl and silver	<i>MMN</i>
Rabbit 1	Frontal	12	Nissl and silver	<i>MP</i>
Rabbit 2	Frontal	18	Nissl and silver	<i>MP, MMN, LMN</i>
Rabbit 3 <i>a</i>	Oblique	8	Silver	<i>MP, F</i>
Rabbit 3 <i>b</i>	Parasagittal	15	Nissl and silver	<i>MMN, LMN</i>
Rabbit 4	Oblique	8	Silver	<i>F</i>
Rabbit 5	Oblique	6	Silver	<i>MT</i>
Rabbit 6	Horizontal	10	Silver	<i>PMT</i>
Rabbit 7	Horizontal	10	Silver	<i>PMT, MT</i>

Cell counts

The cells in the medial and lateral mamillary nuclei have been counted. These nuclei can be clearly recognized in the Nissl preparations, and in the silver preparations they have a dense pericellular fibre plexus which distinguishes them from neighbouring cell groups. The supramamillary, premamillary (Rioch, 1929) and paramamillary (Koiwegami, 1938) nuclei have a comparatively sparse plexus and have not been included in the present counts. A small group of small cells in the anterior part of the medial nucleus, which shares the dense plexus of this nucleus, has been included in the medial mamillary cell counts. This group probably corresponds to the dorsal premamillary nucleus of Krieg (1932).

The sections for all the counts were taken from complete series at intervals of 12–18 sections. The outline of the medial mamillary nucleus was projected on to squared paper at a constant magnification, each square representing $150 \times 150 \mu$ of section. In the medial nucleus the nerve-cell nuclei and parts of nuclei were counted in alternate squares. Only the squares that were completely included in the outline were included in the counts. The area of the medial nucleus was found by weighing tracing paper of uniform thickness which had been cut to the shape of the projected outline. From these results it was possible to calculate the total number of medial mamillary cells per section and hence the number of cells in the medial nucleus. In the lateral mamillary nucleus all the cells in any one section were counted since this nucleus is small in both the rabbit and the cat. The correction factor described by Abercrombie (1946) was used in calculating all the totals. In each of the cell counts between 1.5 and 2.5% of the total number of cells was counted.

Fibre counts

The section of the tract that was to be counted was drawn on to squared paper as above, and the area occupied by the tract was found by the same method. The boundaries of the principal mamillary tract and those of the fornix can be distinguished clearly, but those of the mamillo-thalamic tract and of the mamillary peduncle are less distinct. The error introduced in measuring the area of the mamillary peduncle may be as high as 15%, that introduced in measuring the area of the mamillo-thalamic tract is slightly lower. The fibres were counted in square fields $4.5 \times 4.5 \mu$. Between 100 and 400 such fields, selected from all parts of the tract by means of a table of random numbers, were counted in each section. The number of fibres counted was between 1 and 5% of the total.

Standard deviations of the individual counts have not been given. These would be misleading since neither the cells nor the fibres are evenly distributed throughout the section but occur in groups of varying density. Furthermore, such a measurement of scatter would not include the sampling error due to the measurement of area.

Four of the fornix counts were taken from pairs of closely adjacent sections. The difference between the members of these pairs (Table 2) is less than 10%. The similarity of these counts and the similarity of the pattern that has been found in the fornix counts of different individuals of the same species (see Text-figs. 1-4), shows that the error of the fornix counts is probably less than 10%. The errors of the other fibre counts are of the same order.

RESULTS

The post-commissural fornix

The results of the fornix counts are shown in Table 2. The sections for these counts were taken from a complete series and therefore it has been possible to give their spacing along the course of the post-commissural fornix. The results are shown diagrammatically in Text-figs. 1-4. In both the rabbit and the cat there is a large fall in fibre number between the anterior commissure and the midtuberal region. In the rabbit this is about 100,000 fibres, that is, about one-half of the post-commissural fornix; in the cat it is about 60,000-70,000 fibres, that is, about one-third of the post-commissural fornix. In the cat there is a secondary premamillary increase of about 20,000-25,000 fibres; no such increase was found in the rabbit.

It has not been possible to find the origin of the fibres that are responsible for the secondary increase in the cat. Sections prepared by the rapid Golgi method show that some of the individual fornix fibres branch at the level of the mamillary bodies and the premamillary increase may be due to similar branching at more rostral levels. Parasagittal silver preparations show a small group of fibres curving posterodorsally from the ventro-median hypothalamic nucleus towards the premamillary fornix. These fibres may also contribute to the premamillary increase. Further observations are necessary to show the precise origin of the 20,000-25,000 fibres that appear in the posterior parts of the cat's fornix.

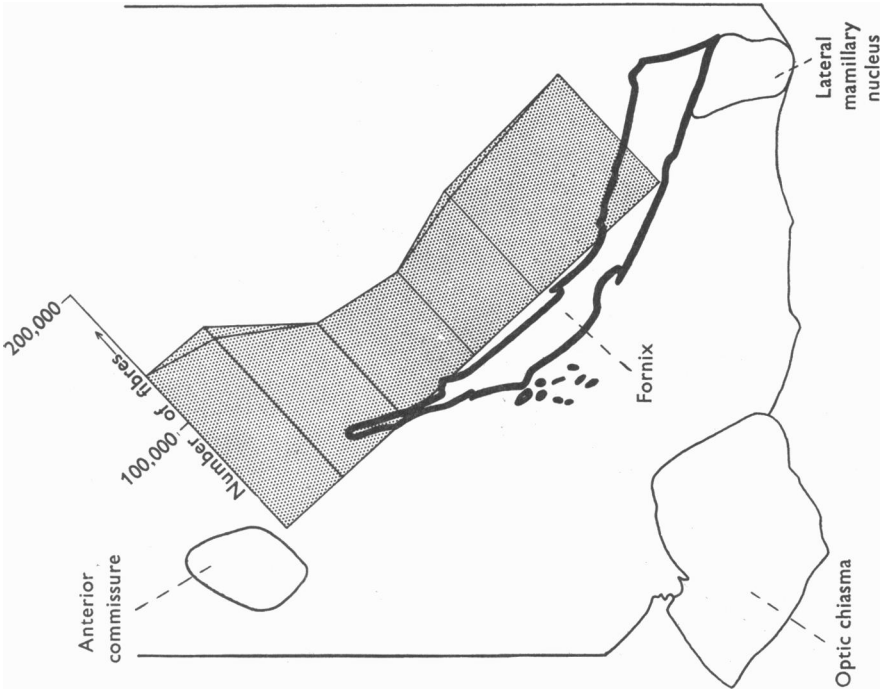
In the anterior part of the hypothalamus, where the fibre loss occurs, a number of fibre bundles can be seen passing from the fornix into the hypothalamus. A small

group of fibres leaves the anterior part of the post-commissural fornix of the rabbit and the cat, to pass ventrally in the periventricular system of the anterior hypothalamus and preoptic region. This group, the medial cortico-hypothalamic tract of Gurdjian (1927), is shown in Pl. 1, fig. 1. The greater part of the tract comes from a loosely organized group of fibres, which lies dorso-medial to the fornix at the level of the anterior commissure (*L* in Pl. 1, fig. 1) and was not included in the counts. A small number of compact bundles (*C* in Pl. 1, fig. 1) from the main bundle of the fornix also join the medial cortico-hypothalamic tract. These were included in the counts but cannot account for more than a small proportion of the total fibre loss.

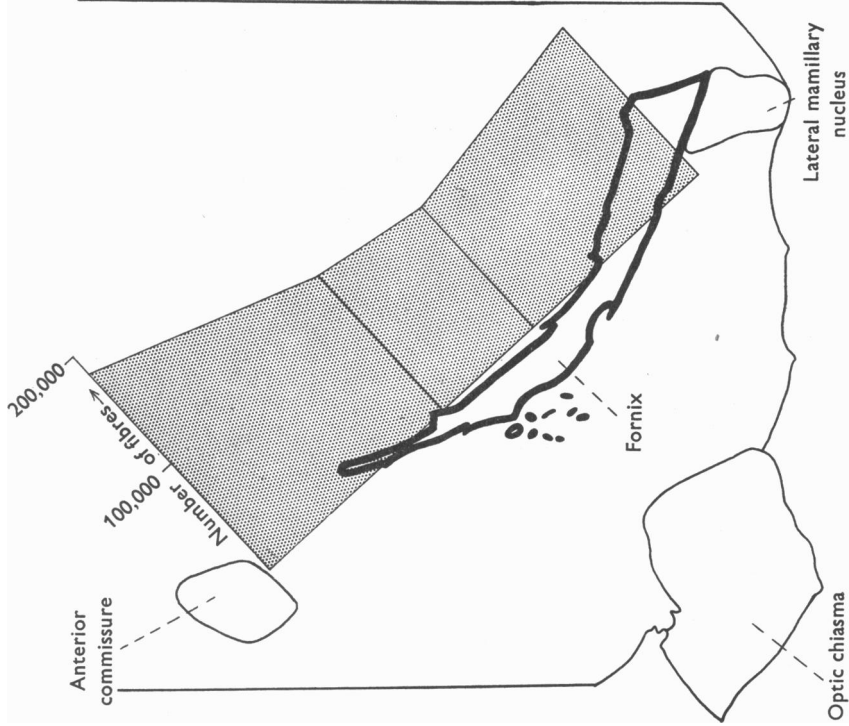
Table 2. *The number of fibres in the parts of the post-commissural fornix*

Distance behind the anterior commissure (expressed as a percentage of the distance between the anterior commissure and the mamillary bodies) (%)	No. of fibres
	Cat 3 (a)
2	143,000
{ 15	131,000 }
{ 15	142,000 }
29	89,000
45	78,000
{ 60	90,000 }
{ 60	96,000 }
88	102,000
	Cat 4
1	184,000
40	127,000
61	114,000
99	138,000
	Rabbit 3 (a)
4	203,000
10	168,000
23	123,000
36	123,000
49	96,000
73	92,000
95	103,000
103	95,000
	Rabbit 4
5	190,000
8	145,000
30	122,000
52	99,000
95	90,000

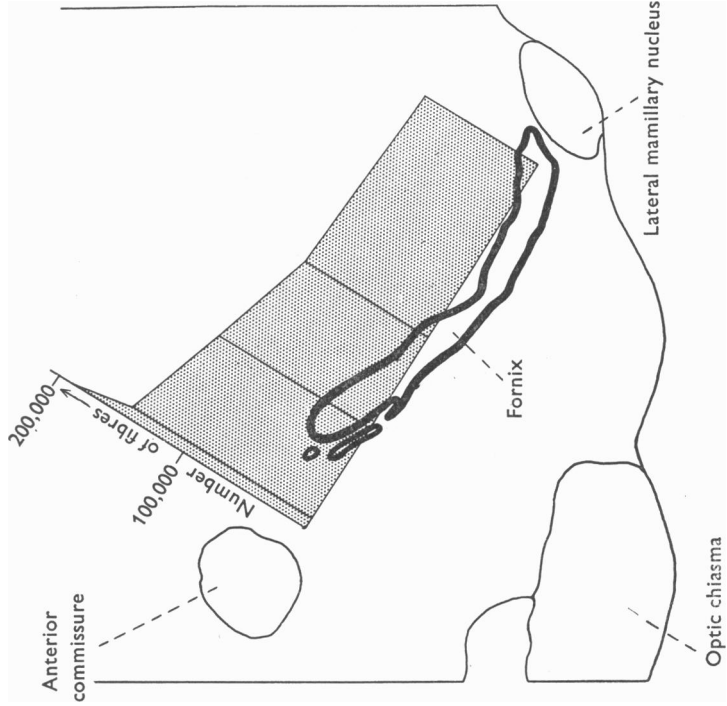
Two other fibre groups can be seen leaving the anterior parts of the cat's fornix. One leaves the fornix laterally, immediately dorsal to the supraoptic nucleus and passes caudally in the medial forebrain bundle (Pl. 1, fig. 2). Some of these fibres can be followed as far as the mamillary bodies, where they lie ventro-lateral to the lateral mamillary nucleus, but the majority are lost in the lateral hypothalamic nucleus. The second group leaves the fornix medially and passes caudally in the



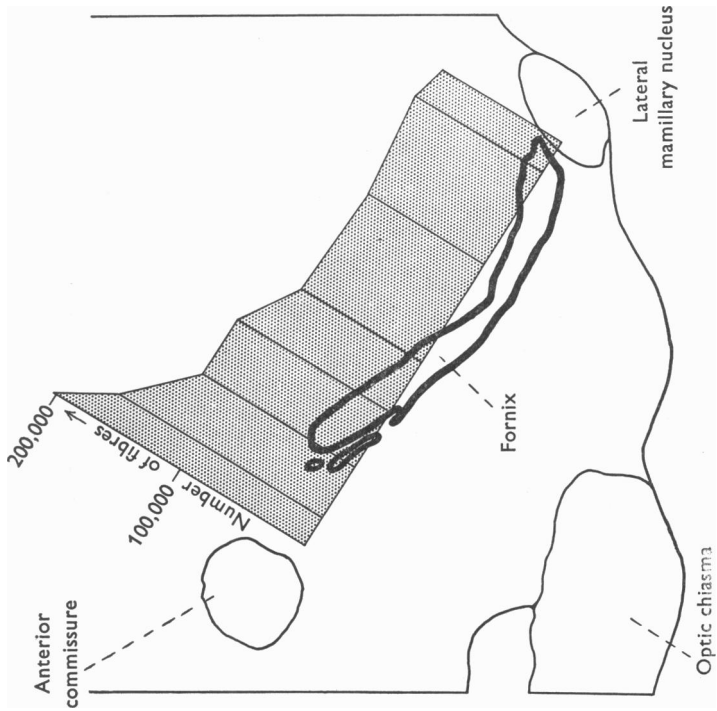
Text-fig. 1. Diagram to show the number of fibres that were counted in the post-commissural fornix of cat 3.



Text-fig. 2. Diagram to show the number of fibres that were counted in the post-commissural fornix of cat 4.



Text-fig. 4. Diagram to show the number of fibres that were counted in the post-commissural fornix of rabbit 4.



Text-fig. 3. Diagram to show the number of fibres that were counted in the post-commissural fornix of rabbit 3.

dorsal part of the hypothalamus (Pl. 1, fig. 3). Some of these fibres can be traced into the posterior hypothalamus almost as far as the principal mamillary tract. It has not been possible to count the number of fibres in either of these groups, or to find their endings. They probably account for a considerable part of the total fibre loss and end among the cells of the premamillary hypothalamus.

No fibres, other than those of the medial cortico-hypothalamic tract, can be seen leaving any part of the rabbit's post-commissural fornix. The great majority of the 100,000 fibres that fail to reach the mamillary bodies must either end close to the fornix, or else leave the main bundle so diffusely that they cannot be seen on normal preparations.

The number of post-commissural fornix fibres that reach the mamillary bodies is about 100,000 in both animals; the number that fail to reach the mamillary bodies is about 100,000 in the rabbit and about 60,000–70,000 in the cat.

The mamillary cells and the efferent mamillary fibres

The mamillary cells send their axons into the principal mamillary tract, which divides to form the mamillo-thalamic and mamillo-tegmental tracts. The fibres in the principal mamillary tract and the mamillo-thalamic tract have been counted, but it has not been possible to count the mamillo-tegmental fibres since these mingle with other tegmental fibres immediately caudal to their origin from the principal tract.

The counts of the mamillary cells are shown in the first two columns of Table 3. The total number of mamillary cells is approximately equal to the total number of fornix fibres that reach the mamillary bodies. In the rabbit there are slightly more than 100,000 cells; in the cat there are slightly fewer than 100,000 cells. The lateral mamillary cells form less than 5% of these totals. Although a number of authors (E. G. Rose, 1939–40; Gudden, 1889) have drawn attention to the large size of the rabbit's lateral mamillary nucleus, this nucleus contains fewer cells than that of the cat, both absolutely and in relation to the number of medial mamillary cells. Rose measured the volume of the lateral mamillary nucleus, whereas the number of cells has been recorded here. Pl. 1, figs. 4 and 5 show that the major difference between the lateral mamillary nuclei of the cat, and the rabbit lies in the packing of the cells, the cells in the cat's lateral nucleus being much more closely packed than the cells in the rabbit's lateral nucleus. The greater part of the volume of the rabbit's lateral nucleus is made up of a dense coarse-fibred plexus. Only a relatively small part of

Table 3. *The number of mamillary cells and the number of fibres in the principal mamillary tract*

	No. of mamillary cells		No. of fibres in the principal mamillary tract	
	Medial nucleus	Lateral nucleus	Under 1.5 μ in diameter	Over 1.5 μ in diameter
Cat	84,000	3,100	86,000	2,200
	74,000	3,000	77,000	2,900
Rabbit	130,000	2,000	72,000	3,300
	104,000	2,100	79,000	2,600

the cat's lateral nucleus is occupied by such a plexus. The fibres of the mamillary peduncle can be followed into this plexus and, since the calibre of the fibres in the peduncle and in the plexus is approximately the same, it is highly probable that the greater part of this coarse-fibred plexus is made up of mamillary peduncle fibres (*vide infra*).

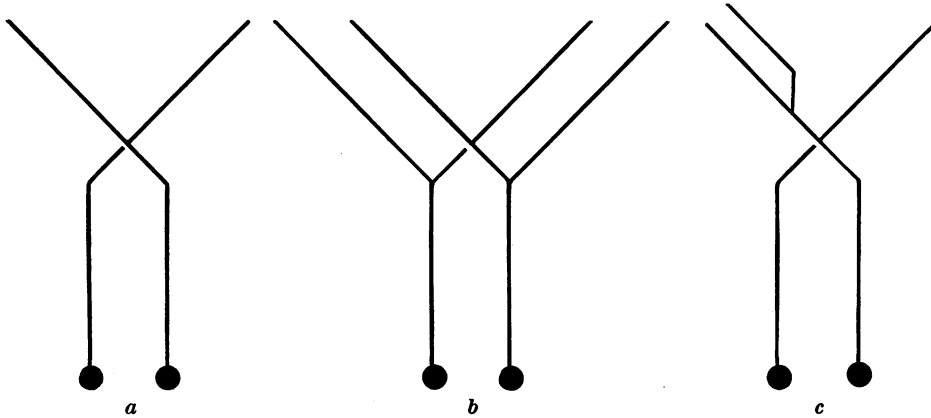
The medial and lateral mamillary nuclei both send their axons into the principal mamillary tract. Horizontal sections through this tract show that there is a group of particularly coarse fibres in its antero-lateral parts, and these can be followed into the lateral mamillary nucleus in frontal sections. A preliminary study of the distribution of fibre sizes (axon diameter, without myelin) showed that the coarse lateral mamillary efferents are over 1.5μ in diameter, while the fibres in the main part of the tract are under 1.5μ . The two size groups have been recorded separately in Table 3.

In Table 3 the counts of the mamillary cells have been compared with the counts of the principal mamillary fibres. In both animals the number of lateral mamillary cells shows close agreement with the number of coarse fibres in the principal tract, indicating that each lateral mamillary cell sends one unbranched axon into the principal tract. Similarly, in the cat there is a close agreement between the number of medial mamillary cells and the number of fine fibres in the principal tract. In the rabbit there appear to be fewer fibres in the principal tract than cells in the medial nucleus. The figures suggest that one-quarter or more of the rabbit's medial mamillary cells have axons which either ramify within the medial nucleus or else pass into the medial forebrain bundle. Although the two sets of figures cannot be regarded as conclusive evidence for the presence of such cells they draw attention to a possibility which is of considerable interest.

The principal mamillary tract divides into the mamillo-thalamic and mamillo-tegmental tracts some distance dorsal to the mamillary bodies. It has not been possible to count the number of fibres in the mamillo-tegmental tract, but it is clear from the literature and from the sections that have been examined that a large number of fibres enter this tract from the principal mamillary tract. In both animals the number of fibres in the mamillo-thalamic tract is approximately equal to, certainly not less than, the number of fibres in the principal mamillary tract (Table 4), showing that there must be a considerable amount of branching of the individual fibres of the principal mamillary tract. The present material is not suitable for showing the pattern of this branching. The fibres may branch as shown in Text-fig. 5*b* or as shown in Text-fig. 5*c*. They cannot leave the mamillary bodies without branching (Text-fig. 5*a*).

Table 4. *The number of fibres in the principal mamillary tract and in the mamillo-thalamic tract*

	No. of fibres in the principal mamillary tract	No. of fibres in the mamillo-thalamic tract
Cat	88,000 80,000	115,000 72,000
Rabbit	75,000 82,000	73,000 82,000



Text-fig. 5.

The mamillary peduncle and post-mamillary fornix

In the ventro-median parts of the midbrain tegmentum, between the mamillary bodies and the exit of the third cranial nerve, the mamillary peduncle is conspicuous as a coarse-fibred bundle. A considerable number of fine fibres also lie scattered among the characteristic coarse fibres of the peduncle. The coarse fibres can be followed rostrally to the mamillary bodies, where they ramify among the cells of the medial and lateral mamillary nuclei, but it has not been possible to trace the finer fibres on the present material. For this reason the coarse and the fine fibres have been recorded separately in the following counts, fibres over 1μ in diameter (axon only) being classed as coarse and fibres under 1μ being classed as fine. The results are given in Table 5, which shows that the coarse fibres form less than a half of the total mamillary peduncle fibres. If all the fibres of the mamillary peduncle reach the mamillary bodies the ratio of fornix afferents to mamillary peduncle afferents is 3:1 or more in the cat, and about 2:1 in the rabbit. If the only coarse fibres reach the mamillary bodies these ratios are as high as 10:1 and 5:1 respectively.

Table 5. *The number of fibres in the mamillary peduncle*

Animal no.	Over 1μ in diameter	Total number of fibres	Medial fornix component
Cat 1	5,000	15,000	—
Cat 2	7,500	18,000	—
Cat 5	12,000	31,500	—
Cat 5	14,000	39,500	—
Rabbit 1	19,000	49,000	11,500
Rabbit 2	17,000	49,000	9,000
Rabbit 3	17,500	55,000	7,000

The counts of cat 5 are considerably higher than those of cats 1 and 2. The mamillary peduncle of the cat 5 occupies an unusually large area but the boundaries of this area are not as definite as they are in cats 1 and 2. It is not possible to assess the significance of this high count until more counts have been done and until the course of the mamillary peduncle fibres is known in more detail. The results from cat 5 make a comparison between the cat and the rabbit material difficult, but the

counts indicate that the mamillary peduncle of the rabbit is larger than that of the cat, suggesting that the mamillary bodies of the rabbit are influenced by tegmental activity to a greater extent than are the mamillary bodies of the cat. These counts also support the view that the dense, coarse-fibred plexus of the rabbit's lateral mamillary nucleus is made up of mamillary peduncle fibres (*vide supra*).

A number of authors have described fornix fibres that pass the mamillary bodies and enter the midbrain tegmentum via the supramamillary commissure (Cajal, 1911; Edinger & Wallenberg, 1902; Morin, 1950) or via the mamillary peduncle (Gerebtzoff, 1941-2; Sprague & Meyer, 1950). On some of the present material (cat as well as rabbit) a few small bundles can be seen passing from the fornix into the supramamillary commissure. It has not been possible to determine either their number or their tegmental course. The fibres that pass into the mamillary peduncle could be identified in the rabbit but not in the cat. The outlines of this group are difficult to define and it is therefore not possible to give an accurate count of the number of fornix fibres in the mamillary peduncle of the rabbit. An approximate estimate has been given in the last column of Table 5. This shows that only about 1/10 of the premamillary fornix fibres pass into the mamillary peduncle and that at least 10,000 of the rabbit's fine mamillary peduncle fibres are not afferent to the mamillary bodies.

DISCUSSION

The cell and fibre counts have shown the gross quantitative relations that hold between the mamillary cells, their afferent and their efferent fibres. They have also shown that a large part of the post-commissural fornix does not reach the mamillary bodies and that there is a considerable amount of branching of the individual fibres in the principal mamillary tract.

The post-commissural fornix

Several authors have described fibres passing from the fornix into the pre-mamillary hypothalamus (e.g. Gudden, 1889, and Edinger & Wallenberg, 1902, for the rabbit; Gurdjian, 1927, for the rat). Daitz (1953) mentions that the fornix gives off small fascicles to the hypothalamus on its way down to the mamillary bodies and Simpson (1952), working on the macaque, found terminal degeneration in the ventro-median hypothalamic nucleus after lesions of the fornix. Simpson, however, points out that his lesions also included the stria terminalis, and that his evidence does not certainly establish a contribution from the fornix to the ventro-median nucleus. Rioch (1931) described the fornix in normal cat material and mentions fibres that leave the fornix through the perifornical nucleus to distribute to the medial preoptic area and to the medial hypothalamic nuclei. Papez (1938) described the brain of a dog in which one hemisphere had been removed, including a part but not the whole of the hippocampus and fornix. He found that the remaining fornix fibres on the affected side did not reach the mamillary bodies but ended in the mid-tuberal region, and he concluded that some of the fornix fibres must end in the hypothalamus.

Although there is good evidence for a hypothalamic ending of fornix fibres, none of the previous evidence shows the size of this fornix component. The present counts show that in the cat about one-third of the post-commissural fornix fibres (60,000-70,000 fibres) fail to reach the mamillary bodies; some of these fibres pass towards the medial, postero-dorsal and lateral parts of the hypothalamus but their precise

end-station is unknown. In the rabbit about one-half of the post-commissural fornix fibres (about 100,000 fibres) fail to reach the mamillary bodies. In the present rabbit material no fibres, other than those of the medial cortico-hypothalamic tract, can be seen leaving the fornix. Sprague & Meyer (1950) found degenerating fornix fibres along the whole length of the perifornical nucleus of the rabbit, but they were unable to find any other fornix degeneration in the hypothalamus. The perifornical endings may, in part, account for the post-commissural fibre loss, but it is doubtful whether as much as one-half of the fornix can end in the perifornical nucleus. If there are fibres passing from the rabbit's fornix into the hypothalamus they must pass diffusely, not in bundles as in the cat, so that their identification in normal or degenerated material would be extremely difficult.

It is probable that the majority of the non-mamillary fibres of the post-commissural fornix end in the hypothalamus. A few pass into the tegmentum. The precise ending of these non-mamillary fibres is not known at present.

The work of Edinger & Wallenberg (1902), Gurdjian (1927) and Krieg (1932) suggests that the hypothalamic component of the fornix arises from the hippocampus as does the mamillary component, but the evidence is not conclusive. Gurdjian describes a bundle of fibres passing from the stria terminalis into the medial cortico-hypothalamic tract, and Morin (1950) describes fibres from the septum that join the post-commissural fornix. It is possible that some of the fibre loss is due to fibres which come from the stria terminalis or the septum, join the post-commissural fornix and leave it again in the premamillary hypothalamus. Further investigations are necessary before the origin and the ending of the non-mamillary component of the fornix can be known in detail, but it is reasonable to assume that at least the greater part of it arises in the hippocampus and ends in the hypothalamus.

The efferent mamillary tracts

The efferent mamillary fibres link the mamillary bodies with the tegmentum on the one hand, and via the anterior thalamus with the cingulate cortex and thence with the hippocampus (Cajal, 1911; Gardner & Fox, 1948; Adey & Meyer, 1952) on the other. Papez (1937) has drawn attention to the circuit that connects the hippocampus, the mamillary bodies, the anterior thalamus and the cingulate cortex. The activity of this circuit is brought into relation with tegmental activity by the tegmental part of the fornix, by the mamillary peduncle and by the mamillo-tegmental tract. Cajal (1911) described the mamillo-thalamic fibres arising as collaterals of the mamillo-tegmental tract, a description which suggests an intimate link between the thalamic and tegmental parts of the mamillary system. The present counts of the principal mamillary tract and of the mamillo-thalamic tract support Cajal's description, but the degeneration experiments reported by van Valkenberg (1911-12) indicate that the two efferent mamillary tracts have an independent origin in separate parts of the mamillary region. The present counts have shown that there must be at least as many points of branching as there are mamillo-tegmental fibres, but they have not shown whether the pattern of this branching is that described by Cajal (Text-fig. 5*b*) or that shown in Text-fig. 5*c*. For an understanding of the relationship between the mamillo-thalamic and mamillo-tegmental pathways the work of van Valkenberg must be repeated in conjunction with quantitative observations.

Quantitative relationships of the mamillary cells and fibres

In the rabbit and the cat the number of afferent mamillary fibres, the number of mamillary cells and the number of efferent mamillary fibres are all in the region of 100,000. The similarity of these figures is striking but their interpretation in terms of mamillary activity is not possible at present. Analyses of the pattern of branching of the mamillary axons and dendrites and more detailed studies of cell:fibre relationships within the mamillary bodies are essential before mamillary activity can be discussed in detail. The gross quantitative relations are presented here as a basis for further studies of mamillary organization.

The literature dealing with the mamillary connexions suggests that the tegmental connexions of the mamillary bodies are relatively small in primates but larger in the rabbit and the rat. The present counts have shown that there are also certain quantitative differences between the mamillary connexions of the rabbit and the cat. These differences are small and are based on only a few animals, but they suggest that further observations of interspecies differences will prove of interest to a study of mamillary organization. The counts show that the hypothalamic part of the fornix is smaller in the cat than it is in the rabbit, that the mamillary peduncle is larger in the rabbit than it is in the cat and that the lateral mamillary nucleus receives proportionally more coarse mamillary peduncle fibres in the rabbit than the cat. These differences suggest that the hippocampus-mamillary system is not as well established in the rabbit as it is in the cat. In the rabbit more of the hippocampal efferents end in non-mamillary parts of the central nervous system and the mamillary bodies receive proportionally more of their afferent fibres from tegmental sources. The tegmental connexions of the mamillary bodies appear to be particularly small in man (Koelliker, 1896), suggesting the hypothesis that the hippocampus-mamillary system increases at the expense of the hypothalamic and tegmental connexions with increasing cortical development. The fornix counts of the macaque and of man that Simpson (1952) and Daitz (1953) have reported are of particular interest in relation to this problem, but at present it is not possible to relate them to counts of any of the other mamillary connexions in these species. Simpson showed that the post-commissural fornix of the macaque contains about 100,000 fibres, whilst Daitz showed that this bundle contains about 1,000,000 fibres in man. Rose measured the volume of the mamillary nuclei in man (3 months old) and in the macaque (*Macaca mulatta*) and found that the human mamillary bodies are 5 times as large as the monkey's. Although cell counts are not available it appears that the relative size of the fornix is particularly great in man. It would be interesting to know how many of the human fornix fibres pass to the hypothalamus and what proportion of the afferent mamillary fibres come from the tegmentum in man.

The afferent and efferent mamillary fibres link the mamillary bodies, directly or indirectly, with the hippocampus, the septum, the hypothalamus and the midbrain tegmentum. The mamillary bodies are in a position to influence the activity of each of these regions and to be influenced by their activity. Investigations of these parts of the nervous system show that they are concerned with a wide variety of visceral and somatic activities (e.g. Ranson & Magoun, 1939; Hess, 1949; Kaada, 1951; Sprague & Chambers, 1954), but the organization of these activities or their relation

to mamillary activity is not clearly understood. It is probable that further investigations of these regions will make a more detailed analysis of the part that the mamillary bodies play in the activity of the central nervous system possible, but the quantitative interspecies differences that have been described here suggest that this part may not be the same in all mammals.

SUMMARY

1. The cells in the mamillary nuclei and the fibres in the mamillary tracts have been counted in the cat and the rabbit.

2. There are about 100,000 cells in the mamillary region; slightly more in the rabbit and slightly fewer in the cat. The lateral mamillary cells form less than 5% of these totals.

3. The number of fibres in the principal mamillary tract is approximately equal to the number of mamillary cells.

4. About 100,000 fibres reach the mamillary bodies in the fornix. The mamillary cells receive less than one-third of their afferent fibres from the mamillary peduncle.

5. The post-commissural fornix loses a large number of fibres between the anterior commissure and the mamillary bodies. This fibre loss is about 60,000 fibres in the cat and 100,000 fibres in the rabbit.

6. The number of fibres in the mamillo-thalamic tract is approximately equal to the number of fibres of the principal tract, showing that a large number of the fibres of the principal tract branch before they enter the mamillo-thalamic and mamillo-tegmental tracts.

7. The counts of the rabbit and the cat material have drawn attention to certain interspecies differences in the relative size of the parts of the mamillary system of connexions. These differences have been discussed in relation to the information that is available for primates.

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EXPLANATION OF PLATE

- Fig. 1. Frontal section through the post-commissural region of the cat. Holmes method. *C*, compact group of fibres passing from the fornix into the periventricular region; *F*, fornix; *L*, loose-fibred group lying dorsomedial to the fornix.
- Fig. 2. Frontal section through the hypothalamus of the cat. Holmes method. *F*, fornix; *OT*, optic tract; *X*, fibres running ventro-laterally from the fornix into the medial forebrain bundle.
- Fig. 3. Parasagittal section through the hypothalamus of the cat. Holmes method. *F*, fornix; *PMT*, principal mamillary tract; *OC*, optic chiasma; *X*, fibres running postero-dorsally from the fornix towards the principal mamillary tract.
- Fig. 4. Frontal section through the lateral mamillary nucleus of the cat. Nissl method.
- Fig. 5. Frontal section through the lateral mamillary nucleus of the rabbit. Nissl method.

