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EXPERIMENTAL ANATOMICAL INVESTIGATIONS CONCERNING THE PROJECTION OF THE RETINA ON THE PRIMARY OPTIC CENTRES IN APES.

By B. BROUWER, PROFESSOR OF NEUROPATHOLOGY, AND W. P. C. ZEEMAN, PROFESSOR OF OPHTHALMOLOGY, UNIVERSITY OF AMSTERDAM.

SOME years ago we started experimental anatomical investigations on the projection of the retina on the primary optic centres in the nervous system of mammals. In 1923 some of the results were published in the *Schweizer Archiv für Neurologie und Psychiatrie*. Previous to this, A. Pick and J. Herrenheiser had given a remarkable description of the secondary degenerations in the optic nerves, in the chiasma and in the tractus opticus of rabbits and cats, observed with the help of the Marchi method after small lesions had been made in the retina. This was also done afterwards by Usher and Dean.

These workers did not, however, investigate the degenerations in the optic centres themselves. Lubsen (1921) went further, and described the projection of the retina on the tectum opticum in fishes. We did the same in rabbits and in a few cats, the results being given in the above-mentioned article. For fuller information readers are referred to it, the following points only being mentioned here.

A very distinct localization of the different parts of the retina was found in the corpus geniculatum externum and in the corpus quadrigeminum anticum. This was especially worked out in the case of rabbits. The uncrossed tract in rabbits is, as is well known, very small. These

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fibres terminate in a rather large but circumscribed part of the external geniculate body, viz., in the medial region of the last two-thirds of this ganglion in a frontocaudal direction. In this respect we agree with Minkowski. The uncrossed fibres in rabbits do not reach the corpus quadrigeminum anticum.

The crossing fibres also terminate in special parts of the external geniculate body. The cells of the lower quadrants of the retina send their fibres to the dorsal part of this ganglion, while those of the upper quadrants reach the ventral part. Hence in the external geniculate body the lower part of the retina is projected above the upper part. Further, the study of our series showed that the inner section of the

FIG. 1.—Position of the various quadrants of the retina in the external geniculate body of rabbits.

retina is always projected lateral from the outer. *Fig. 1* (a drawing of a frontal section of the external geniculate body), gives a picture of the position of the various quadrants of the retina in this primary optic centre. The crossed fibres only are drawn here.

Fig. 2 indicates the projection of the retina in rabbits on the corpus quadrigeminum anticum. From this it is evident that in this additional primary optic centre the various parts of the retina have also a definite localization.

The pulvinar is also generally considered a primary station on the optic path. This is questioned in our article. We doubted whether in cats and rabbits optic fibres terminate in the optic thalamus. Later on in this paper the justice of this contention will be shown.

Since the publication of our first article, we have continued our

investigations. Many more operations have been made on rabbits, cats and apes. The animals are killed eighteen days after the operation, and the central nervous system is examined in complete series through the optic centres by the method of Marchi. In the first place, this has confirmed our previous conclusions in the case of rabbits. The results will be published more fully later on. In this article we give only some facts regarding apes.

The retina of the ape is very similar to that of man. Just as in man, there is a pronounced macula—not found in rabbits and only poorly developed in cats—and, further, the number of uncrossed fibres is very large. This last fact is a consequence of the eyes in the ape not being placed laterally in the head as in rabbits, but frontally as in man. Hence the results of our investigations in apes may be valuable for clinical purposes. It is very probable that the projection of the retina on the primary centres in the ape is similar to that in man, especially since the position and 'build' of the external geniculate body are almost identical in the two.

Our experience in this subject is at present based on a series of twelve apes, where operations have been made on the left eye. The lesions in the periphery were examined during life by the ophthalmoscope and controlled after death. The material must be divided into two groups. In the one, lesions are made in the various quadrants of the retina without injuring the macula. In the other, circumscribed lesions are made in the macula itself without damaging the rest of the retina. For comparative purposes a series of the central nervous system is made after one eye has been totally extirpated.

GROUP A.—LESIONS OF THE RETINA IN THE VARIOUS QUADRANTS WITHOUT INJURY TO THE MACULA.

We have the sections of four apes in which operations have been performed in the upper quadrants of the retina. In one a small lesion is

FIG. 2.—Position of the various quadrants of the retina in the corpus quadrigeminum anticum of rabbits.

made in the nasal half, and we have found degeneration only in the crossed corpus geniculatum externum. In the second this is done in the temporal half, and here degeneration is found only in the corpus geniculatum externum on the same side. In two others lesions are made on both halves of the retina, and here degeneration is observed on both sides. After a small lesion the degeneration is very circumscribed, while in a larger one it is more extended. But it is always very clear that the osmium granules in the geniculate body are situated in close

FIG. 3.—Secondary degeneration on the medial side of the crossed external geniculate body after lesion in the upper half of the retina in apes.

FIG. 4.—Secondary degeneration on the medial side of the uncrossed external geniculate body after lesion in the upper half of the retina in apes.

proximity to one another. This also happens after operations in the lower half of the retina, but as soon as the macula is disturbed this is not so. In the sections of these cases the granules are spread further apart.

In *Figs. 3* and *4* the degeneration following a lesion in both halves of the upper part of the retina is shown. The sections of the corpus geniculatum externum are drawn here at regular intervals in an oro-caudal direction. The degeneration in the optic tract, turning towards the ganglion, is shown dotted, while in the ganglion itself it is darkened except where the number of granules is smaller, these being also pointed. From these drawings it is evident that the degeneration is greater at the

crossed side than at the uncrossed, owing to the injury in the retina being severer in the nasal part.

The Marchi granules are clearly found only in the medial part of the external geniculate body. The same is seen in the other series of this group, and hence we draw the conclusion that the upper part of the retina in apes is projected on the medial side of the corpus geniculatum externum.

We have sections of three cases in which lesions are made in the lower half of the retina. In two of them the degeneration is clearly situated not in the medial but only in the lateral half of the ganglion.

FIG. 5.—Secondary degeneration on the lateral side of the crossed external geniculate body after lesion in the under half of the retina in apes.

FIG. 6.—Secondary degeneration on the lateral side of the uncrossed external geniculate body after lesion in the under half of the retina in apes.

Figs. 5 and 6 give a clear indication of these relations. In this animal two wounds were made in the lower half of the retina, one of them being situated in the nasal half, the other in the temporal. Hence degeneration is seen at both sides.

The difference between the series with lesions in the upper half and those in the lower half can already be seen in the optic tract fibres surrounding the ganglion. After an operation in the upper half the optic fibres are seen to be situated medially and remain there, while after a lesion in the under half the fibres from the beginning have a tendency to pass in a lateral direction.

From these results we may conclude that the lower half of the retina in apes is projected on the lateral part of the corpus geniculatum externum.

In a third series lesions were made in both quadrants of the lower half of the retina. From a study of the central nervous system we find that an extensive degeneration is present in both external geniculate bodies. It is chiefly localized in the lateral part of this ganglion, but not exclusively so. As the degeneration has spread so far through the geniculate body, we conclude that macular fibres must be damaged. Hence a complete series is made through the eye. These preparations show that the radiation of the macular fibres, proceeding to the optic nerve, is partly disturbed. This series forms a transition to the next group.

GROUP B. LESIONS OF THE MACULA WITHOUT INJURY TO ANY OTHER PART OF THE RETINA.

We have sections of five cases in which lesions in the macula were made. In none of them were we successful in extirpating the whole macula. From a histological examination of the eye we learned that in all these experiments some spots of the fovea were spared. The case with the greatest lesion of the macula is drawn in *Figs. 7* and *8*. A complete series of the eye showed there was a lesion in the nasal half of the macula, in the upper quadrant as well as in the under. On the temporal side the upper quadrant only was affected. From this examination of the conditions in the periphery we understand why the crossed degeneration is greater than the uncrossed.

These figures show that the degeneration after a macula lesion is much more extensive than in any other series of the previous group. The granules are, however, more scattered. Most of them are to be seen in the middle part of the external geniculate body. This is just the part where no degeneration is found after lesions in the upper and under half of the retina. But that is not exactly the case, as there is some overlap, observable especially in the oral part of this ganglion. The sections of the uncrossed fibres also show degeneration chiefly in the centre of the corpus geniculatum externum.

In a second series, where a lesion in the macula was made, a very extended degeneration in the geniculate body of the same side was seen. From a microscopical study of the conditions in the periphery we learned that it was almost entirely in the upper temporal quadrant that a disturbance was found. The degeneration was spread through the medial half of the ganglion in the oral part, but reached also more caudally to its centre.

In a third and fourth series of macula lesion we again observed an extended degeneration in the central part of the corpus geniculatum externum, but the medial and lateral parts were not free. Only in the last series of this group the degeneration was small; microscopical examination of the eye showed that the wound in the macula was extremely limited.

Finally, we have still another series. Here the macula itself was not damaged, the lesion being made directly medial from the fovea. In this way we hoped to cut off all the fibres in the retina proceeding from the macula to the optic disc. The result, however, was that the whole of the macula fibres were not destroyed. Besides, a small part of the temporal lower half of the peripheral retina was eliminated.

FIG. 7.—Secondary degeneration in the crossed external geniculate body after lesion in the macula of the ape.

FIG. 8.—Secondary degeneration in the uncrossed external geniculate body after lesion in the macula of the ape.

Here also a very extended degeneration is to be found in both geniculate bodies, especially in the central and lateral parts.

From the series of this group we have to draw the conclusion that the fibres issuing from the macula are spread over a great part of both external geniculate bodies. They terminate more especially in the central part of this ganglion, where the fibres of the peripheral quadrants do not come.

In none of the series of either group did we see degenerated fibres entering the pulvinar. After the extirpation of one eye, degenerated

fibres may be found on the medial edge of the pulvinar. They avoid the geniculate body, but yet do not end in the pulvinar. They take a caudal direction and pass through the anterior arm of the corpus quadrigeminum anticum and terminate in this part of the midbrain. Their number is much smaller than in rabbits and cats. After partial lesions in the periphery, we missed this degeneration. It is a well-established fact that in the ascending scale of mammals the number of the reflex fibres into the midbrain gradually diminishes, at least as far as they are myelinated. From our examinations we draw the conclusion that the pulvinar of apes does not belong to the primary optic stations.

DISCUSSION.

We shall try to define the value of these experimental anatomical results in advancing our knowledge of the visual cerebral organization in men.

Already for many years there have been two lines of thought as to how the optic fibres are spread throughout the central nervous system. The chief representatives in this field are two famous workers, on the one side C. von Monakow, and on the other S. E. Henschen. The former and his school do not believe that the different parts of the retina can thus far be definitely localized in the brain. Further, they deny that the macula has a circumscribed localization in the geniculate body, in the optic radiation to the occipital cortex and in the cortex itself. The high physiological significance of the macula leads v. Monakow to form the theory that the impulses, caught by this part of the retina, are spread over the whole external geniculate body. Thus, it is possible for them to be associated there with impulses from other parts of the retina. In v. Monakow's idea the impulses of the macula must also be diffusely scattered over a great deal of the optic radiation and of the occipital lobe.

Henschen, on the contrary, from the beginning of his studies, has held the localization theory. In his opinion every spot of the retina has a sharp localization in the geniculate body, in the fasciculus longitudinalis inferior as well as in the cortex. The upper part of the retina always lies dorsal in the optic pathways, the under quadrants ventral. Consequently the macula, which forms a small isle in the retina, has also a very circumscribed projection in the brain.

The experiences, especially of the Great War, have led many oculists and neurologists to adopt this theory. They have also fortified Henschen in his views, as may be seen in his recent articles (1923 and 1924). Still, we must not forget that a careful anatomical examination in these war cases is missing, and also that the best clinical observations cannot solve this problem.

As mentioned above, we have found that different parts of the retina in apes have a distinct projection in the external geniculate body, in this sense, that the upper quadrants lie medial, the lower, lateral. In the literature on clinico-anatomical cases of cerebral lesions, results may be found pointing to the same conclusion in men.

Winkler, for example, has described a case of hemianopsia inferior, caused by a cerebral hæmorrhage, where the medial part of the corpus geniculatum externum was degenerated and the lateral spared. From this the deduction may be drawn that the superior quadrants of the retina in men must be situated in the medial part of the external geniculate body. The sight in the upper part of the field of vision being in this case normal, it is evident that the lower half of the retina must be localized in the lateral part of this ganglion. Henschen has also described a case of inferior hemianopsia in men, where, in his opinion, the dorsal part of this ganglion was disturbed. The diagram of this case, however (see article, 1923, *Fig. 3A*, or article, 1924, *Fig. 6*), leads one to suppose that it was the medial part especially which was degenerated.

These facts, arrived at in quite different ways, seem to indicate that the condition in apes and in men may be much alike in regard to the relation between the retina and the external geniculate body.

The chief controversies about the projection of the retina in the central nervous system, as mentioned above, centre round the macula. Our results show that the number of macula fibres is fairly large. The reason may be readily understood from the discussion in a former article by one of us (1917). This region of the macula, it is true, forms a small isle in the retina, but it is very richly provided with ganglion cells, much more so than in other parts. We have described how the fibres, issuing from these cells, are widely spread throughout the corpus geniculatum externum, mostly in the middle, but also reaching the medial part. Here they are mixed with other fibres. Hence we may conclude that the fibres from the macula touch far more cells in the geniculate body than do those of other parts of the retina. Consequently we maintain that the light stimuli, caught in the macular region, must also be widely spread throughout the cortical optic centre.

This conclusion is in contrast to the opinions lately published by a number of neurologists and oculists. The experiences of Rönne, it appears to us, are valuable in this connection. This author studied cases of degeneration of the macular bundle, caused by intoxication, and found cellular changes in the geniculate body. From these investigations he draws the conclusion that the macula has a sharp localization in this ganglion, and that this corroborates the views of Henschen. But it is very clear from his description and from his pictures, that the projection of this small part of the retina is a very large one.

In our former article we mentioned that our results will have to be checked by other methods. The Marchi degeneration alone is not sufficient, hence it will be necessary to examine other cases of retina lesions in the same way as Rönne and Minkowski have done. Still we believe that our results help to advance our knowledge of the cerebral organization of vision.

SUMMARY.

In this paper descriptions are given of secondary degenerations in the external geniculate body, after experimental lesions had been made in the retina of apes. The results convince us that the dorsal quadrants of the retina in apes are projected on the medial part of this ganglion, and the ventral on the lateral. The macula is largely represented in the geniculate body, lying between the other parts of the retina but partly overlapping them. We are at present engaged making investigations to find out whether this is a real overlap or only appears to be one.

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