

Medicine. — *The systematic arrangement of fibres in capsula interna, thalamus opticus and pes pedunculi.* By J. DROOGLEEVER FORTUYN. From the Neurological Institute, Wilhelmina Gasthuis. (Communicated by Prof. B. BROUWER.)

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During recent years the connections between the optic thalamus and the cerebral cortex have been thoroughly investigated. The facts found add to a deeper understanding of the structure of the former. Our more exact knowledge of the connections of the various thalamic nuclei grants us a better insight into their functional significance.

In the neurological institute of the University of Amsterdam various parts of the cerebral cortex of the rabbit's brain have been removed, partly by Prof. Dr. B. BROUWER, partly by myself. Thirty experiments were performed. The animals were killed 14 days after the operations and the brains were treated after MARCHI. Extirpation of different parts of the cortex causes degenerations in different parts of the optic thalamus. In the course of this investigation it appeared to be inevitable to describe once more the anatomy of the normal brain, while the nomenclature of the nuclei was brought in harmony with modern conceptions. We followed closely WINKLER and POTTER's (28) and D'HOLLANDER's (16) description of the rabbit's brain while also other publications, especially those of GURDJIAN (14), RIOCH (23) and LE GROS CLARK (8—12) were consulted. In my thesis (6) a description and discussion of the optic thalamus is to be found, illustrated with photographs of ten transverse sections stained after WEIGERT-PAL. The results of my experiments dealing with the connections of the nuclei are given in fig. 1.

A more extensive discussion does not lie in the scope of this article which intends to deal exclusively with certain facts of a more general character.

The investigations of the past 15 years largely confirmed and completed the findings of several previous investigators, especially of VON MONAKOW. We will discuss one point however where the conclusions do not agree. VON MONAKOW (20) as well as WINKLER (27) stresses the fact that the projection of the thalamus on the cerebral cortex shows a certain degree of overlapping. Recent experiments in rats, rabbits and higher animals corroborate the assumption that the anatomical thalamic units, the nuclei, are connected one by one with anatomical cortical units, the areas of BRODMANN, CAMPBELL, VOGT, e.a. Moreover much evidence exists of a strict spatial arrangement of the whole fibre system connecting telencephalon and diencephalon. This may be expressed in one general formula:

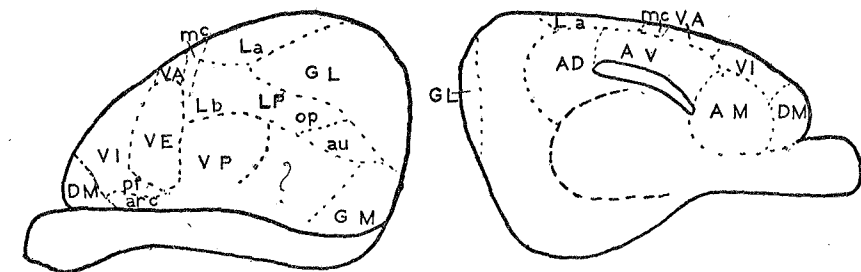


Fig. 1. The cortical fields of projection of the thalamic nuclei in the rabbit.

Nucleus

Field of projection on the cortex
(according to BRODMANN (3) and ROSE (24).)

AM N. antero-medialis	Area 32; part of area 24 dorsal to the former. ROSE: IRaa, IRba, IRca.
AD N. antero-dorsalis	Area 29 b and c.
AV N. antero-ventralis	Area 23 and 24.
DM N. dorso-medialis	Area 8 and 12; oral part of area 6. On the medial surface of the hemisphere area 12 and 6.
N. para-medialis	Oral part of the medial surface of the hemisphere.
VA N. ventralis pars anterior	Between the dorsal end of area 1 + 3 and area 24.
VE N. ventralis externus	Area 1 + 3.
VI N. ventralis internus	Area 4 and 4 + 6.
Arc N. ventralis pars arcuata	Caudal part of area 8; part of area 13 + 16 ventral to area 1 + 3. ROSE: ai1, I1, I2.
pf N. parafascicularis	Ventro-caudal part of area 6; ventral extremity of area 1 + 3. ROSE: dorsal part of I1.
VP N. ventralis pars posterior	Ventral part of area 5 and 5 + 7; probably extending ventrally over area 13—16. ROSE: oral part of area parietalis 5; oral part of 13.
Lb N. lateralis b	Dorsal part of area 5 + 7.
La N. lateralis a	ROSE: area parietalis 3, area parietalis 4. Area 29d, part of area 7 between area 5 + 7 and area 17. ROSE: Rsgβ, area parietalis 3 + area striata.
mc N. magnocellularis	Dorsal part of area 5.
LP N. lateralis pars posterior	Part of area 7 ventral to area 17.
op pars optica	ROSE: oral part of area occipitalis.
au pars auditiva	Dorsal part of area 21.
GL Corpus geniculatum externum	ROSE: caudal part of area occipitalis. Area 17.
GM Corpus geniculatum internum	ROSE: area striata.
N. supra-geniculatus	Area 20.
Lobus superior et N. profundus	Area 21?
N. praetectalis	Area 21?
	Caudal half of the cortex.

fibres, originating from adjacent parts of the cortex terminate in adjacent parts of the thalamus. This formula enables us to discuss various experimental findings from one point of view. In the first place the formula expresses the fact, that adjacent cortical areas project to adjacent thalamic nuclei. WALLER (25) called attention to this fact some years ago. D'HOLLANDER and STOFFELS (17) and GEREBTZOFF (7) worked it out for the rabbit. From this follows a similarity between the topographical relations of a nucleus with its surrounding nuclei and those of its field of projection with the neighbouring cortical areas. Thus a conformity is suggested between the structural pattern of the thalamus and of the cerebral cortex (exposed extensively for the rabbit by D'HOLLANDER, STOFFELS and GEREBTZOFF).

Another experimental fact may be deduced from our formula: the systematic arrangement of the fibre connections between cerebral cortex and thalamus opticus also applies to each cortical area and its corresponding nucleus. The postcentral area as a whole is connected with the nucleus ventralis externus. Within this area we can separate a centre for the arm and one for the leg connected with two separate parts of the nucleus ventralis externus, thus representing the arm and the leg centre in the thalamus. Minute lesions within a cortical area lead to circumscribed degeneration within the corresponding nucleus. This was found to apply to the corpus geniculatum externum already some years ago (V. HEUVEN (15), BIEMOND (1), POLJACK (21), LE GROS CLARK and PENMAN (13), LASHLEY (18), BODIAN (2), POLJACK and REY HAYASHI (22)). A so-called "point-to-point-projection" of the corpus geniculatum externum to the area striata is proved to exist. A similarly differentiated projection of the other nuclei is getting more and more probable. In my experiments not in all nuclei the fields of degeneration are circumscribed. So in the lateral geniculate body, in the ventral nucleus and in the anteroventral nucleus sharp boundaries were seen, corresponding to circumscribed lesions of the cortex. But in other nuclei, such as the anterodorsal nucleus and in the lateral nuclear mass circumscribed fields of degeneration were often but not always found. The differences between the various nuclei can be frequently explained by the different course of the fibres from the cortex: so frontal lobe fibres are often cut obliquely; hence a more diffuse destruction of the connecting system. Our researches on the rabbit with the MARCHI technic lead to the assumption of a sharp projection to all thalamic nuclei, similar to the projection of the geniculate body.

In higher animals this has not been proved. WALKER (26) describes a "laminar" projection in the dorso-medial nucleus of the monkey. According to this author the areas of the various parts of the body represented in the thalamus probably show an overlap, especially in antero-posterior direction. It seems possible to me that diffuse degeneration in the thalamus is often caused by diffuse damage of the cortex. The consequences of even minor lesions are brought to sight easier by MARCHI sections than by NISSL sections. Although WALKER does not assume a point-to-point-projection

of all cortical areas, he describes a "strictly spatially organised arrangement" of all fibres in the Macacus.

We come to the next point. If we follow the fibres parting from the cortex in oro-caudal arrangement the above mentioned formula compels us to expect a certain arrangement in their thalamic endings. Such an arrangement is indeed found to exist. I found degeneration in the *medial* part of the thalamus following lesions in the *frontal* pole, whereas lesion of the *occipital* pole results in degeneration in the *lateral* part of the thalamus. Fronto-occipital arrangement in the cortex corresponds to medio-lateral arrangement in the thalamus. The area frontalis is connected with the dorso-medial nucleus situated next to the midline, whereas the occipital area is connected with the lateral geniculate body which has a lateral position in the thalamus. The connections of the interjacent cortical areas shift in between and end in the ventral and lateral nuclei.

The same systematisation — and this is a remarkable and interesting fact — has been known for a long time to hold true for the various groups of fibre bundles forming the pes pedunculi. DEJERINE (5) worked this out in man. The pes pedunculi may be divided in segments. The medially situated segment contains fibres from the frontal lobe, laterally to this the fibres from the pre-central cortex join; follow the fibres from the postcentral cortex, next those from the parietal cortex and finally extremely laterally the fibres from the temporal and occipital cortex proceed.

So there appears to exist an analogy between the arrangement of the corticofugal fibres to the thalamus opticus and those to the pes pedunculi.

In addition to the medio-lateral system of projection there is a dorso-ventral systematisation of corticofugal fibres in the thalamus. The *dorsal* part of the senso-motor area projects to a *dorsal* part of the ventral nuclear group i.e. the nucleus ventralis anterior; whereas the *insular* regio projects to the *ventrally* situated pars arcuata. According to the above mentioned formula, an analogous systematisation holds true for the connections of each cortical area and their mode of termination in the corresponding nucleus.

In the pes pedunculi again the same arrangement is found: *dorsally* situated cortical lesions cause degeneration in the *dorsal* fibre groups of the peduncle; insular lesions give rise to degeneration in the *ventral* part of the peduncle. Only in the oral parts of the peduncle this localisation is evident, further caudally the fibres of the pes pedunculi intermingle.

Until now we considered two of the three dimensions of the thalamus: the medio-lateral and the dorso-ventral axis. The third, antero-posterior, axis is also subject to systematisation though in a somewhat different way: so the dorsally originating corticofugal fibres end in the anterior part of the thalamus, the ventrally originating fibres in the posterior thalamic parts. So we see that the nucleus ventralis anterior is situated in the anterior

part of the thalamus, the nucleus ventralis pars arcuata in the posterior part of the thalamus.

Following extirpation of parts of the cortex and staining after MARCHI one will find constantly a strict correspondence between the localisation of MARCHI degeneration in the thalamus and in the peduncle. Not only my

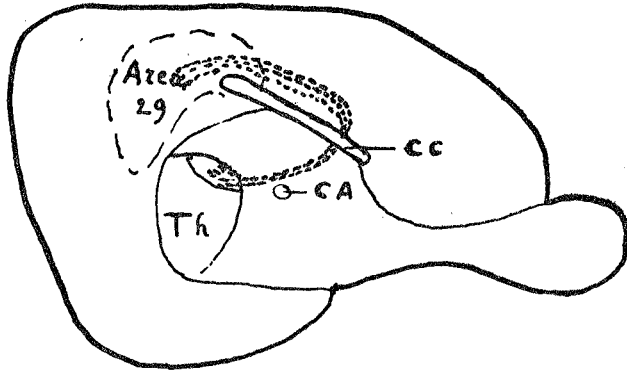


Fig. 2. The projection fibres of Area 29 (retrosplenialis) do not take the shortest route to the thalamus. They run dorsal to the corpus callosum, then bend laterally in a plane oral to the diencephalon. CC Corpus callosum. CA Commissura anterior. Th Thalamus.

own illustrations but also those of LEBLANC (19) and of LE GROS CLARK (11) prove this correspondence.

The connections of the regio cingularis above the corpus callosum need further comment. Fibres from the caudal part of the regio cingularis run via the cingulum orally and bend laterally and ventrally in a plane anterior to the diencephalon (see fig. 2). Probably this remarkable course may be deduced from the phylogenetic development of the callosum, which originally runs together with the commissura anterior. In higher mammals the callosum and regio cingularis extend backwards. The course of the connecting fibres expresses both facts.

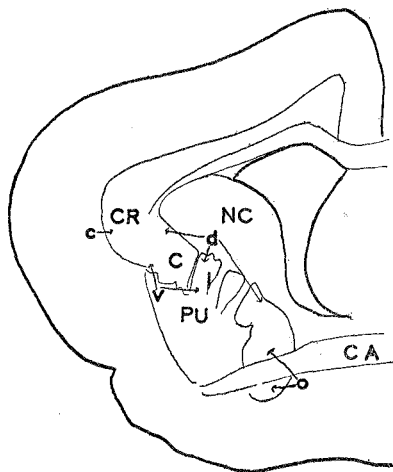


Fig. 3. Arrangement of fibres in the capsula interna (CI) from oral (o), caudal (c), dorsal (d) and ventral (v) parts of the cerebral cortex. CR Corona radiata. CA Commissura anterior. NC Nucleus caudatus. PU Putamen.

bordered laterally by fibres from the sensory and parietal cortex. The

dorso-ventral arrangement is also evident: fibres from the cingular regio run dorso-medially, bordering the caudate nucleus; those from the insular region run along the ventro-lateral side of the capsula interna adjacent to the putamen and the globus pallidus. From the composition of the capsula interna not only the topography of the cortical areas but also of the thalamic nuclei and of the pes pedunculi may be deduced.

The geniculate bodies differ from the remainder of the thalamic nuclei in their topography and in their connecting system.

A large lesion of the occipital cortex encroaching upon the parietal area causes a diffuse field of degeneration in the thalamus, which does not respect the boundaries of the lateral geniculate body but spreads over the lateral nuclear mass. The ventral nucleus however is spared although the nucleus ventralis posterior and the lateral geniculate body are neighbouring structures. Consequently here adjacent thalamic nuclei are not projected to adjacent cortical areas. A transverse section stained after WEIGERT-PAL shows a strong fibre mass separating these two nuclei (see fig. 6). This mass contains fibres connecting the cortex with the lateral geniculate body: they bend laterad to end in this body. The optic tract running along the surface probably only conducts retinal fibres and cortico-pretectal resp. cortico-tectal fibres. Without any doubt the lateral geniculate body is provided with fibres on its medial side, contrary to the remainder of the thalamic nuclei which receives its fibres on its lateral and ventral side from the formatio reticularis and lamina medullaris ventralis. The cortical radiation to the thalamus differs from the cortical radiation to the metathalamus not only in respect to its ending, as described above, but also in the arrangement of the connecting fibres. We may exemplify these differences in opposing the "frontal" radiation to the "occipital" radiation. The following characteristics may be noted:

1. In the mantle the fronto-thalamic radiation forms compact bundles. There is no inner and outer sagittal layer. The optic fibre system on the other hand is spread along the ventricle as a thin band; the fibres run parallel and in transverse sections show an inner and outer sagittal layer containing corticofugal, resp. corticopetal fibres. This arrangement facilitates the possibility of circumscribed experimental and pathological lesions. This gives us the opportunity for a detailed study of this fibre system which for the larger part consists of optic fibres. The primary detection of a finer systematisation of the optic fibre system for this reason may be not fortuitous.

2. The frontal radiation is surrounded by the components of the corpus striatum: the caudate nucleus is situated medially, the globus pallidus and the putamen laterally. The cortico-geniculate radiation, however, runs in a retrolenticular position. The first is "enclosed" by the striatum, the latter "escapes" it and shows the spreading mentioned sub 1.

3. The frontal radiation enters the diencephalon running in oro-caudal

direction. The occipital radiation runs orally first, then turns sharply in a medial direction to reach the diencephalon.

4. After entering the diencephalon the frontal fibres reach the dorso-medial nucleus on its ventral and *lateral* side; the occipital fibres reach the geniculate body on its ventral and *medial* side. Points 3 and 4 are the consequences of one and the same principle (see figs. 4 and 5). In fig. 4

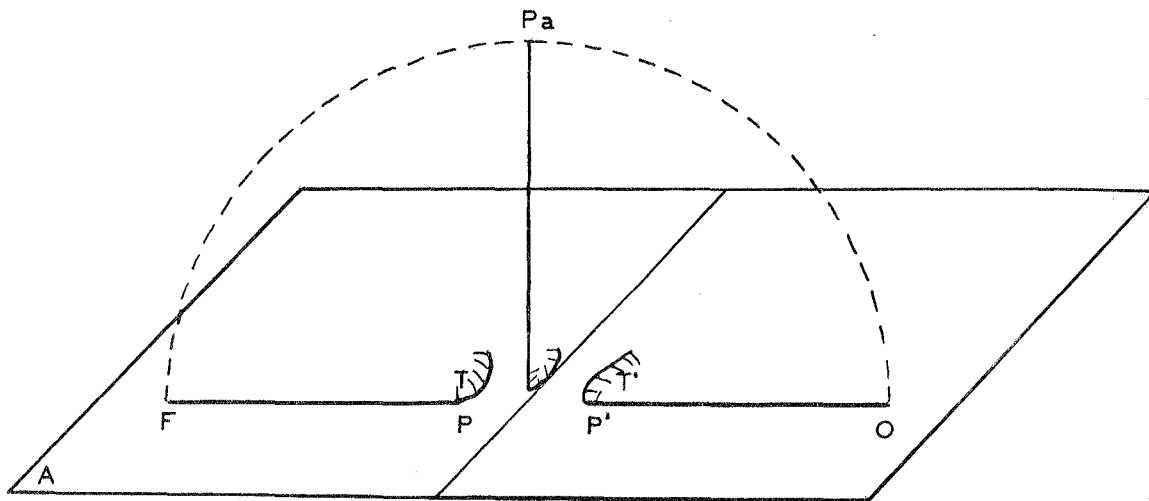


Fig. 4. Scheme of the cortico-thalamic radiation. FPT Fronto-thalamic fibres. Pa Parieto-thalamic, OP'T' Occipito-thalamic fibres.

the frontal radiation is represented by the curve F P T in a horizontal plane A. F is the frontal pole, P the entrance to the diencephalon, T the place of ending in the thalamus. Within the bend P T the nucleus dorso-medialis may be figured. The curve is open frontally. We get the representation of the occipital radiation by rotation of the curve F P T in a

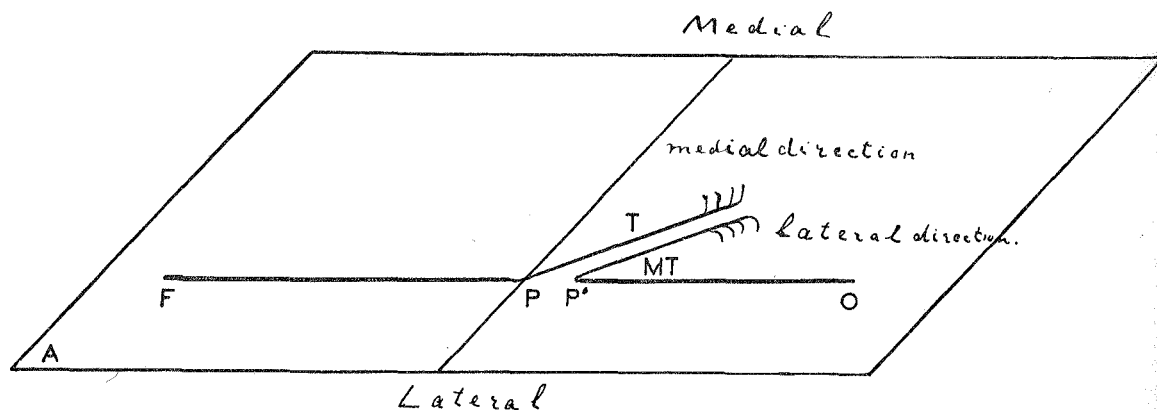


Fig. 5. Scheme of the cortico-thalamic radiation in the rabbit. O P' MT Occipito-(meta)thalamic fibres.

perpendicular plane until the horizontal plane is reached again. This state is represented by the curve O P' T'. Once again the nucleus concerned — i.e. the lateral geniculate body — is found within the bend P'T', this time concave towards the occiput. In the rabbit the fronto-thalamic fibres describe an obtuse angle at their entrance in the diencephalon, whereas the occipito-metathalamic fibres turn sharply. Therefore the next figure approximates the real proportions more closely. It is evident that the fibre supply of the dorso-medial nucleus is medially directed, the supply of the lateral geniculate body laterally (see fig. 5).

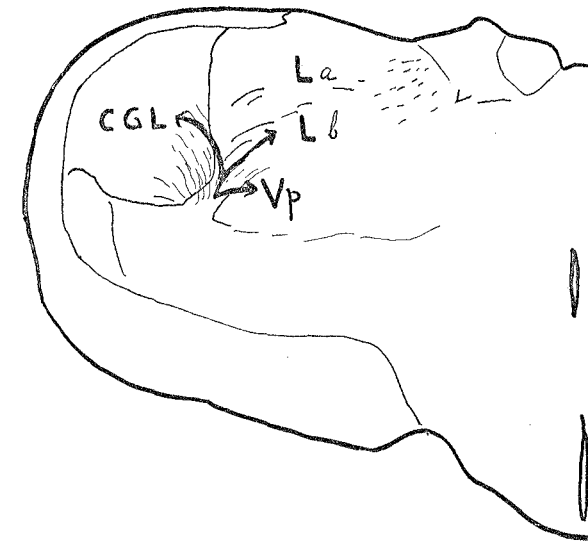


Fig. 6. Transverse section of caudal part of the thalamus. The arrows indicate the direction of the entering fibres. In the phylogenetic development the lateral geniculate body remains on the lateral side of the entering fibres; it becomes expelled and rotated in a direction as indicated by the arrow pointing to the lateral side. CGL Lateral geniculate body, La Nucleus lateralis a, Lb Nucleus lateralis b, Vp Nucleus ventralis pars posterior.

Here a frontal and an occipital radiation are opposed. The remainder of the corticothalamic radiation is pushed in between these two, following for the greater part the frontal, for a smaller part the occipital principle. The connections of the senso-motor and of the parietal cortical areas belong to the former group: fibres from the temporal fields to the latter, leading to a fibre supply of the medial geniculate body on its medial side. Presumably the parieto-occipito-temporal connections to a part of the lateral nuclear mass join this group.

This interpretation throws a light upon the migration of the geniculate bodies in the phylogenetic evolution. The direction of the entering fibres indicates the direction of outgrowth of the posterior thalamic parts. The development of the posterior lateral nucleus to the pulvinar in primates involves an expulsion of the lateral geniculate body laterally and ventrally.

This body remains on the lateral side of the entering fibres. At the same time a rotation takes place (see fig. 6). BROUWER and ZEEMAN (4) found this rotation as a results of their investigations of the different parts of the lateral geniculate body as connected with different quadrants of the retina in monkeys and rabbits. The authors write: "The question now arise whether we can find an analogy with lower animals, for example with rabbits. This is possible if we accept the proposition that the corpus geniculatum externum during its phylogenetic development is not only shifted outwards but is also turned ninety degrees on itself". Our analysis of the structure of the thalamus leads to the same conclusion.

The attempt to correlate the telencephalic and diencephalic course of the cortico-thalamic fibre system stresses the analogous development of telencephalon and diencephalon. Change of the direction of fibre course within one involves a change within the other. Many of these facts may be formulated in terms of neurobiotaxis. Prof. ARIËNS KAPPERS who kindly discussed the subject with me, drew my attention to the fact that the cortico-geniculate fibres take the same course as the cortico-tectal fibres, which represent a very old optic connection. These fibres, running medial to the lateral geniculate body, may determine the route of the cortico-geniculate fibres that consequently have to turn laterally to reach this body. The lateral situation of the latter apparently is determined by the course of the optic tract, the most primitive position of the lateral geniculate body in fishes and amphibians being found always close to the superficially running optic tract in the lateral part of the diencephalon.

Summarizing the above mentioned facts we conclude that the patterns of the cortical surface, of the capsula interna, the thalamus opticus and the pes pedunculi are similar. On the other hand evidence is brought forward for a differentiation of the whole fibre system in two parts: the connections of the frontal, senso-motor and parietal areas are surrounded by the striate body and terminate in the thalamus sensu strictiori. The connections of the occipital, temporal and perhaps of the neighbouring parts of the parietal cortex run retrolenticularly to the metathalamus and to the posterior part of the lateral nucleus. It is tempting to attach a physiological meaning to this differentiation: the anterior part of the cerebral cortex serving motor functions, the posterior part being indispensable for the transmission of optic and auditive stimuli. It may be that the increased spreading of the posterior parts has something to do with a higher degree of local differentiation of sensory mechanics (see also POLJACK (21)).

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