Summary

The incorporation of 3H-thymidine (25μC per animal; incubation times 20 min to 48 hrs; exposition times 28 and 63d) into the DNA of mitotic cells in the CNS of the 9 zebra fish (*Brachydanio rerio* HAM. BUCH.) was investigated by means of radioautography. In the CNS of adult zebra fish numerous cell divisions could be demonstrated only in the valvula cerebelli and the cerebellum. Else, cell divisions are to be seen only in the meningeal and ependymala layers. The optic tectum is nearly free of mitotic cells.

VI. Literatur

BOTSCH, D.: Dressur- und Transpositionsversuche bei Karauschen (Carassius, Teleostei) nach partieller Exstirpation des Tectum opticum. Z. vgl. Physiol. **43**, 173—230 (1960).

FUJITA, S.: Analysis of neuron differentiation in the central nervous system by tritiated thymidine autoradiography. J. comp. Neurol. **122**, 311—327 (1964).

FUJITA, H., and S. FUJITA: Electron microscopic studies on neuroblast differentiation in the central nervous system of domestic fowl. Z. Zellforsch. **69**, 463—478 (1963).

HOMMES, O. R., and C. P. LEBLOND: Mitotic division of neuroglia in the normal adult rat. J. comp. Neurol. **129**, 269—278 (1967).

KAPPERS, C. U. A., G. C. HUBER and E. C. CROSBY: The comparative anatomy of the nervous system of vertebrates, including man. New York: Hafner Publ. Comp. 1960.

KIRSCHE, W.: Experimentelle Untersuchungen zur Regeneration des durchtrennten Rückenmarks von Amblystoma mexicanum. Z. mikrosk. — anat. Forsch. **62**, 521—586 (1956).

KIRSCHE, W.: Die regenerativen Vorgänge am Rückenmark erwachsener Teleostier nach operativer Kontinuitätstrennung. Z. mikrosk.-anat. Forsch. **56**, 190 bis 265 (1951).

KIRSCHE, W.: Zur Frage der Regeneration des Mittelhirns der Teleostier. Verh. Anat. Ges. 56. Vers. (1959). Erg. H. Anat. Anz. **106—107**, 259—270 (1960).

KIRSCHE, W., und K. KIRSCHE: Experimentelle Untersuchungen zur Frage der Regeneration und Funktion des Tectum opticum von Carassius carassius L. Z. mikrosk.-anat. Forsch. **67**, 140—182 (1961).

KIRSCHE, K., und W. KIRSCHE: Regenerative Vorgänge im Telencephalon von Amblystoma mexicanum. J. Hirnforsch. **6**, 421—436 (1963/64).

KRAUSE, R.: Mikroskopische Anatomie der Wirbeltiere. Berlin und Leipzig 1921.

KUHLENBECK, H.: Vorlesungen über das Zentralnervensystem der Wirbeltiere. Jena 1927.

LEGHISSA, S.: La struttura microscopica e la citoarchitettonica del tetto ottico dei pesci teleostei. Z. Anat. Entwickl.-Gesch. **118**, 427—463 (1955).

MARON, K.: Endbrain regeneration in Lebistes reticulatus. Folia Biol. (Krakow) **11**, 3—10 (1963)

PFLUGFELDER, O.: Reparative und regenerative Prozesse nach partieller Zerstörung von Fischgehirnen. Zool. Jb. Physiol. **71**, 301—314 (1965).

RAHMANN, H.: Zum Stofftransport im Zentralnervensystem der Vertebraten. Autoradiographische Untersuchungen mit P-32-Orthophosphat, H-3-Histidin, H-3-Cytidin und H-3-Uridin an Mäusen und Fischen. Z. Zellforsch. **66**, 878—890 (1965).

RAHMANN, H.: Autoradiographische Untersuchungen zum Stofftransport im ZNS der Fische unter besonderer Berücksichtigung der Glucose. Zool. Anz. Suppl. **29**, 485—492 (1966a).

RAHMANN, H.: Zum Vorkommen von RNS im Nervenfaserbereich. Experientia **22**, 762—764 (1966b).

RAHMANN, H.: Darstellung des intraneuronalen Proteintransports vom Auge in das Tectum opticum und die Cerebrospinalflüssigkeit von Teleosteern nach intraocularer Injektion von 3H-Histidin. Naturwissenschaften **54**, 174—175 (1967).

RAHMANN, H.: Syntheseort und Ferntransport von Proteinen im Fischhirn. Z. Zellforsch. **86**, 214—237 (1968).

RICHTER, W.: Mitotische Aktivität in den Matrixzonen des Tectum opticum von juvenilen und adulten Lebistes reticulatus (Peters 1859). J. Hirnforsch. **8**, 195—206 (1966a)

RICHTER, W.: Regeneration im Tectum opticum bei Leucaspius delineatus (Heckel 1843). Z. mikrosk.-anat. Forsch. **74**, 46—68 (1965/1966b).

SEGAAR, J.: Behavioral aspect of degeneration and regeneration in fish brain: a comparison with higher vertebrates. In: Progress in Brain Research, Degeneration Patterns in the Nervous System **14**, 143—231 (1965).

SIBBING, W.: Postnatale Regeneration der verschiedenen Hirnabschnitte bei Urodelen. Wilhelm Roux' Arch. Entwickl.-Mech. Org. **146**, 433—486 (1952/54).

SJÖSTRAND, J.: Proliferative changes in glial cells during nerve regeneration. Z. Zellforsch. **68**, 481—493 (1965).

SMART, J.: The subependymal layer of the mouse brain and its cell production as shown by radioautography after thymidine-H3 injection. J. comp. Neurol. **116**, 325—348 (1961).

SMART, J., and C. P. LEBLOND: Evidence for division and transformation of neuroglia cells in the mouse brain, as derived from radio-autography after injection of thymidine-H3. J. Comp. Neurol. 116, 349—367 (1961).

WAWRZYNIAK, M.: Chemoarchitektonische Studien am Tectum opticum von Teleostiern unter normalen und experimentellen Bedingungen. Z. Zellforsch. **58**, 234 bis 264 (1962).

WIEMER, F. K.: Mittelhirnfunktion bei Urodelen nach Regeneration und Transplantation. Wilhelm Roux' Arch. Entwickl.-Mech. Org. **147**, 560—633 (1954/55).

WINKELMANN, E.: Experimentelle Untersuchungen über die Regeneration des Rückenmarks von Amblystoma mexicanum nach Exstirpation eines kleinen Abschnittes. Z. mikrosk.-anat. Forsch. **66**, 147—176 (1960).

WINKELMANN, E.: Regeneration des Halsrückenmarks von Amblystoma mexicanum nach totaler Durchtrennung. Z. mikrosk.-anat. Forsch. **69**, 279—304 (1962).

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Photometric studies on the myeloarchitecture of the human temporal lobe

By

Adolf Hopf

with 22 figures

The myeloarchitecture of the human temporal lobe was relatively unknown until 1954 (Hopf).

In his combined cyto- and myeloarchitectonic studies Campbell (1905) described only a small "audito-sensory-area" on the dorsal surface of the temporal lobe, an "audito-psychic-area" on the first temporal gyrus and a very large "temporal area" covering the rest of this lobe. He was the first to state that the gyrus of Heschl is the darkest region in myelin preparations, the lateral surface of the T_1 being a little lighter and T_2 and T_3 much lighter in appearance.

Elliot Smith (1907), whose macroscopic studies of the cortex of the fresh brain can also be regarded as a kind of myeloarchitectonics, could differentiate seven temporal areas. They were called area temporalis superior (T_1), area temporalis medialis (T_2), area temporalis inferior (T_3), area temporalis polaris (temporal pole and T_4), area temporalis paradentata (posterior part of T_4), and area para-temporalis (most posterior part of T_2 and T_3).

A more detailed myeloarchitectonic map of the dorsal surface of the temporal lobe was published by C. and O. Vogt in 1910. The same region of the human temporal lobe, i.e., the dorsal surface, was very extensively studied by Beck (1930) who distinguished not less than 79 areas and subareas, also using myeloarchitectonic methods.

The first detailed myeloarchitectonic description of the whole human temporal lobe was published in 1954 (Hopf). Seven main regions could be differentiated (fig. 1).

1. The regio temporopolaris (tp), which is characterized by a broad cortex with only one horizontal stripe of Baillarger namely the outer one in layer 4, the inner sublayer 5b being missed (fig. 2). This type is called singulostriate,

2. The regio temporalis separans (tsep) which separates the pole region from the temporal transverse (auditory) region. Two horizontal stripes can be seen in this region, the inner one is not so well demarcated from the deeper layers. One speaks of a propeunistriate ("nearly unistriate") type,

3. The small regio temporalis parainsularis (tpari) with a very thin cortex and two not very distinct horizontal stripes of Baillarger,
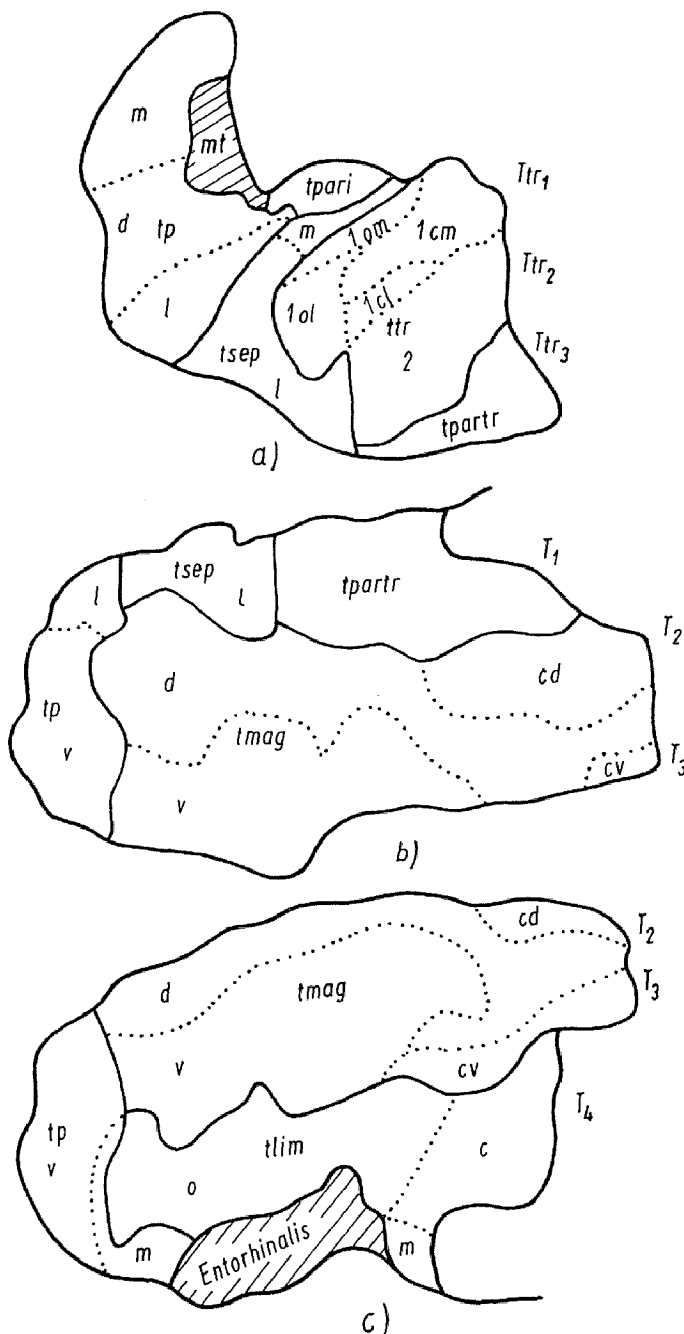
21

Fig. 1. Myeloarchitectonic regions and subregions of the temporal isocortex of man. a) — dorsal (supratemporal) surface, b) — lateral surface, c) — basal surface.

Abbreviations of regions:

tp = regio temporopolaris, tsep = regio temporalis separans, tpari = regio temporalis parainsularis, ttr = regio temporalis transversa, tpartr = regio temporalis paratransversa, tmag = regio temporalis magna, tlim — regio temporalis limitans.

Abbreviations of subregions:

c = caudal, d = dorsal, l = lateral, m = medial, o = oral, v = ventral.

Abbreviations of gyri:

T_1, T_2, T_3, T_4 = first, second, third and fourth temporal gyrus; Ttr_1, Ttr_2, Ttr_3 = first, second, third gyrus temporalis transversus (Heschl). (Reprinted from Hopf, J. Hirnforsch. 1, 216 (1954).

4. The regio temporalis transversa (ttr) on the gyri transversi of Heschl, corresponding approximately to the auditory region, which is the darkest part of the temporal lobe. Two horizontal stripes can be seen, the inner one in 5b mostly not very clearly demarcated from the sublayer 6a, therefore called propeunistriate,

5. The regio temporalis paratransversa (tpartr) around region 4 on the posterior part of convolution T_1, a little less dark, the horizontal stripes a little indistinct, of the propeastriate ("nearly astriate") type,

6. The regio temporalis magna (tmag) on convolutions T_2 and T_3, less dark, with a well demarcated outer horizontal stripe of Baillarger in layer 4 and an indistinct inner stripe in 5b, therefore called unistriate,

7. The regio temporalis limitans (tlim) on convolution T_4 at the border of the entorhinal region, a little darker again, with a pronounced outer horizontal stripe in layer 4, the inner one in 5b mostly not distinguishable from 6a. Therefore most of the areas of this region are called unistriate.

The distribution of the various myeloarchitectonic features was later (HOPF 1955) illustrated by a series of maps. But those myeloarchitectonic descriptions and maps were all based on microscopic observations and therefore subjective to a certain degree.

To demonstrate the main myeloarchitectonic features objectively a photometric method was developed (HOPF 1965, 1966a, 1966b). Striplike photographs of myelin preparations are taken at a magnification of 25 x and registered with the extinction recorder of Zeiss. The whole technical procedure is standardized. The total myelin content and the behaviour of the horizontal stripes can be registered reliably. The curves are exactly reproducible.

Results

1. Regio temporopolaris

All the extinction curves of this region are very characteristic. One can see only two elevations, corresponding to layers 1 and 4.

Figure 3 is taken from the medial subregion (tp. m in fig. 1a) of the temporal pole near the allocortex (mesocortex temporalis, BROCKHAUS 1940). The content in myelinated fibres is very low. Therefore the curve has a course near the

baseline. Besides the dark layer 1 only the outer horizontal stripe of Baillarger in layer 4 is obvious. An inner stripe of Baillarger in sublayer 5b is completely missing. This type is called singulostriate. The photomicrograph of this area shows the very thin myelinated fibres which are typical of areas in the neighbourhood of the allocortex.

If we go a little more lateralward on the dorsal surface of the pole we reach its dorsal subregion (tp. d in fig. 1a). The extinction curve (fig. 4) is more distant from the baseline because of the higher fibre content. Of the two horizontal stripes of Baillarger only the outer one in layer 4 is developed but not an inner one. We have again a singulostriate area.

In the lateral subregion of the temporal pole (tp 1. in fig. 1a and b) the myelin content is still higher (fig. 5). What is demonstrated by these extinction curves is, therefore, a steplike increase in the fibre content from medial to lateral in the polar region of the temporal lobe. This kind of change of architectonic features in a certain direction from area to area was called gradation by VOGT (1919). The singulostriate type with the very prominent layer 4 is obvious in figure 5 but the deeper layers are darker than in the dorsally and medially situated areas of the temporal pole. The next step in this direction is the development of an inner horizontal stripe of Baillarger in 5b which we find not in the temporal pole region but

in the neighbouring areas of T_1 (Regio temporalis separans lateralis, figs. 7—9).

The fourth subregion of the temporal pole is the ventral one (tp. v in fig. 1c), which has a higher myelin fibre content than the medial and dorsal subregions but a little less than the lateral subregion. The ventral subregion is singulostriate too (fig. 6).

2. Regio temporalis separans

The continuation of the gradation in the lateral part of this region (tsep. 1 in fig. 1a and b) is very obvious. An inner horizontal stripe of Baillarger is now developed. The fibre content increases in a caudal direction.

Figure 7 is taken from the anterior area of the subregio temporalis separans lateralis (Area tsep. 1.a). The outer stripe of Baillarger in layer 4 is well demarcated. In sublayer 5b one can see a second elevation but in the following sublayer 6a we have the same fibre content. Therefore the demarcation of the deeper layers from each other is a little blurred. This is called a propeunistriate (nearly unistriate) type.

Figure 8 belongs to the middle area of the lateral subregion (tsep. 1. md). The same propeunistriate type is easy to recognize but the fibre content is higher compared with the more anteriorly situated area (fig. 7).
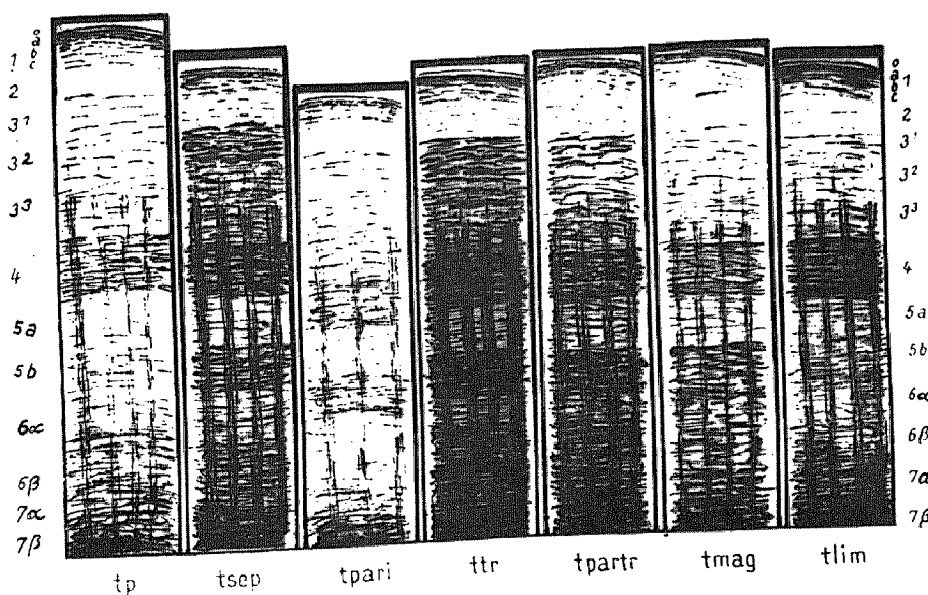

Fig. 2. Scheme of the myeloarchitecture of the seven isocortical temporal regions. For abbreviations see fig. 1.
(Reprinted from Hopf, J. Hirnforsch. 1, 217 (1954)).

21*

Figure 9 from the posterior area of the same subregion demonstrates the same type with a still higher fibre content. We are now in the immediate neighbourhood of the darkest region of the temporal lobe, namely the regio temporalis transversa.
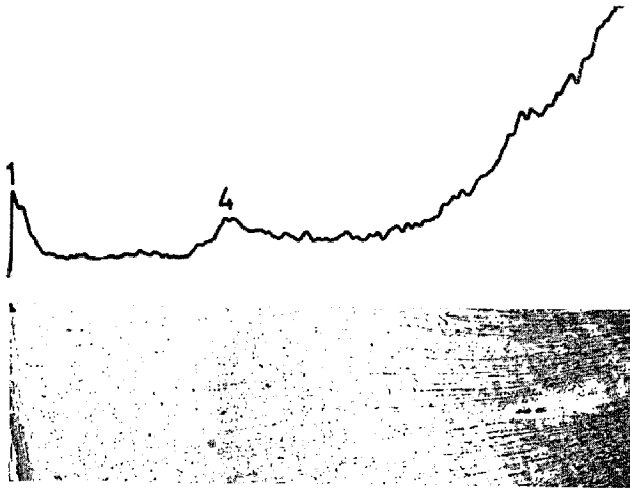

Fig. 3. Photogram and extinction curve from the subregio temporopolaris medialis (tp. m in fig. 1a). Original magnification 25 ×, reduced 4/5 = 20 ×. Myelin preparation, celloidin, 40 μ, Weigert-Wolters staining.
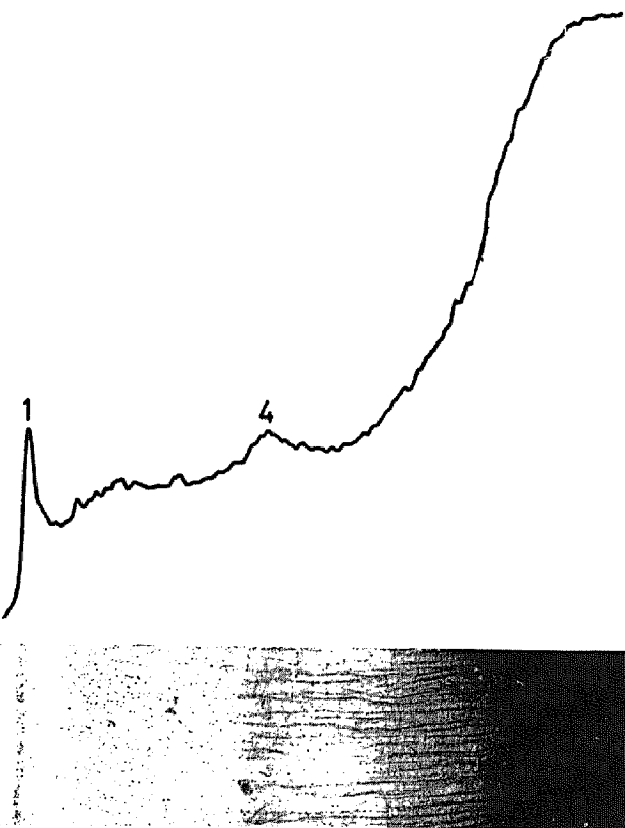

Fig. 4. Photogram and extinction curve from the subregio temporopolaris dorsalis (tp. d in fig. 1), 20 ×.

3. Regio temporalis parainsularis

This region on the medial part of the supratemporal plane (tpari in fig. 1a) is very small. The cortex is thin and of a sulcus type. It was not possible to take a photograph from a place where the cortex is cut perpendicularly. This is demonstrated in the photograph in figure 10 by the discontinuous radial fibres. The deeper layers 4—7 are very thin. That is typical of the cortex in a sulcus formation. The extinction curve shows a clear outer stripe of Baillarger in layer 4 while the inner one is not well demarcated from the adjacent sublayer. Microscopically one can see a not very well developed bistriate type. In the extinction curve such a type is not obvious since the deeper layers are too close together and the decrease in the horizontal fibre content of sublayer 6a is masked by the increasing radial fibre content. This demonstrates a disadvantage of the extinction method, the fact that it does not differentiate between horizontal and radial fibres.

4. Regio temporalis transversa

From this most heavily myelinated region of the temporal lobe only one figure has been chosen, since the principle of gradation was already demonstrated by other examples. All the areas in this region are of a propeunistriate type. They differ from each other only by the fibre content and the behaviour of the radiate fibres and the single fibres in sublayer 3^1.

The extinction curve of an anterior area of the first transversa gyrus of Heschl (ttr 1. ol in fig. 1a) demonstrates a propeunistriate type (fig. 11). Layer 4 is well demarcated. Sublayer 5b is followed not by a descending curve in 6a as in the bistriate type and not by an ascending curve as in the unistriate type, but by a plateau, typical of the propeunistriate type.

In addition a small, but unusual elevation is seen in the thin sublayer 3^1. This elevation is caused by some thick myelinated fibres ("Einzelfasern", single fibres of Vogt). They form what is called the stripe of Kaes-Bechterew. This stripe is characteristic of some areas of the transverse temporal region.

5. Regio temporalis paratransversa

The fibre content of the areas in this region (tpartr in fig. 1a and b) is high but not as high as in the regio temporalis transversa. The outer
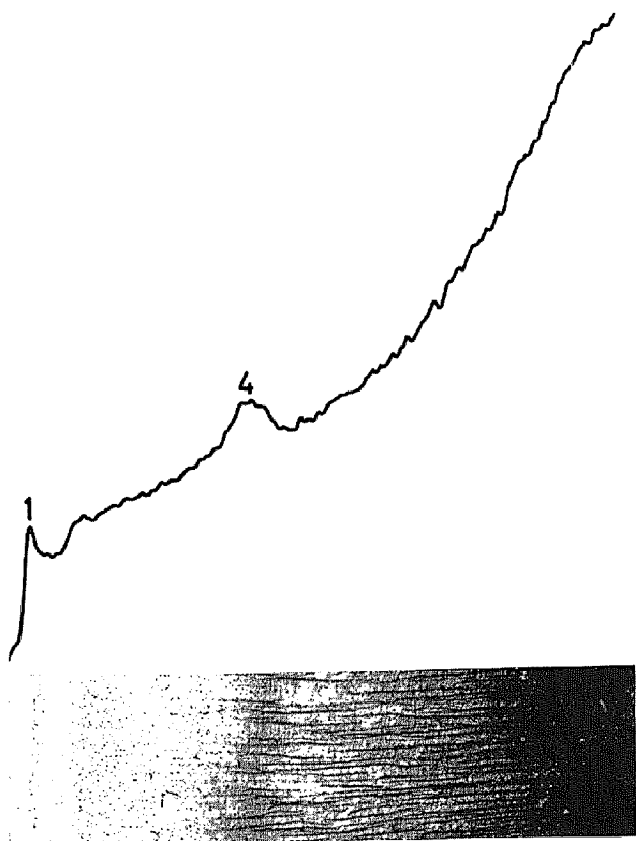
Fig. 5. Photogram and extinction curve from the sub-
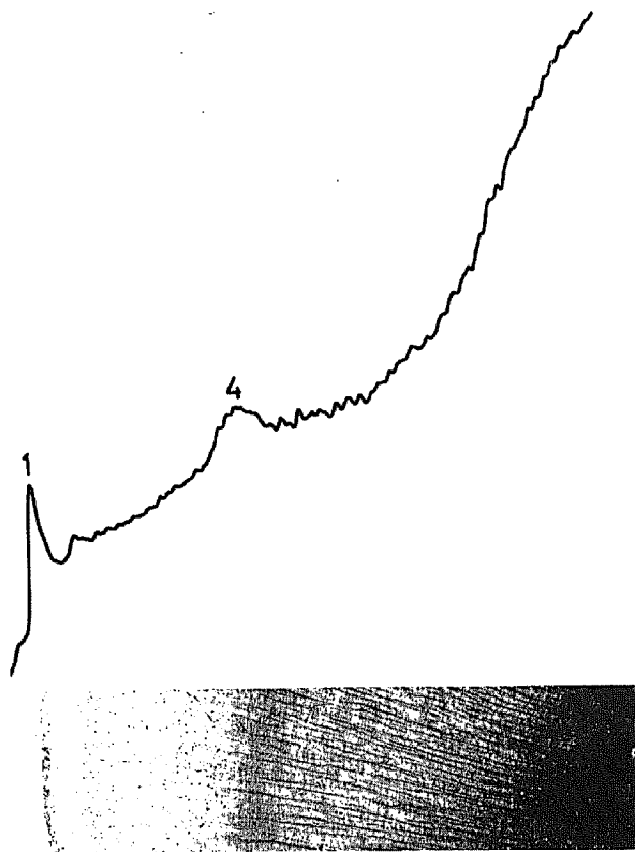regio temporopolaris lateralis (tp. l), 20 ×.

Fig. 6. Photogram and extinction curve from the sub-
regio temporopolaris ventralis (tp. v), 20 ×.
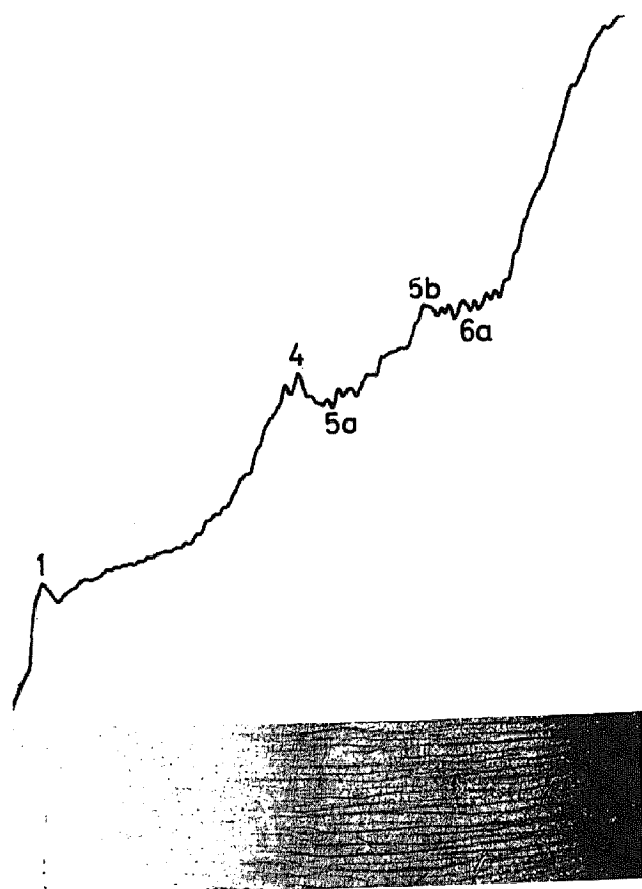

Fig. 7. Photogram and extinction curve from the anterior
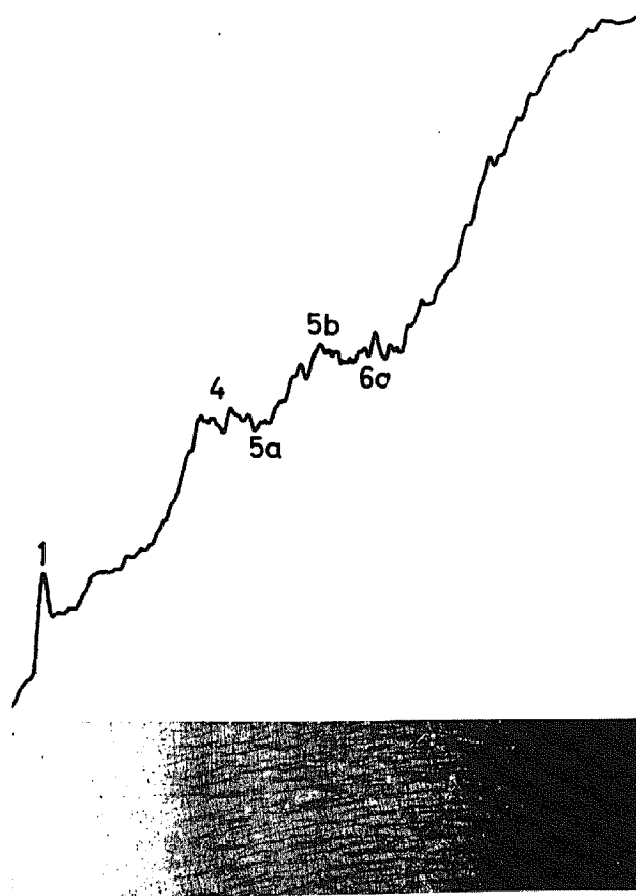area of the subregio temporalis separans lateralis
(tsep l. a), 20 ×.

Fig. 8. Photogram and extinction curve from the middle
area of the subregio temporalis separans lateralis
(tsep. l. md), 20 ×.

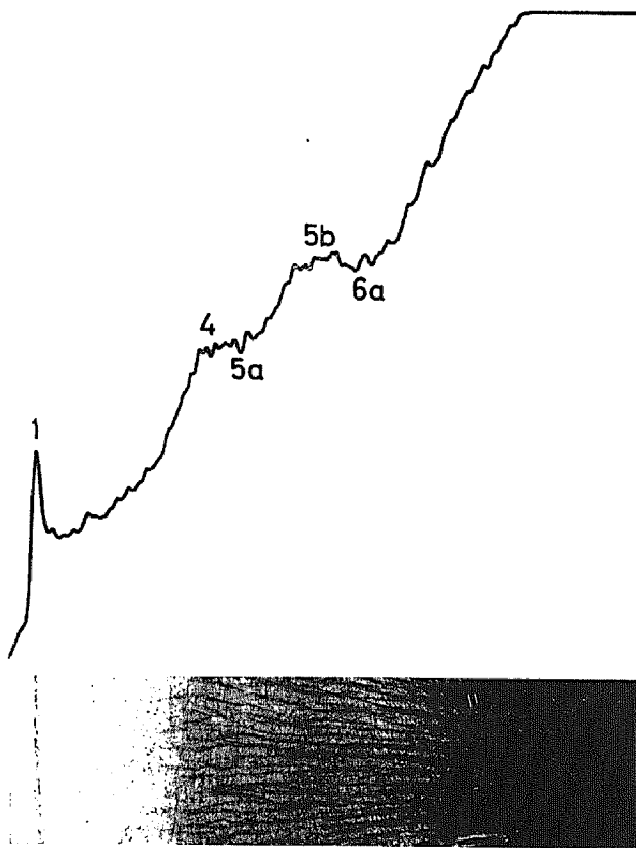Fig. 9. Photogram and extinction curve from the posterior area of the subregio temporalis separans lateralis (tsep. l. p), 20 ×.
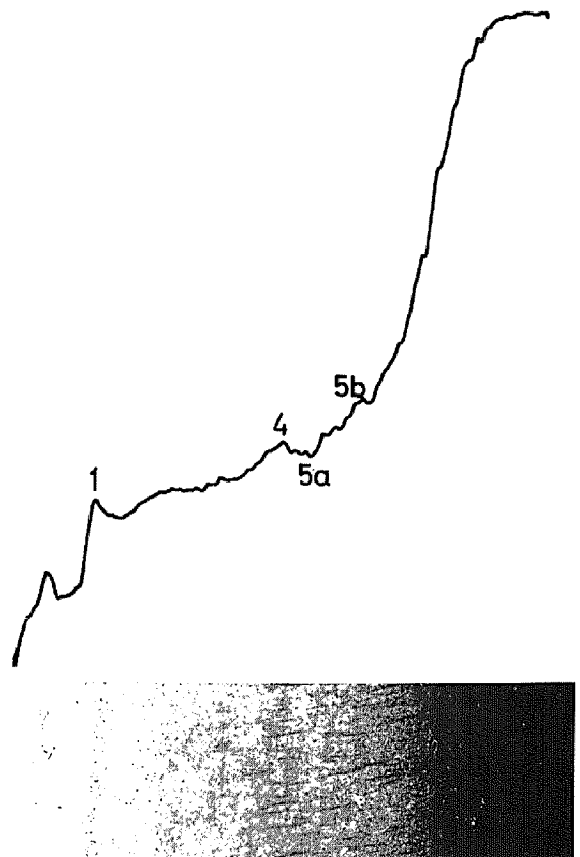

Fig. 10. Photogram and extinction curve from the para-insular temporal region (tpari), 20 ×.
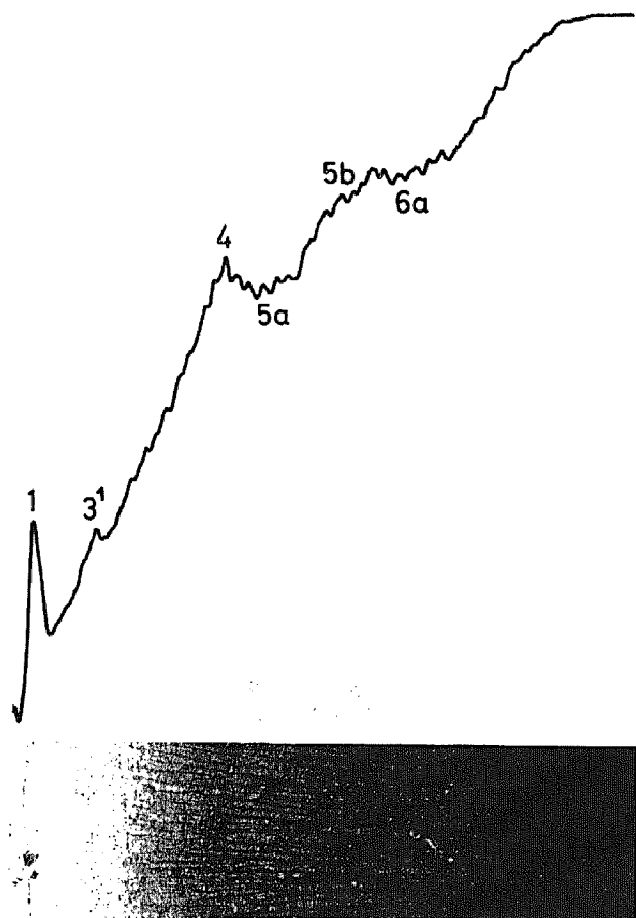

Fig. 11. Photogram and extinction curve from an anterior area of the regio temporalis transversa (ttr 1), 20 ×.

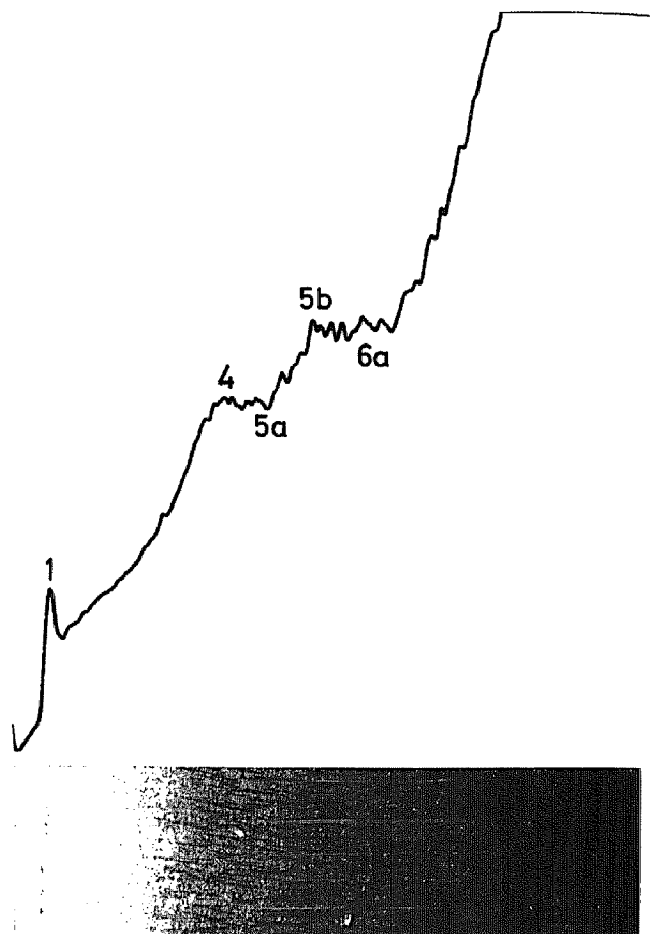
Fig. 12. Photogram and extinction curve from the regio temporalis paratransversa (tpartr), 20 ×.
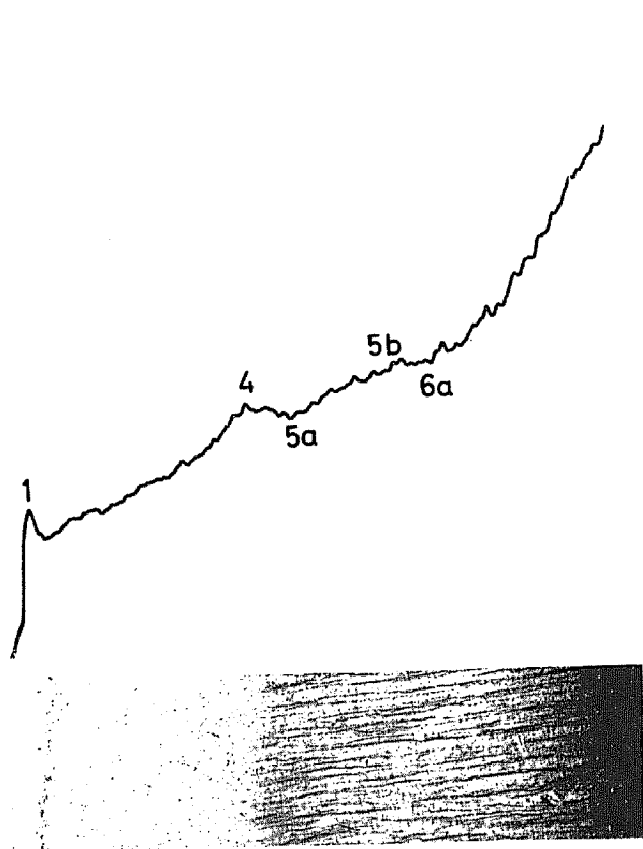
Fig. 13. Photogram and extinction curve from an anterior area of the subregio temporalis magna dorsalis (tmag. d in fig. 1), second temporal gyrus (T_2), 20 ×.
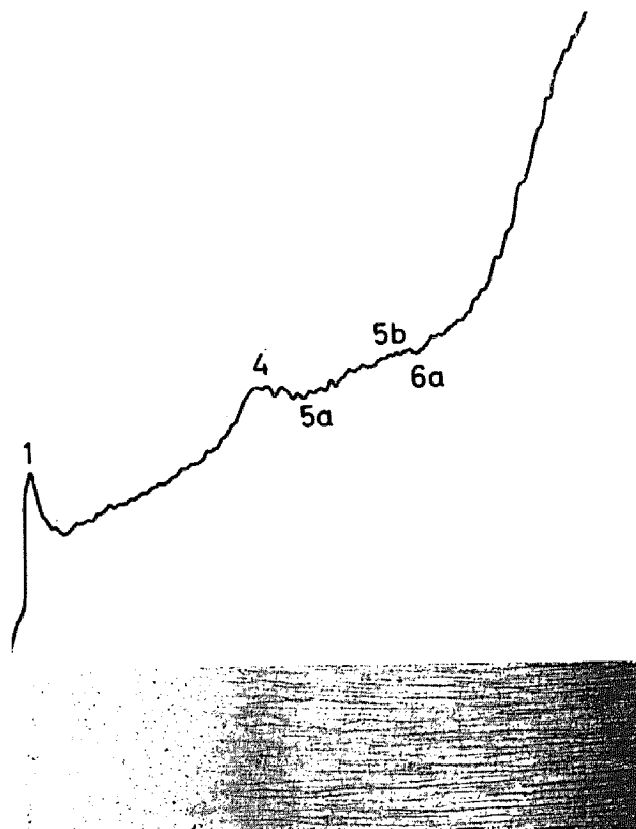

Fig. 14. Photogram and extinction curve from an anterior area of the subregio temporalis magna ventralis (tmag. v), third temporal gyrus (T_3), 20 ×.
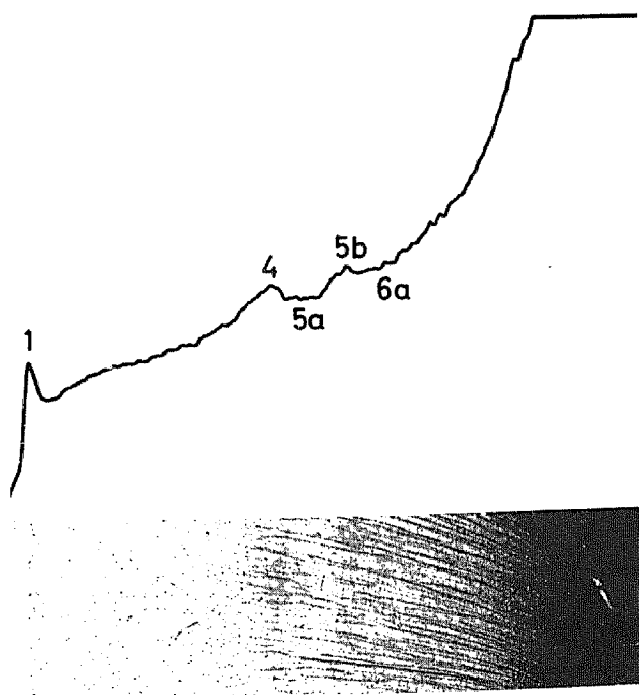

Fig. 15. Photogram and extinction curve from a middle part of the subregio temporalis magna dorsalis (tmag. d), second temporal gyrus (T_2), 20 ×.
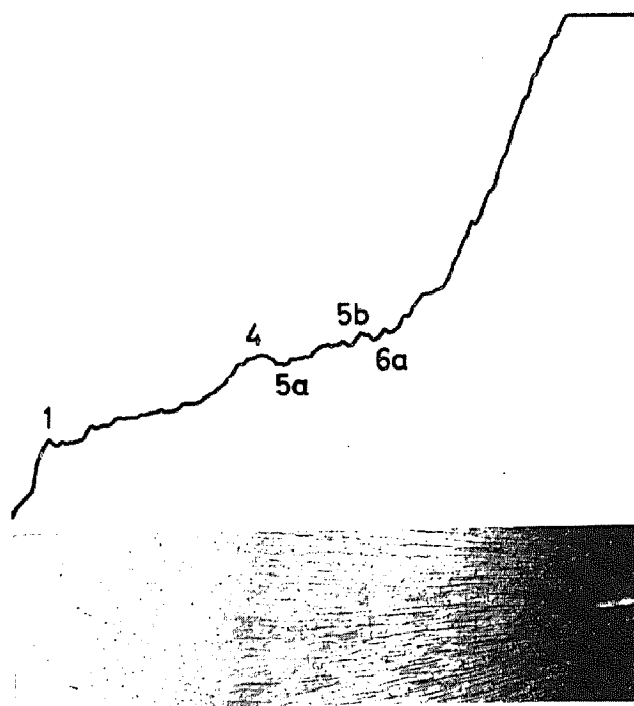

Fig. 16. Photogram and extinction curve from a middle part of the subregio temporalis magna ventralis (tmag. v), third temporal gyrus (T_3), 20 ×.

stripe of Baillarger is well developed. In sublayer
5a there is no decrease in the fibre content (com-
pare figure 12 with figure 11). Therefore the curve
does not descend but shows a plateau. The same
is true of sublayer 6a in relation to sublayer 5b
(inner stripe of Baillarger). Neither of the hori-
zontal stripes stand out very well (fig. 12). This
type is called propeastriate (nearly astriate).

6. Regio temporalis magna

The extinction curves demonstrate a unistriate
or nearly unistriate character of all the areas of
this large region.

Figure 13 is taken from the most anterior part
of the second temporal gyrus (tmag. d in fig. 1b).
The neighbourhood of the temporal pole is indi-
cated by the prominence of the outer stripe of
Baillarger in layer 4. An inner stripe in 5b is
poorly developed. The curve ascends continuously.
We have a transition between a unistriate and a
singulostriate type.

Figure 14 is taken from an anterior part of the
third temporal gyrus (tmag. v in fig. 1b and c).

Fig. 18. Photogram and extinction curve from the sub-
regio temporalis limitans caudalis (tlim. c), posterior
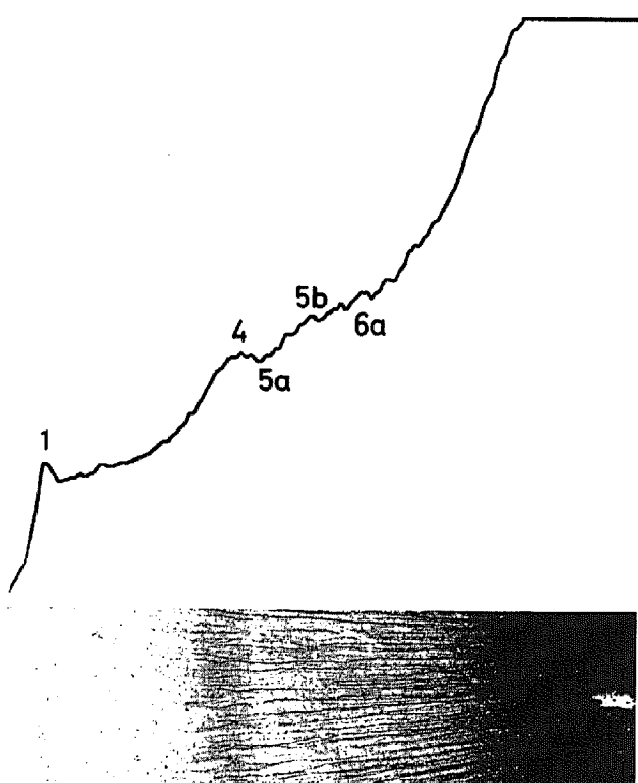part of fusiform gyrus (T_4), 20 ×.

Fig. 17. Photogram and extinction curve from the sub-
regio temporalis magna caudoventralis (tmag. cv in
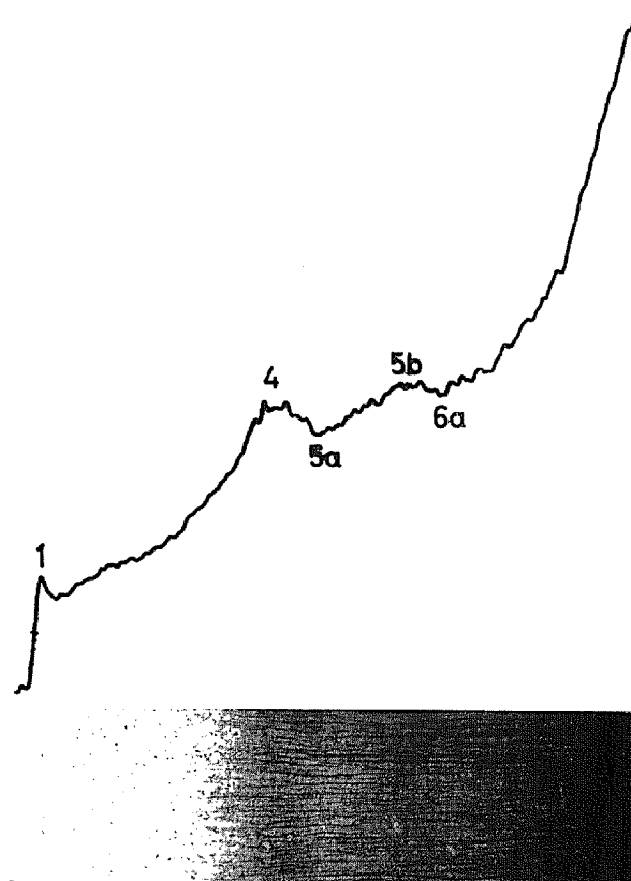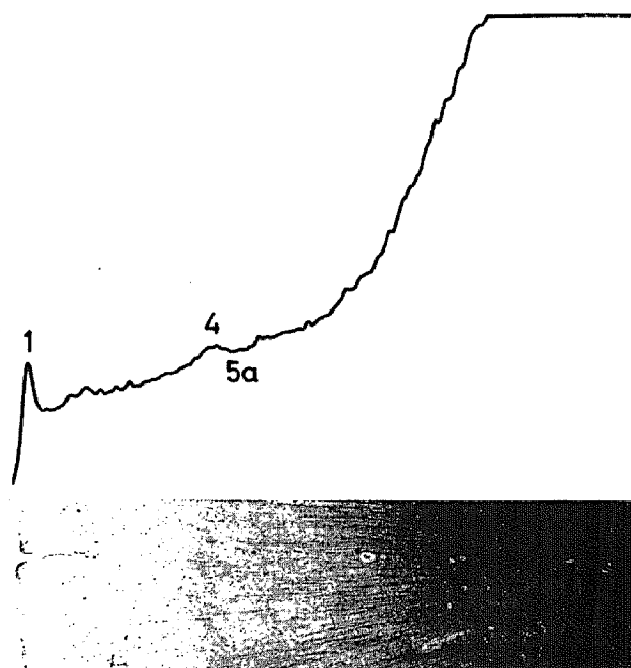fig. 1c), posterior part of the third temporal gyrus (T_3),
20×.

Fig. 19. Photogram and extinction curve from the sub-
regio temporalis limitans medialis (tlim. m in fig. 1c),
parahippocampal gyrus, bordering the caudal entorhinal
region, 20 ×.

The fibre content is a little less as compared with T_2. The outer stripe in 4 stands out very well but not the inner one in 5b. The area is therefore unistriate.

In the occipital direction the prominent character of the outer horizontal stripe of Baillarger is gradually diminished. This is easy to recognize by comparison of the photograms and curves of figures 13 and 14 with those of figures 15, 16 and 17.

In the middle part of T_2 (fig. 15) the outer stripe in 4 is well developed but also the inner one in 5b. The demarcation of the latter from the light sublayer 5a is very clear but not its demarcation from the deeper layers. The area is nearly unistriate.

In the middle part of T_3 (fig. 16) the fibre content is again lower than in T_2. The outer stripe of Baillarger is still well developed but not so prominent as in the anterior part of the gyrus. Then the curve ascends continuously. The unistriate character cannot be doubted.

The fibre content in the most caudal part of the regio temporalis magna (tmag. cv in fig. 1c) is increasing, especially in the deeper layers as figure 17, taken from T_3, demonstrates. The outer stripe of Baillarger is still obvious but then there is a constant ascent of the curve which shows a unistriate character.

There exists therefore a gradation in the regio temporalis magna in the occipital direction. The dominance of the outer stripe is gradually lost and the deeper layers get darker. In the basal direction there is a second gradation in which the general fibre content decreases.

7. Regio temporalis limitans

The whole region (tlim in fig. 1c) is characterized by the prominent outer horizontal stripe of Baillarger. This is especially true of its oral subregion which is similar in this respect to the temporopolar region, of which it seems to be a caudal continuation. But the outer stripe of Baillarger is also well developed in the caudal subregion (tlim. c. in fig. 1c) of the regio limitans as figure 18 demonstrates. The behaviour of the inner horizontal stripe of Baillarger is different in the various areas of this region. Sometimes it is poorly developed, sometimes the stripe is better developed but a clear demarcation from the neighbouring sublayer is always lacking.

In a medial subregion situated behind the entorhinal area (tlim. m in fig. 1c) the cortex is very small. The fibre content is low, and the fibres are very thin, as can be seen in figure 19. But the

outer horizontal stripe of Baillarger is again better developed than the inner layers though layer 4 is also not very impressive.

Discussion

There are many myeloarchitectonic features by which cortical areas can be characterized. They are not all of the same reliability, however. The absolute and relative thickness of the various layers, for example, is influenced by the direction of cutting and the topography (crown of the gyrus, angulus, wall, or the depths of the sulcus). Therefore, the thickness of the layers can only be evaluated if one is sure that the cortex is cut perpendicularly. The correct plane of sectioning is easier to recognize in myelin preparations by the uninterrupted radial fibres than in cell preparations. The position in relation to the gyrus (crown, sulcus) must be known, and only cortical parts with the same relative position may be compared with each other.

Most valuable are the general fibre content of the areas and the behaviour of the two horizontal stripes of Baillarger. These are often sufficient for a characterization of the cortical areas (HOPF 1954 b).

These two characteristics can be proved objectively with the new extinction method. The disadvantage of this method, and of all myelo- and cytoarchitectonic photomicrographs, is that only small cortical sectors can be reproduced or measured. Therefore minor local variations which one can find in every cortical area may have been demonstrated. The main advantage of myeloarchi-
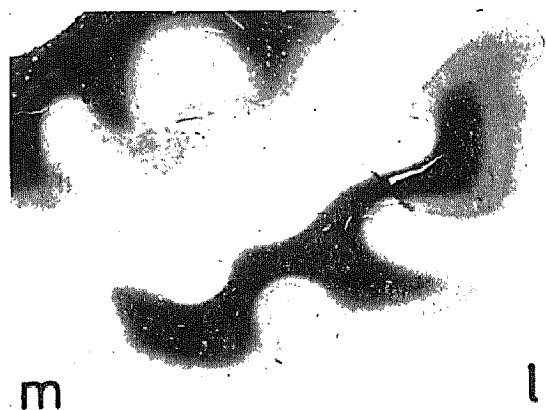

Fig. 20. Temporal pole, frontal section, 1,7 ×. Singulostriate areas with low myelin fibre content medial and dorsal, higher fibre content lateral and ventral.

m — medial, l — lateral.

tectonics is that one can survey large regions of the cortex at a glance. Most areas can be recognized by macroscopic observation or at a very low magnification. In this way it is easy to realize what is typical for an area. And only those features that are typical should be used for the characterization of the area.

With the extinction method the existence of the different regions, subregions, and areas of the temporal cortex which were described on the basis of microscopic observations could be confirmed. There are seven main regions.

The *temporopolar region* is very characteristic and cannot be mistaken for any other cortical region. The temporopolar region has only one fibre band, namely the outer horizontal stripe of Baillarger in layer 4. The inner stripe is missing. Therefore all of the extinction curves have only one elevation in layer 4 (figs. 3—6). This singulostriate type is easy to recognize by macroscopic observation (fig. 20). The same is true of the fibre content which increases from medial to lateral (figs. 20, 3—4—5) and from dorsal to ventral (fig. 6).

The singulostriate type can only be found in the temporal pole, the regio temporalis limitans in

gyrus T_4 (fusiform gyrus or gyrus occipito-temporalis lateralis), a small field of the retrosplenial area in the isthmus of the gyrus fornicatus, and the area striata. Since the oral beginning of the area striata (area 17 of Brodmann) is — according to SANIDES and VITZTHUM (1965) — not surrounded by the parastriate (18) and peristriate (19) area all the regions and areas cited are continuous. With the exception of the area striata and of the lateral parts of the temporopolar region they are situated in the immediate neighbourhood of the periarchicortex, and they have *rhinencephalic* fibre connections. SANIDES and VITZTHUM (1965) speak of a proisocortical belt of areas ("proisocorticaler Feldergürtel") which they consider to be the origin of the area striata. The latter is called a "singulostriate extreme area".

Since the publications of KLÜVER and BUCY (1937) it is generally accepted that the temporal lobe has to do with visual functions. The experiments of RIOPELLE, ALPER, STRONG and ADES (1953) CHOW (1954), MISHKIN (1954), MISHKIN and PRIBRAM (1954), AKERT, GRUESEN, WOOLSEY and MEYER (1961) have demonstrated that the ablation of the temporal neocortex and not of the rhinencephalic parts is responsible for the "psy-
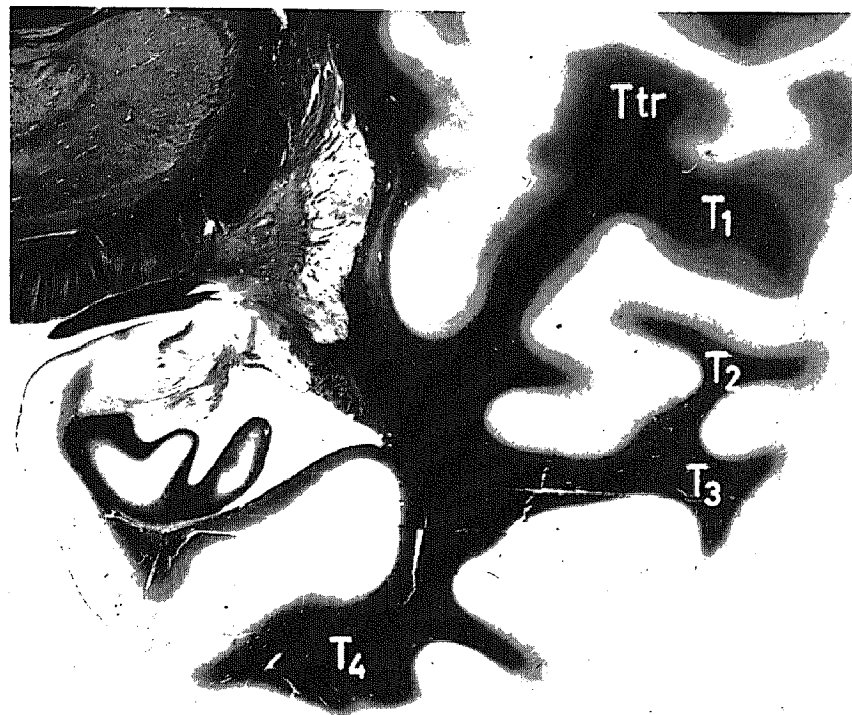

Fig. 21. Temporal lobe, frontal section, 1,7 ×. Highest myelin fibre content in Ttr, steplike decrease in direction of T_1, T_2, T_3. Well demarcated outer stripe of Baillarger (layer 4) in T_4.

chic blindness" in monkeys. In all of the animals of AKERT et al. (1961), not only the temporopolar region and anterior parts of our regio temp. limitans (T_4) were completely removed, but also the anterior parts of the regio temp. magna (T_2 and T_3) as well. Therefore one can only speculate that the deficits in visual discrimination may be mainly correlated to the destruction of the *temporopolar region* and its caudal architectonic continuation, i.e., the *regio temporalis limitans* in the fusiform gyrus. Comparable to the animal experiments in all the human cases of the Klüver-Bucy syndrome anatomically studied by PILLERI (1966), there was found a severe symmetrical atrophy of the temporal neocortex as well as of the hippocampus and amygdaloid nucleus. In his case 1 (Alzheimer's disease) with visual symptoms, the anterior third of the temporal lobe was atrophic and especially the temporal pole and mediobasal parts (T_3, T_4).

In myeloarchitectonic terms, one would say that of the neocortex the singulostriate areas (temporal pole, gyrus fusiformis) were most affected. In PILLERI's case 3 (Pick's disease), which also had visual symptoms, the fusiform gyrus (myeloarchitectonically the singulostriate regio temporalis limitans) was very shrunken as the only part of the neocortex. Only in his case 3 (Pick's disease) no visual symptoms were described. The anterior part of the temporal lobe was atrophic. But in contrast to the other cases there was only a slight atrophy of the cornu Ammonis. The failure of visual symptoms may be partially explained, according to CORDEAU (1960), on the basis that "psychic blindness" is composed of a true optic agnosic disturbance and a loss of recent memory, the former being caused by damage of the temporal neocortex and the latter by that of the archicortex. But further conclusions are not possible from these human cases.

These considerations demonstrate that not only the gyri involved in experiments or in pathologic processes should be described but also the architectonic units. The specific structure of the various cortical areas of the cortex, as revealed by architectonics, is undoubtedly closer related to the physiology or pathophysiology than the gyral pattern.

The highest myelin fibre content in the temporal lobe, (which means the thickest myelinated fibres) is found in the *regio temporalis transversa* on the gyri transversi of Heschl. The extinction curves of this region ascend very steeply (fig. 11). With increasing distance from this region a

steplike decrease in the myelin fibre content is found. The first step is the *regio temp. separans* (fig. 7—9) and the *regio temp. paratransversa* (fig. 12 and 21), the second the *regio temp. magna* (fig. 13—16 and 21) on the lateral surface (T_2 and T_3) and the *regio temp. parainsularis* (fig. 10) on the supratemporal plane.

This steplike decrease is easily recognizable by macroscopic observation of myelin preparations as figure 21 demonstrates. This subjective impression cartographically demonstrated by HOPF in 1955 could now be confirmed by the extinction curves (fig. 22). The general validity of the gradation principle could also be proved by registration of extinction curves of other lobes (frontal lobe, HOPF 1968, parietal lobe, HOPF 1969).
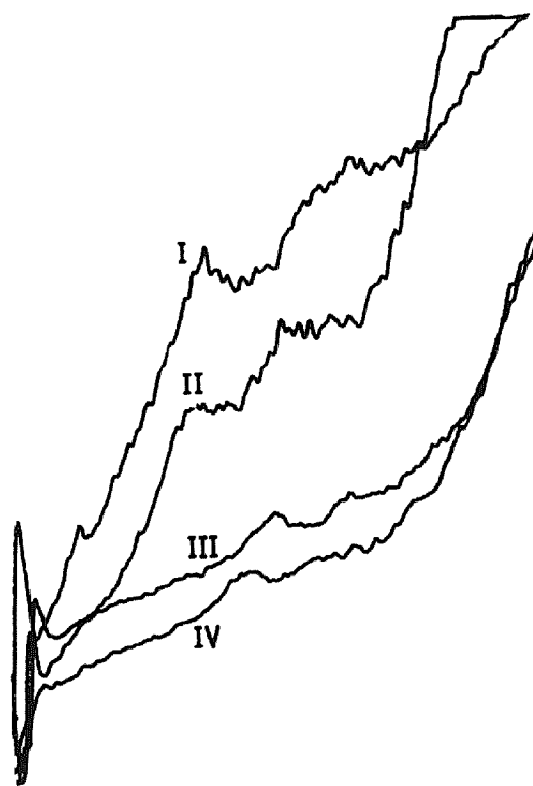

Fig. 22. Extinction curves, confirming the steplike decrease in the myelin content with increasing distance from the auditory region (ttr), 20×.

    I = regio temporalis transversa   (Ttr),
   II = regio temporalis paratransversa   (T_1),
  III = subregio temporalis magna dorsalis   (T_2),
   IV = subregio temporalis magna ventralis (T_3).

Summary

The myeloarchitecture of the human temporal isocortex was studied with a photometric method. Striplike photonegatives of the cortex taken at a magnification of 25 × were registered with the extinction writer of Zeiss.

A standardized technique is necessary for reliable and reproducible results. The most valuable myeloarchitectonic features for a characterization of the cortical areas, namely the myelin fibre content and the behaviour of the two horizontal stripes of Baillarger, can be registered objectively.

With this method the subdivision of the temporal isocortex into seven myeloarchitectonic regions could be confirmed.

The temporopolar region is characterized by a singulostriate type. It has only one horizontal stripe of Baillarger in layer 4.

The same is true of most of the areas of the regio temporalis limitans in the fourth temporal gyrus (fusiform gyrus) in the neighbourhood of the periarchicortex.

The highest myelin fibre content is found in the regio temporalis transversa on the gyri transversi of Heschl (auditory region). This region is of a propeunistriate (nearly unistriate) type because the outer horizontal stripe of Baillarger is well demarcated but not the inner one.

This region is surrounded by the propeunistriate regio temporalis separans (anterior part of T_1 and supratemporal plane) and the propeastriate regio temporalis paratransversa (posterior part of T_1). The horizontal striping in the latter is blurred.

The largest region is the unistriate regio temporalis magna in T_2 and T_3.

The smallest is the bistriate regio temporalis parainsularis.

There is a steplike decrease in the myelin fibre content with increasing distance from the sensory regio temporalis transversa. The phenomenon of gradation in the sense of VOGT can be registered by the extinction curves in all parts of the temporal cortex.

Zusammenfassung

Die Myeloarchitektonik des Isocortex temporalis beim Menschen wurde photometrisch untersucht. Streifenförmige und senkrecht (radiär) zur Rindenoberfläche ausgerichtete Photonegative mit einer Vergrößerung von 25:1 wurden mit dem Extinktionsschreiber von ZEISS ausgewertet.

Eine standardisierte Technik bildet die Voraussetzung für zuverlässige und reproduzierbare Ergebnisse. Die für eine Charakterisierung der corticalen Areae wichtigsten myeloarchitektonischen Merkmale sind der allgemeine Markfasergehalt und das Verhalten der beiden Baillarger'schen Streifen. Diese beiden Merkmale können mit der Extinktionsmethode registriert werden.

Die Gliederung des temporalen Isocortex in 7 myeloarchitektonische Regionen konnte bestätigt werden.

Die Regio temporopolaris ist durch ihr singulostriäres Verhalten charakterisiert. Sie besitzt nur einen Baillarger'schen Streifen, nämlich den äußeren in der 4. Schicht.

Das gleiche Verhalten zeigen die meisten Areae der Regio temporalis limitans auf der 4. Schläfenwindung (Gyrus occipito-temporalis lateralis oder fusiformis) in Nachbarschaft des Periarchicortex.

Die Regio temporalis transversa (Hörregion), die auf den Gyri temporales transversi gelegen ist, besitzt den höchsten Markfasergehalt. Sie ist propeunistriär. Der äußere Horizontalstreifen von Baillarger hebt sich gut gegen die Nachbarschichten ab, der innere dagegen weniger deutlich.

Die Querwindungsregion ist vorn und seitlich umgeben von der propeunistriären Regio temporalis separans, die die Regio transversa von der Polregion trennt und auf der Dorsalfläche des Schläfenlappens und der vorderen T_1 gelegen ist. Caudal schließt sich die propeastriäre Regio temporalis paratransversa an. Sie bedeckt die hinteren Zweidrittel der T_1 und zeigt nur eine undeutliche Horizontalstreifung.

Die größte Region stellt die unistriäre Regio temporalis magna dar. Sie bedeckt die 2. und 3. Schläfenwindung.

Die kleinste Region ist die bistriäre Regio temporalis parainsularis.

Mit zunehmender Entfernung von der sensorischen Regio temporalis transversa findet sich eine stufenweise Verringerung des Markscheidengehaltes der Rinde. Diese Gradation im Sinne von VOGT kann überall in der Temporalrinde mit den Extinktionskurven nachgewiesen werden.

Literature cited

AKERT, K., R. A. GRUESEN, C. N. WOOLSEY, and D. R. MEYER: Klüver-Bucy syndrome in monkeys with neocortical ablations of temporal lobe. Brain 84, 480—498 (1961).

BECK, ED.: Die Myeloarchitektonik der dorsalen Schläfenlappenrinde beim Menschen. J. Psychol. Neurol. Leipzig 41, 129—262 (1930).

BROCKHAUS, H.: Die Cyto- und Myeloarchitektonik des Cortex claustralis und des Claustrum beim Menschen. J. Psychol. Neurol. Leipzig 49, 249—348 (1940).

CAMPBELL, A. W.: Histological studies on the localization of cerebral function. University Press, Cambridge (1905).

CHOW, K. L.: Effects of temporal neocortical ablation on visual discrimination learning sets in monkeys. J. comp. Physiol. Psychol. 47, 194—198 (1954).

CORDEAU, J. P.: Quelques données récentes sur la physiologie du lobe temporale. Bull. Ass. Méd. Lang. franç. Canada 89, 963—975 (1960).

HOPF, A.: Die Myeloarchitektonik des Isocortex temporalis beim Menschen. J. Hirnforsch. 1, 208—279 (1954a).

HOPF, A.: Zur Frage der Konstanz und Abgrenzbarkeit myeloarchitektonischer Rindenfelder. Dtsch. Zschr. Nervenhk. 172, 188—206 (1954b).

HOPF, A.: Über die Verteilung myeloarchitektonischer Merkmale in der isokortikalen Schläfenlappenrinde beim Menschen. J. Hirnforsch. 2, 36—54 (1955).

HOPF, A.: Objektive Registrierung der Myeloarchitektonik der Hirnrinde. Naturwissenschaften 52, 479 (1965).

HOPF, A.: Messungen des Markfasergehaltes der Hirnrinde. Zeiss Mitt. 4, 10—25 (1966a).

HOPF, A.: Über eine Methode zur objektiven Registrierung der Myeloarchitektonik der Hirnrinde. J. Hirnforsch. 8, 301—314 (1966b).

HOPF, A.: Registration of the myeloarchitecture of the human frontal lobe with an extinction method. J. Hirnforsch. 10, 259—269 (1968).

Hopf, A.: Photometric studies on the myeloarchitecture of the human parietal lobe. J. Hirnforsch. (in press).

Klüver, H., and P. C. Bucy: "Psychic blindness" and other symptoms following bilateral temporal lobectomy in rhesus monkeys. Amer. J. Physiol. **119**, 352 (1937).

Klüver, H., and P. C. Bucy: An analysis of certain effects of bilateral temporal lobectomy in the rhesus monkey with special reference to "psychic blindness". J. Psychol. (Princetown) **5**, 33—54 (1938).

Mishkin, M.: Visual discrimination performance following partial ablations of the temporal lobe: II. Ventral surface vs. hippocampus. J. comp. Physiol. Psychol. **47**, 187 (1954).

Mishkin, M., and K. H. Pribram: Visual discrimination performance following partial ablations of the temporal lobe: I. Ventral vs. lateral. J. comp. Physiol. Psychol. **47**, 14—20 (1954).

Pilleri, G.: The Klüver-Bucy syndrome in man. Psychiat. Neurol., Basel **152**, 65—103 (1966).

Riopelle, A. J., R. G. Alper, P. N. Strong, and H. W. Ades: Multiple discrimination and patterned string performance of normal and temporal-lobectomized

monkeys. J. comp. Physiol. Psychol. **46**, 145—149 (1953).

Sanides, F. und H. Gräfin Vitzthum: Zur Architektonik der menschlichen Sehrinde und den Prinzipien ihrer Entwicklung. Dtsch. Zschr. Nervenhk. **187**, 680—707 (1965).

Smith, G. E.: A new topographical survey of the human cerebral cortex. J. Anat. (London) **41**, 237—254 (1907).

Vogt, C. und O. Vogt: Allgemeinere Ergebnisse unserer Hirnforschung. J. Psychol. Neurol. Leipzig **25**, 279 bis 462 (1919).

Vogt, O.: Die myeloarchitektonische Felderung des menschlichen Stirnhirns. J. Psychol. Neurol. Leipzig **15**, 221—238 (1910).

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