Anatomy. — *The diencephalic and some other systems in Xantharpyia amplexicaudata.* II. By NAOKICHI SUZUKI. (Dutch Central Institute for Brain Research, Amsterdam. Department of Anatomy, Manchuria Medical College, Mukden.) (Communicated by Prof. C. U. ARIËNS KAPPERS.)

(Communicated at the meeting of May 23, 1936).

The subthalamic and hypothalamic region.

The most conspicuous nuclei of the subthalamic region are the entopeduncular nucleus, the corpus subthalamicum, (LUYS), separated from it by FOREL's bundle, and caudo-medially to the latter the unpigmented substantia nigra. In the hypothalamus the most distinct cell groups are the autonomic nuclei and the mammillary and ectomammillary nuclei.

The *entopeduncular nucleus,* so conspicuous in all animals below the mammals by the location of its large cells in what is called there the lateral olfacto-hypothalamic and tegmental tract, lies in what RIOCH (l.c. III p. 374) calls the lateral hypothalamic area, consisting of large cells interpolated in the *basal olfactory tract.* This bundle, best described by WALLENBERG [1]), evidently is the homologue of the tr. olfacto-hypothalamicus et tegmentalis lateralis of Submammals.

The basal olfactory bundle of WALLENBERG, indicated by GURDJIAN and RIOCH as medial forebrain bundle [2]), consists of several groups of fibers derived from the basal part of the forebrain chiefly from the lateral olfactory area, partly from the medial olfactory area. It may contain also fibers from the amygdala. Its strongly medullated bundles gather at the rostral pole of the diencephalon over the chiasm (fig. 2: B.O.B.) and from there pass caudally through the lateral preoptic and the hypothalamic area. It can be easily traced (figs. 4—9) to the external mammillary nucleus, while some of its fibers reach the level of the nucleus interpeduncularis and tegmentum. Marchi degeneration of its strongly myelinated fibers enabled WALLENBERG to trace some of them even into the posterior longitudinal fascicle. Normal preparations do not allow to do so but I have no reason to doubt his statement. The cells lying in this tract may be

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1) WALLENBERG, A. Das basale Riechbündel des Kaninchens. Anat. Anz. Bnd. **20**, p. 175 (1901).

2) This bundle is called by several American neurologists medial forebrain bundle, to distinguish it from the laterally running capsular peduncular system. However, in the telencephalon it originates chiefly lateral to the capsula and in the diencephalon runs in the lateral hypothalamic area. The name medial forebrain bundle might be reserved to the septal (fimbrial) part of the fornix, which evidently corresponds to the tr. olfacto-hypothalamicus medialis of lower animals having also the same relation to the autonomic periventricular nucleus.

divided into two groups: 1°. a group of cells lying in the rostral part of the diencephalon (fig. 2), corresponding perhaps to REICHERT's nucleus innominatus; 2°. a more caudal group in front of the external mammillary body and extending from the lateral border of the tuber medially into the direction of the infundibulum, reminding more or less of the large cells of the tubero-mammillary nucleus described by various authors in higher mammals.

The *corpus subthalamicum* of LUYS (C.S. figs. 7, 8, 9), not large but quite evident in my material, is ventrally surrounded by the system of the ansa lenticularis lateralis that will be dealt with in the description of the pes pedunculi, since frontally its fibers run with the cerebral peduncle, gradually leaving it to end partly behind this nucleus. Right in front of the corp. subthalamicum the hypothalamic bundle of FOREL (F. figs. 5, 6 and 7), arising from the ventral edge of the capsula interna, turns medially to approach the bundle of VICQ D'AZYR (M.T.).

The *magnocellular autonomic nuclei* are quite conspicuous by the large size of their cells. The ventro-lateral one, the *nucleus supra-opticus basalis lateralis* extends from in front of the level of the anterior commissure till some sections behind this commissure. A primitive feature of this nucleus in my object, by which it contrasts strongly with rabbits and dogs, is that so few of its cells extend over and behind the chiasm forming a *nucleus basalis postopticus*. A few of such cells occur in fig. 2 (N.B.P.O.). The latter nucleus, however, is very small even compared with Rodents [cf. GRUENTHAL [1])]. Both are indicated by RIOCH as nucl. tangentialis.

The dorso-medial autonomic nucleus, the *nucleus filiformis* or *periventricularis magnocellularis*, extends from immediately behind the anterior commissure, right underneath the commissurae griseae along the upper portion of the infundibulum, to the level of my fig. 3 as a triangular group of cells (P.M. figs. 2, 3). A separation in an anterior and a posterior or principal group (RIOCH) does not exist, but the posterior part is the larger one, as it is in the dog. Laterally to it the finally medullated septal (fimbrial) bundles of the fornix (f.) connect with it, as does the medial (septal) olfacto-hypothalamic tract in fishes. Corresponding with the extension of this nucleus the ependyma of the ventricle is somewhat higher and slightly more folded as first described by KAPPERS (l.c.s.) and CHARLTON [2]), a phenomenon probably due to secretory function of this nucleus [SCHARRER [3]) and KUROTSU [4])]. Ventro-laterally to this nucleus RIOCH's

[1]) GRÜNTHAL, E. Der Zellaufbau im Hypothalamus des Kaninchens und des Macacus rhesus nebst einigen allgemeinen Bemerkungen über dieses Organ. Journ. f. Psychol. u. Neurol. Bnd. **42** (1931).

[2]) CHARLTON. A glandlike ependymal structure in the brain. Proc. Royal Acad. Amsterdam, Vol. **31**, p. 823 (1928).

[3]) SCHARRER, E. Stammt alles Kolloid im Zwischenhirn aus der Hypophysis? Frankfurter Zeitschr. f. Pathol. Bnd. **47**, p. 134 (1934).

[4]) KUROTSU, T. Ueber den Nucleus magnocellularis periventricularis bei Reptilien und Vögeln. Proc. Royal Acad. Amsterdam, Vol. **38** N°. 7 (1935).

area *hypothalamica anterior* extends with small cells which at the bottom of the infundibulum again aggregate in a more distinct group: RIOCH's *nucl. ovoides.*

Further caudally on the ventral and lateral side of the hypothalamus three nuclei are seen: the internal and external mammillary nucleus and the ectomammillary nucleus or nucleus of the tr. peduncularis transversus.

At the frontal pole of the thalamus, behind the com. anterior, the *fornix* (f.) consists of coarse lateral fibers, arising from the hippocampal cortex, and finely medullated medial fibers arising laterally in the fimbrial (supra commiss.) part of the septum and swinging dorsally over the coarser fibers to reach their mesial side. As stated above, the septal fibers end around the nucl. paraventricularis anterior (parvocellularis P.V.A. fig. 1) and the nucl. paraventricularis magnocellularis (sive filiformis). These fibers may have an autonomic function, considering the parasympathetic affects obtained by HESS [1]) in stimulating the septum. They probably are homologous to the medial forebrain bundle of lower animals, whose connection with the periventricular autonomic nucleus was demonstrated by KAPPERS [2]).

The dark fibers running laterally to these, the fornix proper, enter the pars lateralis of the *nucleus mammillaris* at about the same level with the origin of the tractus mammillo-thalamicus. Most of them connect with the lateral body but some of them run into the medial body toward the midline. More caudally some fibers of both sides decussate in the *nucleus supramammillaris,* the bed-nucleus of these crossing fibers, located at the level of the ventral portion of the comm. supramammillaris (S.M.C. fig. 10). As stated before, the tractus mammillo-thalamicus arises from the internal mammillary body, (I. fig. 10), only few fibers originating in the lateral or external mammillary body. (E. fig. 10).

The latter nucleus is conspicuous chiefly by giving origin to the strongly medullated descending *mammillary peduncle,* as experimentally proved for the rabbit by VAN VALKENBURG [3]). Besides, it may receive a component of the medial lemniscus [WALLENBERG [4])]. Laterally to the external mammillary nucleus, between this nucleus and the medial edge of the peduncle, some large cells occur, that would hardly be seen, if they were not connected with the distinct *tr. peduncularis transversus externus* (T.P.T. figs. 10—12), which from here may be traced caudo-laterally over the ventral

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1) HESS, W. R. Le sommeil. Réunion de la Société de Biologie, p. 1 (1931).

2) The phylogenetic development of the hypothalamic autonomic centers. Report for the International Congress of Neurology, London, 1935 (Manuscript).

3) VAN VALKENBURG. Caudale verbindingen van het corpus mammilare. Versl. der Kon. Akad. v. Wetensch. March (1912).

4) WALLENBERG, A. (1900). Notiz über einen Schleifenursprung des Pedunculus corporis mammillaris beim Kaninchen. Anat. Anz. Bnd. VI, N⁰. 5 u. 6. Sekundäre sensible Bahnen im Gehirnstamme des Kaninchens, ihre gegenseitige Lage und ihre Bedeutung für den Aufbau des Thalamus. Anat. Anz. Bnd. XVIII, N⁰. 4 und 5.

surface of the peduncle, as described by FREY [1]), to ascend caudally on its lateral side to the caudal pole of the medial geniculate body. This nucleus corresponds to the ectomammillary nucleus described by KOSAKA and HIRAIWA [2]), the basal optic nucleus of FREY. Curiously enough, the basal optic fibers ending in this nucleus are very difficult to trace, while the tr. peduncularis transversus arising from it is very distinct, so that I agree with FREY in considering the latter not as a continuation but as a secundary neurone of the basal optic system.

The Metathalamus.

Of the *nuclei geniculati laterales* the smaller *ventral nucleus* (G.L.V., figs. 9—10) is separated from the large nucl. geniculatus lateralis dorsalis by a small medullary layer (D.). Receiving fibers of the optic tract, another thick bundle leaves this nucleus to run dorso-medially. Most of these fibers belong to the tractus geniculo-tectalis, others may be connections with the dorsal nucleus. Finer fibers derived from this nucleus run medially into the caudal part of the formatio reticularis and descend medio-ventrally into the zona incerta, as described by various authors.

The *nucleus geniculatus lateralis dorsalis* not labelled in fig. 8—11, but covering the whole area between Pu and G.L.V., is much larger. From this nucleus the geniculo-cortical connection arises, which in this animal is difficult to trace on account of its mixing up with the optic tract fibers. This nucleus continuer gradually in the pulvinar.

In the hilus of the ventral geniculate nucleus a number of well-stained fibers occur, which come from the occipital radiation. These evidently are the fibers described by D'HOLLANDER and RUBBENS [3]) (l.c.p. 306) as „une voie cortifugale dans le tiers externe du pédoncule cérébrale pour aller se terminer dans le tubercule quadrigeminal antérieur". I believe they are the same bundle described long before by K. H. BOUMAN [4]) (l.c.p. 40 and 79) and confirmed by BIEMOND) [5]) as a cortico-fugal system (from the occipital lobe) running in the utmost lateral part of the peduncle and from there through the ventral geniculate nucleus to end in the dorsal geniculate nucleus and in the anterior quadrigeminal body. Some of its fibers remain in the pes pedunculi, as also found by BOUMAN and by D'HOLLANDER.

The *medial geniculate nucleus* (G.M.) is large, owing to the great deve-

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1) FREY. Die basale Optische Wurzel des Meerschweinchens. Proc. Royal Acad. Amsterdam, Vol. 38, p. 781.

2) KOSAKA and HIRAIWA. Zur Anatomie der Sehnervenbahnen. Folia Neurobiologica, Bnd. 9 (1915).

3) D'HOLLANDER and RUBBENS. Recherches anatomo-expérimentales sur la constitution du pédoncule cerébrale et ses constituents sous-thalamiques. Revue neurologique. Tome I, p. 289 (1926) (see specially p. 306 and fig. 19).

4) K. H. BOUMAN. Experimenteele onderzoekingen over het cerebrale optische stelsel. Diss. Amsterdam (1905).

5) A. BIEMOND. Experimenteel-anatomisch onderzoek omtrent de corticofugale optische verbindingen bij aap en konijn. Diss. Amsterdam (1929).

lopment of the lateral lemniscus. The brachium of the inferior colliculus appears at its medio-ventral border and mostly distributes in this area. Some of its fibers enter the upper layer of the anterior colliculus. (fig. 12). The *temporal fibers* originating in this nucleus gather at its dorsal side chiefly and may be traced into the internal capsule passing the medial side of the lateral geniculate (fig. 9). In the rostral pole of the nucleus geniculatus medialis fibers from the GUDDEN's commissure end, in its caudal pole the very distinct tr. peduncularis transversus externus.

The *lateral lemniscus* ascends to enter the posterior colliculus and the medial geniculate body. The most lateral fibers of this lemniscus enter the colliculus posterior, its medial fibers continue more frontally, then swing laterally into the medial geniculate nucleus.

On the level of the IV root exit two groups of large cells are imbedded in the lateral lemniscus. The most ventral group is the frontal end of the nucl. ventralis lemnisci lateralis. The dorsal group corresponds with the magnocellular part of the *ganglion isthmi* of lower animals. It is the same cell group as described by GEREBTZOFF [1]), MARBURG [2]), WINKLER and POTTER [3]) as *nucl. lemnisci lateralis dorsalis*. PRECECHTEL [4]) was the first to realize its homology with the large cells of the ganglion isthmi, a view-point confirmed by LE GROS CLARK [5]). Apart from lateral lemnicus fibers it may receive fibers of the spino-mesencephalic tract, ascending laterally to the lateral lemniscus.

The *brachium conjunctivum anterius* or tractus cerebello-diencephalicus originates from the lateral or dentate nucleus and the nucleus tecti. The dentate nucleus, the largest of the two, lies very lateral, very near the cortex of that part of the hemisphere of the cerebellum that lies on top of the flocculus. The brachium swings ventrally around the ventricle. The first crossing of its fibers occurs directly under the fasciculus longitudinalis medialis (dorsalis). More frontally the crossing extends further ventrally. After decussation, the fibers proceed and most of its dorsal fibers end in the nucleus ruber, (N.R. fig. 12) which — as in most lower mammals — consists of large cells chiefly (cells of the rubro-spinal tract). Some more ventrally and more frontally crossing fibers of this tract leave the chief bundle and join the medial lemniscus in the lamina medullaris externa, running laterally along the lower end of the fasciculus retroflexus. They may be traced frontally in the zona incerta above the corp. subthalamicum.

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1) GEREBTZOFF. Recherches anatomo-expérimentales sur la région du lemniscus latéral et ses commissures. Journ. Belge de Neurologie et de Psychiatrie, p. 73 (1936).

2) MARBURG. Atlas des menschlichen Zentralnervensystems. Wien (1910), (fig. 32).

3) WINKLER and POTTER. An anatomical guide to experimental researches on the cat's brain, Amsterdam (1914), (Plate XXI).

4) PRECECHTEL. Some notes upon the finer anatomy of the brainstem and basal ganglia of Elephas indicus. Proc. Royal Acad. Amsterdam, Vol. **28**, p. 89 (1925).

5) LE GROS CLARK. The medial geniculate body and the nucleus isthmi. Journ. of Anatomy, Vol. **67**, p. 536 (1933).

Pes pedunculi and ansa lenticularis (Kammsystem).

Contrary to most mammals the pes pedunculi of Xantharpyia is easily analyzed, even on normal preparations. It consists of very deeply and faintly myelinated bundles. Of the deeply stained fibers the most lateral group, apparently corresponding to the tempero-pontine tract, is lost in the pons in which they gradually enter, starting at the frontal pole of the pons, swinging medially underneath the pyramidal fibers.

Whether any of the medial fibers of the peduncle enter the pons as fronto-pontine fibers is not sure. If so, they are certainly few.

In the meanwhile the rest of the deeply stained bundles change their flat arrangement to a round bundle. The round bundle thus remaining is the pyramidal tract, most of which fibers decussate on the level of the facial nucleus [proximal pyramidal decussation of DRÄSECKE [1]), HATSCHEK [2]) and FUSE [3])]. Very few fibers of the pyramid reach the beginning of the cervical cord decussating to the dorso-lateral column.

Thus far as concerns the deeply stained fibers of the pes pedunculi.

The faintly stained peduncular fibers form different systems:

A bundle of brownish stained fibers (A.L.) in the lateral part of the peduncle is chiefly connected with the putamen. The light colour of these fibres is very distinct at P.T. fig. 1 and A.L figs. 3, 4 and 6.

They gather at the fronto-lateral side of the globus pallidus. At the level of the anterior commissure they lie underneath its lateral arm, between this and the basal olfactory bundle. Further backward they run between the optic tract and the deeply stained capsule fibers (fig. 6), proceeding in the lateral part of the peduncle, running in the ventral capsule of the corpus Luysii. Their position corresponds exactly to that of the fibers of the corpus Luysii as described by FERRARO (l.c. infra fig. 35, C.C.L.), but they also extend further backward in the lateral part of the substantia nigra. This may be called the *ansa lenticularis lateralis*, or lateral part of EDINGER's "Kammsystem".

I believe that the least myelinated fibers forming the majority of this bundle establish an ascending connection with the putamen. while some of its better myelinated fibers may be descending ones. The first mentioned fibers may be the same as the thalamo-strial tract appearing at the 8 m.m. stage in cat embryos [WINDLE [4])], the more so as also WINDLE found

[1]) DRÄSECKE. Zur mikroskopischen Kenntnis der Pyramidenkreuzung der Chiropteren An. Anz. Bnd. **23**, p. 449 (1903) (Pteropus ursinus).

[2]) HATSCHEK. Ueber eine eigentümliche Pyramidenvariation in der Säugetierreihe. Arb. a. d. Neurologischen Institut der Wiener Universität, Heft **10** (1903). (Pteropus edulis).

[3]) FUSE. Vergl. anat. Beiträge zur Kenntnis über die sog. obere zweite oder proximale Pyramidenkreuzung bei einigen Edentaten sowie bei einigen fliegenden Säugern. Arb. a. d. Anat. Institut der Univ. Sendai, Heft **12** p. 47 (1926). (Pteropus edulis, Pteropus pselephon and one not determined species of Pteropus).

[4]) WINDLE, Neurofibrillar development of cat embryos etc. Journ. of Comp. Neurology, Vol. **63**, p. 139 (1935).

these fibers spreading in the lateral part of the striatum (accompanied by fibers ending in the lateral cortex).

Another bluish stained bundle (A.M. figs. 2—12) arises from the globus pallidus (G.P., fig. 1) and nucl. accumbens. It accompanies the former on its medial side. In front of the corpus Luysii this system is traversed by the hypothalamic bundle of FOREL: *F*. Hence it passes underneath the corpus subthalamicum to continue its course in the medial part of the peduncle. These fibers also finally leave the peduncle, but further backward than the lateral bundle. They end in the medial part of the substantia nigra, right in front of the pons and may be called ansa lenticularis medialis or better ansa pallidalis on account of their main origin. They form the medial part of EDINGER's „Kammsystem" [K. fig. 35 FERRARO [1]]. It is not to be excluded that some cortical fibers of the medial part of the capsula interna join this bundle. The latter however, are, certainly in the minority, so that I can fully confirm FERRARO's statement [2]) that the fronto-nigritic fibers chiefly arise from the striatum, especially in the globus pallidus. Although with normal preparations one cannot make sure whether a system is descending or ascending or both, I suppose, on account of its arising in the globus pallidus, that the medial system is chiefly descending (cf. also FERRARO).

1) FERRARO, A. Etude, anatomique du systême nerveux central d'un chien dont le pallium a été enlevé, Utrecht Hollande (1924).

2) FERRARO, A. Contributo sperimentale allo studio della substantia nigra normale e dei suoi rapporti con la corteccia cerebrale e con il corpo striato. Arrch. generale di Nevrologia, Psichiatria e Psicoanalisi. Vol. **1**, p. 1 (1925).

Embryology. — *Evocation, Individuation, and Competence, in amphibian organiser action.* By C. H. WADDINGTON and J. NEEDHAM. (Cambridge University.) (Communicated by Prof. M. W. WOERDEMAN.)

(Communicated at the meeting of June 27, 1936).

The interpretation of recent work on embryonic induction by chemical substances is one of the most important problems now confronting biologists. A very interesting discussion of it is given in a recent communication to this Academy by Professor M. W. WOERDEMAN [1]). Although this seems to issue in a damaging criticism of the current theories, we desire to suggest that his views in fact agree to a very large extent with those which were originally derived by WADDINGTON [2]) from his studies

1) M. W. WOERDEMAN, Proc. Royal Acad. Amsterdam, **39**, 306 (1936).

2) C. H. WADDINGTON Phil. Trans. Royal Soc. B., **221**, 179 (1932); C. H. WADDINGTON and G. A. SCHMIDT, Arch. Entw. Mech., **128**, 522 (1933).