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Intralobar fibres of the occipital lobe: A post mortem dissection study

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ABSTRACT

Introduction: The atlas by Heinrich Sachs (1892) provided an accurate description of the intralobar fibres of the occipital lobe, with a detailed representation of the short associative tracts connecting different parts of the lobe. Little attention has been paid to the work of Sachs since its publication. In this study, we present the results of the dissection of three hemispheres, performed according to the Klingler technique (1935). Our anatomical findings are then compared to the original description of the occipital fibres anatomy as detailed by Sachs.
Methods: Three hemispheres were dissected according to Klingler's technique (1935). Specimens were fixed in 10% formalin and frozen at −15 °C for two weeks. After defreezing, dissection of the white matter fibres was performed with blunt dissectors. Coronal sections were obtained according to the cuts originally described by Sachs. In addition, medial to lateral and lateral to medial dissection of the white matter of the occipital lobe was also performed.
Results: A network of short association fibres was demonstrated in the occipital lobe, comprising intralobar association fibres and U-shaped fibres, which are connecting neighbouring gyri. Lateral to the ventricles, longitudinal fibres of the stratum sagittale were also identified that are arranged as external and internal layers. Fibres of the forceps major were also found to be in direct contact with the ventricular walls. We were able to replicate all tracts originally described by Sachs. In addition, a previously unrecognised tract, connecting the cuneus to the lingual gyrus, was identified. This tract corresponds to the "sledge runner", described in tractography studies.
Conclusions: The occipital lobe shows a rich network of intralobar fibres, arranged around the ventricular wall. Good concordance was observed between the Klingler dissection technique and the histological preparations of Sachs.

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> *The present work is the first contribution to a series of publications dedicated to the investigation of the brain and its functions in health and pathology. This field of research is still heavily under investigated and nearly every contribution to it is a step forward similar to an expedition into unknown territory comparable to the "deepest Africa".*
>
> *C. Wernicke, introduction to Sachs's atlas*
>
> *Breslau, 1892*

1. Introduction

When it was published, the atlas of Heinrich Sachs ("*The hemispheric white matter of the human brain. Part I: The occipital lobe*", 1892) was saluted by his mentor Wernicke with great enthusiasm. It represented the most accurate description of the intralobar fibres of the occipital lobe ever provided in humans, with a particularly detailed representation of the short associative tracts connecting different portions of the lobe (Fig. 1). At the end of the 19th century, the study of white matter anatomy was revolutionised by the introduction of microscopy and histological preparations of cerebral specimens (Schmahmann and Pandya, 2009). Brains collected at autopsy were fixed, initially using alcohol or chromic acid and only later with formaldehyde. Once the fixation process was completed, thin sections were obtained using the microtome ("*as thin as the microtome allows*" as stated by Sachs). The hereby obtained slices were stained and scrutinised under the microscope, to reveal the complex organisation in layers and fascicles of the white matter. Great neuroanatomists of the time, including Meynert (1833–1892), Flechsig (1847–1929) and Wernicke (1848–1900), applied these novel histological techniques to investigate white matter anatomy (Catani, Forkel, & Thiebaut de Schotten, 2010). Heinrich Sachs, under the tutorage of Wernicke, applied the histological method to the detailed study of the white matter of the occipital lobe. His method consisted of preparing the sections with celloidin, and then treating them with the Pal-haematoxylin and the picrocarmine stains (the former being a specific myelin stain) (Whethered, 1888, Forkel et al., 2014). Surprisingly, little attention has been paid to the work of Sachs after; one reason being that his work was only available in German. The importance of the anatomy and function of the short associative fibres – emphasised in the work of Sachs – has also long been neglected (Catani et al., 2012).

Less than half a century after the publication of Sachs' atlas, a new technique was developed by Joseph Klingler (1935). Working as an anatomical preparator at the University of Basel (Switzerland), Klingler introduced the process of freezing the brains previously fixed in formalin (Agrawal et al., 2011). The freezing process is a crucial step, since the ice that forms between the fibres separates the white matter fascicles, thus facilitating the dissection. The Klingler method greatly improved the techniques of gross dissection of the white matter of the brain, allowing for more accurate anatomical investigations (Ludwig & Klingler, 1956).

In recent years, the advancement of novel in vivo magnetic resonance imaging (MRI) techniques, such as diffusion imaging tractography (Catani & Thiebaut de Schotten, 2008; Jones, Simmons, Williams, & Horsfield, 1999; Le Bihan et al., 2001) and the resurgence, particularly in the neurosurgical community, of post mortem dissection according to the Klingler method (Türe, Yaşargil, Friedman, & Al-Mefty, 2000) has reignited an interest in the study of white matter anatomy. In the last decade, several fibre dissection studies have been reported, providing original anatomical data (Fernandez-Miranda et al., 2008; Martino, Vergani, Robles, & Duffau, 2010; Peltier et al., 2010) and elucidating the cortical termination of some controversial fascicles (Martino, Brogna, Robles, Vergani, & Duffau, 2010; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2011).

In this work, we present original data obtained according to the Klingler dissection of three neuroanatomically healthy

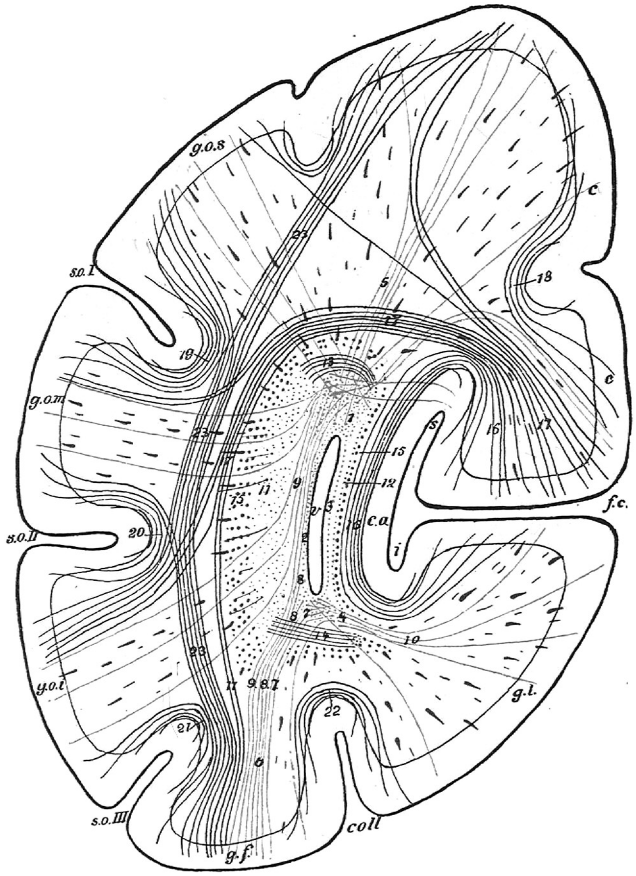

Fig. 1 – Schematic representation of the intralobar white matter fibres of the occipital lobe provided by Sachs (1892). Frontal section through a right hemisphere. *v*: ventricle (occipital horn); *f.c.*: fissura calcarina (calcarine fissure); *coll.*: collateral sulcus; s.o.*I*: sulcus occipitalis superior, s.o.*II*: sulcus occipitalis medium; s.o.*III*: sulcus occipitalis inferior; *g.l.*: gyrus lingualis; *g.f.*: gyrus fusiformis; *g.o.s.*: superior occipital gyrus; *g.o.m.*: middle occipital gyrus; *g.o.s.*: superior occipital gyrus; 1–10: forceps; *11–14*: stratum sagittale internum; 15: stratum sagittale externum; *16*: stratum calcarinum; *17*: stratum cunei transversum; *18*: stratum proprium cunei; *19*: stratum proprium s.o.I; *20*: stratum proprium s.o.II; *21*: stratum proprium s.o.III; *22*: stratum proprium coll.; *23*: stratum profundum convexitatis.

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right hemispheres and compare these results with the original description of the occipital white matter provided by Sachs in 1892.

2. Materials and methods

Klingler dissection was performed on three right hemispheres obtained from the autopsy of two female and one male deceased human subjects, who did not suffer from any neurological and/or psychiatric disease. The specimens were collected at the Newcastle Brain Tissue Resource, Newcastle upon Tyne (UK). The Newcastle Brain Tissue Resource has ethical approval to use post mortem human specimens for research, and it complies with the Human Tissue Act. Specimens were fixed in 10% formalin solution for a minimum of three months. After removal of the pia–arachnoid membrane and cortical vessels, the hemispheres were frozen at −15 °C for 15 days. The water crystallisation induced by the freezing process disrupts the structure of the grey matter (which has a high water content), thus making it easier to peel off the cortex from the brain surface. The freezing process also separates out the white matter fibres, facilitating the dissection of the fibre tracts. The specimens were washed under running water for several hours before performing the dissection.

The surface anatomy of each hemisphere was studied in detail, with identification of sulci and gyri. For the purpose of the current study, coronal cuts were performed at the same levels as originally described by Sachs (Fig. 2). Coronal slices were obtained, from anterior to posterior, at a plane passing through the splenium of the corpus callosum (cut 6), at a plane bisecting the precuneus and passing at the junction between the parieto-occipital sulcus and calcarine fissure (cut 4), at a plane bisecting the cuneus (cut 3) and at a plane dividing the posterior portion of the cuneus (cut 2). The white matter tracts identifiable in each coronal slice were identified and compared to the original dissections described by Sachs.

In addition, stepwise dissection of the white matter was also performed, from lateral to medial and from medial to lateral. To this aim, wooden spatulas were used to peel away the cortex. After removal of the cortical grey matter, the U-shaped fibres (also known as intergyral or short arcuate fibres) were identified. At this point the dissection was completed using blunt metallic dissectors with different tip sizes. Care was taken to separate the fibres using the blunt edge of the instrument, thus avoiding the generation of spurious tracts. Digital high-resolution photographs were taken throughout the procedure.

3. Results

3.1. *Surface anatomy of the occipital lobe*

On the medial surface of the hemisphere, two prominent sulci defining the anatomy of the occipital lobe were identified in all three hemispheres (Fig. 2a). The parieto-occipital sulcus was recognised at the boundary between the parietal and occipital lobe. This sulcus appeared to be uniformly uninterrupted (Ono, Kubik, & Abernathey, 1990) and separated the precuneus (parietal lobe) from the cuneus (occipital lobe). The calcarine fissure, running from the occipital pole towards the splenium of the corpus callosum, divided the cuneus (superior to the fissure) from the lingual gyrus (inferior to the fissure). Both these sulci appeared to be rich in connecting gyri found in the deepest portion of the sulcus. Sachs compared these “gyri brevi” to the insular gyri found in the depth of the Sylvian fissure (Fig. 7a).

On the lateral surface of the brain, the occipital lobe appeared to be in continuity with the posterior part of the parietal and temporal lobes (Fig. 2b). On the dorsal edge of the lateral aspect, the outer margin of the parietoccipital sulcus was identified. Three horizontal sulci were observed on the convexity of the occipital lobe. The transverse occipital sulcus (called by Sachs *sulcus occipitalis superior, s.o.I*) lies lateral to the superior margin of the hemisphere and represents ideally the

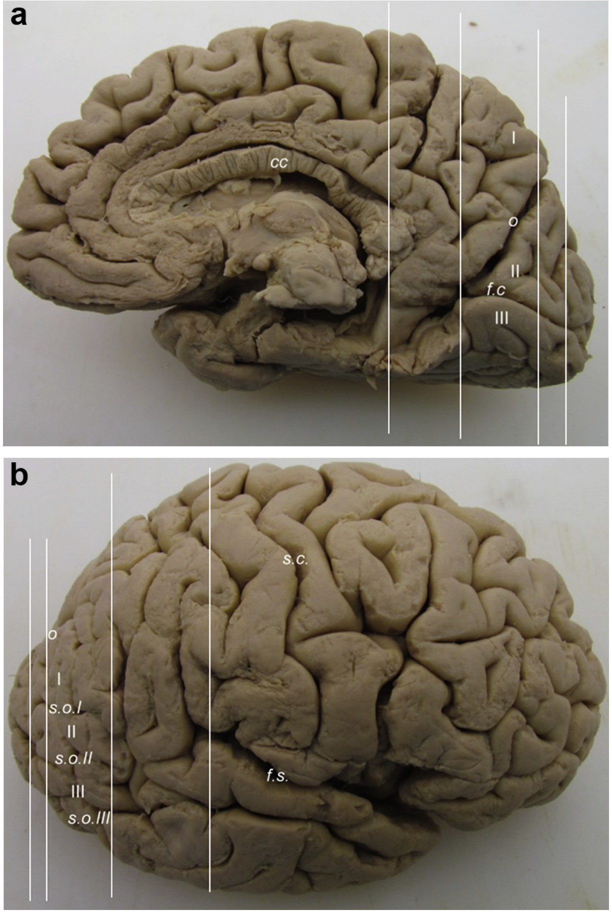

Fig. 2 – a (top panel): medial surface of a right cerebral hemisphere prepared according with Klingler technique. O: occipito-parietal fissure; f.c.: calcarine fissure; cc: corpus callosum; I: precuneus; II: cuneus; III: lingula. b (bottom panel): lateral surface of a right cerebral hemisphere prepared according with Klingler technique. O: occipito-parietal fissure; f.s.: sylvian fissure; s.o.I: sulcus occipitalis superior; s.o.II: sulcus occipitalis medium; s.o.III: sulcus occipitalis inferior. Vertical lines correspond to the coronal sections 6, 4, 3 and 2 (from anterior to posterior) as described by Sachs.

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continuation – in the occipital lobe – of the intraparietal sulcus. The lateral occipital sulcus (*sulcus occipitalis medius, s.o.II* in Sachs' atlas) and the inferior occipital sulcus (*sulcus occipitalis inferior, s.o.III*) lie approximately at the level of the superior and inferior temporal sulci, respectively. These three horizontal sulci identify three gyri on the lateral surface of the occipital lobe: superior, middle and inferior. It has to be noted (as was also recognised by Sachs himself) that the lateral aspect of the occipital lobe shows a great variability in the pattern and presentation of sulci and gyri, with in particular the lateral and inferior sulci being less consistent ("*usually interrupted and branched and therefore less clear*"). The three gyral pattern described here was recognised in two of our three specimens, while in one specimen only two lateral gyri were found (the inferior sulcus not being present). This variability has been also reported for larger cohorts in contemporary studies (Alves, Ribas, Párraga, & de Oliveira, 2012; Iaria & Petrides, 2007; Iaria, Robbins, & Petrides, 2008).

On the basal surface of the brain, the occipital lobe continued with the temporal lobe. The more prominent sulcus at this level was the collateral sulcus that divided the lingual gyrus (medially) from the fusiform gyrus (laterally). More laterally, the occipito-temporal sulcus divided the fusiform gyrus (medially) from the inferior temporal gyrus.

3.2. *Short association fibres*

After removal of the cortex, short U-shaped fibres interconnecting neighbouring gyri were encountered first.

On the medial surface of the brain, dissection of the parietoccipital sulcus showed the presence of U-fibres running in the depth of the sulcus and connecting the superior margin of the cuneus with the inferior aspect of the precuneus (Fig. 7b). Dissection of the calcarine fissure demonstrated a large and relatively thick bundle of U-shaped fibres connecting the upper and lower edges of the calcarine cortex (Fig. 7c). Coronal sections performed just posterior to the junction between the parietoccipital sulcus and the calcarine fissure also clearly demonstrated U-shaped fibres running between the upper and lower bank of the calcarine fissure (Figs. 4–6). These fibres correspond to the *stratum calcarinum* as described by Sachs. As previously mentioned, both the parietoccipital sulcus and the calcarine fissure demonstrate a rich pattern of connecting gyri. Klingler dissection showed that the location of the U-shaped fibres lying in the depth of these two sulci correspond with the surface anatomy of the connecting circonvolutions. It has to be noted with great interest that the dissection of the medial aspect of the calcarine fissure also demonstrated a bundle of fibres previously not described by Sachs or any other post mortem dissection work the authors are aware of. This tract runs deep within the calcarine fissure from the inferior portion of the cuneus to the superior and anterior aspect of the lingual gyrus (where the lingual gyrus blends with the parahippocampal gyrus). The bundle presents with a superior-inferior and anterior curvature. Owing to its peculiar shape, this novel pathway has been named "sledge runner" fasciculus (Catani et al., 2014).

After removing the cortex of the cuneus, U-shaped fibres running between the superior and inferior portion of the cuneus (i.e., to the superior aspect of the calcarine fissure) were exposed (Fig. 7d). These fibres were replicated on coronal sections (Fig. 5). This bundle of fibres corresponds to the *stratum proprium cunei* (layer of the cuneus) of Sachs.

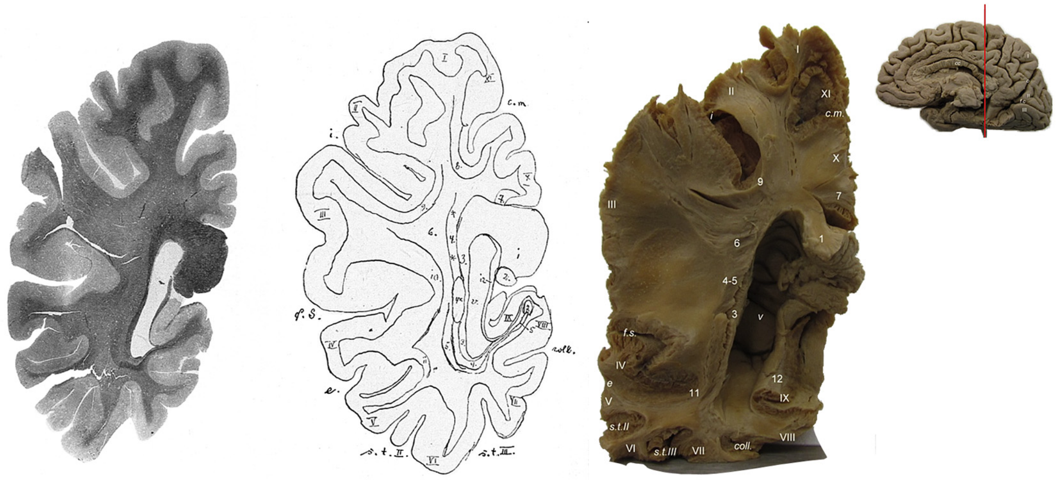

Fig. 3 – Comparison between Sachs's histological atlas and blunt dissections on coronal section through the splenium of the corpus callosum (upper right inset). Histological slice corresponding to section 6 of Sachs (left); schematic diagram of the fibres visualized in photo 6 (middle); coronal cut of a right hemisphere prepared with Klingler's method (right). *I*: posterior central gyrus; *II*: superior parietal lobule; *III*: marginal gyrus; *IV*: superior temporal gyrus; *V*: middle temporal gyrus; *VI*: inferior temporal gyrus; *VII*: fusiform gyrus; *VIII*: hippocampal gyrus; *IX*: Ammon gyrus; *X*: gyrus fornicatus; *XI*: paracentral lobule. *v*: ventricle; *i*: interparietal fissure; *f.s.*: sylvian fissure; *s.t.II*: middle temporal sulcus; *s.t.III*: inferior temporal sulcus; *e*: sulcus parallelis; *coll*: collateral sulcus; *c.m.*: calloso-marginal sulcus; 1: splenium of corpus callosum; 2: inferior portion of forceps; 3: tapetum; 4: stratum sagittale internum; 5: stratum sagittale externum; 6: arcuate fasciculus; 7: cingulum; 8: stratum proprium of the calloso-marginal sulcus; 9: stratum proprium of interparietal sulcus; 10: vertical layer of the convexity; 11: stratum proprium sulcus parallelis. 12: column of the fornix.

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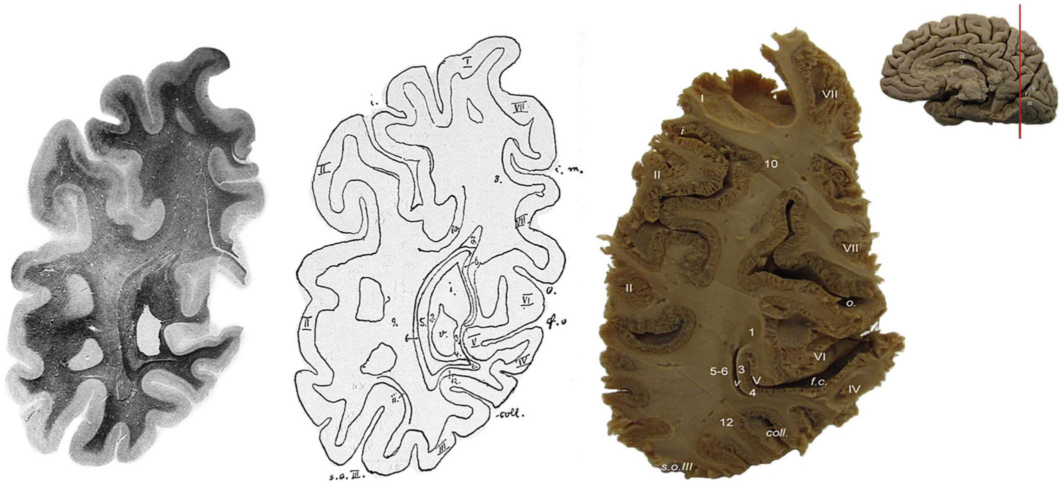

Fig. 4 – Coronal section through the precuneus and anterior edge of the calcarine fissure (upper right inset). Histological slice corresponding to section 4 of Sachs (left); schematic diagram of the fibres visualized in photo 4 (middle); coronal cut of a right-sided hemisphere prepared according to Klingler's method (right) I: superior parietal lobule; II: angular gyrus; III: fusiform gyrus; IV: lingual gyrus; V: calcar avis; VI: cuneus; VII: precuneus; v: ventricle (occipital horn); i: interparietal fissure; s.o.III: inferior occipital sulcus; c.m.: calloso-marginal fissure; o: occipito-parietal fissure; f.c.: calcarine fissure; coll: collateral sulcus; 1–4: fibres of forceps major; 5: stratum sagittale internum; 6: stratum sagittale externum; 7: stratum transversum cunei (transverse layer of the cuneus); 8: stratum proprium of precuneus; 9: vertical layer of the convexity; 10: stratum proprium of interparietal fissure; 11: stratum proprium of inferior occipital sulcus; 12: stratum proprium collateral sulcus.

On the coronal sections, a bundle of fibres originating at the level of the cuneus and running inferiorly and laterally, was also observed (Figs. 5 and 6). This tract was directed towards the lateral wall of the occipital horn, coursing lateral to the stratum sagittale (see below) before pointing more laterally, towards the convexity of the occipital lobe. This bundle corresponds to the *stratum transversum cunei* (transverse layer of the cuneus) described by Sachs. It was unfortunately not possible to trace the cortical terminations of this bundle, as it was difficult to differentiate its fibres from the outer layer of the stratum sagittale medially and from the fibres of the convexity laterally.

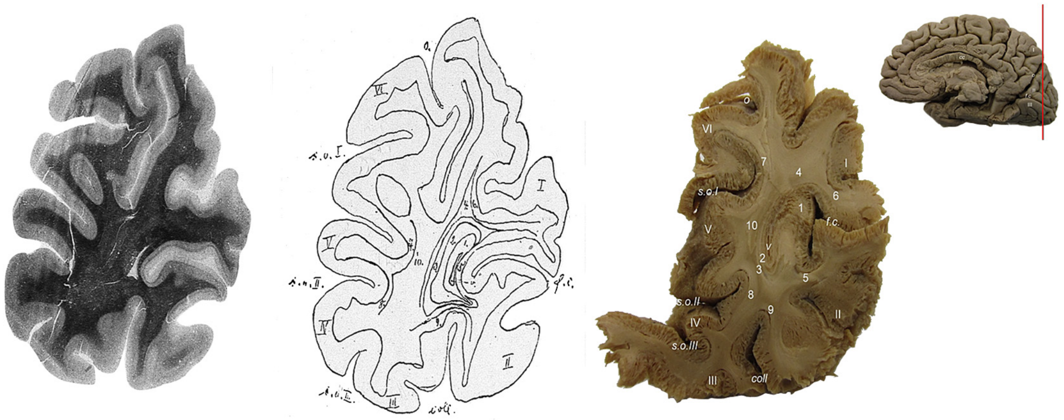

Fig. 5 – Coronal section through the middle portion of the cuneus (upper right inset). Histological slice corresponding to section 3 of Sachs (left); schematic diagram of the fibres visualized in photo 3 (middle); coronal cut of a right-sided hemisphere prepared according to Klingler's method (right) I: cuneus; II: lingual gyrus; III: fusiform gyrus; IV: inferior occipital gyrus; V: middle occipital gyrus; VI: superior occipital gyrus; v: ventricle (occipital horn); f.c.: calcarine fissure; coll: collateral sulcus; s.o.I: superior occipital sulcus; s.o.II: middle occipital sulcus; s.o.III: inferior occipital sulcus; o: occipito-parietal sulcus; 1: forceps; 2: stratum sagittale internum; 3: stratum sagittale externum; 4: transverse layer of the cuneus; 5: stratum calcarinum; 6: stratum proprium of cuneus; 7: stratum proprium of s.o.I; 8: stratum proprium of s.o.II; 9: stratum proprium of collateral sulcus; 10: deep layer of the convexity.

Dissection of the lateral surface of the occipital lobe demonstrated a continuous system of U-shaped fibres connecting neighbouring gyri Thin U-shaped fibres were observed running deep within the cortex of the superior, middle and inferior occipital sulci (Figs. 4–6 and 8a). Sachs named these fibres collectively as "*stratum verticale convexitatis*" (vertical layer of the convexity), naming each individual fibre after the sulcus containing it (e.g., *stratum proprium sulci occipitalis I*, and so on). Deeper to this superficial layer of U-shaped fibres, a vertical bundle running from the superior to the inferior region of the occipital lobe was encountered (Figs. 5 and 8a). This tract, rather thin and running lateral to the stratum sagittale, possibly corresponds to the *stratum profundum convexitatis* of Sachs (deep layer of the convexity). In our dissections it was difficult to follow this bundle for its entire course, as it appeared to merge with the U-shaped fibres of the convexity.

At the basal surface of the occipital lobe, a well-defined U-shaped fibre tract, running deep in the collateral sulcus and connecting the fusiform gyrus with the lingual gyrus was demonstrated (Figs. 4–6). This corresponds to the *stratum proprium sulci collateralis* (layer of the collateral sulcus) identified by Sachs.

3.3. *Stratum sagittale*

A dense bundle of fibres with a sagittal trajectory and extending between the temporal and the occipital lobes was clearly demonstrated in all coronal sections. This represented the *stratum sagittale* described by Sachs (Figs. 4–6). Fibres of the stratum sagittale are contained between the white matter of the convexity and the ventricle. They extend in a C-shaped layer embracing the superior, lateral and inferior walls of the occipital horn of the ventricle; the portion encasing the floor of the ventricle is more pronounced than the portion overlying the roof. The stratum sagittale appears to be larger at the level of the temporal lobe, decreasing progressively in size as it approaches the occipital pole.

Continuing the dissection of the white matter from lateral to medial, two layers of the stratum sagittale were identified; these two layers were named *stratum sagittale internum* (internal layer) and *stratum sagittale externum* (external layer) by Sachs (Fig. 8b). The two layers are contiguous and they are more difficult to appreciate on coronal sections, and in most of our cuts they were not readily identifiable as distinct layers. The two layers can be better appreciated after carefully separating the *stratum externum* from the *stratum internum* with fine blunt dissectors at the level of the lateral and superior wall of the occipital horn. A distinction between the two layers at the level of the floor of the ventricle was not possible in our study.

3.4. *Callosal fibres*

On coronal sections, fibres surrounding the dorsal, lateral and medial portion of the occipital horn of the ventricle were also identified. These fibres were situated medially to the above described stratum sagittale, representing the layer of white matter directly in contact with the walls of the ventricle. These fibres correspond to the forceps major, the radiation of commissural fibres arising from the splenium of the corpus callosum and connecting the occipital cortices. Forceps fibres were mostly evident at the level of the splenium of the corpus callosum (Fig. 3). After leaving the splenium, these fibres follow an inferior trajectory laterally to the lateral wall of the

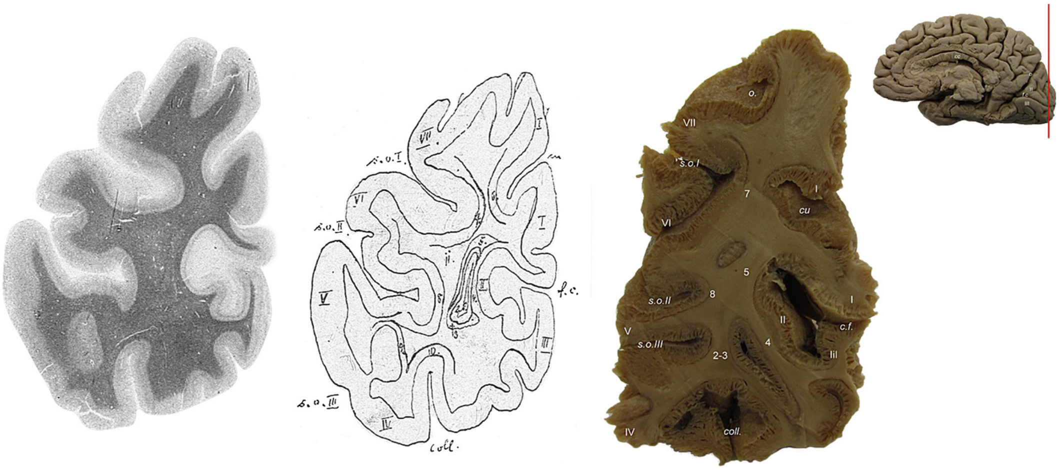

Fig. 6 – **Coronal section through the posterior portion of the cuneus (upper right inset). Histological slice corresponding to section 2 of Sachs (left); schematic diagram of the fibres visualized in photo 2 (middle); coronal cut of a right-sided hemisphere prepared according to Klingler's method I: cuneus; II: calcar avis; III: lingual gyrus; IV: fusiform gyrus; V: inferior occipital gyrus; VI: middle occipital gyrus; VII: superior occipital gyrus; s.o.I: superior occipital sulcus; s.o.II: middle occipital sulcus; s.o.III: inferior occipital sulcus; f.c.: calcarine fissure; coll: collateral sulcus; cu: sulcus of cuneus; 1: forceps; 2: stratum sagittale internum; 3: stratum sagittale externum; 4: stratum calcarinum; 5: transverse layer of the cuneus; 6: stratum proprium of the cuneus; 7: stratum proprium of s.o.I; 8: stratum proprium of s.o.II; 9: stratum proprium of s.o.III; 10: stratum proprium collateral sulcus; 11: deep layer of the convexity.**

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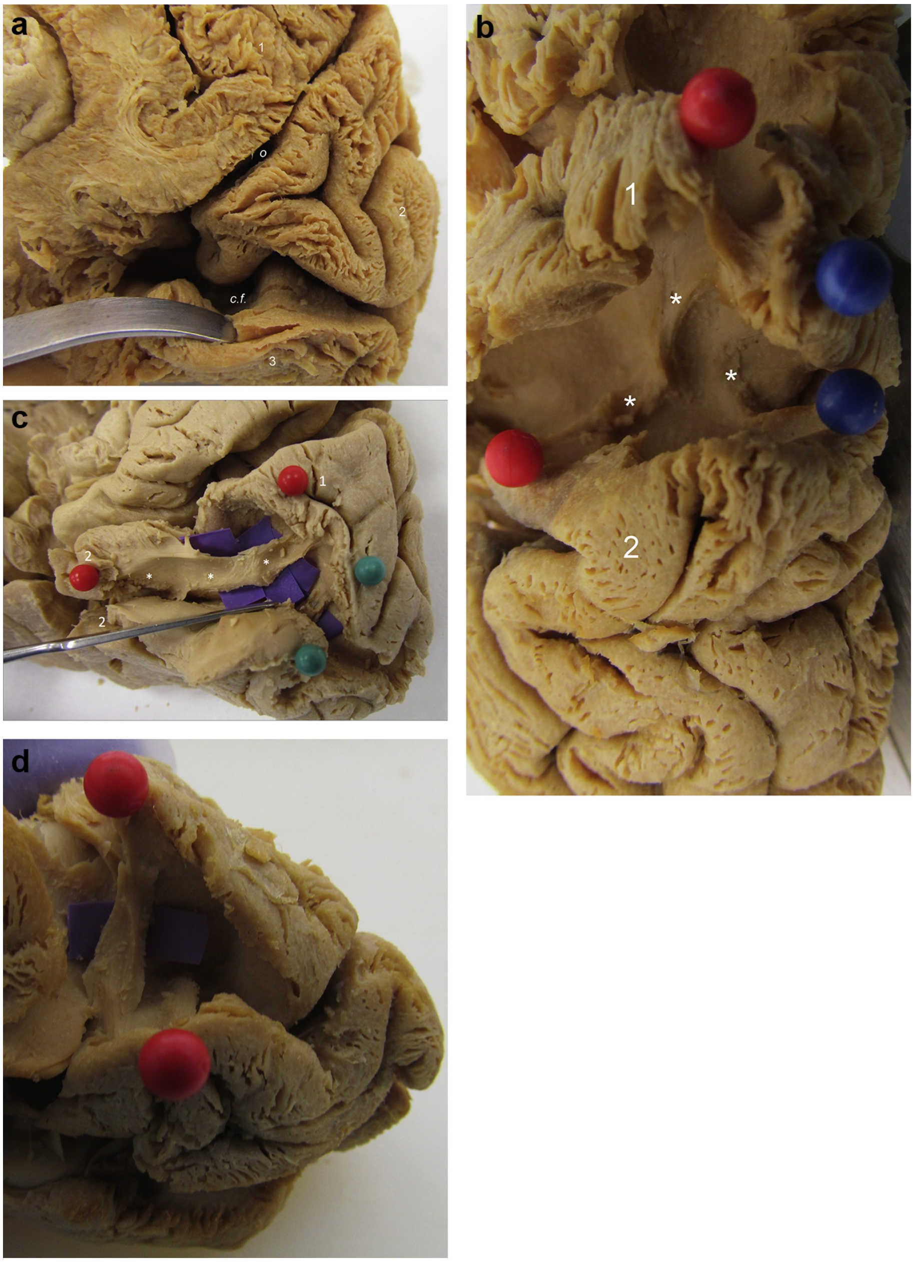

Fig. 7 – Dissection of the medial sulci of the occipital lobe (right hemisphere, sagittal plane). a) Medial surface of the brain prior to dissection. 1: precuneus; 2: cuneus; 3: lingual gyrus. Note the rich pattern of gyri in the calcarine fissure. b) Dissection of the parietoccipital sulcus, showing U-shaped fibres (*) laying in the depth of the sulcus and connecting the precuneus (1) with the cuneus (2). Red and blue pins represent the cortical terminations of the fibres. c) Dissection of the calcarine fissure, showing the "sledge runner" fascicle (*) running from the cuneus (1) to the antero-superior portion of the lingula (2). Red pins indicate the cortical termination of the tract. U-shaped fibres laying in the depth of the sulcus and connecting the upper and lower edges of the calcarine fissure are also demonstrated (green pins). These fibres correspond to the stratum calcarinum of Sachs. Small pieces of purple paper have been inserted to show the complete dissection and continuity of the fibres. d) dissection of the cuneus, showing U-fibres connecting the upper (1) and lower (2) part of the cuneus. These fibres correspond to the *stratum proprium cunei* of Sachs. Red pins indicate the cortical termination of the fibres, while the small pieces of purple paper have been inserted to show the complete dissection and continuity of the fibres.

ventricle and will eventually terminate within the temporal lobe. This branch of the posterior callosal fibres is referred to as *tapetum*. More posteriorly, as the occipital horn of the ventricle decreases in size, callosal fibres appeared less well differentiated from the surrounding white matter. At this level, they were nonetheless recognisable, particularly at the superior and medial portion of the ventricular walls (Figs. 4 and 5).

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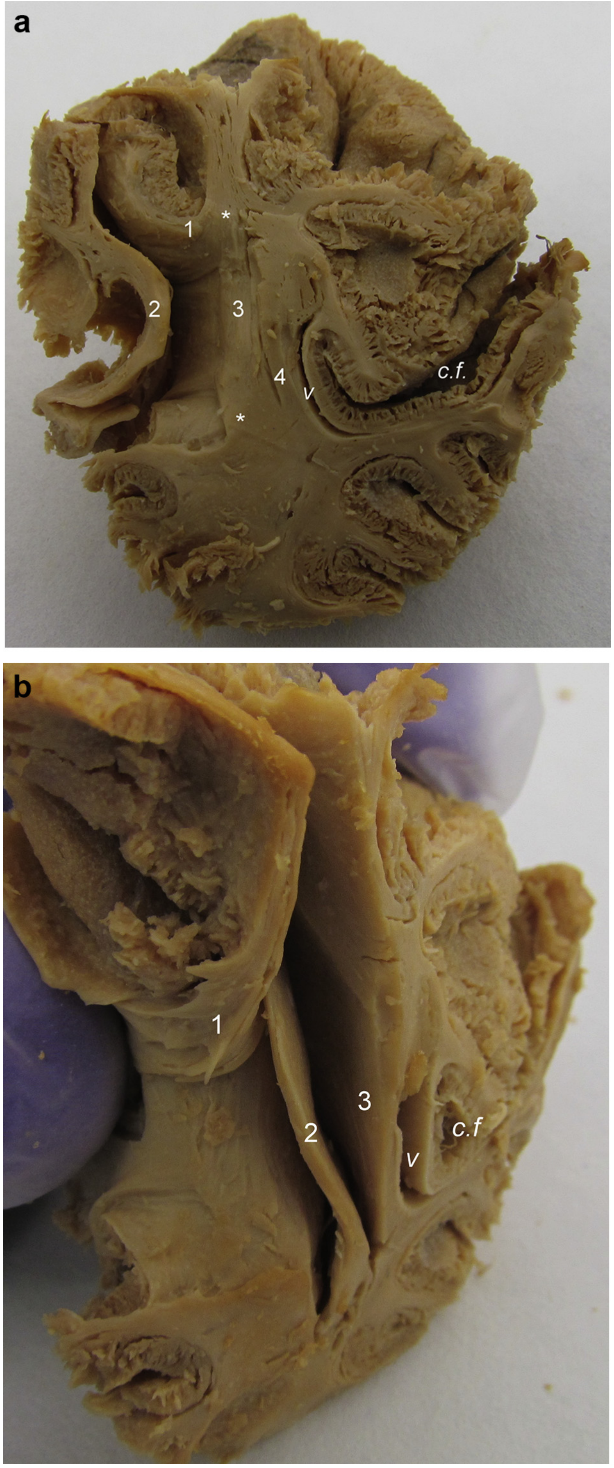

Fig. 8 – Lateral to medial dissection of the occipital lobe (right hemisphere, coronal plane). a) Removal of the cortex overlying the sulci at the convexity revealed a system of U-shaped fibres connecting neighbouring gyri (1 and 2). These fibres correspond to the *stratum proprium sulci occipitalis* according to Sachs. Deeper to these U-shaped fibres, a vertical bundle was identified (3), corresponding to the *stratum profundum convexitatis* described by Sachs. This bundle, lateral to the stratum sagittale (4) appeared to blend with the superficial fibres of the convexity (*). V: ventricle, c.f.: calcarine fissure. b) Dissection more medial than a) within the same hemisphere. The vertical *stratum profundum convexitatis* has been partially removed (1) to expose the external (2) and internal (3) layers of the stratum sagittale at the level of the lateral wall of the ventricle (v). Note the longitudinal course of the fibres of the stratum sagittale.

4. Discussion

4.1. *The anatomy of intralobar occipital fibres*

The atlas of Sachs is one of the most accurate descriptions of the occipital fibres in humans, and it still represents a most valuable basis of comparison for those who want to approach this subject.

In the present study we investigated the intralobar white matter fibres of the occipital lobes preparing three hemispheres according to the Klingler's method. We performed coronal sections of the hemispheres at the same levels described in the historical atlas by Sachs, in order to compare our findings with the original descriptions. Overall, a striking concordance was observed between the two techniques (histology in Sachs's work and dissections in the present work). All major tracts described by Sachs were also clearly identified in our three specimens. The small differences observed in some of the coronal sections (where not every single fibre could be identified with the two methods) can be explained with the law of variability expressed by Sachs in the Introduction to his atlas: "*There are no two brains that are identical in all their details. This variability is also observed in the arrangement and development of the white matter. The cortex and the white matter fibres are mutually dependent on each other. If a particular area of cortex is under-developed in a brain, then there is also a paucity of fibres originating from this area.*" (see Forkel et al., 2014). It is therefore possible that small differences exist, particularly at the level of short arcuate fibres. This may also be reflected by the fact that a coronal cut performed at the same level can show a certain amount of fibres in one specimen and other fibres in another.

One fascicle, although clearly visualized, was particularly difficult to follow with the Klingler's technique. This is the "transverse stratum of the cuneus", running between the cuneus in a medial to lateral direction, curving lateral to the stratum sagittale and eventually pointing towards the convexity. Particular uncertainty persists regarding its cortical terminations, which could not be determined with the dissection method. The main difficulty encountered was to separate this bundle from the stratum sagittale medially and from the fibres of the convexity laterally. At this level in particular the dissection was rendered difficult due to fibre crossing between the "transverse stratum of the cuneus", that shows an horizontal direction, and the "stratum proprium convexitatis", that has a vertical course instead. This problem was also encountered by Sachs who had to conclude the description of the bundle with a note of uncertainty: "*These fibres could thus far not be traced […] along their trajectory through the stratum proprium convexitatis towards the cortex. They potentially reach the cortex of the whole convex part and part of the inferior surface of the occipital lobe and thus form the association* *pathway between the cuneus and the convexity*" (see Forkel et al., 2014). Fibre crossing is a problem common to most, if not all, the different techniques applied to the study of white matter anatomy. The recent development of advanced Magnetic Resonance (MR)-based tractography algorithms, such as spherical deconvolution (that is able to partially overcome the limitation of crossing fibres by identifying multiple fibre orientations within a single brain voxel) may in part overcome this problem (Dell'Acqua et al., 2007, 2010). A limitation of the current study, which is not infrequent to post mortem studies, is the small number of specimens available for dissection. It is possible that with more specimens, a clearer delineation of the "transverse stratum of the cuneus" might be possible. This may be addressed in future studies.

Several differences between the present work and the atlas of Sachs were observed and shall be discussed in detail. The first dissimilarity regards the "stratum profundum convexitatis" (deep stratum of the convexity), which was considered by Sachs as a separate white matter bundle. Although identified as a contingent of vertical fibres running from the superior aspect of the occipital lobe to its inferior surface, this layer of white matter did not appear – with Klingler dissections – to be clearly separated from the superficial U-shaped fibres of the convexity. It is therefore questionable if this "stratum profundum convexitatis" should be considered as an independent white matter tract. Schmahmann and Pandya, in their axonal tracing work on the monkey brain, were also able to identify fibres that link the dorsal and ventral aspects of the occipital lobe, but considered them as being part of a vertical component of the Inferior Longitudinal Fasciculus (ILF) (Schmahmann and Pandya, 2009).

The second discrepancy was found at the level of the stratum sagittale. According to Sachs, the stratum sagittale is divided in an external layer, that conveys corticopetal fibres from the thalamus to the occipital lobe, and an internal segment that conveys corticofugal fibres form the cortex to the thalamus. In Sachs's view, the "stratum sagittale internum" is therefore a projection system, while the "stratum sagittale externum" is an association system, connecting the occipital lobe exclusively with the temporal lobe: "*The occipital lobe has only one long association tract, namely the stratum sagittale externum, that connects to the temporal lobe*" (see Forkel et al., 2014). In our dissections, it was possible to differentiate between the two layers only on the superior and lateral aspect of the ventricular wall. At the level of the floor of the ventricle a thick bundle of white matter, deep in the collateral sulcus, was encountered, with no clear distinction between an external and internal layer. Recent studies, using post mortem dissections and in vivo diffusion tensor imaging tractography, have demonstrated the presence of a long association fascicle that runs along the superior and lateral portion of the ventricular wall, lateral to the optic radiations, before reaching its cortical terminations. This bundle, that connects the frontal to the occipital lobe, corresponds to the inferior fronto-occipital fasciculus (IFOF), originally described by Burdach and later by Curran (Burdach, 1822; Catani, Howard, Pajevic, & Jones, 2002; Curran, 1909; Fernandez-Miranda et al., 2008; Forkel et al., 2012; Martino, Brogna, et al., 2010). The white matter encasing the inferior wall and the floor of the ventricle could correspond to the ILF, a bundle connecting the temporal and the occipital lobe, and running inferolaterally to the optic radiations and the ventricles (Catani, Jones, Donato, & Ffytche, 2003; Fernandez-Miranda et al., 2008).

A final relevant difference was observed in the dissection of the medial aspect of the calcarine fissure. In agreement with Sachs, U-shaped fibres connecting the superior and inferior edges of the fissure were clearly demonstrated in our dissections. However, in contrast to Sachs, we identified an additional fascicle running anteriorly from the inferior portion of the cuneus to the supero-anterior portion of the lingual gyrus. This fascicle, due to its peculiar shape, has been named the "sledge runner" (Catani et al., 2014). It is likely that Sachs missed this fascicle as he only examined coronal sections. The "sledge runner" is a thin fascicle, with a postero-anterior course in the sagittal plane, and can therefore be either lost or confused with the other U-shaped fibres running in the calcarine fissure in the coronal plane. Our findings represent the first demonstration of this fascicle in post mortem human specimens, whilst confirming its discovery in tractography studies (Catani et al., 2014).

4.2. *The functional and connectional anatomy of the occipital lobe*

The study of the occipital lobe anatomy has seen an evolution across the centuries. While early studies (Bolton, 1900; Retzius, 1896; Sachs, 1892) provided a gross anatomical description of the cortical and subcortical anatomy, following reports focused on the cytoarchitecture of the occipital cortex, identifying the existence of distinct cortical areas based on a different neuronal organisation of the six cortical layers (Amunts, Malikovic, Mohlberg, Schormann, & Zilles, 2000; Brodmann, 1909; Von Economo & Koskinas, 1925). These studies established that the primary visual cortex, organised around the calcarine fissure (Brodmann area 17) is surrounded by a cytoarchitectonically different ring of cortex (Brodmann area 18) which is in turn surrounded by an even larger area, corresponding to much of the remaining occipital cortex (Brodmann area 19). A further step was obtained thanks to neurophysiological investigations performed in the nonhuman primate, where direct electrical recording was employed to map the receptive fields of individual neurons after visual stimuli (Kaas, 2004; Sereno & Tootell, 2005). Several visual areas were thus identified, extending beyond the primary visual cortex (referred to as area V1) and even extending beyond the classic boundaries of the occipital lobe, with "visual" areas observed in the temporal and parietal lobes (for a review see Felleman & Van Essen, 1991; Vezoli et al., 2004). The existence of different visual areas has been confirmed in the human brain using non-invasive techniques, such as functional MRI or magnetoencephalography (Anderson, Holliday, Singh, & Harding, 1996; Dougherty et al., 2003; Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Sack, Kohler, Linden, Goebel, & Muckli, 2006; Stiers, Peeters, Lagae, Van Hecke, & Sunaert, 2006; Tootell & Hadjikhani, 2001; Zeki et al., 1991). These studies led to the generation of "functional" maps of the occipital lobe (Van Essen, 2003).

The study of brain connections is the important anatomical correlate for an understanding of function (Mesulam, 2005). In the monkey brain, connections of the occipital lobe have been investigated in great detail, with an emphasis on the intralobar networks. In particular, it has been demonstrated in animal studies that only a minority of stellate cells in layer 4 receive their input from the lateral geniculate nucleus (LGN), while about 80% of the synapses in the occipital lobe receive an input from adjacent occipital areas (Binzegger, Douglas, & Martin, 2004). Such microcircuits may play an important role in the reinforcement of the input from the LGN (Sincich & Horton, 2005). On the basis of these connection studies, it has been possible to delineate "hierarchical" maps of the occipital lobe connections (Felleman & Van Essen, 1991). In the human brain, less attention has been paid to the intralobar connectivity of the occipital lobe (Thiebaut de Schotten, Urbanski, Valabregue, Bayle, & Volle E, 2012). Previous studies employing post mortem Klingler dissection and in vivo tractography focused on the long association tracts connecting the occipital to the frontal lobe via the IFOF (Catani et al., 2002; Fernandez-Miranda et al., 2008; Forkel et al., 2012; Martino, Brogna, et al., 2010; Sarubbo et al., 2011), or to the temporal lobe via the ILF (Catani et al., 2003; Fernandez-Miranda et al., 2008). The optic radiations, with their relationship to the ventricles and their cortical termination at the level of the calcarine fissure have also been studied in detail (Kucukyuruk, Richardson, Wen, Fernandez-Miranda, & Rhoton, 2012; Mahaney & Abdulrauf, 2008; Yogarajah et al., 2009). The anatomy of short association fibres, such as the superficial U-shaped fibres of the convexity, the *stratum calcarinum*, and the "sledge runner" tract have not been described in previous tractography studies (Catani et al., 2014). In the present work, we updated the original work performed by Sachs, describing the detail of intralobar fibres with post mortem dissections.

The putative role of some of the fibres described can be suggested on the basis of the aforementioned functional studies. The stratum calcarinum, with U-shaped fibres connecting the superior and the inferior edges of the calcarine fissure, may play a role in the integration of visual information from the upper and inferior portions of the visual fields. The U-shaped fibres of the superficial layer of the convexity (corresponding to the *stratum superficialis* and *stratum profundus convexitatis* of Sachs), connect the cortical area between the lateral occipital and the inferior occipital sulci (corresponding to functional area middle temporal, MT) with the neighbouring gyri, including area V3A. The area MT has been associated with detection of visual stimuli (Bartels, Logothetis, & Moutoussis, 2008). Damage to the network that is subserved by these superficial fibres might clinically manifest as akinetopsia, the inability to detect moving objects (Thiebaut de Schotten et al., 2012). More anteriorly, at the junction between the temporal and occipital lobe, the system of superficial U-shaped fibres and vertical fibres of the *stratum profundus convexitatis* represent a connection between ventral occipito-temporal regions and superior occipital and parietal regions. These fibres, considered together in the present study, may correspond to the vertical occipital fasciculus (VOF) of Wernicke. A recent study by Yeatman, Rauschecker, and Wandell (2013) has suggested that the VOF has an important role in connecting the Visual Word Form Area (VWFA), a part of the ventral occipito-temporal cortex specialised in the visual formation of words and reading (Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002; Wandell, Rauschecker, & Yeatman, 2012), with language areas including the angular gyrus (Yeatman et al., 2013). Damage to the white matter surrounding the VWFA has been related to the development of pure alexia (Epelbaum et al., 2008; Greenblatt, 1973). The "sledge runner" tract, connecting the superior edge of the calcarine fissure and the anterior portion of the lingual gyrus (where the occipital lobe and the parahippocampal gyrus blends together) can be seen as a tract for the integration of visual stimuli from the inferior portion of the visual field and parahippocampal areas involved in the recognition of places (Arcaro, McMains, & Kastner, 2009; Catani et al., 2014). Finally, the clinical importance of the stratum sagittale of the occipital lobe has been recently emphasised by Viegas, Moritz-Gasser, Rigau, and Duffau (2011). In this retrospective review of patients operated for World Health Organisation (WHO) grade II gliomas encroaching on the occipital lobes, semantic paraphasias were induced after intraoperative stimulation of the IFOF (for lesions located in the language dominant hemisphere). The IFOF therefore constituted the antero-lateral margin of resection, preserving language function in patients undergoing an occipital lobectomy.

5. Conclusions

The human occipital lobe presents a rich and complex network of intralobar fibres, arranged around the ventricular wall. The general principle whereby short association fibres appear to be more superficial, whilst long ranging association fibres are located further away from the cortex and are in contact with the walls of the ventricle, can be confirmed in this study. Overall, good concordance was observed between our Klingler dissection in three right hemisphere specimens and the histological descriptions provided by Sachs's atlas. The most important difference between both studies, is the description of a novel occipital pathway, namely the "sledge runner" connecting the cuneus to the lingual gyrus, described for the first time in a post mortem study. A comprehensive translation of the original work is enclosed to this research work for facilitated comparison and future reference.

Conflict of interest

The authors declare no financial or personal conflict of interest related to the present work.

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REFERENCES

Agrawal, A., Kapfhammer, J. P., Kress, A., Wichers, H., Deep, A., Feindel, W., et al. (2011). Josef Klingler's models of white matter tracts: influences on neuroanatomy, neurosurgery, and neuroimaging. *Neurosurgery, 69*, 238–252.

Alves, R. V., Ribas, G. C., Párraga, R. G., & de Oliveira, E. (2012). The occipital lobe convexity sulci and gyri. *Journal of Neurosurgery, 116*(5), 1014–1123.

Amunts, K., Malikovic, A., Mohlberg, H., Schormann, T., & Zilles, K. (2000). Brodmann's areas 17 and 18 brought into stereotaxic space – where and how variable? *NeuroImage, 11*(1), 66–84.

Anderson, S. J., Holliday, I. E., Singh, K. D., & Harding, G. F. (1996). Localization and functional analysis of human cortical area V5 using magnetoencephalography. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 263*, 423–431.

Arcaro, M. J., McMains, S. A., & Kastner, S. (2009). Retinotopic organization of human ventral visual cortex. *The Journal of Neuroscience, 29*(34), 10638–11152.

Bartels, A., Logothetis, N. K., & Moutoussis, K. (2008). fMRI and its interpretations: an illustration on directional selectivity in area V5/MT. *Trends in Neurosciences, 31*(9), 444–453.

Binzegger, T., Douglas, R. J., & Martin, K. A. (2004). A quantitative map of the circuit of cat primary visual cortex. *The Journal of Neuroscience, 24*(39), 8441–8453.

Bolton, J. S. (1900). The exact histological localization of the visual area of the human cerebral cortex. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 193*, 165–222.

Brodmann, K. (1909). *Vergleichende Lokalizationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Leipzig: Barth.

Burdach, K. F. (1822). *Vom Baue und Leben des Gehirns*. Leipzig: Dyk.

Catani, M., Dell'Acqua, F., Vergani, F., Malik, F., Hodge, H., Roy, P., et al. (2012). Short frontal lobe connections of the human brain. *Cortex, 48*, 271–291.

Catani, M., Forkel, S. J., & Thiebaut de Schotten, M. (2010). Asymmetry of the white matter pathways in the brain. In Hughdhal (Ed.), *The two halves of the brain*. New York: MIT Press (Chapter 7).

Catani, M., Howard, R. J., Pajevic, S., & Jones, D. K. (2002). Virtual in vivo interactive dissection of white matter fasciculi in the human brain. *NeuroImage, 17*, 77–94.

Catani, M., Jones, D. K., Donato, R., & Ffytche, D. H. (2003). Occipito-temporal connections in the human brain. *Brain, 129*, 2093–2107.

Catani, M., & Thiebaut de Schotten, M. (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex, 44*, 1105–1132.

Catani et al. (2014). *Cortex* in press/epub (in this issue).

Curran, E. J. (1909). A new association fiber tract in the cerebrum with remarks on the fiber tract dissection method of studying the brain. *Journal of Comparative Neurology and Psychology, 19*, 645–656.

Dehaene, S., Le Clec, H. G., Poline, J. B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *NeuroReport, 13*(3), 321–325.

Dell'Acqua, F., Rizzo, G., Scifo, P., Clarke, R. A., Scotti, G., & Fazio, F. (2007). A model-based deconvolution approach to solve fiber crossing in diffusion-weighted MR imaging. *IEEE Transactions on Bio-medical Engineering, 54*, 462–472.

Dell'Acqua, F., Scifo, P., Rizzo, G., Catani, M., Simmons, A., Scotti, G., et al. (2010). A modified damped Richardson–Lucy algorithm to reduce isotropic background effects in spherical deconvolution. *NeuroImage, 49*, 1446–1458.

Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., & Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of Vision, 3*, 586–598.

Dupont, P., Orban, G. A., De Bruyn, B., Verbruggen, A., & Mortelmans, L. (1994). Many areas in the human brain respond to visual motion. *Journal of Neurophysiology, 72*, 1420–1424.

Epelbaum, S., Pinel, P., Gaillard, R., Delmaire, C., Perrin, M., Dupont, S., et al. (2008). Pure alexia as a disconnection syndrome: new diffusion imaging evidence for an old concept. *Cortex, 44*(8), 962–974.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1*(1), 1–47.

Fernandez-Miranda, J. C., Rhoton, A. L., Jr., Alvarez-Linera, J., Kakizawa, Y., Choi, C., & de Oliveira, E. (2008). Three-dimensional microsurgical and tractographic anatomy of the white matter of the human brain. *Neurosurgery, 62*, 989–1026.

Forkel, S. J., Thiebaut de Schotten, M., Kawadler, J. M., Dell'Acqua, F., Danek, A., & Catani, M. (2012). The anatomy of fronto-occipital connections from early blunt dissections to contemporary tractography. *Cortex*. http://dx.doi.org/10.1016/j.cortex.2012.09.005 (Epub ahead of print).

Greenblatt, S. H. (1973). Alexia without agraphia or hemianopsia. Anatomical analysis of an autopsied case. *Brain, 96*(2), 307–316.

Iaria, G., & Petrides, M. (2007). Occipital sulci of the human brain: variability and probability maps. *Journal of Comparative Neurology, 501*(2), 243–259.

Iaria, G., Robbins, S., & Petrides, M. (2008). Three-dimensional probabilistic maps of the occipital sulci of the human brain in standardized stereotaxic space. *Neuroscience, 151*(1), 174–185.

Jones, D. K., Simmons, A., Williams, S. C. R., & Horsfield, M. A. (1999). Non-invasive assessment of axonal fiber connectivity in the human brain via diffusion tensor MRI. *Magnetic Resonance in Medicine, 42*, 37–41.

Kaas, J. H. (2004). Early visual areas: V1, V2, V3, DM, DL, and MT. In J. H. Kaas, & C. E. Collins (Eds.), *The primate visual system* (pp. 139–159). New York: CRC Press.

Klingler, J. (1935). Erleichterung der makroskopischen Präparation des Gehirns durch den Gefrierprozess. *Schweizer Archiv für Neurologie und Psychiatrie, 36*, 247–256.

Kucukyuruk, B., Richardson, R. M., Wen, H. T., Fernandez-Miranda, J. C., & Rhoton, A. L., Jr. (2012). Microsurgical anatomy of the temporal lobe and its implications on temporal lobe epilepsy surgery. *Epilepsy Research and Treatment, 2012*, 769825. http://dx.doi.org/10.1155/2012/769825.

Le Bihan, D., Mangin, J. F., Poupon, C., Clark, C. A., Pappata, S., Molko, N., et al. (2001). Diffusion tensor imaging: concepts and applications. *Journal of Magnetic Resonance Imaging, 13*, 534–546.

Ludwig, E., & Klingler, J. (1956). *Atlas Cerebri Humani: Der innere Bau des Gehirns dargestellt auf Grund makroskopischesr Präparate*. Boston: Brown.

Mahaney, K. B., & Abdulrauf, S. I. (2008). Anatomic relationship of the optic radiations to the atrium of the lateral ventricle: description of a novel entry point to the trigone. *Neurosurgery, 63*(4 Suppl. 2), 195–202.

Martino, J., Brogna, C., Robles, S. G., Vergani, F., & Duffau, H. (2010). Anatomic dissection of the inferior fronto-occipital fasciculus revisited in the lights of brain stimulation data. *Cortex, 46*, 691–699.

Martino, J., Vergani, F., Robles, S. G., & Duffau, H. (2010). New insights into the anatomic dissection of the temporal stem with special emphasis on the inferior fronto-occipital fasciculus: implications in surgical approach to left mesiotemporal and temporoinsular structures. *Neurosurgery, 66*, 4–12.

Mesulam, M. M. (2005). Imaging connectivity in the human cerebral cortex: the next frontier? *Annals of Neurology, 57*(1), 5–7.

Ono, M., Kubik, S., & Abernathey, C. D. (1990). *Atlas of the cerebral sulci*. Thieme.

Peltier, J., Verclytte, S., Delmaire, C., Deramond, H., Pruvo, J. P., Le Gars, D., et al. (2010). Microsurgical anatomy of the ventral callosal radiations: new destination, correlations with diffusion tensor imaging fiber-tracking, and clinical relevance. *Journal of Neurosurgery, 112*, 512–519.

Retzius, G. (1896). *Das Menschenhirn*. Stockholm: G. Norstedt and Soener.

Sachs, H. (1892). *Das Hemisphärenmark des menschlichen Grosshirns. I. Der Hinterhauptlappen*. Leipzig: G. Thieme.

Sack, A. T., Kohler, A., Linden, D. E., Goebel, R., & Muckli, L. (2006). The temporal characteristics of motion processing in hMT/V5: combining fMRI and neuronavigated TMS. *NeuroImage, 29*, 1326–1335.

Sarubbo, S., De Benedictis, A., Maldonado, I. L., Basso, G., & Duffau, H. (2011). Frontal terminations for the inferior fronto-occipital fascicle: anatomical dissection, DTI study and functional considerations on a multi-component bundle. *Brain Structure and Function, 18*(1), 21–37.

Schmahmann, J. D., & Pandya, D. N. (2009). *Fiber pathways of the brain*. Oxford: Oxford University Press.

Sereno, M. I., & Tootell, R. B. H. (2005). From monkeys to humans: what do we now know about brain homologies? *Current Opinion in Neurobiology, 15*, 135–144.

Sincich, L. C., & Horton, J. C. (2005). The circuitry of V1 and V2: integration of color, form, and motion. *Annual Review of Neuroscience, 28*, 303–326.

Stiers, P., Peeters, R., Lagae, L., Van Hecke, P., & Sunaert, S. (2006). Mapping multiple visual areas in the human brain with a short fMRI sequence. *NeuroImage, 29*, 74–89.

Thiebaut de Schotten, M., Urbanski, M., Valabregue, R., Bayle, D. J., & Volle, E. (2012 Dec 19). Subdivision of the occipital lobes: an anatomical and functional MRI connectivity study. *Cortex*. http://dx.doi.org/10.1016/j.cortex.2012.12.007. pii:S0010-9452(12)00342-5.(Epub ahead of print).

Tootell, R. B., & Hadjikhani, N. (2001). Where is "dorsal V4" in human visual cortex? Retinotopic topographic and functional evidence. *Cerebral Cortex, 11*, 298–311.

Türe, U., Yaşargil, M. G., Friedman, A. H., & Al-Mefty, O. (2000). Fiber dissection technique: lateral aspect of the brain. *Neurosurgery, 47*, 417–426.

Van Essen, D. C. (2003). Organization of visual areas in macaque and human cerebral cortex. In L. Chalupa, & J. Werner (Eds.), *The visual neurosciences* (p. 507). Bradford: MIT Press.

Vezoli, J., Falchier, A., Jouve, B., Knoblauch, K., Young, M., & Kennedy, H. (2004). Quantitative analysis of connectivity in the visual cortex: extracting function from structure. *Neuroscientist, 5*, 476–482.

Viegas, C., Moritz-Gasser, S., Rigau, V., & Duffau, H. (2011). Occipital WHO grade II gliomas: oncological, surgical and functional considerations. *Acta Neurochirurgica, 153*, 1907–1917.

Von Economo, C., & Koskinas, G. N. (1925). *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen*. Berlin: Springer-Verlag.

Wandell, B. A., Rauschecker, A. M., & Yeatman, J. D. (2012). Learning to see words. *Annual Review of Psychology, 63*, 31–53.

Whethered, F. J. (1888). On a new method of staining sections of the central nervous system. *British Medical Journal, 1*, 150.

Yeatman, J. D., Rauscheker, A. M., & Wandell, B. A. (2013). Anatomy of the visual word form area: adjacent cortical circuits and long-range white matter connections. *Brain and Language, 125*, 146–155.

Yogarajah, M., Focke, N. K., Bonelli, S., Cercignani, M., Acheson, J., Parker, G. J., et al. (2009). Defining Meyer's loop-temporal lobe resections, visual field deficits and diffusion tensor tractography. *Brain, 132*, 1656–1668.

Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience, 11*, 641–649.

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