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Occipital Sulci of the Human Brain: Variability and Morphometry

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Running title: Occipital Sulci of the Human Brain

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Abstract: The external morphology of the occipital lobe was investigated in 15 human post-mortem brains (30 hemispheres) fixed in formalin. We identified, described and measured the lengths of 9 major human occipital sulci and five variable ones, comparing both types between the individuals and hemispheres. Morphological variability of the human occipital sulci is related to the interindividual and interhemispheric differences in their presence, origin, types, segmentation, intersection and length. The major occipital sulci, particularly the parieto-occipital, the calcarine, the inferior lateral occipital and the anterior occipital sulci, as well as two points of their intersections (cuneal point and intersection of the transverse occipital and superior occipital sulcus) may be used as reliable anatomical landmarks for the location of architectonically and functionally defined human visual areas (V1, V2, V3, V3A, V5/MT+, LO1 and LO2) and during less invasive neurosurgical procedures in the cases of the focal lesions of the occipital lobe. The two lateral occipital sulci (inferior or the main and superior or the variable) were defined on the lateral surface of the occipital lobe. The variable lunate sulcus was studied and combining our results with those from histological and functional imaging studies we suggest that the lunate sulci of human and nonhuman primates are not homologous.

Key words: Human brain, Morphology, Occipital lobe, Sulcus, Visual cortex

Abbreviations

Acc – accessory sulcus
AOS – anterior occipital sulcus
CaS – calcarine sulcus
CaS-a – anterior part of the calcarine sulcus
CaS-m – middle part of the calcarine sulcus
CaS-p – posterior part of the calcarine sulcus (retrocalcarine sulcus)
CoS – collateral sulcus
ILOS – inferior lateral occipital sulcus
IOS – inferior occipital sulcus
IPS – intraparietal sulcus
ITS – inferior temporal sulcus
LiS – lingual sulcus
LOTS – lateral occipito-temporal sulcus
LuS – lunate sulcus
OpS – occipitopolar sulcus
PCaS – paracalcarine sulci
PI – preoccipital incisure
POS – parieto-occipital sulcus
SLOS – superior lateral occipital sulcus
SOS – superior occipital sulcus
STS – superior temporal sulcus
TOS – transverse occipital sulcus
\+ – Gyrus descendens

INTRODUCTION

The human occipital sulci show a significant and complex variability (Ono et al. 1990; Iaria and Petrides 2007). The complexity of the sulcal variability is caused mainly by the: 1) degree of regional cortical folding, 2) sulcal presence) or absence (constant or variable sulci), 3) diversity of sulcal origin, 4) sulcal segmentation, 5) differences in sulcal length, 6) differences in sulcal depth and 7) intrasulacal geometry. The position and extent of human occipital cortical areas, defined either architectonically or functionally have characteristic relationships to the occipital sulci, their banks and fundi or to points of sulcal intersections. The spatial covariance between the architectonically defined primary visual area (V1) and the calcarine sulcus (CaS) is well known (Brodmann 1909; Filimonoff 1932; Amunts et al. 2000). The same spatial covariance is found in the case of the functionally defined primary visual area (Hasnian 2006; Hinds et al. 2009; Wilms et al. 2010). Thereby, the variability in CaS location predicts the location variance of the primary visual area.

The primary visual area occupies the upper and lower banks of the CaS and extends in part along the adjacent portions of the cuneus and the lingual gyrus. It contains a map of the contralateral visual hemifield and precise retinotopy. The upper part of the visual hemifield is represented along the lower bank of the CaS, whereas the lower part of the visual hemifield is represented along the upper bank of the CaS (Horton and Hoyt 1991). The horizontal meridian which divides the representations of these parts follows the fundus of the CaS. Retinal representation follows caudorostral axis, with a greatly magnified foveal representation in the posterior calcarine cortex near the occipital pole, and reduced representation of the peripheral parts of retina in the anterior calcarine cortex, below the splenium of the corpus callosum (Horton and Hoyt 1991; Wandell et al. 2007). Neuroradiologically verified focal lesions in the region of the calcarine cortex, correlated with CaS and distinctive representation and retinotopy in the primary visual area may help in predicting and explaining the clinical manifestations of these lesions, as well as in the planning of the neurosurgical procedures.

The spatial covariance between occipital sulci and visual areas defined by functional neuroimaging techniques in humans has also established for areas V3A (Tootell et al. 1997), V3v (VP) and V4v (V4), (De Yoe et al. 1996; Hasnian et al. 2006) and V5 (MT+) (Dumoulin et al. 2000; Huk et al. 2002). Additionally, a similar spatial covariance was found in the cases of the putative anatomical correlates of the human visual motion area V5 (MT+) defined either by the quantitative myeloarchitectonic (Annese et al., 2005) or by the quantitative cytoarchitectonic approach (Malikovic et al. 2007).

The aim of the present study was to define the variability of the human occipital sulci with particular regard to the sulcal: 1) presence, 2) position, 3), extent, 4) intersections and 5) length. such knowledge can contribute to a better definition of the position, extent, size and the spatial variability of the human architectonic and functional occipital areas. Well established and constant occipital sulci, or the points of their intersections, may be used as useful anatomical landmarks during the less invasive neurosurgical procedures.

MATERIAL AND METHODS

Investigation of the occipital sulci was performed on 15 human post-mortem brains (10 male: brain numbers 1, 2, 4, 5, 8-10 and 12-14; 5 female: brain numbers 3, 6, 7, 11 and 15; mean age 56.6 years, range from 30 to 69 years). The brains were obtained in accordance with the ethical and legal recommendations of the Faculty of Medicine, University of Belgrade. The post-mortem delay was < 30 h. All of the brains were from the subjects with no history of neurological or psychiatric diseases in their clinical records.

The brains were removed from the skull and fixed in buffered formalin (4% neutral solution of formaldehyde) for at least 2 months. The fixation was performed by suspending the brains on their vertebral arteries in the fixative in order to avoid compression or distortion in brain shape. After fixation, the cerebellum and brain stem were removed above the mesencephalon and the cerebral hemispheres were separated by a midline sagittal section. The leptomeninges and blood vessels were carefully removed from the brain surface and occipital sulci and gyri were exposed.

The occipital sulci were traced using the transparent and adherent folia along the medial, lateral and inferior surfaces of the hemisphere. The tracing process was carefully performed in order to preserve existing course of the occipital sulci and their relationships. The resulting drawings of the occipital sulci on transparent folia were additionally copied on the tracing paper, and these images were scanned (Scanjet G2710; Hewlett-Packard, Palo Alto, CA; resolution of the digitized images 600 dpi). The occipital sulci were identified directly from the hemispheres and marked in the digitized images after the scanning process. Photographs of the occipital lobes were also taken for each post-mortem brain.

In order to avoid possible inconsistencies or confusion related to the terminology frequently present in descriptions of the occipital sulci, we used the terminology introduced by Duvernoy (1999) based on: 1) the position of the sulcus, 2) the relationship to the sulcus to gyri and 3) the shape or the course of the sulcus. A number of alternate terms, which have been employed for the occipital sulci, were also kept in order to establish the correlation between the different names used for the same sulcus.

The length of each occipital sulcus was measured three times in the digitized images using free image processing program ImageJ (National Institute of Health, MD), and the mean was used as the valid sulcal length. Statistical analyses were performed using in-house program (Institute of Medical Statistics and Informatics, Faculty of Medicine, University of Belgrade). The differences among sulcal types (incidences for the sulcal types) i n relation to the side of the hemisphere were tested using a Pearson chi-square test. Sulcal lengths were compared between hemispheres (interhemispheric differences) using a *t* test. The degree of association between the sulcal lengths (for the left and right hemispheres separately, and between hemispheres, respectively) was tested using a Pearson correlation. These parametric methods (both for the differences and correlations) were assessed due to the normal distribution of our numerical variables which were tested by Kolmogorov-Smirnov test.

RESULTS

Parieto-occipital sulcus. The parieto-occipital sulcus (POS) is constant, continuous and clearly defined sulcus. Its longer portion occupies the medial surface of the hemisphere separating neighboring parts of the occipital (cuneus) and parietal lobe (precuneus). The shorter portion of the POS extends to the lateral surface of the hemisphere by crossing its superior margin, partly representing the border between the occipital and parietal lobes (Figs. 1 and 2). The anterior bank of the POS belongs to the parietal lobe while its posterior bank belongs to the occipital lobe. With respect to the course and ramification, we found three types of the POS (Table 1).

There are no significant interhemispheric differences ($p > 0.05$) between the incidences of the POS types, but the type II (Y-shape ramified form of POS with two superolateral branches, anterior and posterior) (Fig. 1a, d) is more often present in the left hemisphere (9 cases) than in the right hemisphere (7 cases).

The POS connects to CaS in all 30 investigated hemispheres. The junction of these 2 sulci on the medial surface of the hemisphere is defined as the cuneal point (CP) (Fig. 1). The mean length of the POS is 51.9 mm (Table 4). The POS is longer in the left hemisphere (53.6 mm) than in the right hemisphere (50.1 mm), although this difference is not significant ($p > 0.05$). In the right hemisphere there is a significant correlation between the types and the lengths of the POS. In the right hemisphere, Type I of the POS (the POS with the straight course and without ramification) (Fig. 1c) is the shortest, while type III (T-shape ramified form of the POS with a horizontal superolateral branch near the superior margin of the hemisphere) is the longest (ρ = 0.493, p = 0.049).

Calcarine sulcus. The CaS is a constant sulcus which extends along the medial surface of the occupying the inferior parts of the latter when reaching the CP. The part of the CaS in front of the CP extends into the temporal lobe, just below the splenium of the corpus callosum.

With respect to the relationships with the CP and the occipital pole, there are three parts of the CaS: the anterior, middle and posterior parts (Fig. 1). The anterior part of the CaS is located in front of the cuneal point (CP), extending in an anteroposterior direction to reach the posteromedial portions of the temporal lobe. The middle, which is the longest part of the CaS (truncus), is located between the CP and the occipital pole, interposed between the cuneus and lingual gyrus. The posterior part or the tail-end of the CaS that reaches the occipital pole, is also known as the retrocalcarine sulcus. In 79.9% of cases (24 hemispheres), the posterior part of the CaS ramifies into upper and lower branches. In most of the hemispheres (20 hemispheres), the point of this bifurcation is located on the medial surface of the occipital pole; in rare cases, the point of bifurcation is located on the lateral surface of the occipital pole (4 hemispheres). In most of the cases (86.6% of cases, 26 hemispheres) the posterior part of the CaS is a direct posterior continuation of the middle part of the CaS; in the remaining 13.3% of cases (4 hemispheres) it is separated from the middle part of the CaS, where the cuneus and lingual gyrus are fused by the small bridge-like cuneolingual gyrus (Fig. 1c).

According to the shape of its course, we defined four types of CaS (Table 2). There are no significant differences ($p > 0.05$) between the incidences of these CaS types related to the side of the hemisphere. The most common type I (CaS with a single apex) is found slightly more often in the left hemisphere (10 cases) than in the right hemisphere (9 cases). There are also no significant correlations between the types of the CaS and their lengths. The most frequent sulcal intersections of the CaS are to the POSs and paracalcarine sulci (PCaS) (Table 3; Fig. 1b). The mean length of the calcarine sulcus (including all 3 parts) is 104.6 mm (109.5 mm in the left and 99.7 mm in the right hemisphere).

The paracalcarine sulci. The PCaS are defined as constant sulci that extend along the cuneus (Fig. 1). They are situated above to the middle part of the CaS running more or less parallel to it. In most cases there is only one PCaS (66.6% of cases, 20 hemispheres). In two hemispheres (6.7% of cases) we identified 2 PCaS, i.e. superior and inferior ones; in the remaining cases we found three, four and five clearly separated and short PCaS. Retzius (1896) and Economo and Koskinas (1925) referred to these sulci as the sagittal sulci (superior and inferior) of the cuneus, indicating their position and direction. The mean length of the PCaS was 41.6 mm (42.5 mm in the left; 40.7 mm in the right hemisphere) and their lengths are highly variable (CV=40.7) (Table 4).

Lingual sulcus. The lingual sulcus (LiS) is a constant sulcus which extends along the lingual gyrus, interposed between the middle part of the CaS and the posterior (occipital) end of the collateral sulcus (CoS) (Fig. 1). The LiS divides the lingual gyrus into superior and inferor portions, and 73.3% of cases (22 hemispheres) it is a prominent sulcus which extends along the lingual gyrus (Fig. 3b, d). In the remaining

26.7% of cases (8 hemispheres), the LiS is the medial branch of the CoS (Fig. 2c) as indicated by Ono et al. (1990).

In most of cases (93.3% of cases, 28 hemispheres) the LiS is a continuous sulcus, and only rarely (6.7% of cases, 2 hemispheres), the LiS is discontinuous, composed of two or three short segments. The most frequent sulcal connection of the LiS was the intersection with the posterior end of the CoS (Table 3; Fig. 1a). The LiS has been referred as the intralingual sulcus by Ono et al. (1990). The mean length of the LiS is was 27.6 mm (29.9 mm in the left and 25.3 mm in the right hemisphere), but its length is highly variable (CV=43.6) (Table 4).

Collateral sulcus or medial occipito-temporal sulcus. The CoS medial occipito-temporal sulcus is constant, continuous and long. The CoS extends along the inferomedial parts of the occipital and the temporal lobes, interposed between the lingual and lateral occipito-temporal sulci (Figs. 1, 3c). The posterior (occipital) end of CoS separates the lingual gyrus from the occipital part of the fusiform gyrus (lateral occipito-temporal gyrus). In three hemispheres (10.0% of cases) the CoS is associated with an accessory sulcus (Fig. 3c).

Lateral occipito-temporal sulcus or occipito-temporal sulcus. The lateral occipito-temporal sulcus or occipito-temporal sulcus (LOTS) is constant and the longest of measured sulci, extending along the inferolateral parts of the occipital and temporal lobes. The LOTS is located between the CoS and the inferolateral border of the hemisphere (Figures 1, 3c). The posterior (occipital) end of this sulcus separates the occipital part of the fusiform gyrus from the inferior occipital gyrus. In 70.0% of cases (21 hemispheres) the LOTS is continuous sulcus, while in the remaining cases it is composed of two or three segments. The posterior end of the LOTS is occasionally

(16.7% of cases or 5 hemispheres) connected to the preoccipital incisure (Fig. 1a, 3c). In the left hemisphere there is significant positive correlation between the lengths of the LOTS and the CaS (ρ =0.517, p <0.048).

Transverse occipital sulcus. The transverse occipital sulcus (TOS) is constant and continuous. It has mediolateral (transverse) orientation along the border between the occipital and parietal lobes on the lateral surface. The TOS is located behind the lateral part of the POS. This sulcus was very often connected to the superior occipital sulcus (SOS) (76.6% of cases, 23 hemispheres; Table 3, Figs. 2, 3a) and this is the most frequent sulcal interconnection on the lateral surface of the occipital lobe. The TOS crosses the SOS, more or less at a right angle and is thus divided into medial and lateral segments (Fig. 3a). The medial segment is directed toward the superior margin of the occipital lobe. The lateral segment of the TOS is directed inferiorly along the lateral surface of the occipital lobe toward the anterior ends of the superior and inferior lateral occipital sulci. It is connected to the superior or inferior lateral occipital sulci and the incidence of these sulcal intersections is equal (16.7% of cases, 5 hemispheres each). The TOS has been referred as the sulcus occipitalis primus by Economo and Koskinas (1925). The mean length of the TOS is 43.4 mm (47.4 mm in the left and 39.5 mm in the right hemisphere) and it varies considerably (CV=36.2) (Table 4). In the right hemisphere there is a significant positive correlation between the lengths of the TOS and the SOS (ρ = 0.604, p < 0.022).

Superior occipital sulcus. The SOS is a variable, simple sulcus found in 86.7% of cases (26 hemispheres). It extends in anteroposterior direction along the lateral surface of the occipital lobe, more or less parallel to the superior margin of the hemisphere (Figs. 2, 3a). This sulcus has been referred as the paroccipital sulcus (sulcus paroccipitalis) by

Kuhlenbeck (1928). The superior occipital gyrus is situated between the SOS and the superior margin of the hemisphere, where it merges with the cuneus on the medial surface of the occipital lobe. In only four of the hemispheres the SOS was found to be discontinuous with two segments, namely anterior and posterior segments, respectively. In most of cases (80.8% of cases, 21 hemispheres) the SOS is a direct posterior continuation of the intraparietal sulcus (IP). The SOS is connected to the TOS as mentioned previously. The mean length of the SOS is 35.3 mm (Table 4).

Superior lateral occipital sulcus. The superior lateral occipital sulcus (SLOS) is a variable sulcus which we found in 76.7% of cases (23 out of 30 hemispheres). It is always located immediately above the inferior lateral occipital sulcus (ILOS) and extends in an anteroposterior direction along the lateral surface of the occipital lobe (Fig. 2a-c). The middle occipital gyrus covers the main part of the lateral occipital surface, which is situated between the superior and inferior occipital sulci, when they are present. When there is a single and continuous ILOS (23.3% of cases, 7 out 30 hemispheres), the middle occipital gyrus comprise two parts: the superior and inferior ones. When there is a coexistence of two lateral occipital sulci, the superior and inferior sulci (76.7% of cases), the middle occipital gyrus comprises three parts: the superior, middle and inferior ones. The anterior end of the SLOS is connected to the superior temporal sulcus (STS) (34.8% of cases, 8 hemispheres) and less often to the anterior occipital sulcus (AOS) (21.7 % of cases, 5 hemispheres). The posterior end of the SLOS was connected to the lunate sulcus in 17.4% of cases (4 hemispheres). The mean length of SLOS is 20.2 mm (Table 4). There is a negative correlation between the lengths of the SLOS and the side of hemisphere (ρ= - 0.686, $p < 0.060$), which indicates significant morphological asymmetry.

Inferior lateral occipital sulcus. The ILOS is a constant, continuous and clearly defined. This horizontally oriented sulcus is located between the SLOS and the inferior occipital sulcus (IOS), when both are present (Figs. 2, 3d). The anterior end of the ILOS can be connected to the AOS, and this type of intersection we found in 30.0 % of cases (9 hemispheres). Less often, the anterior end of the ILOS is connected to the STS (23.3% of cases, 7 hemispheres). The posterior end of the ILOS was connected to the LuS in one-fifth of cases (20.0% of cases, 6 hemispheres). The ILOS as a constant of two lateral occipital sulci has been referred to as the prelunate sulcus by Elliot Smith (1907). The mean length of the ILOS is 53.2 mm (53.8 mm in the left and 52.5 mm in the right hemisphere).

Inferior occipital sulcus. The IOS is a variable sulcus found in 86.7% of cases (26 hemispheres). It is situated immediately below the ILOS, near the inferolateral margin of the occipital lobe (Figs. 2, 3d). The inferior occipital gyrus is situated between the IOS (when it exists) and the posterior end of the LOTS. The length of this sulcus is the most variable among the occipital sulci (CV = 60.8) (Table 4).

Anterior occipital sulcus. The AOS is a constant sulcus with vertical or oblique orientation along the border between the occipital and temporal lobes on the lateral surface of the hemisphere (Figs. 2, 3d). The AOS is continuous sulcus which has various origins. In 60.0% of cases (18 hemispheres) this sulcus is the continuation of the ascending branch of the inferior temporal sulcus (Figure 3d). In the remaining 40.0% of cases, the AOS is the superior continuation of the preoccipital incisure (temporo-occipital incisure) directed upward from the inferolateral margin of the hemisphere (Fig. 2b). When it appears in this way, the preoccipital incisure is connected to one lateral branch of the LOTS on the inferior surface of the hemisphere (16.7% of cases or 5 hemispheres) and the AOS apears to be connected to the LOTS (Fig. 1a, 1c). Additionally, in both hemispheres the lengths of the anterior occipital and those of the lateral occipito-temporal sulci are highly significantly and positively correlated, both in the left hemisphere (ρ=0.654, p<0.008), and in the right hemisphere (ρ=0.670, p<0.006). The AOS has been referred as the preoccipital sulcus (sulcus preoccipitalis) by Meynert (1877) or as the ascending branch of the inferior temporal sulcus (Watson et al. 1993; Dumoulin et al. 2000).

The superior end of the AOS was connected to the STS in 40.0% of cases (12 hemispheres) (Fig. 2a). There are also two important sulcal intersections of the AOS: the intersections with the IOS (33.3% of cases, 10 hemispheres) and with the ILOS (33.3% of cases, 9 hemispheres) (Table 3). The mean length of the AOS is 49.6 mm (52.9 mm in the left and 46.3 mm in the right hemisphere).

Figure 3 about here, please

Lunate sulcus. The LuS, found in one-third of the investigated hemispheres (33.3% of cases, 10 hemispheres), is a variable and continuous sulcus situated near the occipital pole on the lateral surface. The second criterion used to define this sulcus is its origin in relation to the lateral occipital sulci. The LuS is the posterior continuation of either the ILOS (60.0% of cases, 6 hemispheres), or the SLOS (40.0% of cases, 4 hemispheres). The LuS is a curved sulcus with a vertical or oblique orientation (Figs. 2d, 3d).

Occipitopolar sulcus. The OpS is a variable sulcus, found only in one-third of the investigated hemispheres (10 of 30 hemispheres). It is a vertically oriented sulcus of the occipital pole interposed between the retrocalcarine and the lunate sulci- when they exist. When the retrocalcarine and the OpS coexist in the region of the occipital pole, these two sulci demarcate the gyrus descendens (Duvernoy 1999) (Fig. 3b).

DISCUSSION

In this study, human occipital sulci were we divided the into two categories based on the frequency of their appearance: 1) major or constant sulci, which may be used as anatomical landmarks (POS, CaS, PCaS, LiS, TOS, ILOS, AOS, as well as occipital parts of the CoS and LOTS) and 2) the variable sulci (SOS, SLOS, IOS, LuS, OpS). The POS and CaS are reliable anatomical landmarks of the occipital lobe. We found that these two sulci were consistently present and that their positions and lengths are less variable than those of other major occipital sulci (the length of the ILOS is an exception). In addition, their depths are significant compared to those of other occipital sulci: 22.0-24.2 mm (POS) and 15.2-16.5 mm (CaSs) (Ono et al. 1990).

The complexity of the POS and the CaS, manifested by the presence of the multiple types we found, is similar to those reported by Ono et al. (1990). We also identified three parts of the CaS, which corresponds with findings of Kuhlenbeck (1928) and Duvernoy (1999). Our particular interest was directed to the retrocalcarine sulcus and its terminal bifurcation, which is predominantly located along the medial surface of the occipital pole. This finding explains the posterior extent of the primary visual area (V1), which may be restricted to the more medial aspects of the occipital pole. The separation of the retrocalcarine sulcus from the middle part of the CaS (13.3% of cases) is another remarkable morphological entity when the variable cuneolingual gyrus interposes between the completely separated parts of the CaS, an observation also made by Retzius (1896), Ono et al. (1990) and Duvernoy (1999). In this case, V1 extending along the CaS reaches extrasulcal medial surface of the occipital lobe, which may explain its more superficial location in one of two hemispheres found in functional imaging studies.

We identified two lateral occipital sulci: superior (variable) and inferior (major) ones, which is in agreement with our previous findings (Malikovic et al. 2007). The coexistence of two or even three lateral occipital sulci was reported by Retzius (1896) and Kuhlenbeck (1928). The SLOS was present in 76.7% of cases with a mean length of 20.2 mm, which we regarded as a significant value and therefore decided not to classify SLOS as ”the accessory lateral occipital sulcus” as presented by Iaria and Petrides (2007). These two lateral occipital sulci differ from each in terms of their position, incidence and length, as well as their intersections. We found that the ILOS (major sulcus) was more often associated (connected) with the AOS, while the SLOS (variable) was more often associated to the STS (Table 3). The ILOS is a constant sulcus located along the inferior portion of the lateral occipital surface, and its length is the least variable comparing of all occipital sulci located along the lateral occipital surface (Table 4). The ILOS is also an important anatomical landmark related to the location of three extrastriate visual areas. Its most anterior part, near to the point of intersection with the AOS, contains motion -sensitive area V5 (MT+) (Watson et al. 1993). The cortical region that extends along the anteroposterior axis of the ILOS immediately behind area V5 (MT+) contains two lateral occipital areas: anterior (LO2) and posterior (LO1) ones involved in visual object perception (Larsson and Heeger 2006).

Our criterion to define the LuS as the posterior continuation of either the SLOS or the ILOS corresponds with the findings reported by Elliot Smith (1907) and Kuhlenbeck (1928), both of whom found LuS in 28.3% of cases (compare to 33.3% of cases in our study), Duvernoy (1999) and, in part, Iaria and Petrides (2007). In nonhuman primates, the LuS is constant structure that forms the border between the occipital and temporal lobes along the lateral surface of the hemisphere. It also represents the anterior lateral border of expanded primary visual area (Elliot Smith 1907; Allen et al. 2006). On the other hand, LuS in humans is a variable structure and its position is considerably posterior compared to nonhuman primates, while the occipito-temporal border along the lateral surface of the hemisphere is formed by the AOS. Furthermore, the posterior extent of the human primary visual area along the occipital pole is highly variable and it can not be related to sulcal patterns (Amunts et al. 2000). Based on these arguments, we suggest that the LuS of human and nonhuman primates are not homologous structures.

The two most constant points of the occipital sulcal intersections that we found were the CP and the TOS-SOS intersection. The CP, an easily observed and reliable constant anatomical landmark, is located in the most anterior position of the occipital lobe, along or near, its inferomedial margin. It represents the most inferior point of the POS. The cortical region above the CP, which extends along the posterior (occipital) bank of the POS and anterior portion of the cuneus, contains parts of two extrastriate visual areas: dorsal part of V2 and dorsal part of V3 (Wilms et al. 2010). The point of the TOS-SOS intersection we found in 76.7% of cases was always located behind the parieto-occipital transition along the superolateral aspect of the occipital lobe. In addition, the length of the transverse occipital and that of the superior occipital sulci was also highly correlated in the right hemisphere. The point of the TOS-SOS intersection may serve as an anatomical landmark, which was already propopsed by Tootell et al. (1997) in the case of the V3A area. According to this study, the functionally defined area V3A was located in the region of the TOS-SOS intersection along the superolateral portion of the occipital lobe.

In comparing mean sulcal lengths, we found that seven of the nine main occipital sulci (POS, CaS, PCaS, LiS, TOS, ILOS, AOS) are longer in the left hemisphere than in the right one. PCaS length and the lengths of the lingual and the transverse occipital sulci were highly variable (Table 4). Therefore these sulci are less reliable structures, especially if we estimate the length of each compared to the length of each of the remaining four main occipital sulci (the POS, CaS, ILOS and AOS). Although these differences did not reach statistical significance, they indicate a certain degree of the interhemispheric difference in the sulcal lengths. Ono et al. (1990) found that the POS and the LiS are longer in the left hemisphere, which is not the case with the CaS, while the length of the remaining occipital sulci were not measured. Interhemispheric differences in the length among the main sulci may be related to the degree of spatial covariance between architectonically and functionally defined occipital areas, such as “stronger sulcus-function covariance” in the left than in the right occipital lobe in the cases of visual areas V1, V2, V3 and V3A (Hasnian et al. 2006).

The human visual cortex beyond area V3 is organized into groups of areas that share common functional properties (Wandell et al. 2007; Arcaro et al. 2009). The main area among those involved in motion perception is V5 (MT+) (Watson et al. 1993; Tootell et al. 1995). V5 (MT+), which has been identified by the functional neuroimaging methods, is located on the lateral surface of the anterior part of the occipital lobe, within or near to the AOS (Dumoulin et al. 2000; Huk et al. 2002). In the same region Malikovic et al. (2007) found a distinct cytoarchitectonic area considered to be the anatomical correlate to the functionally defined area V5 (MT+). A focal brain lesion in this region results in the syndrome of cerebral akinetopsia, a deficit in perception of moving stimuli (Zihl et al. 1983; Zeki 1991).

There is intense debate about the location of the principal color center in the human brain. According to McKeefry and Zeki (1997) the center corresponds to area V4 in the ventral occipito-temporal cortex which represents a visual hemifield, while according to other Hadjikhani et al. (1998), this cenete (referred to as area V8) is in the inferior occipito-temporal region but only with quarter-field retinotopic representation. It seems that these two candidates share similar locations in the inferolateral part of the occipital lobe, where they occupy the most anterior segment in the occipital part of the fusiform gyrus. However, V4 as an area extending from the lateral bank of the CoS anterolaterally to the fusiform gyrus cannot be precisely distinguished from a more medially located V8, which was originally described as ”located midway along the length of the CoS” (Hadjikhani et al. 1998). A focal brain lesion in the inferior occipito-temporal cortex results in cerebral achromatopsia, a syndrome which causes deficient color vision (Meadows 1974) that is very often a partial deficit (Bouvier and Engel 2006). We believe that these unsolved controversies related to exact spatial definition of human visual areas are related to insufficient anatomical data on the presence, position, intersections and length of sulci in the human occipital lobe. Our results will contribute to a solution of these controversies.

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FIGURES

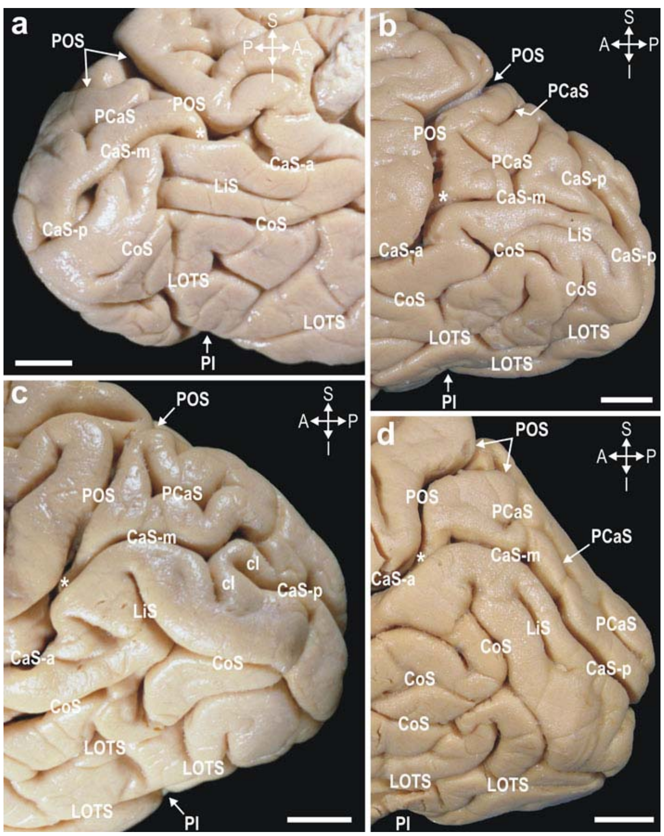

Figure 1. Sulci on the medial and inferior surfaces of the occipital and temporal lobes, the left (**a**, brain number 1), and the right hemispheres (**b**, brain number 12); c, brain number 1; **d**, brain number 14) of four post-mortem brains fixed in formalin. *Asterisks* indicate position of the cuneal point. *cl* – Cuneolingual gyrus. Orientation: *A* – anterior; *P* – posterior; *S* – superior; *I* – inferior. *Scale bar* 1 cm. For abbreviations see Abbreviation list

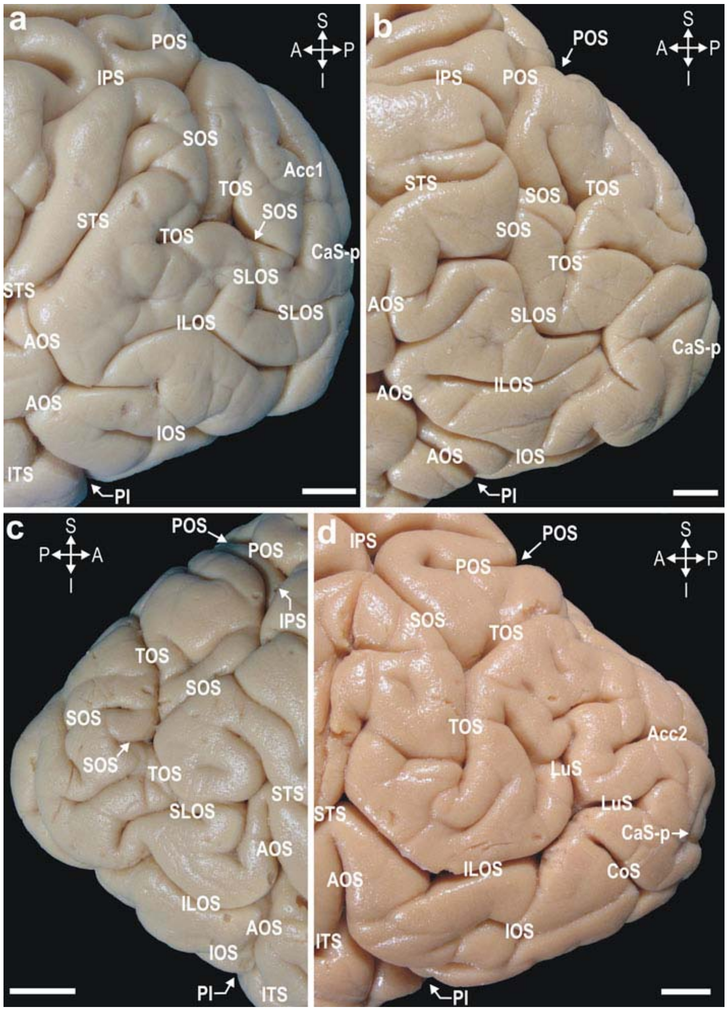

Figure 2. Sulci on the lateral surface of the occipital lobe, the left hemispheres (a, brain number 3; b, brain number 11; d, brain number 12) and the right hemisphere (c, brain number 4)) of four post-mortem brains fixed in formalin. Orientation as given in Fig. 1. *Scale bar* 1 cm. For abbreviations, see Abbreviation list.

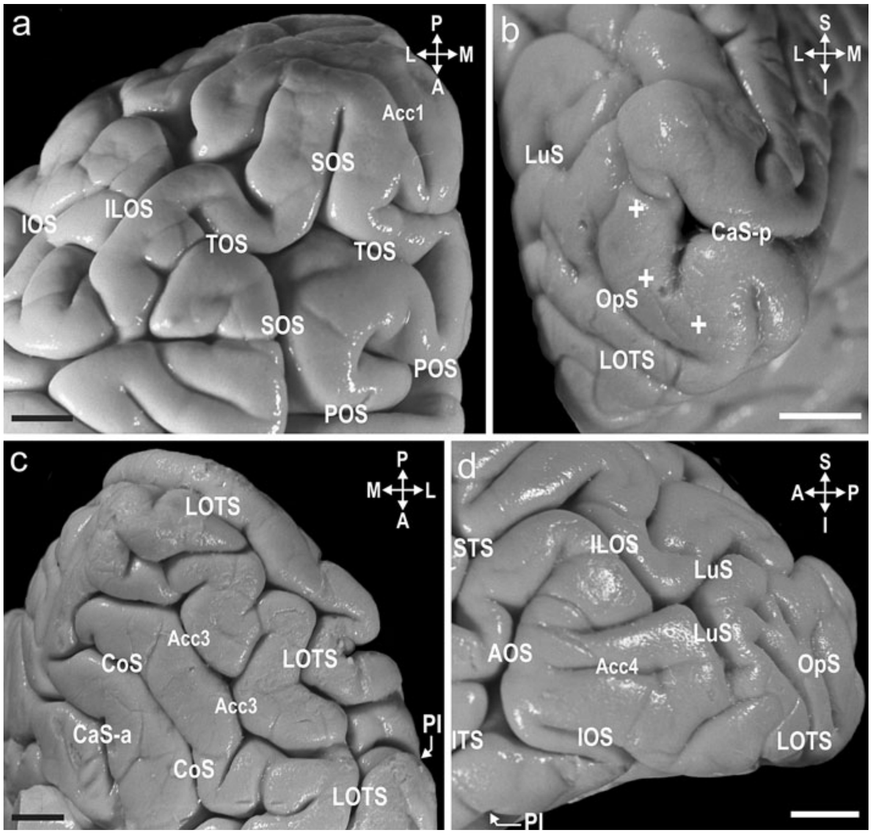

Figure 3. a Superolateral aspect of the occipital lobe (the right hemisphere of brain number 8) with the intersection of the transverse occipital and the superior occipital sulci. **b** Polar aspect of the occipital lobe (left hemisphere of brain number 9) and gyrus descendens (indicated by *crosses*). **c**. Inferior aspect of the occipital and temporal lobes (right hemisphere of brain number 9) and an accessory sulcus *(Acc3)* associated with the collateral sulcus.
d Inferolateral aspect of the occipital lobe (the left hemisphere of brain number 9) and locations of the lunate and occipitopolar sulci. Orientation: A – anterior; P – posterior; S – superior; I – inferior. *Scale bar* 1 cm. For abbreviations see Abbreviation list.

TABLES

Table 1 Types of the parieto-occipital sulcus according to its course and ramification, criteria and incidences

Type	Criteria	Incidence (%)
I	Straight course without ramification	36.7% (11 hemispheres)
II	Y-shape form with two superolateral branches	53.3% (16 hemispheres)
III	T-shape form with horizontal superolateral branch	10.0% (3 hemispheres)

Table 2 Types of the calcarine sulcus (CaS) with respect to its shape and course, the criteria and incidences

Type	Criteria	Incidence (%)
I	CaS with a single apex	63.3% (19 hemispheres)
II	CaS with two apexes	10.0% (3 hemispheres)
III	S-shaped CaS	20.0% (6 hemispheres)
IV	CaS in the form of horizontal sulcus	6.7% (2 hemispheres)

Table 3 The most frequent sulcal intersections of the occipital lobe.

Intersection	Incidence (%)
POS-CaS	100% (30 hemispheres)
TOS-SOS	76.6% (23 hemispheres)
CoS-LiS	43.3% (13 hemispheres)
CoS-LOTS	43.3% (13 hemispheres)
AOS-STS	40.0% (12 hemispheres)
SLOS-STS	33.3% (10 hemispheres)
AOS-IOS	33.3% (10 hemispheres)
AOS-ILOS	30.0% (9 hemispheres)
POS-IPS	26.7% (8 hemispheres)
CaS-PCaS	20.0% (6 hemispheres)
ILOS-LuS	20.0% (6 hemispheres)

For abbreviations, see the Abbreviation list

Table 4 The incidence of identified human occipital sulci (15 brains, 30 hemispheres), their mean lengths, standard deviations and coefficients of variation

Sulcus	Incidence (%)	Mean length (mm)	SD	CV
POS	100	51.9 (25-76)	15.7	30.3
CaS	100	104.6 (54-144)	29.7	28.4
PCaS	100	41.6 (19-83)	16.9	40.7
LiS	100	27.6 (5-50)	12.1	43.6
CoS	100	83.6 (54-114)	16.7	19.9
LOTS	100	121.9 (48-196)	33.7	27.7
TOS	100	43.4 (16-78)	15.7	36.2
ILOS	100	53.2 (32-91)	13.9	26.1
AOS	100	49.6 (18-90)	14.9	30.1
SOS	86.7	35.3 (16-57)	10.4	29.3
IOS	86.7	37.8 (14-97)	22.9	60.8
SLOS	76.7	20.2 (13-27)	3.83	18.9
LuS	33.3	25.7 (15-42)	8.6	33.5
OpS	33.3	23.8 (14-45)	9.2	38.5

For abbreviations, see the Abbreviation list