Title

Sulcal pattern variation in extant human endocasts

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Abstract

Our knowledge of human brain evolution primarily relies on the interpretation of palaeoneurological evidence. In this context, an endocast or replica of the inside of the bony braincase can be used to reconstruct a timeline of cerebral changes that occurred during human evolution, including changes in topographic extension and structural organisation of cortical areas. These changes can be tracked by identifying cerebral imprints, particularly cortical sulci. The description of these crucial landmarks in fossil endocasts is, however, challenging. High-resolution imaging techniques in palaeo-neurology offer new opportunities for tracking detailed endocranial neural characteristics. In this study, we use high resolution imaging techniques to document the variation in extant human endocranial sulcal patterns for subsequent use as a platform for comparison to the fossil record. We selected 20 extant human crania from the Pretoria Bone Collection (University of Pretoria, South Africa), which were detailed using X-ray microtomography at a spatial resolution ranging from 94 to 123 µm (isometric). We used Endex to extract, and Matlab to analyse the cortical imprints on the endocasts. We consistently identified superior, middle and inferior sulci on the frontal lobe; and superior and inferior sulci on the temporal lobe. We were able to label sulci bordering critical functional areas such as

Broca's cap. Mapping the sulcal patterns on extant endocasts is a prerequisite for constructing an atlas which can be used for automatic sulci recognition.

Key Words

sulci detection; brain cast; cerebral variation; human neuroanatomy; palaeoneurology

Introduction

Together with comparative anatomy, the endocast or replica of the internal table of the bony braincase can be used to reconstruct the timeline and mode of cerebral changes in human evolution (Holloway, 1978; Holloway et al., 2004; de Sousa and Cunha, 2012). Identifying cerebral imprints in endocasts of fossil hominin specimens is challenging due to poor preservation of fossils and inconsistencies in characterisation and identification of landmarks. Longstanding concerns exist regarding the correlation between the gyral and sulcal patterns on the brain, and the bulges and furrows imprinted on the braincase (Le Gros Clark et al., 1936; Kobayashi et al., 2014; Minh and Hamada, 2017; Bruner and Ogihara, 2018). Controversy also surrounds early descriptions of these patterns in fossil endocasts, which mostly relied on visual inspection and palpation of the endocranial surface (Falk, 1980a; Falk, 1980b; Falk, 1983; Holloway, 1981). The accuracy of the cerebral details on the endocranial surface is also affected by the presence of intracranial components, including arterial supply of the brain, cerebrospinal fluid, and meningeal membranes (Neubauer, 2014). The sulcal patterns in extant human brains are also variable, further complicating anatomical comparisons (Ribas, 2010).

The accurate identification of sulcal imprints on fossil endocasts is of prime interest in palaeoneurology. Despite the uncertainty surrounding the correspondance of cerebral areas delimited by sulci and the functional areas of the brain (Amunts et al., 1999), sulcal variation may reliably predict the location of primary and secondary areas in the brain, such as visual, somatosensory and motor areas (Fischl et al., 2008). The ability to identify sulci in endocasts of fossil hominoids may inform our understanding of evolutionary trends in cortical areas involved in specific functions. For example, the evolution of the visual cortex and the Broca's cap have been intensively discussed in non-human and human fossil hominin taxa (Falk, 1980b; Falk, 1980a; Falk, 1983; Holloway, 1981; Carlson et al., 2011; Falk, 2014; Beaudet, 2017; García-Tabernero et al., 2018; Holloway et al., 2018).

Technological advances in medical imaging techniques have enabled palaeoneurologists to compare anatomical features in more detail. Endocasts of fragmented fossil cranial vaults can be virtually extracted, reconstructed and interpreted without damaging the specimen (Spoor et al., 2000; Gunz et al., 2010; Neubauer et al., 2012; Neubauer, 2014; Neubauer et al., 2018; Beaudet and Gilissen, 2018). We used high-resolution microtomography to investigate endocranial structural organisation and variation in extant human skulls. This non-invasive, observer independent approach was recently used to automatically detect sulcal imprints on fossil endocasts (Beaudet et al., 2016a; Beaudet and Gilissen, 2018). These studies identified a need for an atlas of variation in sulcal patterns in extant human crania. This study documents the variation in sulcal pattern on extant human endocasts for subsequent use as a reference in palaeoneurological studies.

Materials and Methods

We selected 20 individual, non-pathological adult crania from the Pretoria Bone Collection (University of Pretoria, South Africa) (L'Abbé et al., 2005), consisting of 10 individuals of African and 10 individuals of European ancestry with equal proportions of females and males . The crania were from individuals of known age, ranging from 30 to 80 years old. We scanned the crania using micro X-ray computer-tomography at the MIXRAD facility, housed at Necsa, Pelindaba, South Africa, at a spatial resolution ranging from 94 to 123 µm (isometric) (Hoffman and De Beer, 2012).

The endocasts were virtually extracted and reconstructed using Endex software (Subsol et al., 2010) (Fig. 1A). Based on previous studies (Subsol et al., 1996; Subsol et al., 1998), we detected the cortical relief in endocasts using an algorithm that automaticallydetects topographical variations in, for example, crest lines on 3D meshes (Yoshizawa et al., 2007; Yoshizawa et al., 2008) (Fig. 1C). We manually removed the structures of no interest, for example, the imprints formed by the middle meningeal arteries and cranial sutures by referring to brain atlases (Connolly, 1950; Ono et al., 1990). We manually labelled the detected sulci using a program created with MATLAB R2013a v8.1 (Mathworks) which assigns a label to the selected curves (Beaudet et al., 2016b) (Fig. 1D).

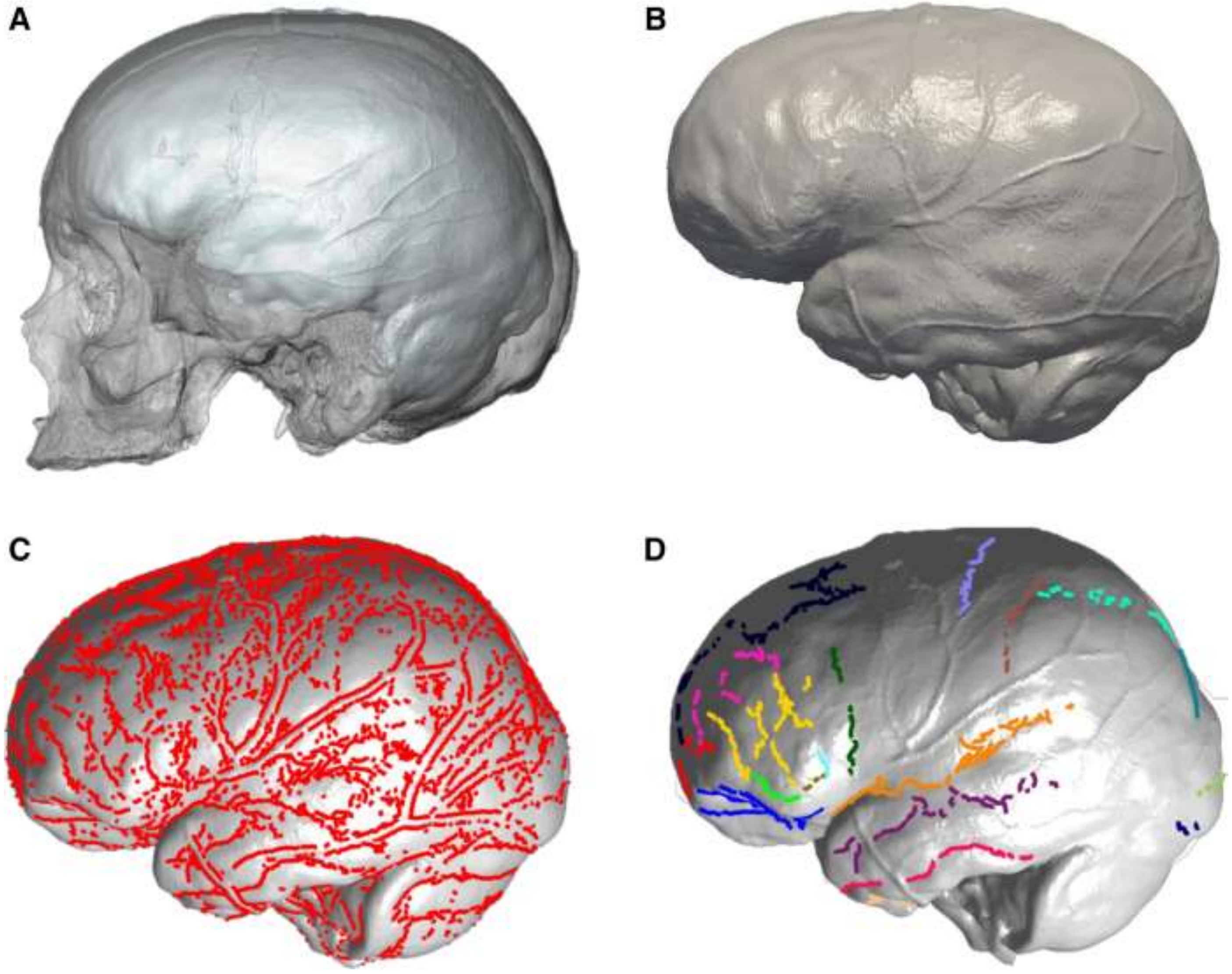

Figure 1 . Automatic extraction of an extant human endocast using Endex (A). Resulting endocast mesh (B). Application of crest line detection algorithm (C). Endocast after cleaning of crest lines and labelling (D).

Table 1: Frequency of sulci observed for left and right hemispheres in human

Sulcus	**Left**	**Right**
anterior horizontal ramus (*hr*)	40%	20%
ascending ramus (*ar*)	40%	20%
central (*c*)	55%	50%
collateral (*col*)	25%	0%
fronto-marginal (*W*)	85%	100%
fronto-orbital (*fo*)	75%	60%
inferior frontal (*if*)	85%	90%
inferior temporal (*it*)	100%	95%
middle frontal (*fm*)	90%	75%
intraparietal (*ip*)	30%	15%
lateral calcarine (*lc*)	55%	20%
inferior/lateral occipital (*oci*)	50%	60%
lunate (*L*)	80%	70%
occipitotemporal (*oct*)	35%	45%
orbital sulci (*o*)	100%	100%
postcentral (*pt*)	20%	15%
precentral (*pc*)	35%	40%
retro-calcarine (*rc*)	20%	10%
rhinal (*rh*)	25%	60%
superior frontal (*sf*)	95%	90%
superior temporal (*st*)	75%	90%
sylvian fissure (*S*)	95%	85%
transverse occipital (*otc*)	70%	55%

Results

The frequencies of sulci identified on the left (LH) and right (RH) hemispheres of the crania are alphabetically listed in Table 1.

Frontal lobes

We identified impressions of the branches of the orbital sulcus on the orbital surface of all cranial endocasts. We identified a clear transverse orbital sulcus impression on nine crania, resulting in the generally known "H" or "Y" pattern. We did not consider the olfactory sulcus in any of the crania due to the distortion caused by the impression from the cribriform plate.

We clearly identified the fronto-orbital sulcus of the frontal lobe (sensu Ono et al., 1990) in 75% of LHs and 60% of RHs (Figs. 2-3). We identified the fronto-marginal sulcus in 85% of LHs and in 100% of RHs (Fig. 2h).

We clearly identified the superior frontal sulcus in 95% of LHs and in 90% of RHs. We observed connections between the superior frontal sulcus and the fronto-marginal sulcus (n=12), middle frontal sulcus (n=7) and the precentral sulcus (n=2) (Figs 2-3).

We identified the middle frontal sulcus in 90% of LHs and in 75% of RHs. We mostly observed a segmental pattern (n=13) (Fig. 3a).

We identified impressions of the inferior frontal sulcus in 85% of LHs and in 90% of RHs. We observed up to seven side branches in one cranium, some of which extended onto the orbital surface and others connecting with the middle frontal sulcus (Fig. 3r). The inferior frontal sulcus was not clearly defined in five crania; which may be due to distortion caused by overlaying blood vessels (Fig. 3f). We could only observe the precentral sulcus in 35% of the LHs and 40% of the RHs (Figs 2-3). We clearly identified the Sylvian fissure in 95% of LHs and 85% of RHs. We could only identify the anterior horizontal ramus and ascending ramus in eight LHs and four RHs (Figs 2-3).

Parietal lobes

We identified the central sulcus in 55% of LHs and 50% of the RHs (Fig. 2). We observed the postcentral sulcus in 20% of LHs and 15% of RHs (Fig. 2a).

We identified the intraparietal sulcus on the LH of six crania and on the RH of three crania (Fig. 2a). We identified the transverse occipital sulcus, or posterior branch of the intraparietal sulcus (Ono et al., 1990), in 70% of LHs and 55% of RHs (Fig. 2e-f).

Occipital lobes

We identified the lateral occipital sulcus in 50% of LHs and 60% of RHs, as a small sulcus along the most lateral and inferior border of the occipital lobe. We identified fragments of the lunate sulcus in

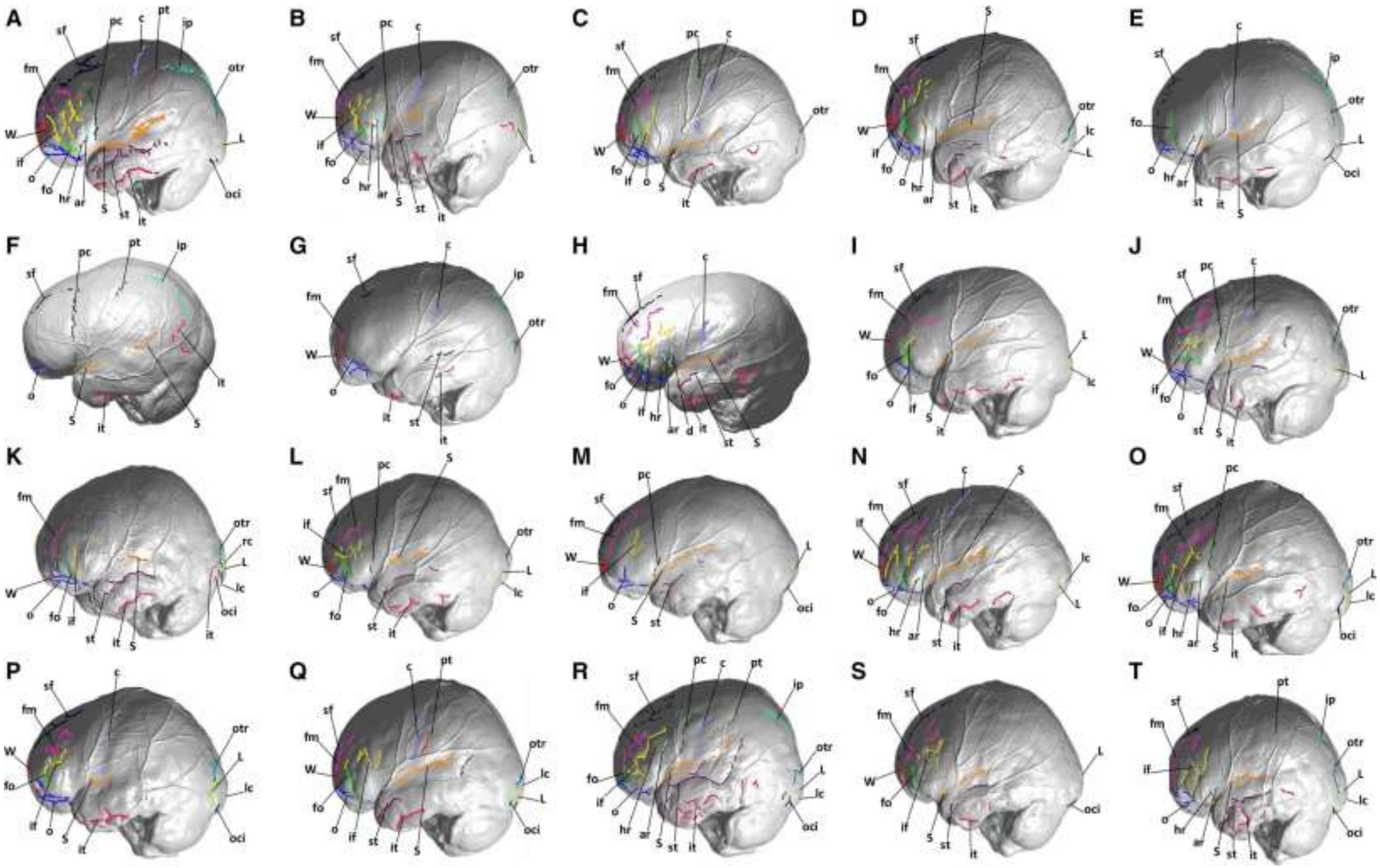

Figure 2. Sulcal imprints observed on the left hemisphere of 20 individuals. ar = ascending ramus, c = central, d = diagonal, W = fronto-marginal, fo = fronto-orbital, hr = anterior horizontal ramus, if = inferior frontal, ip = intraparietal, it = inferior temporal, L = Lunate, lc = lateral calcarine, fm = middle frontal, o = orbital, oci = inferior/lateral occipital, otr = transverse occipital, pc = precentral, pt = postcentral, rc = retro-calcarine, S = Sylvian fissure, sf = superior frontal, st = superior temporal.

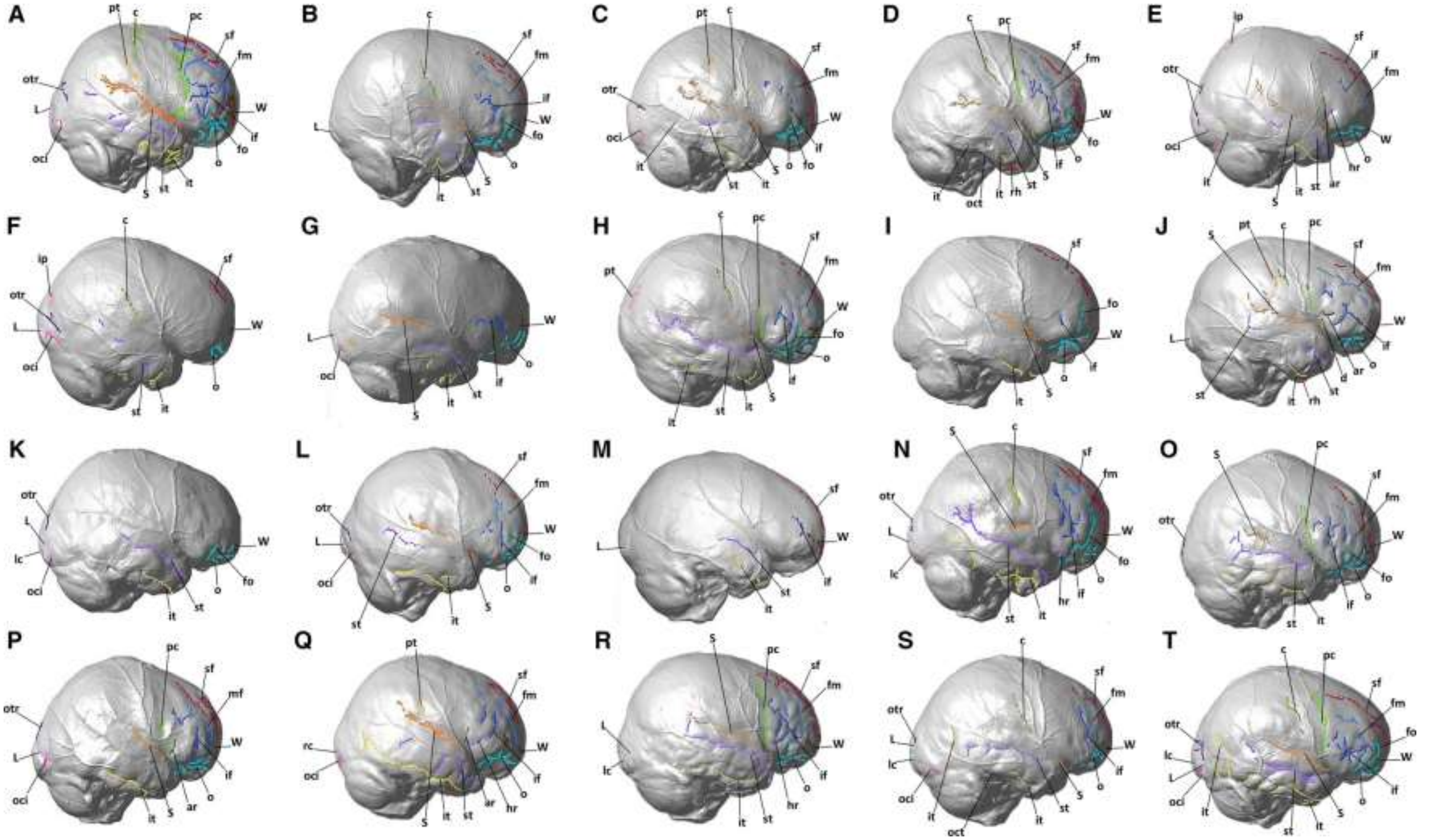

Figure 3. Sulcal imprints observed on the right hemisphere of 20 individuals. ar = ascending ramus, c = central, d = diagonal, W = frontomarginal, fo = fronto-orbital, hr = anterior horizontal ramus, if = inferior frontal, ip = intraparietal, it = inferior temporal, L = Lunate, lc = lateral calcarine, fm = middle frontal, o = orbital, oci=inferior/lateral occipital, oct = occipitotemporal, otr = transverse occipital, pc = precentral, pt = postcentral, rc = retro-calcarine, rh = rhinal, S = Sylvian fissure, sf = superior frontal, st = superior temporal.

80% of LHs and 70% of RHs (Figs 2-3). We could also identify the lateral calcarine sulcus (LHs= 55%; RHs= 20%) and retro-calcarine sulcus (LHs= 20%; RHs= 10%), medial to the lunate sulcus (Fig. 4).

Temporal lobes

We observed the superior temporal sulcus in 75% of LHs and 90% of RHs, with the anterior segment clearly imprinted. We observed the inferior temporal sulcus in 100% of LHs and 95% of RHs with most crania exhibiting an anterior extension to the temporal pole (Figs 2-3).

When observing the basal surface of the temporal lobe, we identified the rhinal sulcus in 25% of LHs and 60% of RHs. The rhinal sulcus is frequently subject to a substantial degree of distortion due to the presence of the middle meningeal artery. We observed similar results for the collateral sulcus (LHs= 25%; RHs= 0%) and the occipitotemporal sulcus (LHs= 35%; RHs= 45%).

Left vs. Right hemisphere

We noted left-right hemisphere asymmetry for the lateral calcarine sulcus (LHs= 55%; RHs= 20%, $p<0.05$), the rhinal sulcus (LHs= 25%; RHs= 60%, $p<0.05$) and the collateral sulcus (LHs= 20%; RHs= 0% $p<0.05$) (Fig. 5).

Male vs. Female

We did not observe any differences in sulcal patterns between male and female crania ($p>0.05$). In general, we more readily identified sulci in female (~3% more frequent) crania compared to male crania (Fig. 6). We saw sex differences in the RHs in the impression of the fronto-orbital sulcus (M= 40%; F= 80%), precentral sulcus (M= 50%; F= 30%), transverse occipital sulcus (M= 40%; F= 70%), lunate sulcus (M= 80%; F= 60%), lateral calcarine (M= 30%; F= 10%), superior temporal sulcus (M= 80%; F= 100%), rhinal sulcus (M= 50%; F= 70%), occipitotemporal sulcus (M= 30%; F= 60%) and ascending ramus (M= 30%; F= 10%). We noted sex differences in the LHs in the impression of the precentral sulcus (M= 20%; F= 50%), postcentral sulcus (M= 30%; F= 10%), intraparietal sulcus (M= 40%; F= 20%), transverse occipital (M= 60%; F= 80%), lunate sulcus (M= 70%; F= 90%), retro-calcarine sulcus (M= 30%; F= 10%), anterior horizontal ramus (M= 30%; F= 50%) and ascending ramus (M= 30%; F= 50%).

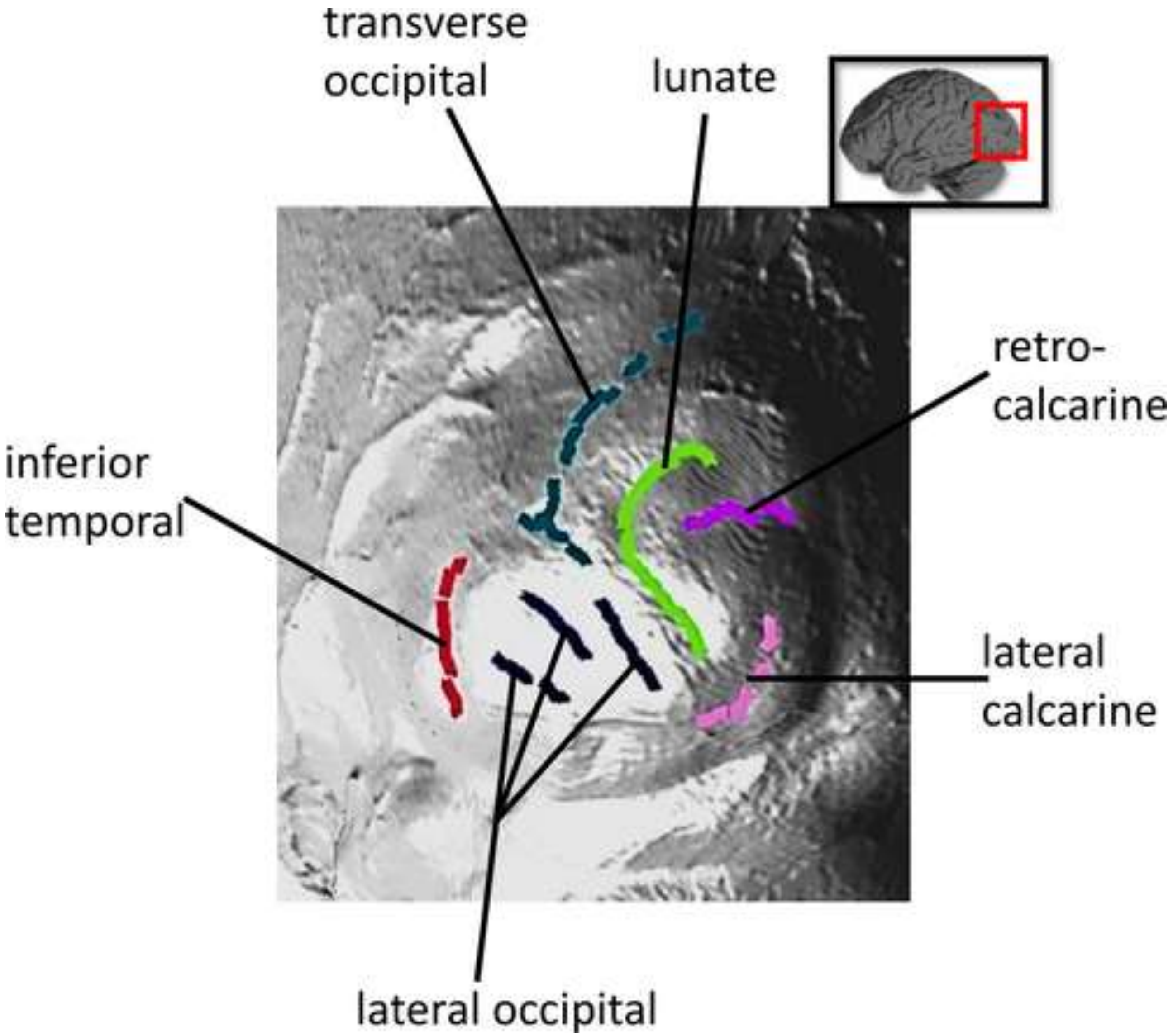

Figure 4. Occipital view showing the lunate sulcus impression in one selected individual..

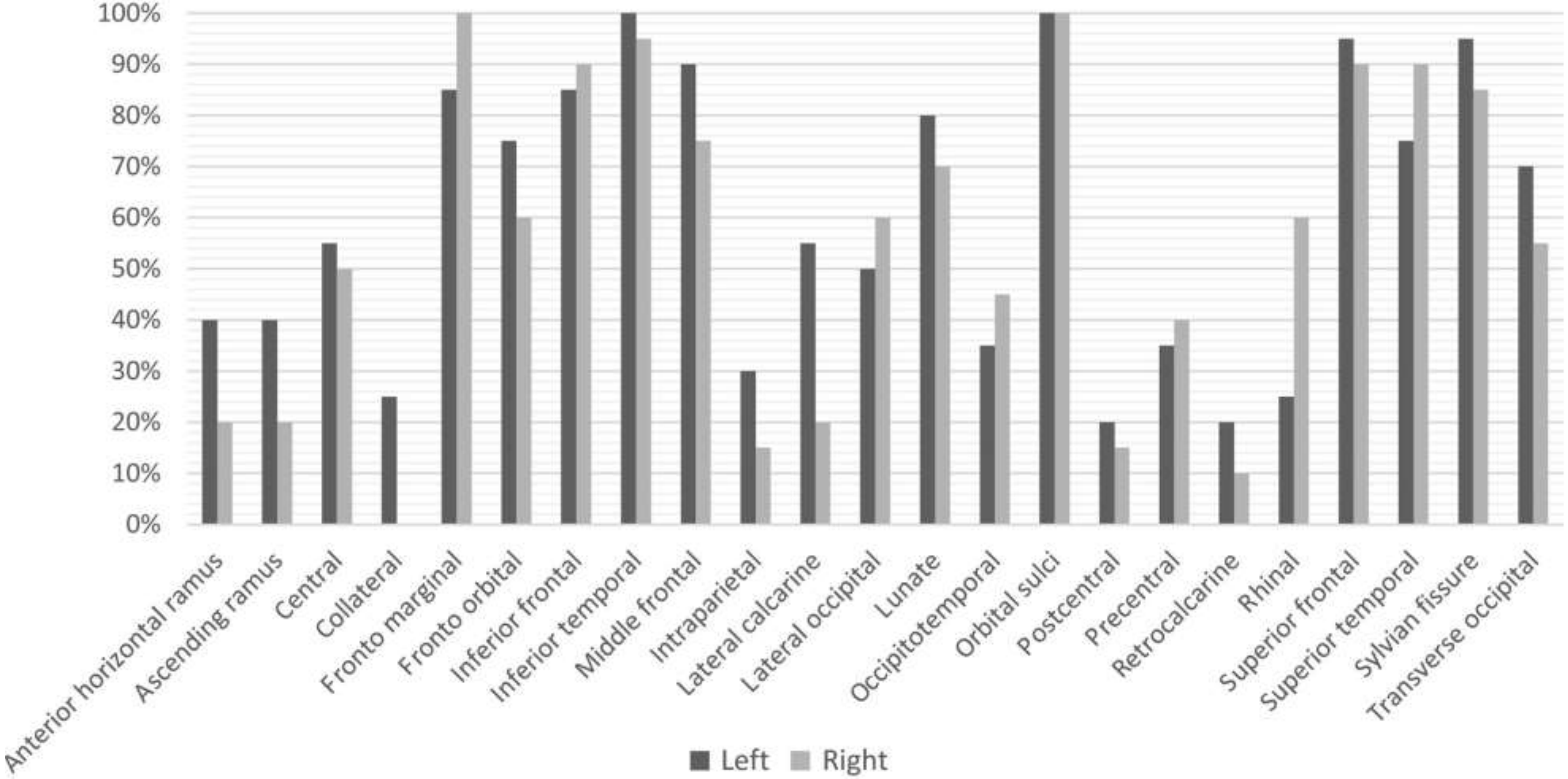

Figure 5. Frequency of sulci observed in the left and right hemispheres of human endocasts..

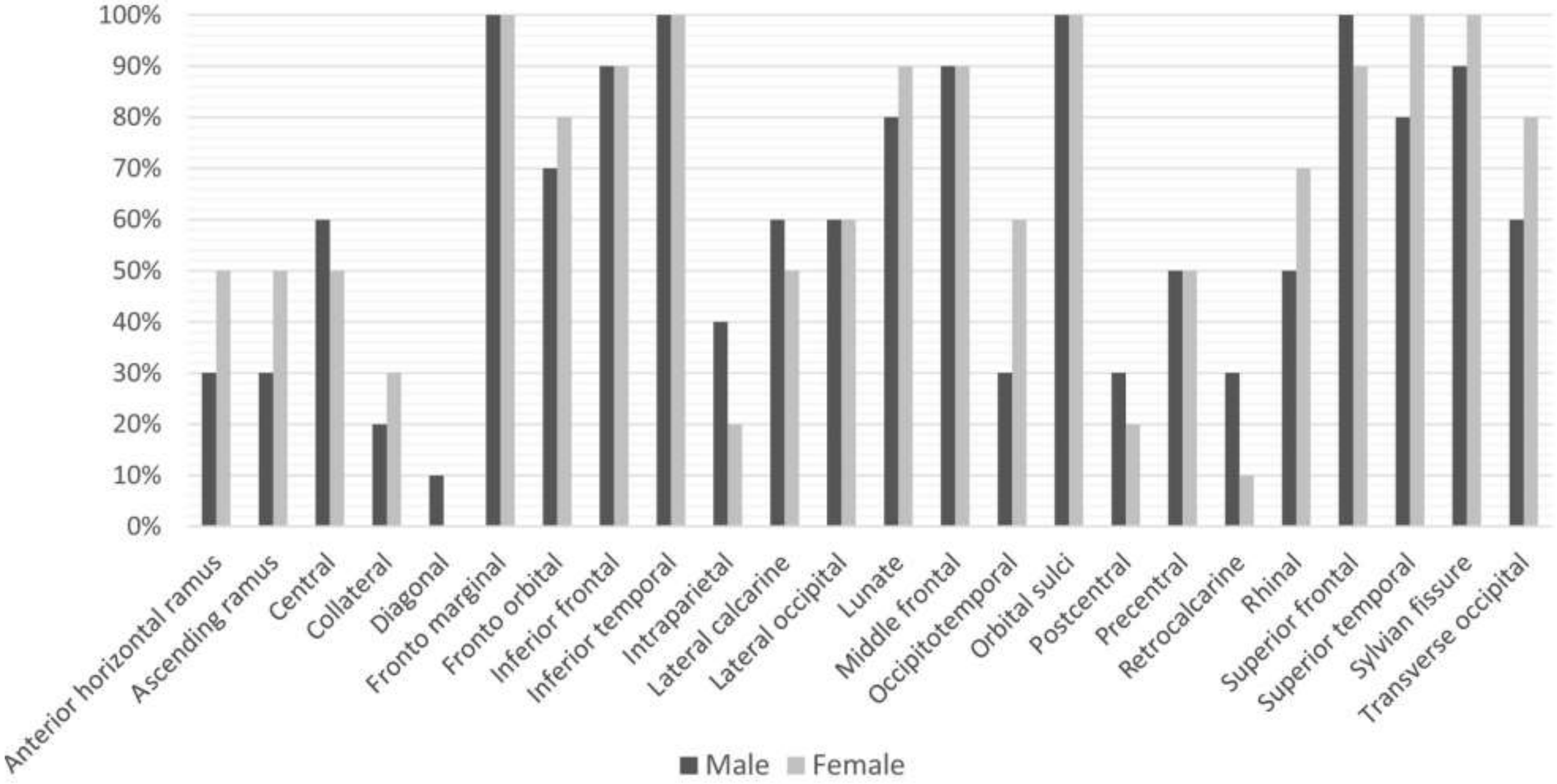

Figure 6. Frequency of sulci observed in male and female human endocasts..

Discussion

Sulci identification

In this study, we used high definition x-ray microtomography to explore variation in sulcal patterns in 20 extant human endocasts. Using this method, we could reliably identify the orbital, temporal and frontal sulci and the Sylvian fissure in more than 80% of the endocasts. Descriptions of frequency and configuration of the orbital sulci, fronto-marginal, fronto-orbital, and lateral occipital sulci are consistent with previous descriptions of brain sulci (Ono et al., 1990; Chiavaras and Petrides, 2000; Iaria and Petrides, 2007). We were able to identify both the fronto-marginal and fronto-orbital sulci on the endocasts, despite identification of these features in humans being a rather controversial topic (see Connolly, 1950; Falk et al., 2018; Petrides and Pandya, 2012).

We could only identify the precentral sulcus in fewer than half of the individuals, this may be due to distortion by the anterior bregmatic branch of the middle meningeal vessels (Bruner et al., 2018). Similarly, we could not reliably identify the postcentral sulcus, which may be due to the complex branching networks of blood vessels covering this area. Cerebrospinal fluid and blood vessels usually fill the main sulci delineated functional areas and may not reproduce well on endocasts (Zollikofer and León, 2013). Additionally, the transverse occipital sulcus can easily be misidentified on endocasts due to the tendency of the intraparietal sulcus to terminate posteriorly close to the lambdoid suture, which frequently creates phantom markings on the endocast.

Various morphological and functional differences have been noted between male and female brains (Holloway and de Lacoste, 1986; Zilles et al., 2001; Liu et al., 2010; Glezerman, 2016). While morphological differences may exist between male and female brains, these differences may not extend to sulcal patterns or sulcal imprint visibility (this study). We noted significant asymmetry between the left and right hemispheres, when identifying the lateral calcarine sulcus, rhinal sulcus and collateral sulcus. The rhinal and collateral sulcal imprints are frequently misidentified on endocasts due to their vulnerability to distortion imposed by localised bony elements, which may also explain the perceived asymmetry. The lateral calcarine sulcus may also be asymmetrical (LHs= 55%; RHs= 20%), due to distortion occasionally created by overlay of the right dominant dural venous sinus groove (García-Tabernero et al., 2018).

Minh and Hamada (2017) found that the expression of sulcal imprints on endocasts of Japanese macaques decreased with age, and other studies have proposed that no new brain expansion occurs in older individuals (Liu et al., 2010), making it harder to identify sulcal imprints in crania of older individuals. We excluded age as a variable due to sample size constraints.

Implications for palaeoneurological studies

We identified sulci delimiting crucial cortical areas in the brain in more than one third of the crania, including the lunate sulcus and the anterior horizontal and ascending rami of the Sylvian fissure, which are involved in critical debates in human palaeoneurology (Sherwood et al., 2008; Falk, 2014). In particular, frontal sulci delimit crucial functional areas in neuroscience, including language, memory and motor functions (Petrides, 2005; Petrides and Pandya, 2012). The horizontal and the ascending rami of the Sylvian fissure, which we identified in nearly half of the samples on the LH, are suggested to have emerged with the genus *Homo* but the recent discovery of a non-human hominin endocast with an intermediate pattern between the ape-like and human-like patterns suggests a more complex scenario (Falk, 1983; Tobias, 1987; Carlson et al., 2011; but see discussion in Falk et al., 2018) . The middle frontal sulcus is also of particular interest in palaeoneurology due to its presence in non-human hominin endocasts and its relationship to the dorsolateral prefrontal cortex, which is involved in executive functions (Connolly, 1950; Van Essen, 2007; Falk, 2014). From a comparative perspective, the rostral part of the middle frontal sulcus is considered to be a homolog of the sulcus rectus in monkeys, while the caudal part is unique to humans, and is associated with the expansion of the frontal lobe (Eberstaller, 1890; Connolly, 1950; Falk, 2014).

The lunate sulcus has been extensively described in association with human brains and is highly variable (Smith, 1903; Connolly, 1950; Ono et al., 1990; Duvernoy et al., 1999; Holloway et al., 2004; Allen et al., 2006). Although our sample size was small, the lunate sulcus was observed in 75% of the crania, which is more than the 62% in Ono et al. (1990) and 51.8% in Allen et al. (2006). Larger sample sizes (studied using similar methods or other populations) could shed more light on this matter. We observed the lunate sulcus anterior to the caudal pole of the occipital lobe as fragmented, vertically orientated impressions, usually depicting a curve (Fig. 4). In one case we could visualize a lunate sulcus as described by Allen et al. (2006), traversing a substantial portion of the lateral surface of the posterior portion of the occipital lobe. As observations were made on endocasts and not cerebral surfaces, we are not able to comment whether this impression is made by a ‘true’ or a composite lunate sulcus, however, humans generally do not have ‘true’ lunate sulci (Connolly, 1950; Allen et al., 2006; Alves et al., 2012). Nevertheless, our ability to detect the lunate sulcus (or at the very least, fragments thereof) is important due to the past and ongoing debate regarding the homology of the lunate sulcus in humans and apes and the identification of the lunate sulcus in early hominin endocasts (Falk, 1980b; Holloway, 1981; Falk, 2014). The caudal placement of the lunate sulcus in hominins older than 2 million years may indicate early changes in the occipital lobes, probably related to the expansion of the parietal association cortex and a mosaic evolution of the cerebral areas (Falk, 1980b; Falk, 2014; Holloway, 1981; Holloway, 2001).

We were also able to identify the lateral calcarine sulcus more often than previously reported, namely in half of the crania (see Connolly, 1950), whereas Alves and co-authors (2012) identified a calcarine fissure on the superolateral surface of the brain at the level of the lateral occipital sulcus in 40% of brains. The size of the calcarine sulcus and its association with the primary visual cortex was recently discussed in Neanderthal brain endocasts, which revealed potential differences in visual capacity when compared to *Homo sapiens* (García-Tabernero et al., 2018).

In conclusion, our semi-automatic sulcal detection approach allowed us to identify sulci involved in crucial functions and long-standing debates in palaeoanthropology. Despite the automatic sulci detection applied in this study, the identification of sulci by human observers may represent a potential bias that should be taken into account when interpreting sulcal imprints in the fossil record. Accordingly, this atlas will subsequently be used to construct a statistical model documenting sulcal variation in extant humans and, ultimately, to develop a protocol for the automatic recognition of cerebral imprints in fossil hominin endocasts, which will aid investigations pertaining to cortical evolution in the fossil record (Beaudet, 2017).

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