Published in final edited form as:
Neuroimage. 2018 June ; 173: 604–609. doi:10.1016/j.neuroimage.2018.02.040.

On object selectivity and the anatomy of the human fusiform gyrus

Kevin S. Weiner[a,b,*], **Vaidehi S. Natu**[c,d], and **Kalanit Grill-Spector**[d,e]

[a]Department of Psychology, University of California, Berkeley, Berkeley, CA 94720, USA

[b]Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA 94720, USA

[c]Department of Neurological Surgery, University of Texas Southwestern Medical Centre, TX 75390, USA

[d]Department of Psychology, Stanford University, Stanford, CA 94305, USA

[e]Stanford Neurosciences Institute, Stanford University, Stanford, CA 94305, USA

Abstract

pFs is a functionally-defined region in the human brain that is involved in recognizing objects. A recent trend refers to pFs as the *posterior fusiform sulcus*, which is a neuroanatomical structure that does not exist. Here, we correct this mistake. To achieve this goal, we first recount the original definitions of pFs and then review the identification of sulci within and surrounding the fusiform gyrus (FG) including the mid-fusiform sulcus (MFS), which is a tertiary sulcus within the FG. We highlight that tertiary sulci, such as the MFS, are often absent from brain atlases, which complicates the accurate localization of functional regions, as well as the understanding of structural-functional relationships in ventral temporal cortex (VTC). When considering the location of object-selective pFs from previously published data relative to the sulci surrounding the FG, as well as the MFS, we illustrate that (1) pFs spans several macroanatomical structures, which is consistent with the original definitions of pFs (Grill-Spector et al., 1999, 2000), and (2) the topological relationship between pFs and MFS has both stable and variable features. To prevent future confusion regarding the anatomical location of functional regions within VTC, as well as to complement tools that automatically identify sulci surrounding the FG, we provide a method to automatically identify the MFS in individual brains using FreeSurfer. Finally, we highlight the benefits of using cortical surface reconstructions in large datasets to identify and quantify tertiary sulci compared to classic dissection methods because the latter often fail to differentiate tertiary sulci from shallow surface indentations produced by veins and arteries. Altogether, we propose that the inclusion of definitions and labels for tertiary sulci in neuroanatomical atlases and neuroimaging software packages will enhance understanding of functional-structural relationships throughout the human brain.

---

[*]Corresponding author. Department of Psychology, University of California, Berkeley, Berkeley, CA 94720, USA. kweiner@berkeley.edu (K.S. Weiner).

Conflicts of interest
None.

Keywords

Cortical folding; Inferior temporal cortex; Fusiform gyrus; Mid-fusiform sulcus; High-level visual cortex; pFs

Introduction

Functional magnetic resonance imaging (fMRI) studies that examine the neural underpinnings of object recognition in humans localize the lateral occipital complex (LOC; Malach et al., 1995). The LOC is a swath of cortex activated more strongly to images of objects compared to scrambled versions of these objects. The LOC has been parcellated into anatomically and functionally distinct occipital and ventral temporal components (Grill-Spector et al., 1999, 2000). Researchers agree on the anatomical definition and nomenclature of the occipital component (lateral occipital – LO). However, the ventral-temporal component has been referred to in many ways: pFs (Grill-Spector et al., 2000), vTO (James et al., 2002), PF (Halgren et al., 1999), LOa (Grill-Spector et al., 1999), vLOC (Sorger et al., 2007; Drucker and Aguirre, 2009), and there are likely others. Of these labels, *pFs* is the most commonly used. A recent trend defines this acronym as the posterior fusiform sulcus.[1] This is puzzling because the posterior fusiform sulcus is an anatomical structure that does not exist. Therefore, the goal of the present paper is to correct this mistake and prevent it from being perpetuated.

To achieve our goal, this paper is divided into five main sections. First, we discuss the original definition of the pFs as a functional region and highlight that this definition does not reference a posterior fusiform sulcus. Second, we review recent definitions of sulci surrounding the fusiform gyrus (FG) and the mid-fusiform sulcus (MFS), which is located within the FG. We also provide a way to automatically identify the MFS in individual brains to prevent future confusion between the MFS and sulci that surround the FG. Third, we highlight that tertiary sulci,[2] such as the MFS, are more accurately identified and quantified using cortical surface reconstructions from a large sample size compared to classic postmortem dissection methods in a small set of brain specimens. Fourth, we discuss how accurate characterization of the MFS, FG, and surrounding sulci illustrates that functionally-defined pFs spans multiple macroanatomical structures with stable and variable features across individuals. Fifth, due to its extensive use in the literature, we propose to continue to refer to this object-selective region as pFs, but we underscore that pFs is an acronym that stands for the posterior fusiform gyrus. Finally, a theme that propagates throughout the manuscript is the importance of including definitions and labels for tertiary sulci in neuroanatomical atlases and neuroimaging software packages. We believe that this will not

---

[1] Specifically, from our research, there are nearly two dozen papers (and likely more) in prominent journals authored by well-respected research groups that use this label starting around 2005 and appearing as recently as August 2017. However, we do not include these references here as the point of this paper is not to single out particular research groups, but instead, to prevent this misrepresentation from being perpetuated.

[2] Primary, secondary, and tertiary sulci form during different gestational periods in which primary sulci (sometimes referred to as fissures) form first and tertiary sulci form last. The former are considered the most similar from one person to the next, while the latter are considered the most variable and hard to quantify. For example, Tamraz and Comair (2006) write there are “Various individual variations” (Pg. 65) for tertiary sulci in the occipital lobe and that there is an “absence of consensus” (Pg. 65) regarding their definition.

only prevent mischaracterization of tertiary sulci in future studies, but will also enhance accurate quantifications of the correspondence between macroanatomy and functional representations throughout the brain.

The origin of pFs

In 1995, the LOC was discovered (Malach et al., 1995), and in 1999, it was divided into two functionally and anatomically distinct components (Grill-Spector et al., 1999). A caudal-dorsal component was differentiable from an anterior-ventral component based on size and position sensitivity in which the latter was more invariant to changes in object position compared to the former (Grill-Spector et al., 1999). Since then, the distinction between two functionally and anatomically distinct components of the LOC has been widely implemented. The caudal component, LO, is defined based on anatomical (within lateral occipital cortex) and functional (posterior to MT) boundaries (Malach et al., 1995).

However, the labeling of the ventral component has been less consistent. In 1999, Grill-Spector and colleagues first defined area PF/LOa as follows: “The anterior–ventral subdivision (PF/LOa, yellow arrows in Figure 6a and LOa in Figure 6c) was located within the fusiform gyrus anterior to areas V4/V8, extending into the occipitotemporal sulcus.” (Pg. 193). We now note that as we prepared that study for publication, we originally referred to this region with one label, LOa. However, during the same time period of our paper, Halgren et al. (1999) identified a functional region selective for faces in a similar location macroanatomically, as well as topologically relative to visual field maps. As they referred to this region as ‘PF,’ and our experiments also used images of faces, we incorporated PF with LOa to generate the PF/LOa label.

Just one year later, we re-named PF/LOa as pFs (Grill-Spector et al., 2000). Here is the direct text of that re-naming: “The anterior-ventral subdivision in the posterior to mid-fusiform gyrus (pFs; orange in Figure 2) is anterior and lateral to areas v4/v8, extending into the occipitotemporal sulcus.” (Pg. 837). While we did not include the original motivation for this re-labeling in the paper, it was because we thought that ‘PF’ was ambiguous and could be interpreted by readers as referring to ‘prefrontal.’

Despite the change in nomenclature between the two years, the functional and anatomical delineation of pFs is consistent. Of note, we emphasize that the original definitions do not reference a posterior fusiform sulcus. Instead, the commonality between the two original definitions describes pFs as being located on the fusiform gyrus extending into the occipitotemporal sulcus. We revisit this shared commonality with recently published data (Natu et al., 2016) later on in the manuscript. Now that we have clarified the origin of pFs, we turn to the next section in which we review the definitions of sulci within and surrounding the FG in order to guide researchers examining the structural-functional organization of high-level visual cortex.

Sulci within and surrounding the fusiform gyrus

The fusiform gyrus (FG) is a relatively large anatomical structure located in the ventral portion of the temporal lobe. The FG is hominoid-specific, which means that humans and non-human hominoids such as chimpanzees have an FG, but non-human primates such as macaques do not have an FG (Weiner and Zilles, 2016). The FG is approximately 5 cm in length and it is bounded laterally, medially, and posteriorly in a consistent manner by the following three sulci: (1) laterally, the FG is bounded by the occipito-temporal sulcus (OTS), (2) medially, the FG is bounded by the collateral sulcus (CoS), and (3) posteriorly, the FG is bounded by the posterior transverse collateral sulcus (ptCoS; Ono et al., 1990). On cortical surface reconstructions, the ptCoS often appears as a hook and can be considered as a landmark separating the ventral portions of the occipital and the temporal lobes (Fig. 1A). In some cases, the anterior boundary of the FG is defined by another transverse component of the CoS known as the anterior transverse collateral sulcus (atCoS; Ono et al., 1990). Together, the OTS, atCoS, CoS, and ptCoS contribute to the spindle-like appearance of the FG, which is the etymology of its namesake: 'fusiform' is Latin for spindle (Huschke, 1854; Weiner and Zilles, 2016). These sulci are identifiable in most brains, and therefore, they can be automatically defined on an average cortical surface, such as the one available in FreeSurfer (Destrieux et al., 2010, Fig. 1A).

In addition to these sulci surrounding the FG, there is also a longitudinal sulcus that bisects the FG into lateral and medial partitions. Originally identified as the *sulcus sagittalis gyri fusiformis* by Gustav Retzius in 1896 (Retzius, 1896; Weiner and Zilles, 2016), more recent cognitive neuroscience studies refer to this sulcus as the mid-fusiform sulcus, or MFS (Puce et al., 1996; Nobre et al., 1998; Allison et al., 1999; Nasr et al., 2011; Weiner and Grill-Spector, 2010; Weiner et al., 2014; Weiner and Zilles, 2016). The MFS has both stable and variable morphological features. In terms of stability, the MFS is identifiable in all brains and is consistently about half as deep compared to the OTS and CoS (Weiner et al., 2014). In terms of variability, the MFS varies in its fractionation, morphology, and length. Previous data from our lab indicates that in nearly half of the hemispheres examined (48.55% of 138 hemispheres), the MFS appears as a single longitudinal sulcus independent of the OTS and CoS in both children and adults (Weiner et al., 2014). In the other half of the hemispheres (51.45%), the MFS varies in terms of its fractionation, as well as its intersection with the OTS and CoS. The MFS length also significantly varies – ranging from 2.0 mm to 56.3 mm (Weiner et al., 2014; Nasr et al., 2011). This difference in length generates extensive inter-individual variability in the location of the posterior tip of the MFS. In contrast, the anterior tip of the MFS relative to other macroanatomical structures is stable across individuals. For example, the anterior tip of the MFS consistently aligns with the posterior end of the hippocampus (Grill-Spector and Weiner, 2014).

Despite the fact that the MFS is identifiable in every brain, it can be tricky to identify the MFS in individual hemispheres. However, present neuroanatomical atlases and neuroimaging software packages do not include the MFS, which could help identification in these tricky cases. Thus, to guide researchers, we provide a definition of the MFS as a label on the FreeSurfer average cortical surface (Fig. 1A). This label can be back-projected to individual cortical surfaces using cortex-based alignment (Dale et al., 1999; Fischl et al., 1999), which results in accurate identification of the MFS in the brains of individual subjects despite differences in morphology mentioned above (Fig. 1B). For instance, despite differences in fractionation (S1 and S2) or in length (S3–S5), the MFS back-projected from the FreeSurfer average cortical surface accurately identifies the MFS from the OTS and the CoS in individual hemispheres. This label can serve as a guide for researchers examining the structural-functional organization of high-level visual cortex – especially in those cases in which the MFS is hard to identify.

Taken together, there are four sulci that consistently bound the perimeter of the FG (posterior: ptCoS; lateral: OTS; anterior: atCoS; medial: CoS) and one sulcus (MFS) that longitudinally bisects the FG. Researchers do not need to be anatomists to identify these sulci as the four former sulci are included within the FreeSurfer software package (which is freely available) and the latter sulcus is available for download with this paper (https://github/VPNL/MFS). We are hopeful that the definition of the MFS will be included in future FreeSurfer releases. Using cortex-based alignment, each sulcus can be back-projected to individual hemispheres, which (a) results in accurate identification of these five sulci within and surrounding the FG and (b) will help prevent future confusion in labeling sulci and functional representations (such as pFs) in ventral temporal cortex.

Cortical surface reconstructions and large datasets identify and quantify tertiary sulci better than classic dissection methods

While we use the MFS as an example, the exclusion of tertiary sulci from commonly used brain atlases and neuroimaging software packages is a general concern for the field. The exclusion of tertiary sulci from neuroanatomical reference sources likely has occurred for at least two main reasons: (1) historically, neuroanatomists had a hard enough time agreeing on the definition of primary sulci that tertiary sulci were often considered too variable to quantify (Weiner and Zilles, 2016) and (2) in classic dissection methods of postmortem brains (which often serve as the foundation for modern brain atlases), the variability of tertiary sulci is exacerbated by the difficulty to distinguish tertiary sulci from indentations produced by veins and arteries on the outer surface of the cerebrum (Fig. 2B-left). On the contrary, tertiary structures are clearly visible on cortical surface reconstructions from MRI images and not affected by these vessel indentations. This is because these reconstructions are generated from segmentations of the brain at the boundary between gray and white matter in which definitions of tertiary sulci are not occluded by these vessels (Fig. 2B-right).

Examining and quantifying tertiary sulci on cortical surface reconstructions with modern MRI tools rather than with classic dissection methods has not only improved the understanding of sulcal patterning within the FG, but also generalizes to additional tertiary sulci. For example, contrary to classic dissection methods that identified one longitudinal sulcus within the lingual gyrus (Huschke, 1854), a recent MRI study identified two transverse sulci (Mangin et al., 2015). This latter finding was replicated and – importantly – improved understanding of structural-functional organization in ventral temporal cortex in over 500 participants (Weiner et al., 2017a). Concomitantly, if you are interested in understanding the structural-functional organization within your favorite part of the brain, but cannot find what appears to be either a small, shallow sulcus or even a branch (or ramus) of a sulcus within neuroanatomical atlases or neuroimaging software packages, it may be for the two reasons mentioned in the prior paragraph. Thus, what you may be observing, but cannot find in reference atlases, may be worth quantifying. Luckily, we are in an age of big data – and data sharing – that provides us with thousands of MRI brain images at our fingertips, which makes the quantification of tertiary sulci even more feasible since the data have already been acquired. Indeed, the human connectome project (www.humanconnectomeproject.org), together with modern software tools that enable accurate cortical surface reconstructions (http://www.freesurfer.net/; www.brainvoyager.com) and morphological analyses of gyri and sulci (http://brainvisa.info/web/index.html), can significantly advance accurate identification and analyses of tertiary sulci. Once these tertiary structures are identified and quantified using modern tools, it will be important to assess if deviations between cortical folding patterns observed in postmortem specimens and in-vivo cortical surface reconstructions are artificial or meaningful (Fig. 2). Altogether, the combination of modern and classic approaches will further advance understanding of stable and variable features of tertiary sulci throughout the brain and prevent mischaracterization of tertiary sulci in future studies.

pFs traverses several macroanatomical structures and is lateral to the MFS

To bring this Comments and Controversies paper full circle, using previously published data (Natu et al., 2016, Fig. 3; 12 subjects, ages = 22–36, $N_{females} = 4$), we have projected the functionally-defined pFs to cortical surface reconstructions from each of the 12 adults who participated in that study. To remind the reader, the first studies differentiating pFs from LO (Grill-Spector et al., 1999, 2000) identified pFs on the posterior FG extending into the OTS. This definition still holds nearly two decades later. Indeed, in each of the 12 individual subjects, pFs extends from the posterior FG into the OTS and sometimes extends over to the inferotemporal gyrus (ITG). Additionally, there are both stable and variable topological features between the pFs and the MFS. In terms of stability, pFs is consistently lateral to the MFS in all 12 subjects. In terms of variability, pFs can be (1) adjacent to the MFS (S1–4, S7–S9, S11–12) or (2) cortically distant from the MFS – either laterally (S5) or postero-laterally (S6 and S10). Immediately relevant for the present discussion is the fact that a subset of the cases in (1) either abut (S1–S4, S9) or overlap (S8) the posterior extent of the MFS.

Thus, despite the focality of its name, pFs actually traverses multiple macroanatomical structures and there is no single landmark that serves as an identifier for the location of pFs in individual subjects. To accommodate this fact, our solution over the years has been to include multiple anatomical structures in the name when referring to this region (e.g. pFus/OTS). This is not an ideal solution as (1) it has resulted in 6 different names for this same object-selective region across studies from our lab alone (Grill-Spector, 2003a, 2003b, 2008; Grill-Spector et al., 1999, 2000, 2001, 2006; Grill-Spector and Malach, 2001, 2004; Grill-Spector and Weiner, 2014; Sayres and Grill-Spector, 2006, 2008; Vinberg and Grill-Spector, 2008; Natu et al., 2016), and (2) referring to the same brain region with 6 different names is not good practice for reproducible science. However, we also note that describing the anatomical location of a brain region based on a non-existent neuroanatomical structure prohibits scientific reproducibility. We also underscore that while it is possible that previous studies used “posterior fusiform sulcus” to refer to the posterior extent of the MFS, we believe it is unlikely as these studies did not describe or identify a specific sulcus to which they were referring. Instead, it is more likely that researchers assumed that the “s” in “pFs” stood for sulcus and that this assumption was perpetuated. In actuality, as described in the beginning of this paper, “Fs” stands for fusiform. Further, as the posterior extent of the MFS is the least stable morphological feature of the MFS (Weiner et al., 2014; Grill-Spector and Weiner, 2014) and pFs has a variable topological relationship with the MFS, we suggest that labelling a brain region according to the least stable, and least predictive, morphological feature of an anatomical structure also does not generate good practice to promote reproducibility.

As such, we propose that going forward, the easiest solution is to keep the acronym pFs when referring to this object-selective region, but to accurately define pFs as an acronym that stands for the posterior fusiform gyrus (while acknowledging that pFs extends to other macroanatomical structures as well). The reader may wonder why we do not suggest an alternative name for this functional region – especially because we have suggested alternative names for other regions, such as those selective for faces (Weiner and Grill-Spector, 2010, 2012), bodies (Weiner and Grill-Spector, 2011), and places (Weiner et al., 2017a). We emphasize that in each of these prior cases, functional regions are tightly coupled to macroanatomical structures. For example, mFus-faces and pFus-faces are reliably identifiable relative to cortical folding of the FG, as well as represent functionally (Weiner et al., 2010; Kay et al., 2015) and cytoarchitectonically (Weiner et al., 2017b) distinct portions of the FG that are behaviorally and developmentally (Gomez et al., 2017) relevant. However, the structural-functional coupling between object selectivity and macroanatomical structures in VTC seems to be more variable than in these prior cases and has yet to be explicitly quantified. We are of course open to a different name for pFs, but are firm believers that extensive quantifications are prerequisites for renaming and therefore, leave that possibility open for future studies.

That being said, we underscore that there is still much to study regarding the relationship between the pFs and other nearby anatomical structures, as well as functionally-defined regions that are in the cortical neighborhood of pFs. For instance, important topics for future studies will be (1) to directly compare the anatomical location of pFs relative to regions selective for other domains such as words (Cohen et al., 2000; Ben-Shachar et al., 2007), bodies (Schwarzlose et al., 2005; Peelen and Downing, 2005; Weiner and Grill-Spector, 2010), and faces (Kanwisher et al., 1997; Weiner and Grill-Spector, 2010), as well as retinotopic maps (Brewer et al., 2005; Kolster et al., 2010) and (2) to examine the effect of methodological parameters, stimuli, and task on the localization of pFs relative to cortical folding and these nearby functional regions. Such studies will continue to improve our understanding of object selectivity and the anatomy of the human fusiform gyrus relative to the functional-structural organization of the surrounding ventral temporal cortex.

Conclusion

In sum, the goal of this *Comments and Controversies* paper was to correct a mistake in the literature that refers to an object-selective region, pFs, as being located within the posterior fusiform sulcus. To correct this mistake, we have clarified the sulci located within and surrounding the FG. In doing so, we have shown that the posterior fusiform sulcus does not exist. Using recently published data (Natu et al., 2016), we have also illustrated that (1) pFs spans several macroanatomical structures, which is consistent with the original definitions of pFs (Grill-Spector et al., 1999, 2000) and (2) the topological relationship between pFs and the MFS has both stable and variable features. To prevent future mistakes – similar to the one that has been perpetuated with pFs – from happening to other regions within or outside occipito-temporal cortex, we believe that it is necessary to incorporate tertiary sulci into neuroanatomical atlases and neuroimaging software packages. As a first step toward achieving this goal, we share the definition of the MFS aligned to the FreeSurfer average brain (https://github/VPNL/MFS). Together, we are hopeful that future studies will improve our understanding of additional tertiary cortical sulci, which in turn, will also make it possible for improved quantifications and insights regarding the structural-functional organization of the living human brain.

Acknowledgements

This research was funded by NEI grants 1 RO1 EY 02391501A1 and 1 RO1 EY 02231801A1. We would like to thank Ed Plowey and Christoph Leuze for help with the dissection included in Fig. 2.

References

Allison T, Puce A, Spencer DD, McCarthy G, 1999 Electrophysiological studies of human face perception. I: potentials generated in occipitotemporal cortex by face and non-face stimuli. Cerebr. Cortex 9, 415–430.

Ben-Shachar M, et al., 2007 Differential sensitivity to words and shapes in ventral occipito-temporal cortex. Cerebr. Cortex 17, 1604–1611.

Brewer AA, Liu J, Wade AR, Wandell BA, 2005 Visual field maps and stimulus selectivity in human ventral occipital cortex. Nat. Neurosci 8, 1102–1109. [PubMed: 16025108]

Cohen L, Dehaene S, Naccache L, Lehericy S, Dehaene-Lambertz G, Henaff MA, Michel F, 2000 The visual word form area: spatial and temporal char-acterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123, 291–307. [PubMed: 10648437]

Destrieux C, Fischl B, Dale A, Halgren E, 2010 Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. Neuroimage 53 (1), 1–15. [PubMed: 20547229]

Dale AM, et al., 1999 Cortical surface-based analysis. I. Segmentation and surface reconstruction. Neuroimage 9, 179–194. [PubMed: 9931268]

Drucker DM, Aguirre GK, 2009 Different spatial scales of shape similarity representation in lateral and ventral LOC. Cerebr. Cortex 19, 2269–2280.

Fischl B, et al., 1999 High-resolution intersubject averaging and a coordinate system for the cortical surface. Hum. Brain Mapp. 8, 272–284. [PubMed: 10619420]

Gomez J, Barnett MA, Natu VS, Mezer A, Palomero-Gallagher N, Weiner KS, Amunts K, Zilles K, Grill-Spector K, 2017 Microstructural proliferation in human cortex is coupled with the development of face processing. Science 355 (6320), 68–71. [PubMed: 28059764]

Grill-Spector K, 2003a Occipital lobe In: Aminoff M, Daroff R (Eds.), Encyclopedia of Neurological Sciences. Academic Press, pp. 1–7.

Grill-Spector K, 2003b The neural basis of object perception. Curr. Opin. Neurobiol 13, 1–8.

Grill-Spector K, 2008 Visual priming In: Eichenbaum H, Bryne J (Eds.), Learning and Memory: A Comprehensive Reference. Elsevier, Oxford, UK, pp. 219–236.

Grill-Spector K, Malach R, 2001 fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107, 293–332.

Grill-Spector K, Malach R, 2004 The human visual cortex. Annu. Rev. Neurosci 27, 649–677. [PubMed: 15217346]

Grill-Spector K, Weiner KS, 2014 The functional architecture of the ventral temporal cortex and its role in categorization. Nat. Rev. Neurosci 15, 336–548. [PubMed: 24739788]

Grill-Spector K, et al., 1999 Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24, 187–203. [PubMed: 10677037]

Grill-Spector K, et al., 2000 The dynamics of object-selective activation correlate with recognition performance in humans. Nat. Neurosci 3, 837–843. [PubMed: 10903579]

Grill-Spector K, et al., 2001 The lateral occipital complex and its role in object recognition. Vis. Res 41, 1409–1422. [PubMed: 11322983]

Grill-Spector K, et al., 2006 High-resolution imaging reveals highly selective nonface clusters in the fusiform face area. Nat. Neurosci 9, 1177–1185. [PubMed: 16892057]

Halgren E, et al., 1999 Location of human face-selective cortex with respect to retinotopic areas. Hum. Brain Mapp. 7, 29–37. [PubMed: 9882088]

Huschke E, 1854 Schaedel, Hirn und Seele des Menschen und der Thiere nach Alter, Geschlecht und Race, dargestellt nach neuen Methoden und Un-tersuchungen. Mauke, Jena.

James TW, et al., 2002 Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. Neuron 35, 793–801. [PubMed: 12194877]

Kanwisher N, McDermott J, Chun MM, 1997 The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci 17, 4302–4311. [PubMed: 9151747]

Kay KN, Weiner KS, Grill-Spector K, 2015 Attention reduces spatial uncertainty in human ventral temporal cortex. Curr. Biol 25 (5), 595–600. [PubMed: 25702580]

Kolster H, Peeters R, Orban GA, 2010 The retinotopic organization of the human middle temporal area MT/V5 and its cortical neighbors. J. Neurosci 30 (29), 9801–9820. [PubMed: 20660263]

Malach R, et al., 1995 Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. Unit. States Am. 92, 8135–8139.

Mangin JF, Auzias G, Coulon O, Sun ZY, Riviere D, Regis J, 2015 Sulci as landmarks In: Toga AW (Ed.), Brain Mapping: an Encyclopedic Reference. Academic Press, New York.

Nasr S, Liu N, Devaney KJ, Yue X, Rajimehr R, Ungerleider LG, Tootell RB, 2011 Scene-selective cortical regions in human and nonhuman primates. J. Neurosci 31, 13771–13785. [PubMed: 21957240]

Natu VS, et al., 2016 Development of neural sensitivity to face identity correlates with perceptual discriminability. J. Neurosci 36, 10893–10907. [PubMed: 27798143]

Nobre A, et al., 1998 Modulation of human extrastriate visual processing by selective attention to colours and words. Brain 121 (7), 1357–1368. [PubMed: 9679786]

Ono M, Kubik S, Abernathy CD, 1990 Atlas of the Cerebral Sulci. Thieme, New York.

Peelen MV, Downing PE, 2005 Selectivity for the human body in the fusiform gyrus. J. Neurophysiol 93, 603–608. [PubMed: 15295012]

Puce A, Allison T, Asgari M, Gore JC, McCarthy G, 1996 Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J. Neurosci 16, 5205–5215. [PubMed: 8756449]

Retzius G, 1896 In: Buchdr PA (Ed.), Das Menschenhirn: Studien in der makroskopischen Morphologie. Kgl Norstedt and Söner, Stockholm.

Sayres R, Grill-Spector K, 2006 Object-selective cortex exhibits performance-independent repetition suppression. J. Neurophysiol 95, 995–1007. [PubMed: 16236787]

Sayres R, Grill-Spector K, 2008 Relating retinotopic and object-selective responses in human lateral occipital cortex. J. Neurophysiol 100, 249–267. [PubMed: 18463186]

Schwarzlose RF, Baker CI, Kanwisher N, 2005 Separate face and body selectivity on the fusiform gyrus. J. Neurosci 25, 11055–11059. [PubMed: 16306418]

Sorger B, et al., 2007 Understanding the functional neuroanatomy of acquired prosopagnosia. Neuroimage 35, 836–852. [PubMed: 17303440]

Tamraz J, Comair Y, 2006 Atlas of Regional Anatomy of the Brain Using MRI: with Functional Correlations. Springer, New York.

Vinberg J, Grill-Spector K, 2008 Representation of shapes, edges, and surfaces across multiple cues in the human visual cortex. J. Neurophysiol 99, 1380–1393. [PubMed: 18171705]

Weiner KS, Grill-Spector K, 2010 Sparsely-distributed organization of face and limb activations in human ventral temporal cortex. Neuroimage 52, 1559–1573. [PubMed: 20457261]

Weiner KS, Grill-Spector K, 2011 Neuroimage Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. Neuroimage 56 (4), 2183–2199. [PubMed: 21439386]

Weiner KS, Grill-Spector K, 2012 The improbable simplicity of the fusiform face area. Trends Cognit. Sci 16 (5), 251–254. [PubMed: 22481071]

Weiner KS, Zilles K, 2016 The anatomical and functional specialization of the fusiform gyrus. Neuropsychologia 83, 48–62. [PubMed: 26119921]

Weiner KS, Golarai G, Caspers J, Chuapoco MR, Mohlberg H, Zilles K, Amunts K, Grill-Spector K, 2014 The mid-fusiform sulcus: a landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex. Neuroimage 84, 453–465. [PubMed: 24021838]

Weiner KS, et al., 2017a Defining the most probable location of the parahippocampal place area using cortex-based alignment and cross-validation. Neuroimage S1053–8119 (17), 30333–30336.

Weiner KS, Barnett MA, Lorenz S, Caspers J, Stigliani A, Amunts K, Zilles K, Fischl B, Grill-Spector K, 2017b The cytoarchitecture of domain-specific regions in human high-level visual cortex. Cerebr. Cortex 27, 146–161.

Weiner KS, Sayres R, Vinberg J, Grill-Spector K, 2010 fMRI-adaptation and category selectivity in human ventral temporal cortex: regional differences across time scales. J. Neurophysiol 103, 3349–3365. [PubMed: 20375251]

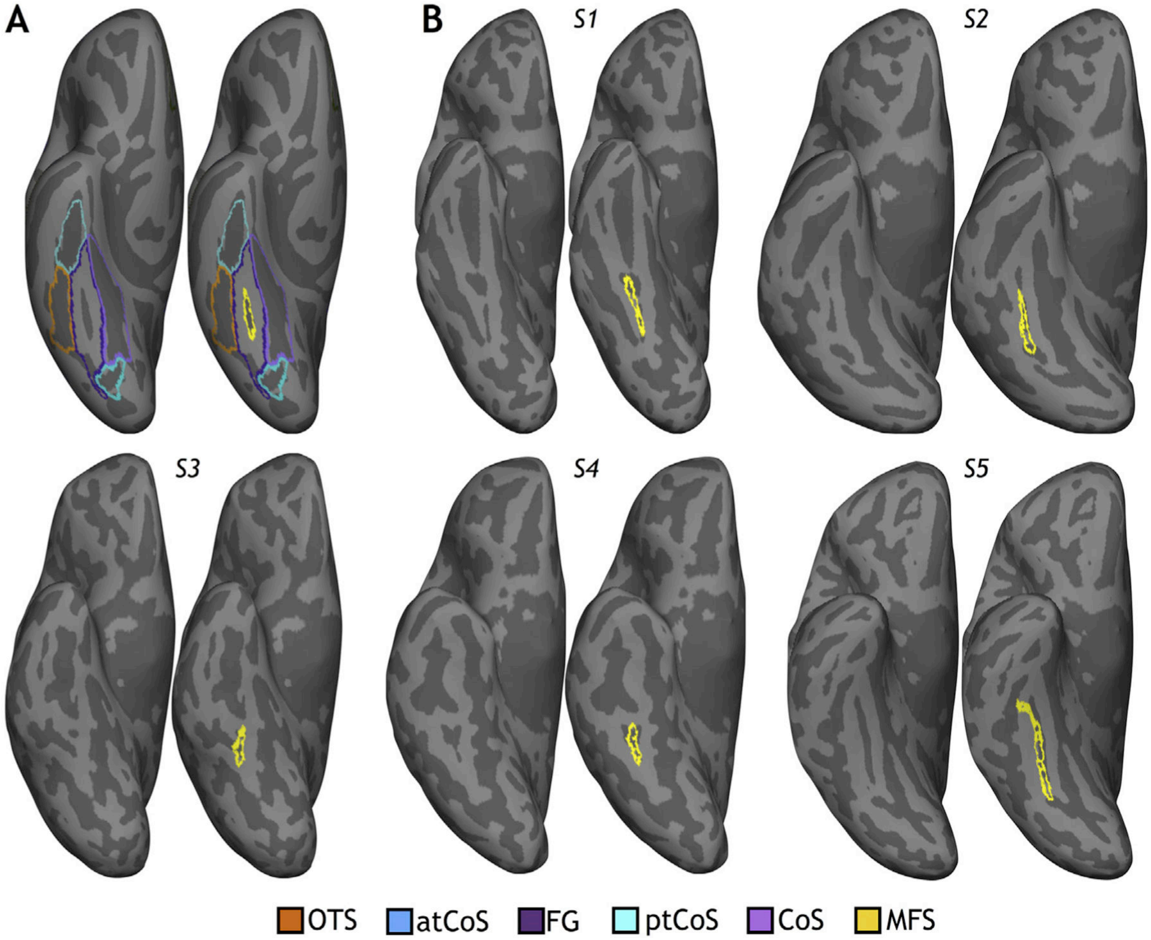

Fig. 1. Automatic identification of the mid-fusiform sulcus (MFS) irrespective of morphological variability using cortex-based alignment.

(A) An inflated cortical surface reconstruction of the right hemisphere from 39 adults provided by the Freesurfer software package (http://freesurfer.net/). *Left:* Colored outlines illustrate automatic definition of macro-anatomical structures within ventral temporal cortex from Destrieux et al. (2010) (See legend). Note that the sulcus within the FG is undefined. *Right:* The MFS is defined on the fsaverage cortical surface in yellow, which we provide as a label file with this paper. (B) Inflated cortical surface reconstructions of the right hemisphere from 5 adults (S1–S5). The left image does not include any anatomical definitions, while the right image includes the location of the MFS (yellow) that is predicted from using cortex-based alignment to project the label file in (A) to individual subjects. There is good predictability in each subject even if the MFS is fractionated into two (S1) or three (S2) components or if the MFS is short (S3 and S4) or long (S5). atCoS: anterior transverse collateral sulcus; CoS: collateral sulcus; FG: fusiform gyrus; MFS: mid-fusiform sulcus; OTS: occipito-temporal sulcus; ptCoS: posterior transverse collateral sulcus.

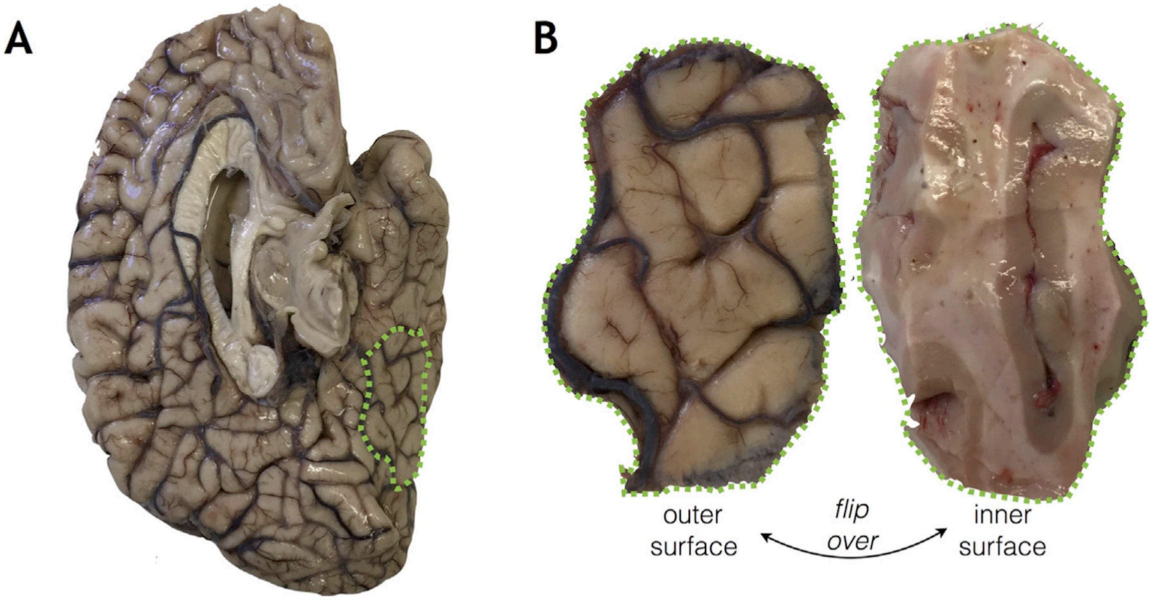

Fig. 2. The identification of tertiary sulci in classic dissection methods are impeded by indentations on the outer surface of the brain caused by veins and arteries.

Recent neuroimaging studies have made progress in identifying and quantifiying tertiary sulci within occipitotemporal cortex (Weiner et al., 2014, 2017a; Mangin et al., 2015), while classic dissection methods have had difficulty in doing so. We propose that the arteries and veins on the outer surface of the brain may make the appearances of tertiary sulci seem more variable than they actually are. As cortical surface reconstructions that are commonly used in neuroimaging studies are generated based on the boundary between gray and white matter, an easy test of this proposal is to see if the morphological pattern of sulci on the inner surface of a piece of cortical tissue is different than the appearance on the outer surface of the tissue. **(A)** Medial view of a left hemisphere from a post-mortem brain. Dotted green outline: mid-fusiform gyrus. **(B)** *Left:* The mid-fusiform gyrus (dotted green outline) was carefully extracted from the left hemisphere in (A). There are many veins and arteries that are on the surface of the brain that align with deep and shallow indentations on the surface of the brain. There are two alternatives: (1) these arteries and veins can produce random indentations on the outer surface of the cerebrum or (2) these arteries and veins often align with sulci corresponding to these deep (primary) and shallow (tertiary) indentations. If (2) is true, then the pattern generated by the veins and arteries on the outer surface should match the pattern on the inner surface. If (1) is correct, then the patterns on the outer and inner surface should be different. *Right:* The mid-fusiform gyrus extracted from (A) has been flipped over to show the inner surface. The patterns are clearly different on the inner and outer surface in support of the first alternative. This qualitative exercise is important because it illustrates that the pattern of tertiary sulci on the outer surface of the brain may be artificially compounded by indentations produced by veins and arteries. As cortical surface reconstructions are generated from the inner boundary between gray and white matter, we propose that non-invasive morphological assessments of the human brain are better-suited for the clear identification of tertiary structures compared to classic dissection methods.

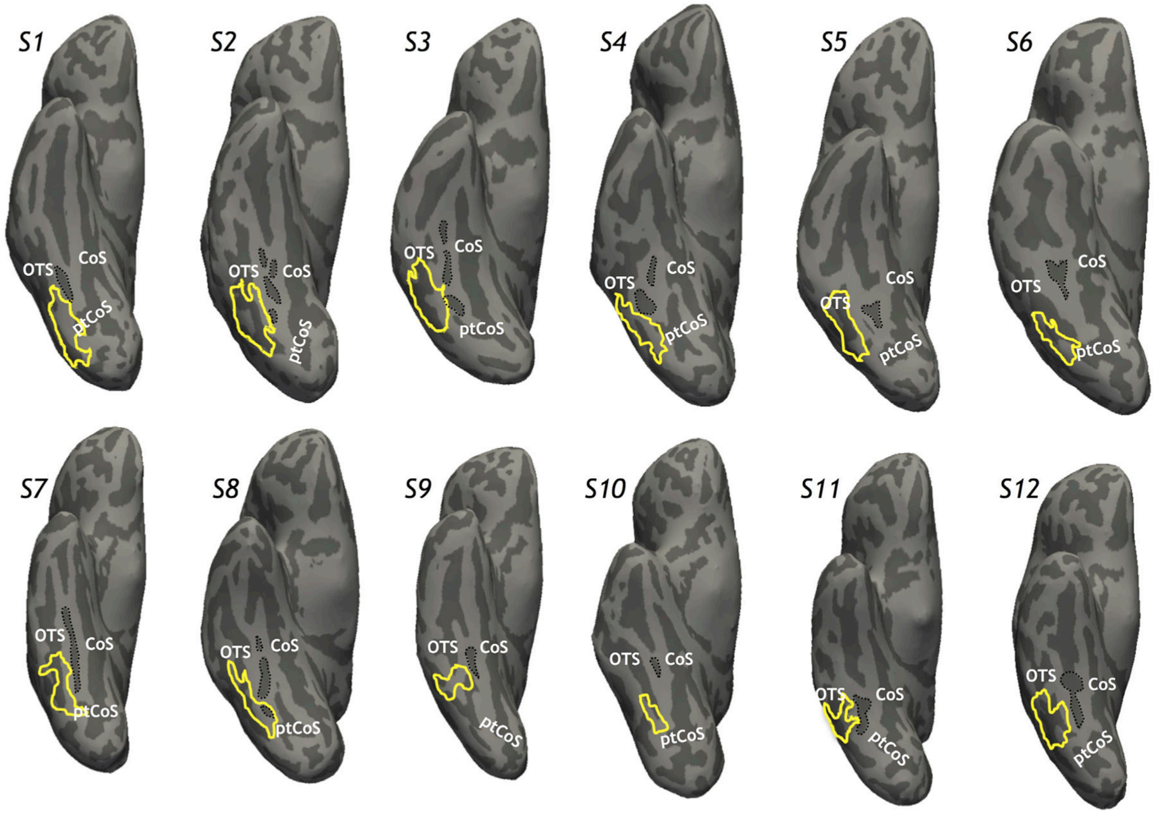

Fig. 3. Stable and variable features between object-selective pFs and the MFS.

(A) pFs (yellow) in 12 individual right hemispheres from previously published data (Natu et al., 2016). Consistent with the first studies to differentiate pFs from LO (Grill-Spector et al., 1999, 2000) and described in the text, pFs overlaps the occipitotemporal sulcus (OTS) and fusiform gyrus (FG). However, there are both stable and variable features between object-selective pFs and MFS (dotted black outline). In terms of stability, pFs is consistently lateral to the MFS. In terms of variability, pFs can be (1) adjacent to the MFS (S1–4, S7–S9, S11–12) or (2) cortically distant from the MFS either laterally (S5) or postero-laterally (S6 and S10). Immediately relevant for the present discussion is the fact that a subset of the cases in (1) either abut (S1–S4, S9) or overlap (S8) the posterior extent of the MFS. CoS: collateral sulcus; OTS: occipito-temporal sulcus; pFs: posterior fusiform gyrus; ptCoS: posterior transverse collateral sulcus.