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# The mid-fusiform sulcus: A landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex

Kevin S. Weiner [a,*], Golijeh Golarai [a], Julian Caspers [c,d,g], Miguel R. Chuapoco [a], Hartmut Mohlberg [d], Karl Zilles [d,e,f], Katrin Amunts [c,d], Kalanit Grill-Spector [a,b]

[a] Department of Psychology, Stanford University, Stanford, CA 94305, USA
[b] Neuroscience Institute, Stanford University, Stanford, CA 94305, USA
[c] C. and O. Vogt Institute for Brain Research, Heinrich Heine University Düsseldorf, 40001 Düsseldorf, Germany
[d] Institute for Neuroscience and Medicine (INM-1), Research Centre Jülich, 52425 Jülich, Germany
[e] JARA-BRAIN, Jülich–Aachen Research Alliance, 52425 Jülich, Germany
[f] Department of Psychiatry, Psychotherapy and Psychosomatics, RWTH Aachen University, 52074 Aachen, Germany
[g] Department of Diagnostic and Interventional Radiology, University Düsseldorf, Medical Faculty, D-40225 Düsseldorf, Germany

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ABSTRACT

Human ventral temporal cortex (VTC) plays a pivotal role in high-level vision. An under-studied macroanatomical feature of VTC is the mid-fusiform sulcus (MFS), a shallow longitudinal sulcus separating the lateral and medial fusiform gyrus (FG). Here, we quantified the morphological features of the MFS in 69 subjects (ages 7–40), and investigated its relationship to both cytoarchitectonic and functional divisions of VTC with four main findings. First, despite being a minor sulcus, we found that the MFS is a stable macroanatomical structure present in all 138 hemispheres with morphological characteristics developed by age 7. Second, the MFS is the locus of a lateral–medial cytoarchitectonic transition within the posterior FG serving as the boundary between cytoarchitectonic regions FG1 and FG2. Third, the MFS predicts a lateral–medial functional transition in eccentricity bias representations in children, adolescents, and adults. Fourth, the anterior tip of the MFS predicts the location of a face-selective region, mFus-faces/FFA-2. These findings are the first to illustrate that a macroanatomical landmark identifies both cytoarchitectonic and functional divisions of high-level sensory cortex in humans and have important implications for understanding functional and structural organization in the human brain.



## Introduction

Human ventral temporal cortex (VTC) plays a pivotal role in perceptual and cognitive tasks spanning high-level vision (Haxby et al., 2000; Malach et al., 2002; Martin, 2007; Op de Beeck et al., 2008; Tarr and Gauthier, 2000; Weiner and Grill-Spector, 2013), memory (Henson et al., 2000; Wagner et al., 1999), and multi-sensory integration (Amedi et al., 2002; James et al., 2002; Kitada et al., 2009). One of the most replicable organizational features of human VTC documented by functional magnetic resonance imaging (fMRI) is a large-scale lateral–medial functional distinction. For instance, inanimate (Mahon and Caramazza, 2009; Martin, 2007), place (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Nasr et al., 2011), and peripherally-biased (Hasson et al., 2002; Levy et al., 2001; Malach et al., 2002) representations are located in medial VTC encompassing the medial FG and collateral sulcus (CoS), while animate (Connolly et al., 2012; Mahon and Caramazza, 2009; Martin, 2007), face (Kanwisher et al., 1997), and foveally-biased (Hasson et al., 2002; Levy et al., 2001; Malach et al., 2002) representations are located in lateral VTC, encompassing the lateral fusiform gyrus (FG) and occipito-temporal sulcus (OTS). Intriguingly, in addition to this lateral–medial functional distinction, a lateral–medial cytoarchitectonic distinction has recently been identified (Caspers et al., 2012). Using novel tools detecting transitions in both cell density and layering across gray matter, Caspers et al. (2012) reported two cytoarchitectonic regions in the posterior aspect of VTC: FG1 and FG2. Macroanatomically, FG1 is located on the medial FG extending into the CoS, while FG2 is located on the lateral FG extending into the OTS. Cytoarchitectonically, FG1 displays a columnar arrangement of small pyramidal cells, while FG2 contains large pyramidal cells in layer III and a prominent layer IV, but no columnar arrangement. If and how these functional and cytoarchitectonic parcellations are related to one another is presently unknown.

A major obstacle preventing the full understanding of cytoarchitectonic and functional correspondences in VTC is that macroanatomical structures are yet to be fully characterized. For instance, an often over-looked feature of VTC is that the FG is divided longitudinally by a minor sulcus referred to as the mid-fusiform sulcus, or MFS (Allison et al., 1999; Nasr et al., 2011; Nobre et al., 1998; Puce et al., 1996; Weiner and Grill-Spector, 2010, 2012, 2013; Weiner et al.,

* Corresponding author.
*E-mail address:* kweiner@stanford.edu (K.S. Weiner).

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2010). Indeed, although the MFS was first labeled as such in the late nineties (Allison et al., 1999; Nobre et al., 1998; Puce et al., 1996), it has been mentioned in the literature less than ten times (Davidenko et al., 2012; Nasr et al., 2011; Parvizi et al., 2012; Schultz et al., 2003; Weiner and Grill-Spector, 2010, 2012, 2013; Weiner et al., 2010). Despite the paucity of studies mentioning the MFS, recent research in adults provides insight into how incorporating the MFS into functional neuroimaging might enhance the understanding of VTC functional organization. Specifically, these studies show that the MFS serves as a lateral–medial functional boundary dividing face-selective regions (Davidenko et al., 2012; Nasr et al., 2011; Parvizi et al., 2012; Weiner and Grill-Spector, 2010, 2012, 2013; Weiner et al., 2010) from place-selective regions (Nasr et al., 2011), and also dissociates differential repetition suppression mechanisms (Weiner et al., 2010). However, it is unknown (1) if the morphology of the MFS is stable across development, (2) if the MFS is coupled with cytoarchitectonic partitions of VTC, (3) whether the MFS predicts additional lateral–medial functional gradients in VTC such as eccentricity bias representations, and (4) if the MFS also predicts the fine-scale clustering of face-selective regions.

To address these questions, we conducted four separate studies. First, we characterized the morphology of the MFS in 69 subjects (ages 7–40), determining the developmental and stable features of the MFS in children, adolescents, and adults. Second, we examined the relationship between the MFS and cytoarchitectonic regions FG1 and FG2 using an independent set of 10 postmortem brains. Third, using a novel classification approach, we tested if the MFS serves as a functional boundary separating the large-scale eccentricity bias map (Hasson et al., 2002; Levy et al., 2001; Malach et al., 2002) in 36 subjects (ages 7–40). We chose eccentricity bias measurements because they show a medial–lateral gradient across VTC and constitute a large-scale category-independent representation. Fourth, we tested if the MFS serves as a functional landmark identifying the fine-scale functional organization of face-selective regions pFus-faces/FFA-1 and mFus-faces/FFA-2 (Weiner and Grill-Spector, 2010) using high-resolution fMRI (HR-fMRI) in 14 adult subjects. To our knowledge, this is the first in depth analysis of human high-level visual cortex spanning cytoarchitectonics, macroanatomy, and functional organization at multiple spatial scales. We demonstrate that the MFS is a stable macroanatomical feature across development, as well as a crucial landmark identifying both cytoarchitectonic and functional divisions of VTC.

## Materials and methods

We describe the methods in two sections, one for the anatomical and functional MRI scans and a separate section for the cytoarchitectonical analysis.

### *Participants*

To obtain macroanatomical data, 69 subjects participated in an anatomical MRI session. Subjects included 20 children (ages 7–11, 7 females), 14 adolescents (ages 12–17, 8 females), and 35 adults (ages 18–40, 18 females), all of whom were healthy with no report of neurological or psychiatric disease. To obtain data on the functional organization of VTC, 36 (12 children, 12 adolescents, and 12 adults) of these 69 subjects also participated in an fMRI session. Written consent was obtained from each subject. Procedures were approved by the Stanford Internal Review Board on human subjects research.

### *Anatomical scans and analysis*

*Scanning.* All subjects were scanned on a GE 3-Tesla Signa scanner at Stanford University. A high-resolution anatomical volume of the whole brain was acquired with a whole head coil using a T1-weighted SPGR pulse sequence (TR = 1000 ms, flip angle = 45°, 2 NEX, FOV = 200 mm, resolution of 0.78 × 0.78 × 1.2 mm).

*Data analysis.* Data were analyzed with MATLAB (MathWorks) using the mrVista toolbox (http://white.stanford.edu/software).

*Cortical surface reconstruction.* Anatomical volumes were aligned to the AC-PC plane and resampled to 1 mm isotropic voxels. Using a combination of automated (FreeSurfer: http://surfer.nmr.mgh.harvard.edu) and manual segmentation tools (ITK-SNAP: http://white.stanford.edu/itkgray), each anatomical volume was segmented to separate gray from white matter, from which we reconstructed the cortical surface for each subject (Wandell et al., 2000).

*Identification of the MFS on single slices and cortical surface reconstructions.* The MFS is a longitudinal sulcus dividing the FG into lateral and medial partitions as viewed on the cortical surface (Fig. 1). Here, we determined the identifying features of the MFS relative to surrounding sulci on single sections in order to define the MFS consistently on anatomical MRIs as well as in single histological sections. As illustrated in Fig. 1, the MFS is positioned between the OTS and CoS on the cortical surface (Fig. 1a), resulting in a distinct omega (ω) pattern on single coronal slices (Fig. 1b). This ω pattern (red outline in Figs. 1–2) is a characterizing feature of the MFS despite differences in how it may appear on the cortical surface.

*Sulcal length measurements.* Lines were manually drawn along the fundus of the MFS on the cortical surface for each subject and hemisphere. The length of this line was determined using a modified version of Dijkstra's algorithm (as in Wandell et al., 2000). As the cortical surface reconstruction is composed of a series of connected vertices, the algorithm computes the length by determining the shortest path between endpoints on the line taking into consideration their actual distance in gray matter. When the MFS was fractionated into more than one component (Table 1, Fig. 2, and Results), the total length was based on the sum of the independent sulcal components excluding the interspersed

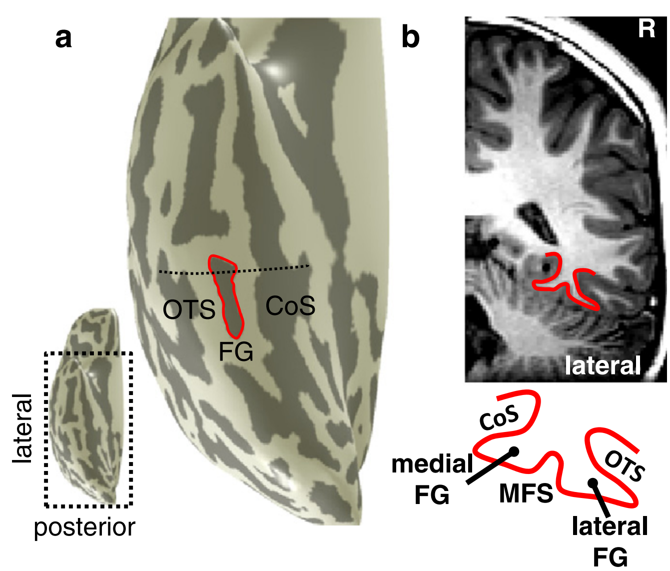


**Fig. 1.** The mid-fusiform sulcus (MFS). Example right hemisphere from a ten-year old male. (a) Inflated cortical surface with sulci illustrated in dark gray. The MFS (outlined in red) is a longitudinal sulcus dividing the fusiform gyrus (FG) into lateral and medial partitions, flanked by the occipito-temporal sulcus (OTS) laterally and the collateral sulcus (CoS) medially (inset for location of zoomed portion). (b) The MFS, OTS, and CoS have a distinctive ω pattern on single coronal slices where the MFS is the shallower sulcus flanked by the much deeper CoS and OTS. Top: Example coronal slice from the position of the dotted line in (a). Bottom: Schematic of the ω pattern of the MFS, OTS, and CoS.