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SHORT COMMUNICATION

Hominoid-specific sulcal variability is related to face perception ability

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Abstract

The relationship among brain structure, brain function, and behavior is of major interest in neuroscience, evolutionary biology, and psychology. This relationship is especially intriguing when considering hominoid-specific brain structures because they cannot be studied in widely examined models in neuroscience such as mice, marmosets, and macaques. The fusiform gyrus (FG) is a hominoid-specific structure critical for face processing that is abnormal in individuals with developmental prosopagnosia (DPs)—individuals who have severe deficits recognizing the faces of familiar people in the absence of brain damage. While previous studies have found anatomical and functional differences in the FG between DPs and NTs, no study has examined the shallow tertiary sulcus (mid-fusiform sulcus, MFS) within the FG that is a microanatomical, macroanatomical, and functional landmark in humans, as well as was recently shown to be present in non-human hominoids. Here, we implemented pre-registered analyses of neuroanatomy and face perception in NTs and DPs. Results show that the MFS was shorter in DPs than NTs. Furthermore, individual differences in MFS length in the right, but not left, hemisphere predicted individual differences in face perception. These results support theories linking brain structure and function to perception, as well as indicate that individual differences in MFS length can predict individual differences in face processing. Finally, these findings add to growing evidence supporting a relationship between morphological variability of late developing, tertiary sulci and individual differences in cognition.

Keywords Developmental prosopagnosia · Neuroanatomy · Developmental disorders · Sulcal morphology · Cortical folding

Introduction

The relationship among brain structure, brain function, and behavior is of major interest in neuroscience, evolutionary biology, and psychology. This relationship is especially intriguing when considering hominoid-specific brain structures because they cannot be examined in widely studied animal models in neuroscience such as mice, marmosets, and macaques (Armstrong et al. 1995; Connolly 1950; Weiner 2019). For example, the fusiform gyrus (FG) is a hominoid-specific structure critical for face processing (Duchaine and Yovel 2015; Kanwisher et al. 1997), object recognition (Gauthier and Tarr 2016), and reading (Cohen et al. 2000; Wandell et al. 2012).

The FG contains a shallow tertiary sulcus—the mid-fusiform sulcus (MFS)—that reliably divides the FG into lateral and medial partitions in both hemispheres and serves as a functional and microarchitectural landmark in humans (Grill-Spector and Weiner 2014; Weiner et al. 2014; Parvizi

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et al. 2012). By definition, tertiary sulci such as the MFS are smaller in surface area and shallower in depth compared to primary and secondary sulci, emerge last in gestation, continue to develop after birth, and many are hominoid-specific (Welker 1990; Sanides 1964). Immediately relevant for the present study, the MFS exhibits extensive variability across hominoids: it can be as short as a few millimeters or as long as several centimeters in both humans and chimpanzees (Miller et al. 2020; Weiner et al. 2014). While previous (McGugin et al. 2016, 2020) and ongoing (Chen et al. 2023) work provides evidence linking anatomical features to functional representations and face perception ability, including anatomical differences between individuals with developmental prosopagnosia (DPs) and neurotypical controls (NTs; Behrmann et al. 2007; Garrido et al. 2009; Gomez et al. 2015; Song et al. 2015), it is presently unknown if the extensive individual differences in MFS morphology previously identified (Weiner et al. 2014; Miller et al. 2020) reflect individual differences in perception. Further motivating this question are recent findings showing a relationship between either the depth or length of tertiary sulci and cognition in clinical populations and NTs. For example, tertiary sulcal depth predicts reasoning skills in children (Voorhies et al. 2021), while tertiary sulcal length is related to whether individuals with schizophrenia will hallucinate or not (Garrison et al. 2015).

Motivated by these findings, we pre-registered analyses (https://osf.io/ydqc4) that leveraged two previously published datasets (Garrido et al. 2009; Jiahui et al. 2018) in which behavioral and anatomical brain data were acquired in 82 participants. A main benefit of these datasets is that they contain data from both NTs as well as DPs—individuals who have severe deficits recognizing the faces of familiar people without accompanying insult to the brain (Avidan and Behrmann 2021; Susilo and Duchaine 2013). Our pre-registered analyses focused on two main questions: (1) Do morphological features of the MFS differ between DPs and NTs? and (2) Is morphological variability of the MFS predictive of face processing ability in NTs, DPs, or both?

Materials and methods

Here, we include the materials and methods as written in our pre-registered analyses (modified to use the past tense). We also include our original predictions and rationale as well if we specified them in the pre-registration (https://osf.io/fzb48/). We emphasize that our pre-registration is focused on the proposed analyses as the datasets were acquired previously (Garrido et al. 2009; Jiahui et al. 2018). In the present study, we focus on the CFMT for two main reasons. First, the CFMT is a well-established test with high reliability: previous studies by Wilmer and colleagues (2010, 2012) show a Spearman–Brown split-half reliability for CFMT of 0.91, as well as a test–retest reliability of 0.70 and alternate forms of reliability of 0.76. Second, we focus on the CFMT in order to maximize the number of participants included in the present measurements. Specifically, since the present analyses consisted of two datasets, not all individuals were tested with the same tasks. Nevertheless, each participant completed the CFMT. For these reasons, the CFMT was the main focus in our pre-registered analyses.

Data acquisition

Our analyses were conducted using two previously published datasets from Garrido et al. 2009 (Dataset 1) and Jiahui et al. 2018 (Dataset 2), which we describe in turn below.

Dataset 1 (Garrido et al. 2009).

Participants. Dataset 1 consisted of data from seventeen individuals with developmental prosopagnosia (DPs; 11 females, mean age 30.94 years (SD = 7.54, range 20–46)) and 18 neurotypical controls (NTs; 11 females, 28.94 (SD = 5.70, range 23–43)). All reported being right-handed. All 35 participants showed normal or corrected-to-normal visual acuity when tested with Test Chart 2000 (Thompson Software Solutions, Hatfield, UK). DP participants contacted the Duchaine lab through http://www.faceblind.org and reported significant difficulties recognizing familiar faces in everyday life. To ascertain that the face recognition deficits that the participants were reporting were consistent with DP, each individual was tested on the Cambridge Face Memory Test (CFMT; Duchaine and Nakayama 2006) and on a Famous Faces Test. All DPs performed significantly below the mean of published NT means for these two tests.

Brain data acquisition. Each participant was scanned on a 3 T whole-body MRI scanner (Magnetom TIM Trio, Siemens Medical Systems, Erlangen, Germany) operated with a radio frequency body transmit and 12-channel receiver head coil. For each participant, a T1-weighted (T1w), 3D-modified driven equilibrium Fourier transform (MDEFT) dataset was acquired in sagittal orientation with 1 mm isotropic resolution (176 partitions, field of view = 256×240 mm^2, matrix $256 \times 240 \times 176$) with the following parameters: repetition time = 7.92 ms, echo time = 2.48 ms, inversion time = 910 ms (symmetrically distributed around the inversion pulse; quot = 50%), flip angle $\alpha = 16$x, fat saturation, bandwidth 195 Hz/pixel. The sequence was specifically optimized for reduced sensitivity to motion, susceptibility artifacts, and B1 field inhomogeneities.

Behavioral tasks. All participants were tested on a battery of tests tapping different aspects of face and object processing. Results on 11 behavioral tasks were published in Garrido et al. 2009, including the CFMT and the Famous Faces

Test described above, as well as three Old–New Recognition Tasks (faces, cars, and horses) (Duchaine and Nakayama 2005), the Cambridge Face Perception Test (Duchaine et al. 2007), the Cambridge Hair Memory Test (Garrido et al. 2009), a Sequential Matching Task for Face Identity and a Sequential Matching Task for Face Emotion (Garrido et al. 2009), the Reading the Mind in the Eyes Test (Baron-Cohen et al. 2001), and the Films Facial Expression Task (Garrido et al. 2009).

The following tests show significant correlation with CFMT in control participants: Cars ($F(68, 1) = 24.8$; $p < 0.001$), Cars Reaction Time ($F(68, 1) = 29.6$; $p < 0.001$), Baldwomen ($F(68, 1) = 111.28$, $p < 0.001$), Baldwomen Reaction Time ($F(68, 1) = 43.3$; $p < 0.01$), Horses ($F(68, 1) = 11.01$; $p < 0.002$), Horses Reaction Time ($F(68, 1) = 16.7$, $p < 0.001$), Famous Faces ($F(68, 1) = 167.47$, $p < 0.001$). CFPT ($F(68, 1) = 37.0$, $p < 0.001$). All other tasks (Eyes Test – Emotion, Films Task, CHMT, WASI Full Scale, WASI Verbal, and WASI Performance) were non-significant after Bonferroni correction ($F(68, 1) < 4$, $p > 0.01$). As such, to test if a relationship between sulcal morphology and face processing ability is specific to the CFMT, we also used PC1 scores from principal component analyses conducted by Garrido and colleagues (2009) in Dataset 1.

Dataset 2 (Jiahui et al. 2018).

Participants. Twenty-two DPs (7 males, mean age 41.9 years) and 25 NTs (10 males, mean age 42.3 years) participated in the study. DPs were recruited from www.faceblind.org, and all reported problems in daily life with face recognition. To assess their face recognition, DPs were tested with the Cambridge Face Memory Test (CFMT), a famous face test, and an old–new face discrimination test. All but one DP performed two or more standard deviations (SDs) below the mean of published control results in at least two of the three diagnostic tests. The DP participant who did not reach − 2 SD on two tests scored poorly on two of the three tasks (CFMT: $z = -1.9$; famous face: $z = -7.1$; old– new: $z = -0.5$), so we included them to increase the sample size. All participants had normal or corrected-to-normal vision and had no current psychiatric disorders. Participants provided written informed consent before doing the tasks, and all procedures were approved by Dartmouth's Committee for the Protection of Human Participants.

Brain data acquisition. All participants were scanned in a 3 T Philips MR scanner (Philips Medical Systems, WA, USA) with a SENSE (SENSitivity Encoding) 32-channel head coil. A high- resolution anatomical volume was acquired at the beginning of the scan using a high-resolution 3D magnetization-prepared rapid gradient-echo sequence (220 slices, field of view = 240 mm, acquisition matrix = 256 × 256, voxel size = 1 × 0.94 × 0.94 mm).

Face processing tasks. All participants (except one NT) were tested on the CFMT, and DP participants were also tested on a Famous Faces Test (all except two DPs) and on the Old–New Recognition Test for faces (all but one DP).

Data analyses

For our analyses, we implemented a twofold approach. First, we compared morphological features of three sulci in VTC (MFS, CoS, and OTS) between DPs and NTs. Second, we quantified the relationship between morphological features and behavioral performance on face processing tasks. Each approach is explained in turn below.

Morphological analyses. All sulci were defined by BP, EW, TH, and KSW, blind to the identity of all participants. Specifically, from each T1w scan in Datasets 1 and 2, BP, EW, TH, and KSW generated cortical surface visualizations using FreeSurfer (FS). The authors then manually identified the three sulci of interest in each hemisphere using protocols from our previously published work (Weiner et al. 2014; Miller et al. 2020). The location and definition of each sulcus was identified separately in every individual by three trained independent raters (authors BJP, EHW, and TH) from pial and inflated screenshots of each hemisphere in the ventral view. The raters compared independent ratings and modified the definitions accordingly on the annotated images. These sulcal definitions were then reviewed, further modified, and finalized by a neuroanatomist (KSW). This process expedites the definition of manual sulcal definitions as each sulcus is only defined once in FreeSurfer (in the next step); however, it does not allow the quantification of inter-rater reliability since the sulci are only defined in the final step of our tiered process. This approach is similar to other approaches that manually define sulci in other software packages such as BrainVisa (Borne et al. 2020; Rivière et al. 2022). Once finalized, the surface vertices for each sulcus were then selected using tools in FreeSurfer and saved as surface labels for vertex-level analysis of morphological statistics. As it can sometimes be difficult to determine the precise start and end points of a sulcus on one surface (Borne et al. 2020), all definitions were also guided by the pial and smoothwm surfaces of each individual. Using multiple surfaces allowed us to form a consensus across surfaces and clearly determine each sulcal boundary as in our previous work (Miller et al. 2021; Voorhies et al. 2021). Specifically, a three-tiered approach was implemented to identify the MFS, OTS, and CoS. First, the FG was identified as the major gyrus in VTC. Second, once the FG was identified, the OTS, CoS, and MFS were identified based on the following criteria: (1) the CoS was identified as a deep and long sulcus identifying the medial extent of the FG, (2) the OTS was identified as a deep and long sulcus identifying the lateral extent of the FG, and (3) the MFS was identified as either a single

shallow longitudinal sulcus dividing the FG into lateral and medial partitions or it was identified as two or more shallow sulcal components dividing the FG into lateral and medial partitions. In addition to these criteria, the MFS varies morphologically across participants and between hemispheres regarding its intersections with the CoS and OTS, as well as regarding the number of components. Third, as the MFS has predictable anterior (posterior extent of the hippocampus) and posterior (posterior transverse collateral sulcus) landmarks, but the OTS and CoS can extend longitudinally from the occipital pole to the temporal pole, we restricted our OTS and CoS definitions to the portions in VTC surrounding the MFS. This is consistent with our previous protocols and assures that the portions of the OTS and CoS being compared to the MFS are within the VTC. Building from previous analyses among the CoS, OTS, and MFS (Weiner et al. 2014) as well as previous anatomical comparisons between DPs and NTs (Garrido et al. 2009; Behrmann et al. 2007), morphological analyses focused on three main anatomical features: (1) sulcal depth for MFS, OTS, and CoS, (2) cortical thickness for MFS, OTS, and CoS, and (3) sulcal length for the MFS (since we restricted the length of the OTS and CoS to the portions surrounding the MFS; "Materials and methods"). Using functions in FS and custom software, we measured mean sulcal depth and cortical thickness for each of the three sulci. As in our previous work (Miller et al. 2020), mean sulcal depth was normalized in each individual based on the deepest point in cortex. In addition, cortical thickness was normalized based on the thickest point in cortex. As our previous work showed that sulcal length is the most variable morphological feature of the MFS across both human and non-human hominoid participants (Weiner et al. 2014; Miller et al. 2020), we measured sulcal length of the MFS (in units of millimeters).

Group differences of morphological measures. After manually defining all sulci in both groups, GJ, LG, and BD provided a list of participants' codes and their group to BP, EW, TH, WV, JM and KSW. DPs and NTs from both datasets ($N = 82$) were then included together for morphological analyses. Specifically, groups were included for each of the dependent measures with three main statistical tests outlined below with rationale and predictions:

(1) Rationale: From our previous work, sulcal depth of the MFS is the shallowest compared to OTS (2nd shallowest) and CoS (deepest; Weiner et al. 2014; Miller et al. 2020). As such, we conducted an N-way analysis of variance (ANOVA) on sulcal depth, with sulcus (CoS, MFS, OTS), hemisphere (RH, LH), natal sex (male, female) and group (DP, NTs) as factors.

Prediction: The MFS depth should be shallowest, CoS should be deepest, and OTS should be in between for both groups. In addition, we hypothesized that (a) there will not be group differences in sulcal depth between DPs and NTs for the CoS and OTS given previous findings (Behrmann et al. 2007), and (b) there will be group differences in sulcal depth for the MFS, but we do not make any predictions regarding the directionality of the differences.

(2) Rationale: From our previous work (Garrido et al. 2009), voxel-based morphometry (VBM) analyses showed differences in the fusiform gyrus between DPs and NTs. As gray matter volume as measured with VBM may also be related to cortical thickness, we plan to conduct a 3-way ANOVA on cortical thickness, with sulcus (CoS, MFS, OTS), hemisphere (RH, LH), natal sex (male, female) and group (DP, NTs) as factors.

Prediction: As our previous findings showed that DPs had reduced gray matter volume in the middle FG compared to NTs (Garrido et al. 2009) and portions of each of these three sulci were likely included in the region identified in this previous work, we hypothesized that there will be group differences in cortical thickness for all or a subset of these three sulci. Specifically, we hypothesized that it may be the case that each sulcus is thinner in DPs compared to NTs, which would be consistent with reduced gray matter volume, but we cannot be sure as the region identified previously also contained gyral components. Thus, we did not make an explicit prediction regarding directionality, but did predict that there will be group differences in cortical thickness for all or a subset of these three sulci.

(3) Rationale. While the shallowness of the MFS is its most stable feature, the length of the MFS is its most variable feature: it can be as short as just under 3 mm or as long as 5.5 cm (Weiner et al. 2014; Miller et al. 2020). Thus, we measured the length of the MFS in both DPs and NTs, and then compared the length of the MFS between DPs and NTs in both hemispheres.

Prediction: Based on previous studies showing that the length of the MFS is its most variable feature (Weiner et al. 2014; Weiner 2019; Miller et al. 2020), it may be the case that the MFS will be equally variable between DPs and NTs. Nevertheless, given the large variability in MFS length, it may also be the case that we find group differences in the length of the MFS. As such, we do not explicitly predict one or the other as both outcomes are possible.

Exploratory analyses

Examining the relationship between brain and behavior. We aimed to perform exploratory analyses examining the relationship between morphological features of VTC sulci and behavior in our two datasets. For any anatomical features that either showed a main effect of group or were included in any interactions from our ANOVA analyses, we performed correlation analyses to explore the relationship between these anatomical features and behavioral performance, including age and natal sex as covariates. We

started with the CFMT as a behavioral measure, as that is the only measure that we have for all participants. We then repeated all analyses within each dataset with the behavioral measures available for each dataset. We also tested if the relationship between MFS length and face recognition ability was specific to the CFMT or if it generalized to a composite score. To do so, we used the result from a principal component analysis (PCA) from Garrido et al. (2009) as Dataset 1 is from that paper.

Relationship between morphological measures. Our recent work (Miller et al. 2020) showed a relationship between cortical thickness and depth particularly with the MFS in a group of NTs from the Human Connectome Project. Building on this work, we calculated the correlation between thickness and depth for each of the three sulci and for each of the two groups. Based on these previous findings, we predicted that there would be a relationship between thickness and depth for the MFS in our cohort of subjects. However, we did not make an explicit prediction regarding if this relationship would (a) occur in one group, but not the other, or (b) would be stronger in one group compared to another. Thus, this analysis was also exploratory in nature.

Results

As outlined in our pre-registration, we first reconstructed the cortical surface for all participants (39 DPs (26 females, mean age 37.1 years); 43 NTs (26 females, mean age: 36.7 years)) using FreeSurfer (Dale et al. 1999). We then manually defined the MFS and the two sulci surrounding the FG (occipito-temporal, OTS; collateral, CoS) in each hemisphere ($N = 492$ total sulci; Fig. 1A) and implemented a two-pronged analysis approach. First, we compared sulcal morphological features between groups. Second, for those features that were significantly different between groups, we tested if there was a relationship between morphological variability and scores on the Cambridge Face Memory Test (CFMT) within each group. Results from all pre-registered anatomical and behavioral analyses are included in the Supplementary Materials.

For the first time, we show that MFS length, but not MFS depth, is predictive of face processing in two ways. First, the MFS is shorter in DPs (32.94 ± 12.34) compared to NTs (NTs: 37.36 ± 12.33). A 3-way ANOVA with group, hemisphere, and participant natal sex as factors revealed a main effect of group ($F(1, 153) = 4.61$, $p = 0.03$; Fig. 1B)

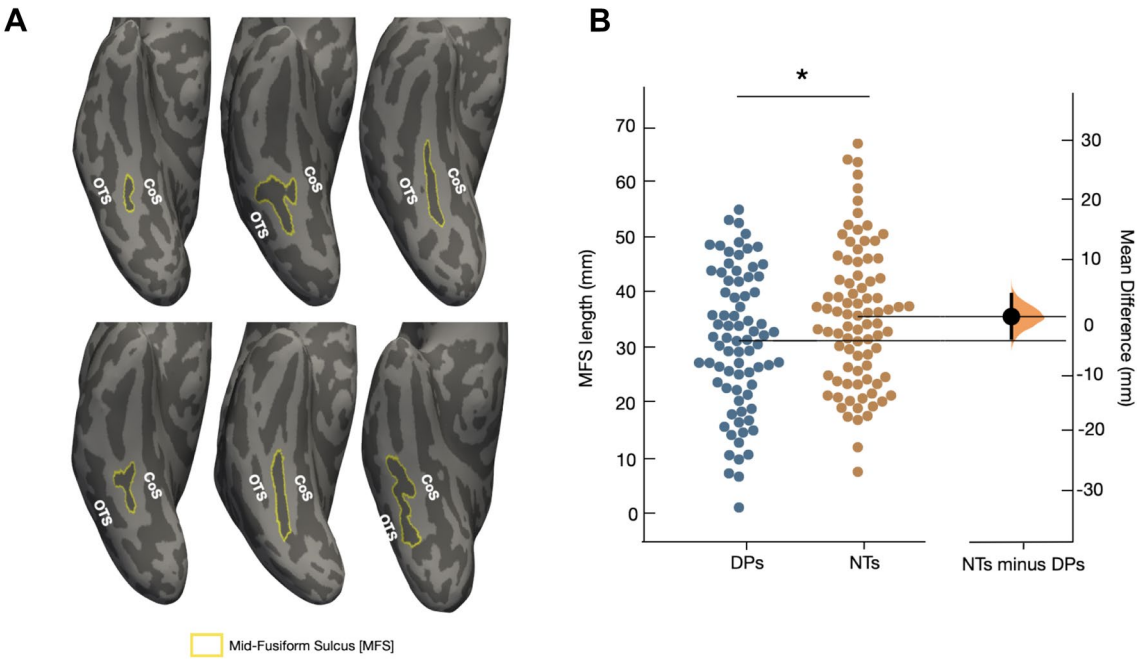

Fig. 1 The mid-fusiform sulcus (MFS) is morphologically different between developmental prosopagnosics (DPs) and neurotypical controls (NTs). **A** Three example inflated cortical surface reconstructions of right hemispheres from DPs (top) and NTs (bottom); the leftmost hemisphere belongs to the 25th percentile of MFS (yellow) length for its respective group, the center to the 50th percentile, and the rightmost to the 75th percentile. The collateral (CoS) and occipito-temporal (OTS) sulcal components within ventral temporal cortex ("Materials and methods") are labeled. Dark gray: sulci. Light gray: gyri. **B** Swarm plot showing MFS length as a function of group (DPs, blue; NTs, orange). On the right y-axis, a bootstrap of 5,000 iterations was used to generate a confidence interval (black bar) displayed with a density plot (orange) which depicts the mean difference in MFS length for each iteration (plot generated with Python package DABEST; Ho et al. 2019). On average, the MFS is shorter in DPs compared to NTs (*$p = 0.03$)

and a group × hemisphere × natal sex interaction ($F(1, 153) = 6.40$, $p = 0.02$; Supplementary Fig. 6). Second, the length of the MFS in the right ($r = 0.34$, $p = 0.03$), but not left ($r = -0.11$, $p = 0.47$), hemisphere predicted CFMT scores in NTs and these correlations were significantly different from one another (Fisher's $Z = 2.08$, $p = 0.04$; Fig. 2A). In DPs, the length of the MFS in the left ($r = -0.34$, $p = 0.04$), but not right ($r = -0.14$, $p = 0.35$), hemisphere predicted CFMT score, but these correlations were not significantly different from each other (Fisher's $Z = 0.89$, $p = 0.38$). While this difference between groups and hemispheres may seem surprising, when including all

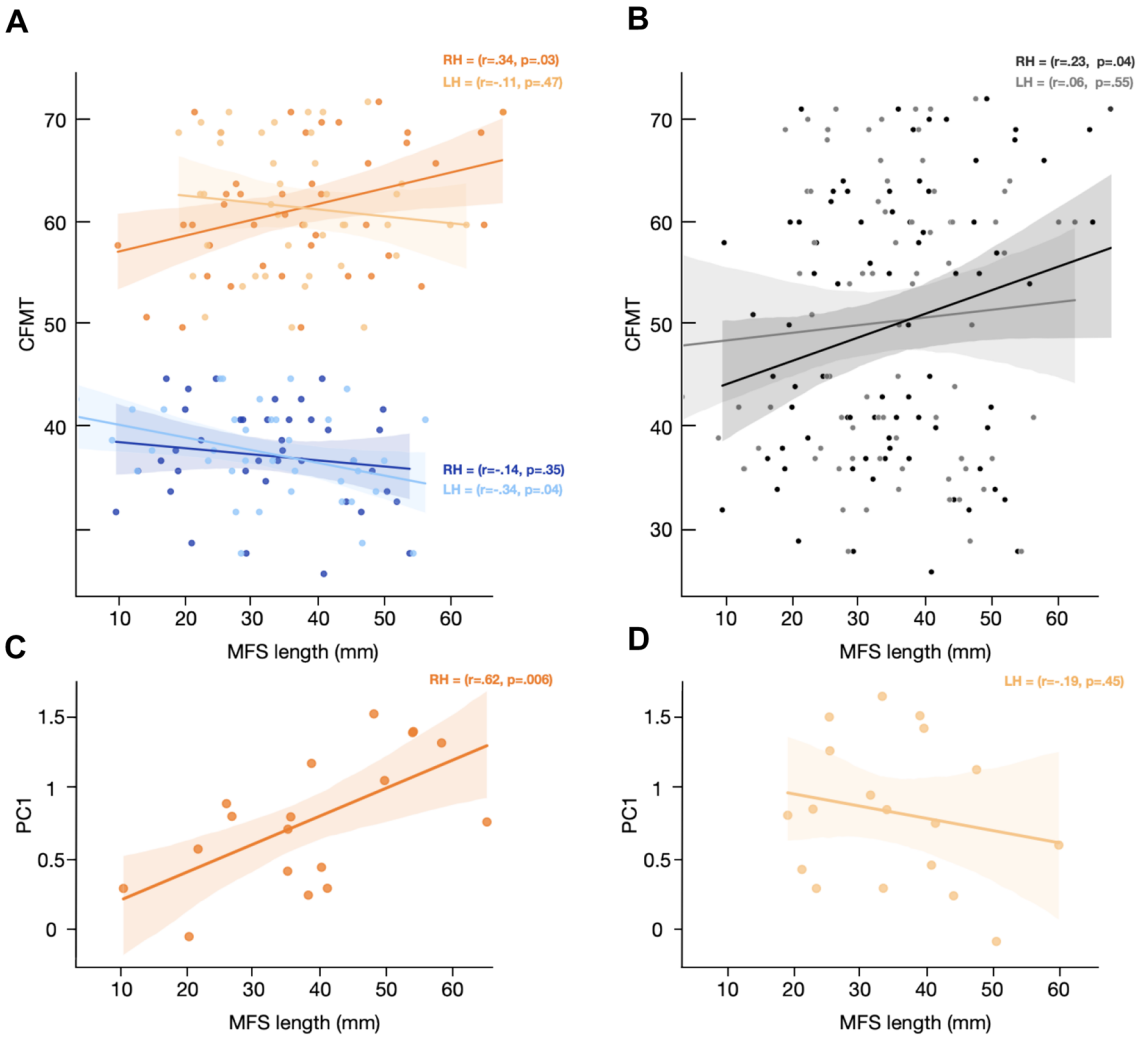

Fig. 2 The length of the mid-fusiform sulcus (MFS) is correlated with face recognition ability. **A** CFMT performance as a function of MFS length in NTs (orange) and DPs (blue) for the right (darker shade) and left (lighter shade) hemispheres. The length of the MFS in the NT right ($r = 0.34$, $p = 0.03$), but not NT left ($r = -0.11$, $p = 0.47$), hemisphere predicted CFMT scores, and these correlations were significantly different from one another (Fisher's $z = 2.08$, $p = 0.04$). In DPs, the length of the MFS in the left ($r = -0.34$, $p = 0.04$), but not right ($r = -0.14$, $p = 0.35$), hemisphere predicted CFMT score, but these correlations were not significantly different from each other (Fisher's $z = 0.89$, $p = 0.38$). **B** CFMT performance as a function of MFS length collapsed across groups for the left (lighter shade; $r = 0.06$, $p > 0.50$) and right (darker shade; $r = 0.23$, $p < 0.05$) hemispheres. While it may seem surprising that a longer MFS is related to higher CFMT scores in NTs, while the opposite is true in DPs, it is important to remember that a "high" CFMT score in DPs is actually impaired and DPs also have a shorter MFS. Indeed, when considering all of the data together, collapsed across groups and hemispheres, there is a positive correlation between MFS length and CFMT score ($r = 0.15$, $p = 0.05$). **C** The relationship between MFS length and face recognition ability is not limited to CFMT performance. Regression of MFS length in the right hemisphere of NTs against PC1 scores from Garrido et al. (2009) also revealed a positive relationship between MFS length and behavioral performance ($r = 0.62$, $p = 0.006$). PC1 loadings included tasks closely associated with facial identity, requiring encoding and recognizing faces, plus perceptual matching of faces (including Famous Faces, CFMT, Old–New Faces, Sequential Matching—identity). **D** Regression of MFS length in the left hemisphere of NTs against PC1 scores from Garrido et al. (2009) once again showed that the relationship between MFS length and behavioral performance was not significantly correlated in the left hemisphere ($r = -0.19$, $p = 0.45$)

participants as a single distribution with a range of CFMT scores (in which DPs are on the lower end of this distribution) separately in each hemisphere, the length of the MFS still predicts CFMT score in the right (Fig. 2B; $r = 0.23$, $p = 0.04$) but not the left (Fig. 2B; $r = 0.06$, $p = 0.55$) hemisphere. Thus, the positive correlation between MFS length in the right hemisphere and CFMT scores is stronger in NTs, but also reflects a general relationship when considering both groups together. However, the negative correlation between MFS length in the left hemisphere and CFMT scores in DPs does not reflect a general relationship when considering both groups together. Further, to remind the reader, CFMT scores for DPs (i) reflect poor task performance and (ii) have a truncated range of values. In addition, a qualitative observation from our previous publications (Garrido et al. 2009; Jiahui et al. 2018) is that differences in scores in the DP group may not be accurate estimates of their face recognition ability since we observed that some DPs gave up during the test whereas others persevered (with little predictability regarding who would quit or persevere).

The relationship between MFS length and face recognition ability is not limited to CFMT performance. Specifically, regression of MFS length in the right hemisphere of NTs against PC1 scores from Garrido and colleagues (2009) also revealed a positive relationship ($r = 0.62$, $p = 0.006$). Impressively, this relationship between MFS length in the right hemisphere and PC1 scores is even stronger in this analysis, which only includes 18 NTs from Dataset 1, compared to the previous analysis which included more than double the sample size (43 NTs across both Datasets). PC1 loadings included tasks closely associated with facial identity, requiring encoding and recognizing faces, plus perceptual matching of faces (including Famous Faces, CFMT, Old–New Faces, Sequential Matching—identity). In addition, this analysis once again showed that the relationship between MFS length and behavior (PC1 scores) was specific to the right hemisphere as this relationship was not significantly correlated when considering MFS length in the left hemisphere ($r = -0.19$, $p = 0.45$). We suspect that the stronger relationship between PC1 scores and MFS length compared to CFMT scores and MFS length is likely because PC1 scores are a purer measure of face recognition ability compared to CFMT scores.

Finally, while there was no difference in depth between groups for any of the three sulci ($F(1, 156) = 0.60$, $p = 0.40$), the MFS was shallower in NTs compared to DPs who identified as male, while the opposite was true for those who identified as female (natal sex × group interaction: $F(1, 156) = 5.10$, $p = 0.03$); Supplementary Fig. 3A). Despite this interaction, MFS depth did not predict CFMT score in either group (NTs: $F(1, 76) = 2.7$, $p = 0.10$; DPs: $F(1,70) = 2.40$, $p = 0.12$).

Discussion

Together, our results reveal that hominoid-specific sulcal variability is related to face perception ability in two ways. First, the length of the MFS was shorter in DPs than NTs. Second, MFS length in the right hemisphere was positively correlated with face recognition. As the MFS is a hominoid-specific structure, together, these findings empirically support that hominoid-specific sulcal variability is related to face perception for the first time.

These two main findings support a classic anatomical theory (Sanides 1962, 1964) positing that tertiary sulci are important landmarks in association cortices. They also complement previous and recent findings showing a relationship between either the depth or length of tertiary sulci and cognition in clinical populations and NTs (Voorhies et al. 2021; Yao et al. 2021; Brun et al. 2016; Garrison et al. 2015; Fornito et al. 2006; Fujiwara et al. 2007). Extending these findings, the present results are the first to (i) relate individual differences in tertiary sulcal length to individual differences in face perception and (ii) differentiate DPs from NTs based on tertiary sulcal length.

As the MFS is a functional and anatomical landmark (Weiner 2019; Grill-Spector and Weiner 2014), the relationship between MFS length and face perception identified here is likely associated with several functional and anatomical differences across NTs and DPs, which can be explored in future research. Importantly, this structural–functional coupling is not epiphenomenal: electrical charge delivered to electrodes on cortex lateral, but not medial, to the MFS produces causal, face-specific perceptual distortions (Jonas and Rossion 2021; Parvizi et al. 2012). Thus, future research can quantify the relationship between MFS length and (i) transitions in large-scale functional maps, (ii) the location of fine-scale functional regions, and (iii) decreased category- selectivity in DPs compared to NTs in VTC (Jiahui et al. 2018). In addition, the MFS also identifies microstructural transitions in VTC based on cytoarchitecture, myelin content, and receptor architecture (Weiner and Yeatman 2020). As such, the relationship between MFS length and face perception identified here could also be related to differences in the microstructure within and around the MFS in DPs compared to NTs, which would be consistent with an influential theory of selective developmental disorders that suggests neural migration problems may give rise to behavioral deficits like those seen in DP (Ramus 2004). Furthermore, recent findings show that anatomical features of longitudinal white matter tracts positioned lateral to the MFS differ in DPs and NTs and that these differences correlate with face perception (Gomez et al. 2015). Altogether, the seemingly simple relationship between MFS

length and face perception likely reflects complex, multi-scale functional and anatomical differences between NTs and DPs. For example, previous work provides evidence linking anatomical features to functional representations and face perception ability (McGugin et al. 2016, 2020). Yet, the effect size of the previous work focusing on cortical thickness within face-selective regions is substantially larger than that identified in the present work. Thus, a natural next question is: How much additional variance is explained when MFS length is included? This is a critical question which can be explored in future studies considering face selectivity, cortical thickness, sulcal morphology, and behavior.

More broadly, individual differences in MFS morphology may not only be linked to individual differences in face perception and DP but may also extend to additional disorders. For example, a recent study found that MFS morphology predicts behavioral performance on a theory of mind task in individuals with Autism Spectrum Disorder (Ammons et al. 2021). In addition, Bouhali and colleagues (2019) recently identified a cortical region selective for graphemes overlapping with the MFS (Bouhali et al. 2019). Thus, the morphology of the MFS may also be a critical biomarker in individuals with dyslexia or even predict phonological skills across individuals without dyslexia. Finally, in line with previous work (Brun et al. 2016; Garrison et al. 2015; Fornito et al. 2006; Fujiwara et al. 2007), our study empirically supports the utility of morphological analyses of tertiary sulci in different syndromes and diseases. As tertiary sulci emerge later in gestation, continue to develop after birth, and are either hominoid- or human-specific, they are ideal targets for future studies striving to better understand the neuroanatomical underpinnings of human developmental disorders.

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Data availability Data used for this project have been made freely available on GitHub (https://github.com/cnl-berkeley/stable_projects/tree/main/SulcalVariability_FacePerception). Requests for further information or raw data should be directed to the Corresponding Author, Kevin Weiner(kweiner@berkeley.edu).

Declarations

Conflict of interest The authors declare no competing financial interests.

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