



Sulcal variability in anterior lateral prefrontal cortex contributes to variability in reasoning performance among young adults

Ethan H. Willbrand¹ · Samantha Jackson² · Szeshuen Chen³ · Catherine B. Hathaway⁴ · Willa I. Voorhies³ · Silvia A. Bunge^{2,3} · Kevin S. Weiner^{2,3}

Received: 31 August 2023 / Accepted: 12 November 2023 / Published online: 6 January 2024
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2024

Abstract

Identifying structure–function correspondences is a major goal among biologists, cognitive neuroscientists, and brain mappers. Recent studies have identified relationships between performance on cognitive tasks and the presence or absence of small, shallow indentations, or sulci, of the human brain. Building on the previous finding that the presence of the ventral para-intermediate frontal sulcus (pimfs-v) in the left anterior lateral prefrontal cortex (aLPFC) was related to reasoning task performance in children and adolescents, we tested whether this relationship extended to a different sample, age group, and reasoning task. As predicted, the presence of this aLPFC sulcus was also associated with higher reasoning scores in young adults (ages 22–36). These findings have not only direct developmental, but also evolutionary relevance—as recent work shows that the pimfs-v is exceedingly rare in chimpanzees. Thus, the pimfs-v is a key developmental, cognitive, and evolutionarily relevant feature that should be considered in future studies examining how the complex relationships among multiscale anatomical and functional features of the brain give rise to abstract thought.

Keywords Comparative biology · Cortical folding · MRI · Neuroanatomy · Prefrontal cortex · Reasoning

Introduction

Identifying structure–function correspondences is a major goal across subdisciplines in the biological sciences. In neurobiology and cognitive neuroscience, there is a broad interest in uncovering relationships between neuroanatomical features of the human brain and cognition—especially

for structures in parts of the brain that are largely human specific. Given that 60–70% of the human cerebral cortex is buried in indentations, or sulci (Zilles et al. 1988, 2013; Van Essen 2007), there is continued interest in the relationships among sulcal morphology, functional representations, and cognition. Previous work exploring this relationship has largely focused on the consistent and prominent sulci within primary sensory cortices (Yousry et al. 1997; Boling et al. 1999; Hinds et al. 2008; Cykowski et al. 2008; Li et al. 2010; Wandell and Winawer 2011; Sun et al. 2012; Benson et al. 2012). Nevertheless, recent work has begun to explore the small and shallow sulci in association cortices (e.g., putative tertiary sulci) that are only present in humans and non-human hominoids.

The main aims of this recent work are to better understand (1) the relationship between individual differences in the morphology of putative tertiary sulci that are present in every hemisphere and individual differences in brain structure, brain function, and cognition (Weiner et al. 2014; Grill-Spector and Weiner 2014; Miller et al. 2021b; Willbrand et al. 2022a, 2023c; Miller and Weiner 2022) and (2) how the presence or absence of a variably present putative tertiary sulcus relates to functional and structural brain

Silvia A. Bunge and Kevin S. Weiner are co-senior authors.

✉ Silvia A. Bunge
sbunge@berkeley.edu

✉ Kevin S. Weiner
kweiner@berkeley.edu

¹ Medical Scientist Training Program, School of Medicine and Public Health, University of WI–Madison, Madison, WI, USA

² Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA, USA

³ Department of Psychology, University of California, Berkeley, Berkeley, CA, USA

⁴ Cognitive Science, University of California, Berkeley, Berkeley, CA, USA

organization, as well as cognitive performance, which is the focus of the present paper. For example, regarding the second main approach, previous studies have focused on how the presence or absence of the paracingulate sulcus (pcgs) in the medial prefrontal cortex relates to core executive functions in children and young adults (Fornito et al. 2004; Whittle et al. 2009; Huster et al. 2009; Buda et al. 2011; Borst et al. 2014; Amiez et al. 2018), as well if individuals with schizophrenia will hallucinate or not (Garrison et al. 2015; Rollins et al. 2020). Furthermore, the presence or absence of the pcgs has been related to changes in local gray matter cytoarchitecture (Vogt et al. 1995; Palomero-Gallagher et al. 2008; Amiez et al. 2021).

In terms of function, the cortical gray matter/cytoarchitecture is considered the neural hardware that performs the computations necessary for the function of a given cortical area, while white matter/myeloarchitecture is considered the neural hardware sending and receiving information to and from other brain areas, respectively. In this regard, changes in the computational (gray matter) or communicative hardware (white matter) due to the presence or absence of sulci/sulcal features could underlie these previously observed relationships to cognition. Building on the foundation of these structure–function relationships that have cognitive and clinical implications, theories, as well as computational and experimental studies, implicate the differential expansion of inner and outer layers of the gray matter, as well as white matter architecture, on the emergence and development of sulci in utero (Richman et al. 1975; Van Essen 1997, 2020; Kriegstein et al. 2006; White et al. 2010; Zilles et al. 2013; Kelava et al. 2013; Garcia et al. 2018; Holland et al. 2018; Wang et al. 2022).

Here, we focus on the anterior lateral prefrontal cortex (aLPFC) and reasoning, given several sequential findings linking the individual variability of an aLPFC sulcus to reasoning performance. Our recent work implementing a data-driven approach on 12 LPFC sulci showed that the morphology of the para-intermediate frontal sulcus (pimfs) in aLPFC was the best predictor of performance on a widely used test of reasoning in a pediatric sample (ages 6–18) (Voorhies et al. 2021). However, since we recently documented that the pimfs is composed of two variably present components [dorsal (pimfs-d) and/or ventral (pimfs-v) component(s)] (Voorhies et al. 2021; Willbrand et al. 2022b) that are also functionally dissociable from one another (Willbrand et al. 2023a), we then tested whether the presence of specific pimfs components was also related to reasoning scores in this pediatric sample. Indeed, we found that the presence of the pimfs-v in the left hemisphere, specifically, was associated with better reasoning performance (Willbrand et al. 2022b).

Therefore, in the present study, we tested the targeted prediction that this pattern of results across the four pimfs

components (left and right pimfs-v and pimfs-d) holds across age groups and studies. To this end, we first defined the pimfs components in a sample of young adults from the Human Connectome Project (HCP; $N=72$, 144 hemispheres, 50% female, 22–36 years old), as in our pediatric sample. We then assessed whether the presence or absence of the left or right pimfs components related to scores on a reasoning task from the NIH toolbox. We also tested whether presence/absence of pimfs-v or pimfs-d in either hemisphere was related to performance on measures of processing speed and working memory for two reasons. First, these cognitive abilities are theorized to be foundational for reasoning (Kail and Salthouse 1994; Fry and Hale 2000; Ferrer et al. 2013; Kail et al. 2016). Second, we had previously found that the presence of left pimfs-v was related to our measure of reasoning, but not to processing speed or working memory (Willbrand et al. 2022b). We also conducted exploratory analyses testing a relationship between presence/absence of the pimfs components and two executive function tests, as well as one episodic memory test, given previous findings showing that these measures (or similar ones) have been linked to PFC function (executive functions: Milner 1963; Posner et al. 1988; Botvinick et al. 1999; Ezekiel et al. 2013; control processes operating on episodic memory: Shimamura et al. 1990; Wagner et al. 2005; Blumenfeld and Ranganath 2019).

Materials and methods

Participants

Data for the young adult human cohort analyzed in the present study were taken from the Human Connectome Project (HCP) database (<https://db.humanconnectome.org>). Here, we used a sample of 72 randomly selected participants, balanced for gender (following the terminology of the HCP data dictionary), from the HCP database (50% female, 22–36 years old, 90% right handed). We selected this sample for three reasons. First, these participants have also been used in our previous work in multiple cortical expanses (Miller et al. 2020, 2021b; Willbrand et al. 2022a, 2023b, c, d, e); continuing to comprehensively label these same participants will afford future multi-sulcal and cross-region investigations. Second, this sample size mirrors that of our prior analyses relating the presence/absence of the pimfs and reasoning in children and adolescents (Willbrand et al. 2022b). Third, previous neuroanatomical investigations at the level of individual participants emphasize that a sample size of at least 20 can be large enough to capture individual differences and detect reliable group differences (e.g., Fornito et al. 2004, 2006; Amiez et al. 2006; Borst et al. 2014; Amunts and Zilles 2015; Zlatkina et al. 2016;

Lopez-Persem et al. 2019; Amunts et al. 2020). HCP consortium data were previously acquired using protocols approved by the Washington University Institutional Review Board. Informed consent was obtained from all participants.

Imaging data acquisition

Anatomical T1-weighted (T1-w) MRI scans (0.7 mm voxel resolution) were obtained in native space from the HCP database as well as cortical reconstructions generated through the HCP's version of the FreeSurfer pipeline (Dale et al. 1999; Fischl et al. 1999; Glasser et al. 2013). All sulcal labeling and anatomical metric quantification were done on the cortical surface reconstructions of each participant.

Behavioral data

Overview

In addition to structural and functional neuroimaging data, the Human Connectome project also included a wide range of behavioral metrics (motor, cognitive, sensory, and emotional processes) from the NIH toolbox that illustrates a set of core functions relevant to understanding the relationships between human behavior and the brain (Barch et al. 2013); task details: <https://wiki.humanconnectome.org>. As with the neuroimaging data, the behavioral data were acquired from the HCP database. 71 of 72 participants in the present project had behavioral scores. We used the non-age adjusted scores for all tests provided by the HCP (as opposed to scores normalized to a different sample) to assess the extent to which sulcal variability helps to explain the distribution of scores in our sample. Below, we describe the six behavioral tests used in our analyses. The first three were selected a priori; the others were added later for the purpose of exploratory analyses.

Relational reasoning task

The ability to reason about the patterns, or relations, among disparate pieces of information—i.e., relational reasoning—has long been recognized as central to human reasoning and learning (James 1890a, b; Cattell 1943). Tests of relational reasoning assess the ability to integrate and generalize across multiple pieces of information, and help to predict real-world performance in a variety of domains (Alexander 2016). Here, we used scores obtained for each participant on a measure of relational reasoning, the Penn Progressive Matrices Test from the NIH toolbox (Bilker et al. 2012). This test is similar to the classic Raven's Progressive Matrices (Raven 1941), the WISC-IV Matrix Reasoning task (Wechsler 1949) used in our pediatric sample (Willbrand et al. 2022b), and other task variants that are ubiquitous in

assessments of what is often termed “fluid intelligence.” In this task, participants must consider how shapes in a 2×2 , 3×3 , or 1×5 stimulus array are related to one another, for example, an increase, across a row or column, in the number of lines superimposed on a circle. Specifically, participants must identify the abstract relations among items in the array (Carpenter et al. 1990) and select, among five options, the shape that completes the matrix. The task is composed of 24 different matrices, presented in order of increasing difficulty. Testing is discontinued after five incorrect choices in a row, and the total score is calculated as the number of correct responses (with a maximum possible score of 24).

List sorting working memory task

Participants also completed the List Sorting Working Memory Test from the NIH toolbox (Tulsky et al. 2014). In this task, each participant sequences different visually and orally presented stimuli (alongside a sound clip and written text for the name of the item) in two conditions: 1-List and 2-List. In the former, participants order a series of objects (food or animals) from smallest to largest. In the latter, participants are presented with both object groups (food *and* animals) and must report the food in order of relative size in real life and then the animals in order of size. Testing is discontinued after two trials of the same length are failed, and the total score is calculated as the combined total number of correct items on both conditions (maximum of 28).

It is important to note that this is not a standard test of working memory (WM), such as the digit span test—used in our previous study (Willbrand et al. 2022b)—which requires immediate recall of items in a forward or backward order. Although the List Sorting task is not characterized as such, we posit that completing this task not only requires working memory manipulation and maintenance but also relational reasoning. That is, to report the items in order of size it is necessary to compare pairs of stimuli and then engage in transitive inference across multiple items. Indeed, size ordering has been cited as an example of relational reasoning (Halford et al. 1998).

Processing speed task

Participants also completed the Pattern Comparison Processing Speed Test from the NIH toolbox (Carlozzi et al. 2014, 2015). This test was designed to measure the speed of cognitive processing based on the participant's ability to discern whether two adjacent pictures are identical as quickly as possible. Here, participants consider several possible differences (addition/removal of an element or the color or number of elements on the pictures). A yes–no button press is used to determine whether the two stimuli are identical, and the final

score corresponds to the number of trials answered correctly during a 90-s period (maximum of 130).

Episodic memory task

Participants also completed the Picture Sequence Memory Test, which measures episodic memory (Bauer et al. 2013). This task involves encoding a thematically similar series of images presented on a computer screen (e.g., hiking, fishing, making a fire, and setting up a tent), and then there is a three second delay. The images are then presented out of order and participants must rearrange them into the correct temporal order. The number of images presented in a series gets longer and longer across three trials; the longest series presented ranges from 6 to 18 pictures, depending on the participant's age. There is a no stopping rule. One point is awarded for each correct adjacent pair of pictures. The maximum score is the total length minus one (e.g., if there are 15 pictures in a sequence, the maximum score is 14). The total score is the sum of adjacent-pair scores across the three trials.

Executive function tasks

Executive functioning was assessed using two widely used tasks: the Dimensional Change Card Sort Test and Flanker Test. The Dimensional Change Card Sort Test is commonly used as a measure of cognitive flexibility, or, more specifically, set-shifting (Milner 1963; Zelazo 2006; Zelazo et al. 2013, 2014). The task consists of showing the participant two target pictures that vary based on two dimensions (e.g., shape and color). Participants must match a series of bivalent test pictures (e.g., red rabbit and blue boat) to the target pictures based on one of the dimensions (e.g., color) which then changes to the other (e.g., shape) after a number of trials. Switch trials are also included, in which the participant is asked to match based on the other dimension and then return to the previous dimension. The total score is computed with a two-vector method combining accuracy, and for participants with high accuracy (> 80% correct), response time (for additional information see (Zelazo et al. 2013, 2014).

The Flanker Test is widely used to assess selective attention and response inhibition. In the classic version of the test (Eriksen and Eriksen 1974), implemented in the NIH Toolbox (Zelazo et al. 2013, 2014), the participant is asked to selectively attend to a central arrow in a horizontal array of arrows. Each arrow points either to the left or right, and the participant's task is to press either a left or right button in response to the direction in which the central arrow is facing. On congruent trials, the direction of the central and flanker arrows matches; on incongruent trials, the flanker arrows point in the opposite direction of the central arrow. Thus,

accurate performance requires overriding the tendencies to both attend and respond to the more numerous, flanking stimuli. The total score is a combination of accuracy (across both congruent and incongruent trials) and response times, computed in the same manner as the Dimensional Change Card Sort Test (Zelazo et al. 2013, 2014).

Morphological data

Defining the presence and size of the para-intermediate middle frontal sulcus

Individuals typically have anywhere from three to five putative tertiary sulci within the middle frontal gyrus (MFG) in LPFC (Miller et al. 2021a, b; Voorhies et al. 2021; Yao et al. 2022). The posterior MFG contains three of these sulci, which are present in all participants: the anterior (pmfs-a), intermediate (pmfs-i), and posterior (pmfs-p) components of the posterior middle frontal sulcus (pmfs). In contrast, the tertiary sulcus within the anterior MFG, the para-intermediate middle frontal sulcus (pimfs), is variably present. A given hemisphere can have zero, one, or two pimfs components (Fig. 1). As described in prior work (Petrides 2013, 2019; Willbrand et al. 2022b), the dorsal and ventral components of the pimfs (pimfs-d and pimfs-v) were generally defined using the following two-fold criterion: (i) the sulci that appear immediately ventrally and lateral to the horizontal and ventral components of the intermediate middle frontal sulcus (imfs-h and imfs-v), respectively (with the intersection/gyral border of the imfs-h and imfs-v being the border separating the pimfs-d from pimfs-v), and (ii) superior and/or anterior to the mid-anterior portion of the inferior frontal sulcus (ifs) (Fig. 1A). It is worth noting that although the two pimfs components are most commonly separate from other sulci, in some cases, they do intersect with nearby sulci with common patterns. For instance, the pimfs-d may intersect with the pmfs-a, which resides just posterior to it. Further, the pimfs-v may intersect ventrally with the pretriangular sulcus (prts; see Fig. 1A “ventral pimfs only” for example) or lateral frontomarginal sulcus (lfms). In some cases, the pimfs-d and pimfs-v may intersect with the imfs or with the ifs (see Fig. 1A “dorsal pimfs only” for an example). For comprehensive examples of individually-defined pimfs components in this sample and other samples, see (Willbrand et al. 2022b, 2023a).

We first manually defined the pimfs within each individual hemisphere with *tksurfer* (Miller et al. 2021b). Manual lines were drawn on the *inflated* cortical surface to define sulci based on the most recent schematics of pimfs and sulcal patterning in LPFC by Petrides (Petrides 2019) and from our own expertise in defining these components from our previously published work (Willbrand et al. 2022b, 2023a), as well as by the *pial* and *smoothwm* surfaces of each

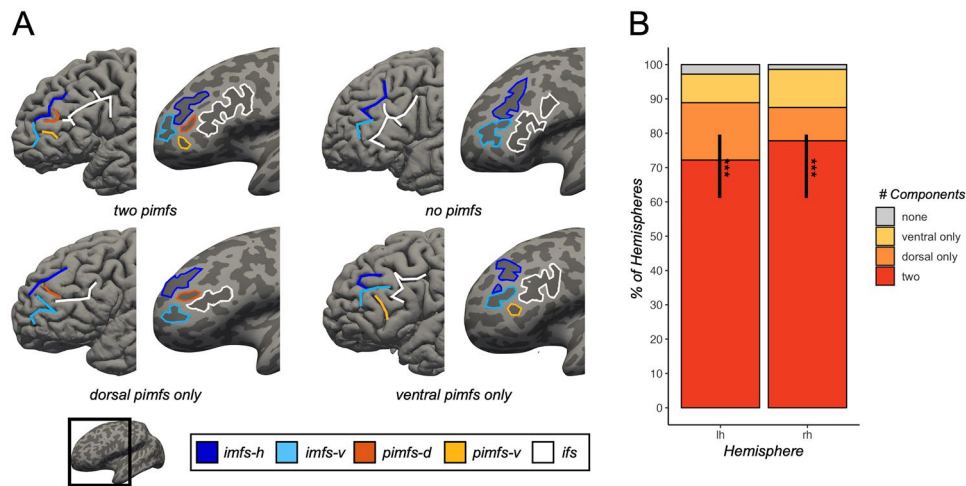


Fig. 1 The para-intermediate frontal sulcus (pimfs) is variable across individuals and hemispheres. **A** Left hemispheres (sulci: dark gray; gyri: light gray; cortical surfaces are not to scale) depicting four types of the pimfs: (i) both pimfs-v/d present, (ii) neither present, (iii) pimfs-d present, (iv) pimfs-v present. For each set, the cortical surface reconstruction from the same hemisphere is shown in both the pial (left) and inflated (right) versions. Prominent sulci surrounding

the pimfs components are shown: two components of the intermediate frontal sulci—horizontal (imfs-h) and ventral (imfs-v)—and the inferior frontal sulcus (ifs; see legend). See Willbrand et al. (2023a, b, c, d, e) and Willbrand et al. (2022a, b) for additional examples of the pimfs patterning in individual hemispheres. **B** Stacked bar plot depicting pimfs incidence in left (lh) and right (rh) hemispheres ($N=72$; see rightward legend). (***) $p < 0.001$

individual (Miller et al. 2021b). Using multiple surfaces allows for the establishment of a consensus across surfaces and clearly determines sulcal boundaries. The location of the pimfs was confirmed by three trained independent raters (E.H.W., S.M., S.C.) and finalized by a neuroanatomist (K.S.W.). Although this project focused on a single sulcus, the manual identification of all LPFC sulci (2877 sulcal definitions across all 144 hemispheres) was required to ensure the most accurate definitions of the pimfs components.

The size of the pimfs was quantified as surface area (in mm^2), as a quantitative comparison to the qualitative metric of sulcal incidence. The surface area of each pimfs label was extracted with the `mrisc_anatomical_stats` FreeSurfer function (Fischl and Dale 2000). For participants with two pimfs components, the surface area was quantified as a sum of both components. For participants with one pimfs component, the surface area was quantified as that single component. As in previous work (Clark et al. 2010; Rollins et al. 2020), the surface area was set to zero for participants with no pimfs component. To control for individual differences in brain size, as in prior work (Willbrand et al. 2022b, 2023d; Hathaway et al. 2023), we normalized the surface area as a percent of the hemispheric surface area.

Probability map generation

As in prior work (Miller et al. 2020, 2021b; Voorhies et al. 2021; Willbrand et al. 2022a; Hathaway et al. 2022), sulcal probability maps were calculated to display the vertices with the highest alignment across participants for a given

sulcus. The label files for the pimfs-d, pimfs-v, imfs-h, imfs-v, and ifs were first transformed from the individual to the fsaverage surface. Once transformed to this common template space, the proportion of participants for whom a given vertex was labeled as the given pimfs component was then calculated. For vertices where the pimfs components overlapped, we employed a “winner-take-all” approach. Here, the component with the highest overlap across participants was assigned to that overlapping vertex. Unthresholded maps and constrained versions of these maps—i.e., maximum probability maps (MPMs), which improve map interpretability (Miller et al. 2021b)—are available (Data accessibility statement). MPMs for these five sulci are shown in Fig. 2.

Analysis I: comparing the incidence rates of the pimfs components

We first compared the incidence rates of the pimfs components—both as number of components (2 vs < 2) and as the presence of the specific pimfs component (dorsal vs ventral)—in each hemisphere with Chi-squared (χ^2) tests. Note that all statistical tests in the present project were implemented in R (v4.1.2; <https://www.r-project.org/>) and each set of analyses was corrected for multiple comparisons (with the false-discovery rate; FDR). Chi-squared tests were carried out with the `chisq.test` function from the stats R package.

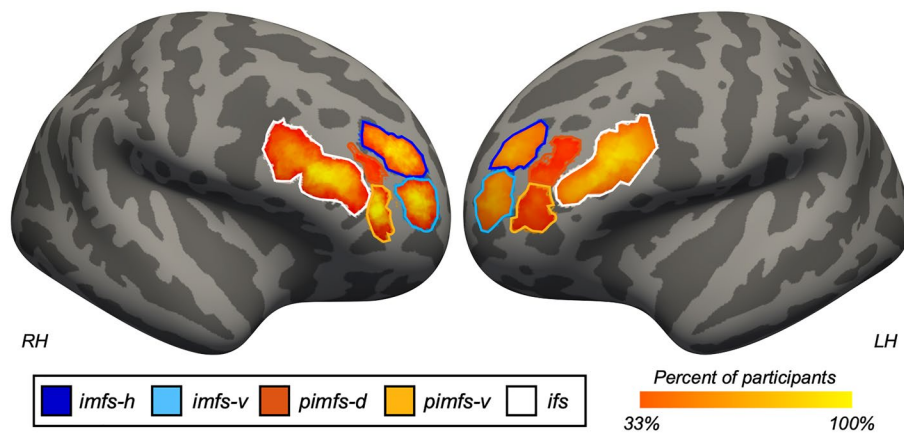


Fig. 2 Maximum probability maps (MPMs) of the pimfs and surrounding sulci. MPMs of the pimfs-d, pimfs-v, and three surrounding sulci (imfs-h, imfs-v, and ifs) on the inflated fsaverage cortical surface (left surface: right hemisphere, RH; right surface: left hemisphere, LH). Sulci are outlined according to their colors in Fig. 1A. For vis-

ual clarity, as in our prior work (Miller et al. 2020, 2021b; Voorhies et al. 2021; Willbrand et al. 2022a; Hathaway et al. 2022), the MPMs were thresholded at 33% overlap across participants (the warmer the color, the higher the overlap)

Analysis II: relating the presence and size of the pimfs to hemisphere, age, and gender

Prior work has indicated that the presence of variable sulci may differ between hemispheres and by participant gender (Paus et al. 1996; Clark et al. 2010; Wei et al. 2017; Amiez et al. 2019, 2021). Further, although sulcal patterning emerges before birth and is stable across the lifespan (Cachia et al. 2021), there could have been an age imbalance in pimfs incidence in our sample, purely by chance. There could have also been an imbalance in pimfs incidence between genders in our sample. Thus, we sought to test for differences in incidence rates as a function of hemisphere, gender, and age. To this end, we implemented three binomial logistic regression GLMs with hemisphere (left, right), age, and gender (male, female), as well as their interactions, as factors for (i) number of components [0 (fewer than 2 components), 1 (2 components)], (ii) pimfs-d presence [0 (absent), 1 (present)], and (iii) pimfs-v presence [0 (absent), 1 (present)]. Finally, in addition to these categorical analyses, we examined a continuous variable, conducting a multiple linear regression for normalized total surface area of the pimfs component(s). GLMs were implemented with the glm function from the stats package. ANOVA χ^2 tests were applied to each GLM with the Anova function from the car package. Linear regressions were performed with the lm function from the stats package.

Analysis III: relating the presence of the pimfs to reasoning performance

These analyses were performed on the 71 participants with behavioral scores. Participant age and gender were not

considered in these analyses, as Analysis II showed that they did not differ in terms of pimfs presence (Results) or reasoning performance (*age*: unstandardized $\beta=0.01$, $p=0.98$; *gender*: $\chi^2=0.04$, $p=0.84$). We first ran two-sample t-tests to assess whether the number of components in each hemisphere (*two* vs. *less than two*) related to reasoning performance (Penn Progressive Matrices Test). In the main text, we report differences between groups as the percentage increase in average scores (μ) from the “less than two” group to the “two” group with the following equation:

$$\frac{\mu(\text{two}) - \mu(\text{less than two})}{|\mu(\text{less than two})|} \times 100$$

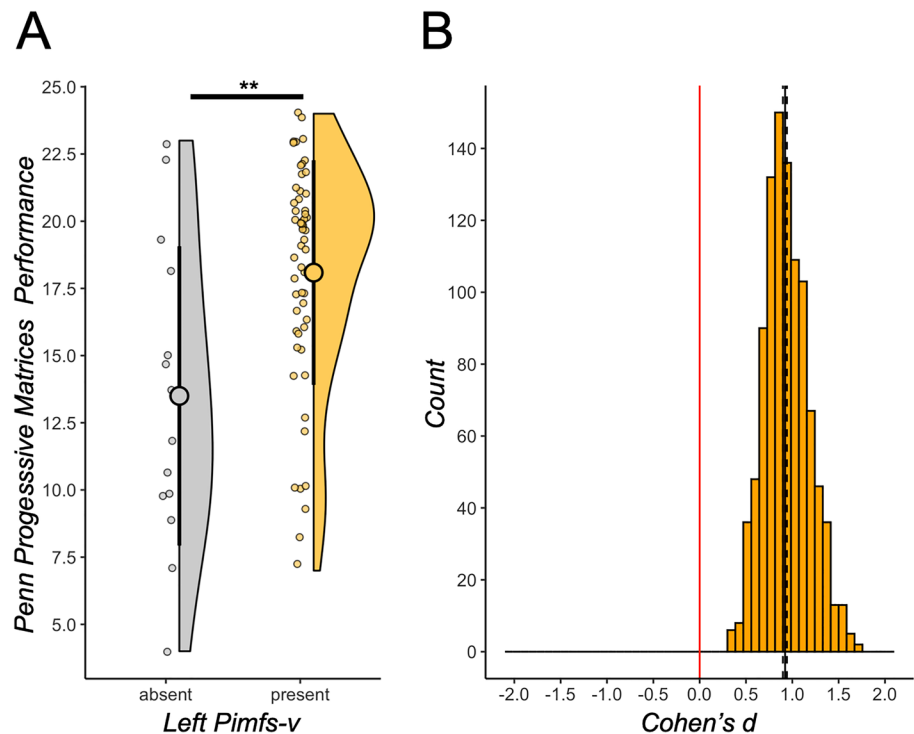
Next, to determine if the presence of a specific pimfs component was related to reasoning performance, we ran additional two-sample t-tests to test for an effect of the presence of the pimfs-v and pimfs-d (*present* vs *absent*) in each hemisphere. As in the prior analysis, we report differences between groups as the percentage increase in μ from the “absent” group to the “present” group.

To determine whether the observed relationship between the left pimfs-v presence and reasoning (Fig. 3B) was impacted by differences in sample size between participants with and without this sulcus, we iteratively sampled a subset of participants from the left pimfs-v present group ($N=57$) to match that of the left pimfs-v absent group ($N=14$) 1000 times and conducted a Welch’s *t*-test for each sampling (to account for potential unequal distributions when resampling). To evaluate the bootstrapped effect size, we report the median and 95% confidence interval for the effect size.

Next, given the wide age range (22–36 years old) and prior work indicating that reasoning performance peaks

Fig. 3 Relational reasoning is related to left pimfs-v presence.

A Raincloud plots (Allen et al. 2021) depicting Penn Progressive Matrices task score as a function of left pimfs-v presence in young adults (present, $N=57$; absent, $N=14$). Large dots and error bars represent mean $\pm$ std reasoning score; violin plots represent kernel density estimate. Small dots indicate individual participants. **B** Histogram visualizing results of the iterative resampling (1000 times) of left pimfs-v presence in A. Distribution of the effect size (Cohen's d) is shown, along with the median (black line) and 95% CI (dotted lines). Red line corresponds to zero, highlighting that left pimfs-v absence was never associated with higher reasoning scores than left pimfs-v presence. (** $p < 0.01$)



in the early 20 s (McArdle et al. 2002), we implemented a 3-step procedure to ensure that age did not confound the results and to further evaluate the model fit. First, we ran a linear regression with left pimfs-v presence and age as predictors for reasoning in the full sample ($N=71$ with reasoning scores). We then ran a Chi-squared test to compare the previously described regression model to one including age only. Second, to test more conclusively that age did not drive the effect of left pimfs-v presence on reasoning scores, we conducted variable-ratio matching on age (ratio = 3:1, min = 1, max = 5; optimal ratio parameters were based on the calculation in (Ming and Rosenbaum 2000)) with the MatchIt package. Here, the distance between each member of each group (left pimfs-v presence, left pimfs-v absence) was calculated with a logit function:

$$\text{Estimate } \pi_i = \Pr(\text{noPimfs}_i = 1|X) = \frac{1}{1 + e^{-X_i\beta}}$$

$$\text{Distance}(X_i, X_j) = \pi_i - \pi_j$$

where X is participant age in groups without (i) and with (j) a left pimfs-v. Matches were based on a greedy nearest-neighbor interpolation where each participant in the smaller group (left pimfs-v absent) received 1–5 unique matches from the larger group (left pimfs-v present). Afterwards, we ran a weighted linear regression in the matched sample, with left pimfs-v presence and age as predictors of reasoning, to further test the robustness of our initial finding with the

whole sample. Third, we employed a two-pronged analysis to assess and verify the unique variance explained by left pimfs-v presence, while accounting for age-related effects on reasoning (see Supplementary Results and Supplementary Fig. 2). We began by running a Chi-squared test to compare the previously described weighted-regression model to one with age only. Then, as described and implemented in prior work (Voorhies et al. 2021; Yao et al. 2022; Willbrand et al. 2022b), we fit these weighted-regression models with repeated K-fold cross-validation (CV; five-fold, 10 repeats). Since these are nested models, the best fit was determined as the model with the lowest cross-validated RMSE_{cv} and the highest R^2_{cv} value. We did not conduct this second procedure with gender given the lack of relation between gender and either (1) pimfs incidence (in this sample; Results) or (2) reasoning, both in this sample (Materials and Methods) and in a larger sample ($N=523$) (Wendelken et al. 2017).

T -tests were implemented with the `t.test` function from the R stats package. T -test effect sizes are reported with Cohen's d (d) metric. The median and 95% confidence intervals were calculated with the `MedianCI` function from the DescTools R package. Linear regressions were run with the `lm` function from the stats package. Variable-ratio matching was implemented with the `matchit` function from the MatchIt package.

Analysis IV: control behavioral analyses

To ascertain whether the observed relationship between sulcal morphology and cognition is specific to reasoning

performance, or generalizable to other measures of cognitive processing, we conducted planned tests of sulcal-behavior relationships for measures of list-sorting working memory (List Sorting Working Memory Test), and processing speed (Pattern Comparison Processing Speed Test) in line with our previous work (Voorhies et al. 2021; Willbrand et al. 2022b). We also conducted exploratory analyses on tests of episodic memory (Picture Sequence Memory Test) and executive function (Dimensional Change Card Sort Test and Flanker Test). Participant age and gender were not considered in these analyses, as they were not reliably associated with any of these measures ($p > 0.34$). Two-sample *t*-tests were run to test for differences in performance on each measure as a function of left pimfs-v presence (*present* vs *absent*). If any comparison was statistically significant, we then used the Akaike Information Criterion (AIC) to compare the model predictions to reasoning predictions. Briefly, the AIC provides an estimate of in-sample prediction error and is suitable for non-nested model comparison. By comparing AIC scores, we are able to assess the relative performance of the two models. If the ΔAIC is > 2 , it suggests an interpretable difference between models. If the ΔAIC is > 10 , it suggests a strong difference between models, with the lower AIC value indicating the preferred model (Wagenmakers and Farrell 2004; Burnham and Anderson 2004).

Given that there was also a significant correlation between the Penn Matrices and List Sorting test scores (unstandardized $\beta = 1.42$, $p < 0.001$), and that List Sorting performance varied as a function of left pimfs-v sulcal presence/absence (Fig. 4A), we tested whether this relationship was mediated by reasoning performance, consistent with the hypothesis that the behavioral-sulcal association for List Sorting is explained by relational reasoning demands of this specific working memory task. To this end, we implemented a bootstrapped causal mediation analysis (1000 simulations)

to quantify the average causal mediation effect (ACME) of reasoning on the left pimfs-v presence and working memory relationship (mediation diagram in Fig. 4B).

T-tests were implemented with the *t.test* function from the R stats package. *T*-test effect sizes are reported with Cohen's *d* (*d*) metric. AIC values were quantified with the AIC function from the stats R package. The causal mediation analysis was implemented with the *mediate* function from the mediation package.

Analysis V: relating the size of the pimfs to reasoning performance

As in prior work (Clark et al. 2010; Garrison et al. 2015; Cachia et al. 2018; Rollins et al. 2020; Willbrand et al. 2022b), to determine whether it was truly a discrete sulcal metric that mattered, we followed up by testing whether a related continuous metric—the size, i.e., normalized surface area, of the pimfs—was also related to reasoning performance. To do so, we implemented a multiple linear regression with normalized total surface area of the pimfs component(s) in left and right hemispheres as predictors. Age and gender were not included, as they were not related to pimfs surface area (Results) or to reasoning performance. Linear regressions were implemented with the *lm* function from the stats package.

Analysis VI: relating the probabilistic location of the pimfs-v to a meta-analysis of fMRI studies that include the term “reasoning”

To situate the pimfs-v within the current state of fMRI research on reasoning, we downloaded the association and uniformity test meta-analysis maps for the search term ‘reasoning’ ($N = 182$ studies) from Neurosynth (<https://neuro>

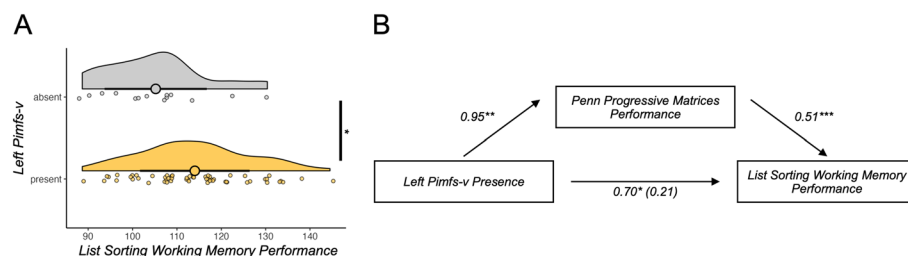


Fig. 4 Relationship between List Sorting Working Memory performance and left pimfs-v presence is mediated by reasoning performance. **A** Same format as Fig. 3, but for the List Sorting Working Memory Test. **B** Mediation diagram showing that the relationship between left pimfs-v presence and working memory is fully mediated by reasoning performance (via an indirect effect computed for 1,000 bootstrapped samples with the bias-corrected method; average causal mediation effect [95% CI] = 0.49 [0.18, 0.93], $p = 0.006$). Standardized parameter estimates (numbers) and p -values (asterisks) are

included for each relationship. The standardized parameter estimate for the direct effect between left pimfs-v presence and list sorting performance is shown outside of parentheses. The standardized parameter estimate for this relationship, controlling for reasoning performance, is shown in parentheses. Note that this effect disappears in the latter case (standardized $\beta = 0.21$, $p = 0.44$), indicating that this relationship is fully mediated by reasoning performance. (***) $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; no asterisks $p > 0.05$

[synth.org/](https://neurosynth.org/); Yarkoni et al. 2011). The uniformity test map was generated from a χ^2 test comparing the activation in each voxel for studies containing the term ($N=182$) compared with what one would expect if activation were uniformly distributed throughout the gray matter. The association test map was generated from a χ^2 test comparing the proportion of studies demonstrating activation in each voxel for studies containing the term ($N=182$) of interest compared with all other studies in the Neurosynth database ($N>14,000$). Both tests were whole-brain FDR-corrected ($p=0.01$). These maps were then projected to fsaverage surface space with the `mri_vol2surf` FreeSurfer function so that the pimfs-v probabilistic maps in each hemisphere could be spatially related (data shown in Fig. 5).

Results

The pimfs was variably present within the 144 young adult hemispheres examined (four example hemispheres depicting different types of pimfs patterning are presented in Fig. 1A). It was more common for participants to have two components in a given hemisphere (*left*: 72.22% of participants; *right*: 77.78%) than either one (*left*: 25%; *right*: 20.83%) or none (*left*: 2.78%; *right*: 1.39%; $\chi^2s > 54$, $ps < 1.59\text{e-}12$ in both hemispheres). When only one pimfs component was present, it was equally likely to be a dorsal or ventral component ($\chi^2s < 2$, $ps > 0.31$ in both hemispheres; Fig. 1B). The number of pimfs components and the presence of the pimfs-d and pimfs-v did not differ between hemispheres ($ps > 0.23$; Fig. 1B) or by participant age and gender ($ps > 0.23$); nor did the surface area of the pimfs differ by these features ($ps > 0.60$). There were no significant interactions between these variables in any analysis ($ps > 0.23$). These incidence rates were similar to those observed in our previous sample of children and adolescents (Willbrand et al. 2022b). To aid

future identification in other samples, we share probabilistic maps of the pimfs components (Fig. 2).

Since the pimfs was variably present among young adults, we statistically tested whether this variability was related to reasoning performance (quantified as scores on the Penn Progressive Matrices Test), as previously found for children and adolescents using a similar matrix reasoning task (Willbrand et al. 2022b). The presence of two pimfs components in the left hemisphere was associated with 21% better reasoning performance on average (mean $\pm$ std = 18.1 ± 4.21) relative to either one or none (mean $\pm$ std = 15.0 ± 5.59 ; $t(69)=2.54$, $p=0.026$, $d=0.67$). This effect was not driven by the fact that individuals with two components tended to have a larger overall pimfs surface area, since pimfs surface area (normalized by hemisphere surface area) was not related to reasoning ($ps > 0.90$; Supplementary Fig. 1). As previously found in children and adolescents (Willbrand et al. 2022b), this effect was driven by the presence or absence of the left pimfs-v: participants with a left pimfs-v (mean $\pm$ std = 18.1 ± 4.18) had on average 34% higher reasoning scores relative to those without it (mean $\pm$ std = 13.5 ± 5.57 ; $t(69)=3.44$, $p=0.004$, $d=1.03$; Fig. 3A). Neither the right pimfs-v nor pimfs-d showed this effect ($ts < 1.32$, $ps > 0.38$, $ds < 0.47$). To account for the difference in sample sizes between adults with and without the left pimfs-v, we iteratively sampled a size-matched subset of the left pimfs-v present group 1,000 times. This procedure supported the behavioral difference (median [95% CI] $d=0.92$ [0.90–0.94]; Fig. 3B). Finally, although reasoning performance was unrelated to age in this young adult sample (unstandardized $\beta=0.01$, $p=0.98$), we conducted additional analyses to provide additional evidence that age did not confound the results (Supplementary Results; Supplementary Fig. 2).

To assess the generalizability and/or specificity of this brain-behavior relationship, we tested whether left pimfs-v presence was associated with performance on the List

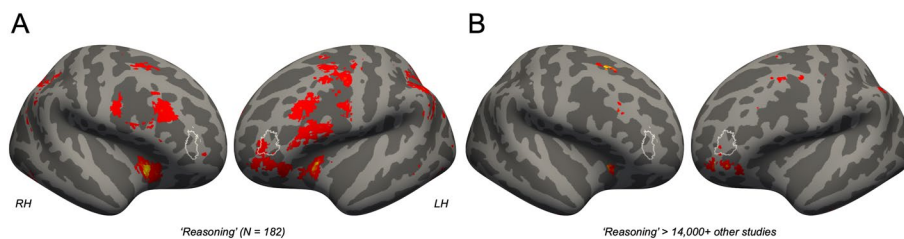


Fig. 5 **A** Neurosynth meta-analysis shows that the most probable location of the left, but not right, pimfs-v includes and forms the dorsal border of a functional region that has been preferentially implicated in reasoning. **A** Left and right hemisphere inflated *fsaverage* cortical surfaces (left surface: right hemisphere, RH; right surface: left hemisphere, LH) displaying overlap of a whole-brain FDR-corrected ($p=0.01$) uniformity-test meta-analysis z-score map of the “reasoning” term (warm-colored heatmap; downloaded from Neu-

rosynth (<https://neurosynth.org/>) and the left pimfs-v MPM (white outline; from Fig. 2). **B** Same format as **A** for a whole-brain FDR-corrected ($p=0.01$) association-test meta-analysis z-score map of the “reasoning” term. Since the association test is more stringent than the uniformity test in **A**, it is unsurprising that there is less overlap between the left pimfs-v MPM and the clusters identified by the meta-analysis

Sorting Working Memory Test or the Pattern Comparison Processing Speed Test, as working memory and processing speed are foundational cognitive skills that support reasoning (Kail and Salthouse 1994; Fry and Hale 2000; Ferrer et al. 2013; Kail et al. 2016; Holyoak and Monti 2021). The List Sorting task requires reordering items according to their relative size, thus requiring relational reasoning, in the form of transitive inference, in addition to working memory (Materials and Methods). Participants with a left pimfs-v (mean $\pm$ std = 114 ± 12.3) had on average 9% better performance on the List Sorting task on average relative to those without it (mean $\pm$ std = 105 ± 11.5 ; $t(69) = 2.42$, $p = 0.035$, $d = 0.72$; Fig. 4A). While significant, this effect was not as large as for the Penn Matrices task ($\Delta AIC_{(\text{working memory} - \text{reasoning})} = 142.23$). Additionally, the relationship between left pimfs-v presence and List Sorting scores was significantly fully mediated by Penn Matrices scores (via an indirect effect computed for 1,000 bootstrapped samples with the bias-corrected method; average causal mediation effect [95% CI] = $0.49 [0.18, 0.93]$, $p = 0.006$; Fig. 4B), further indicating that the relationship between left pimfs-v and relational reasoning is the stronger one. By contrast, left pimfs-v presence was not related to the processing speed task performance ($t(69) = 0.24$, $p = 0.81$, $d = -0.07$; Supplementary Fig. 3A).

Finally, to further explore the generalizability and/or specificity of this relationship, we also tested whether left pimfs-v presence was related to three other tests of cognitive skills that rely on PFC function: the Picture Sequence Memory, Dimensional Change Card Sort, and Flanker tests. However, left pimfs-v presence was not related to scores on any of these three measures (Supplementary Fig. 3; *Picture Sequence Memory*: $t(69) = 2.05$, $p = 0.13$, $d = 0.61$; *Dimensional Change Card Sort Test*: $t(69) = 0.09$, $p = 0.93$, $d = 0.03$; *Flanker Test*: $t(69) = 1.02$, $p = 0.46$, $d = 0.31$). Taken together, left pimfs-v presence was related most strongly to the test of relational reasoning, and to a lesser extent to the test of list-sorting working memory—for which the relationship was fully mediated by reasoning performance—but was not related to the measures that tax processing speed, episodic memory, or executive functioning.

Discussion

The pimfs exhibits prominent variability in humans that is robustly linked to variability in relational reasoning performance across age groups: in young adulthood, as reported here, and in childhood and adolescence (ages 6–18), as reported previously (Willbrand et al. 2022b). The pattern of results across the two studies was strikingly similar, with left pimfs-v—but not right pimfs-v or left or right pimfs-d—implicated in a test of matrix reasoning. We found that

children and adults with left pimfs-v had on average 28% and 34% higher reasoning scores, respectively, than those without it. In the same sample of young adults, we recently showed that pimfs-v and pimfs-d exhibited different patterns of large-scale resting-state functional connectivity, whereby the pimfs-v was associated with control-related networks and the pimfs-d was associated with attention-related networks (Willbrand et al. 2023a). Thus, the present behavioral dissociation between these sulcal components likely stems from participation in different brain networks and cognitive functions.

In addition to being associated with better reasoning scores, we also found that the presence of left pimfs-v was associated with better performance on a test of working memory in the present study on adults—albeit not on a different working memory test completed by our pediatric sample. Children and adolescents completed a standard task involving repeating a series of numbers in order or in reverse order (WISC-IV Digit Span working memory task; Wechsler 1949). By contrast, adults completed a List Sorting task that requires participants to encode a series of objects into working memory and reorder them according to their size in real life. Size ordering, an example of transitive inference, is recognized as a form of relational reasoning (Halford et al. 1998). We found an effect of left pimfs-v presence on List Sorting in adults, but not on Digit Span in children. We posit, based on part on a prior fMRI study of transitive inference implicating aLPFC in relational, but not non-relational, working memory (Wendelken et al. 2008a), that the apparent discrepancy between these findings relates to substantive differences in task demands, whereby only List Sorting requires relational reasoning. Consistent with this hypothesis, we found that the relationship between left pimfs-v presence and List Sorting was fully mediated by performance on the matrix reasoning task. Future research is also necessary to confirm that the left pimfs-v is not involved in the Digit Span working memory task in young adults as well.

Importantly, this sulcal-behavioral relationship did not generalize to all cognitive tasks—just as it did not generalize to all sulci. In both the adult and pediatric samples, the incidence of left pimfs-v was not related to tests of processing speed. The studies covered different age ranges—ages 22–36 vs. 6–18—and also used different tests of processing speed (children: Woodcock-Johnson Psychoeducational Battery Cross Out task; Brown et al. 2012; young adults: Pattern Comparison Processing Speed Test; Carlozzi et al. 2014, 2015). Here, we provide additional evidence of some level of specificity of this relationship, as the incidence of the left pimfs-v in adults was not related to a task assessing episodic memory or two tasks assessing executive functioning. Taken together, these findings establish a robust anatomical-behavioral association that does not generalize to

all forms of cognition or to all sulci, which converges with the observed functional dissociation between neighboring sulcal components (Willbrand et al. 2023a). Future investigations can seek to further replicate these results in similar and additional (e.g., older adults) age groups, with yet more cognitive measures, and with additional analysis methods (e.g., Bayesian statistics).

This extension of our previous pattern of results across four sulcal components to a new sample, involving different age ranges (22–36 as opposed to 6–18) using different variants of a reasoning task, is a notable finding given a timely discussion among researchers regarding the reliability and generalizability of brain-behavior relationships (Marek et al. 2022; Gratton et al. 2022; Westlin et al. 2023). It is also notable because it converges with other types of evidence implicating aLPFC in reasoning. We now discuss these findings in the context of (i) the role of aLPFC in reasoning, (ii) hypothesized relationships among the presence/absence of sulci, the morphology of sulci, and the efficiency of network communication contributing to performance on cognitive tasks, and (iii) the translational implications of aLPFC sulcal variability.

The anatomical-behavioral link reported here and in our previous study (Willbrand et al. 2022b) appears to provide converging evidence with fMRI research on relational reasoning. Neurosynth, a meta-analytic tool drawing on over 14,000 fMRI studies (Yarkoni et al. 2011), shows that the most probable location of the left pimfs-v includes, and forms the dorsal border of, a functionally defined area in aLPFC often referred to as rostralateral prefrontal cortex that has—particularly in the left hemisphere—been implicated in higher-order relational thinking of the kind taxed by matrix reasoning and transitive inference (Fig. 5; for examples see Christoff et al. 2001; Kroger et al. 2002; Bunge et al. 2005; Wendelken et al. 2008a, b; Crone et al. 2009; Wendelken and Bunge 2010; Dumontheil et al. 2010; Krawczyk 2012; Vendetti and Bunge 2014; Hobeika et al. 2016; Hartogsveld et al. 2018; Assem et al. 2020; Holyoak and Monti 2021). Future research should investigate this intriguing overlap, directly testing the spatial correspondence between the pimfs-v and reasoning-related task activations in individual participants, as well as further explore underlying features contributing to the hemispheric specificity identified in previous fMRI studies and the present study. Further, it would be useful for future work to also address why, given these converging lines of evidence, some neuropsychological studies show that damage to aLPFC affects reasoning task accuracy (Urbanski et al. 2016; Bendetowicz et al. 2018) while others have not (Burgess 2000; Tranel et al. 2008; Waechter et al. 2013).

While we focus on the pimfs in the present study, and do show a sizeable relationship to reasoning performance, we hypothesize that variable morphology of this sulcus reflects

and/or drives neural differences more broadly. Indeed, the presence/absence and morphology of sulci are theorized to be anatomically linked to cortical white matter development (Sanides 1962, 1964; Van Essen et al. 2014; Reveley et al. 2015; Van Essen 2020; Cottaar et al. 2021; Miller et al. 2021b; Cachia et al. 2021), and the presence of sulci relates to changes in the local cytoarchitectonic organization of gray matter (Vogt et al. 1995; Palomero-Gallagher et al. 2008; Amiez et al. 2021). Neural efficiency is the foundation of our hypothesis regarding relationships between sulcal anatomy and reasoning observed in these and other studies (Voorhies et al. 2021; Willbrand et al. 2023c). Specifically, we (and others; Garrison et al. 2015) hypothesize that these sulcal-behavioral relationships stem from individual differences in white matter projections and, in turn, the distributed functional brain networks that underlie higher-level cognition. Consistent with this possibility, we have previously shown relationships between reasoning development and both whole-brain white matter (Ferrer et al. 2013) and white matter fiber bundles originating from aLPFC (Wendelken et al. 2017), along with the strength of functional connectivity of aLPFC (Wendelken et al. 2017). Future research should investigate this multiscale, mechanistic relationship describing the neural correlates of reasoning, integrating structural, functional, and behavioral data.

Given that the pimfs is rare in non-human hominoids (Hathaway et al. 2022; Amiez et al. 2023), the presence of left pimfs-v could reflect evolutionarily expanded white and gray matter properties that enhance neural communication in this higher cognitive area (Van Essen 1997, 2020; White et al. 2010; Zilles et al. 2013). Additionally, given (i) evidence implicating sulcal incidence to cognition in chimpanzees (Hopkins et al. 2021) and (ii) hypotheses that the disproportionate expansion of aLPFC in humans compared to non-human primates contributes to species differences in reasoning capacity (Semendeferi et al. 2001; Vendetti and Bunge 2014), another testable hypothesis is whether the incidence of the pimfs is also cognitively relevant in chimpanzees.

Although the cognitive relevance of the pimfs has only been examined in neurotypical populations (Voorhies et al. 2021; Yao et al. 2022; Willbrand et al. 2022b), numerous studies have shown that variations in sulcal incidence are clinically relevant (Yücel et al. 2002, 2003; Le Provost et al. 2003; Fornito et al. 2006, 2008; Shim et al. 2009; Meredith et al. 2012; Gay et al. 2017; Nakamura et al. 2020; Harper et al. 2022). Thus, the present results raise the question: Does the incidence and/or morphology of the pimfs differ in clinical populations exhibiting impaired reasoning? Schizophrenia is a prime candidate for future investigations, given that it is marked by impaired reasoning (Weickert et al. 2000; Bowie and Harvey 2006; Keefe and Harvey 2012; Zhang et al. 2017; Alkan et al. 2021; McCutcheon

et al. 2023) and has repeatedly been associated with altered aLPFC structure and function (Barnes et al. 2011; Tu et al. 2012; Kaplan et al. 2016; Kang et al. 2018; Pillinger et al. 2019; Nazli et al. 2020; Shinba et al. 2022). To help guide future studies examining the cognitive, evolutionary, developmental, clinical, and functional relevance of the pimfs, we share probabilistic predictions of the pimfs from our data (Fig. 2; Data accessibility statement).

In conclusion, we have shown that left pimfs-v presence is cognitively relevant in young adulthood, which extends previous work showing that left pimfs-v presence is cognitively relevant in childhood and adolescence. The combination of findings across studies establishes pimfs-v presence/absence as a novel developmental, cognitive, and evolutionarily relevant feature that should be considered in future studies in neurotypical and clinical populations examining how the complex relationships among multiscale anatomical and functional features of the brain give rise to abstract thought.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00429-023-02734-8>.

Acknowledgements We thank Jewelia Yao and Jacob Miller for their assistance defining other additional lateral prefrontal cortex sulci across age groups. We also thank the HCP researchers for participant recruitment and data collection and sharing, as well as the participants who took part in the study.

Author contributions EHW, SAB, and KSW designed research; EHW, SJ, SC, CBH, WIV, and KSW performed manual sulcal labeling; EHW, SAB, and KSW analyzed data; EHW, SAB, and KSW wrote the paper; all authors gave final approval to the paper before submission.

Funding This research was supported by NICHD R21HD100858 (Weiner, Bunge), NIH Medical Scientist Training Program Training Grant T32 GM140935 (Willbrand), an NSF CAREER Award 2042251 (Weiner), and an NSF-GRFP fellowship (Voorhies). Young adult neuroimaging and behavioral data were provided by the HCP, WU-Minn Consortium (Principal Investigators: David Van Essen and Kamil Ugurbil; NIH Grant 1U54-MH-091657) funded by the 16 NIH Institutes and Centers that support the NIH Blueprint for Neuroscience Research, and the McDonnell Center for Systems Neuroscience at Washington University.

Data availability Data, code, analysis pipelines, and sulcal probability maps, are on GitHub (https://github.com/cnl-berkeley/stable_projects/tree/main/CognitiveRelevance_PrefrontalStructure).

Declarations

Conflict of interest The authors declare no competing financial interests.

References

Alexander PA (2016) Relational thinking and relational reasoning: harnessing the power of patterning. *NPJ Sci Learn* 1:16004. <https://doi.org/10.1038/npjscilearn.2016.4>

- Alkan E, Davies G, Evans SL (2021) Cognitive impairment in schizophrenia: relationships with cortical thickness in fronto-temporal regions, and dissociability from symptom severity. *NPJ Schizophr* 7:20. <https://doi.org/10.1038/s41537-021-00149-0>
- Allen M, Poggiali D, Whitaker K et al (2021) Raincloud plots: a multi-platform tool for robust data visualization. *Wellcome Open Res* 4:63. <https://doi.org/10.12688/wellcomeopenres.15191.2>
- Amiez C, Kostopoulos P, Champod A-S, Petrides M (2006) Local morphology predicts functional organization of the dorsal premotor region in the human brain. *J Neurosci* 26:2724–2731. <https://doi.org/10.1523/JNEUROSCI.4739-05.2006>
- Amiez C, Wilson CRE, Procyk E (2018) Variations of cingulate sulcal organization and link with cognitive performance. *Sci Rep* 8:1–13. <https://doi.org/10.1038/s41598-018-32088-9>
- Amiez C, Sallet J, Hopkins WD et al (2019) Sulcal organization in the medial frontal cortex provides insights into primate brain evolution. *Nat Commun* 10:1–14. <https://doi.org/10.1038/s41467-019-11347-x>
- Amiez C, Sallet J, Novek J et al (2021) Chimpanzee histology and functional brain imaging show that the paracingulate sulcus is not human-specific. *Commun Biol* 4:54. <https://doi.org/10.1038/s42003-020-01571-3>
- Amiez C, Sallet J, Giacometti C et al (2023) A revised perspective on the evolution of the lateral frontal cortex in primates. *Sci Adv* 9:eadf9445. <https://doi.org/10.1126/sciadv.adf9445>
- Amunts K, Zilles K (2015) Architectonic mapping of the human brain beyond brodmann. *Neuron* 88:1086–1107. <https://doi.org/10.1016/j.neuron.2015.12.001>
- Amunts K, Mohlberg H, Bludau S, Zilles K (2020) Julich-brain: a 3D probabilistic atlas of the human brain's cytoarchitecture. *Science* 369:988–992. <https://doi.org/10.1126/science.abb4588>
- Assem M, Glasser MF, Van Essen DC, Duncan J (2020) A domain-general cognitive core defined in multimodally parcellated human cortex. *Cereb Cortex* 30:4361–4380. <https://doi.org/10.1093/cercor/bhaa023>
- Barch DM, Burgess GC, Harms MP et al (2013) Function in the human connectome: task-fMRI and individual differences in behavior. *Neuroimage* 80:169–189. <https://doi.org/10.1016/j.neuroimage.2013.05.033>
- Barnes MR, Huxley-Jones J, Maycox PR et al (2011) Transcription and pathway analysis of the superior temporal cortex and anterior prefrontal cortex in schizophrenia. *J Neurosci Res* 89:1218–1227. <https://doi.org/10.1002/jnr.22647>
- Bauer PJ, Dikmen SS, Heaton RK et al (2013) III. NIH Toolbox Cognition Battery (CB): measuring episodic memory. *Monogr Soc Res Child Dev* 78:34–48. <https://doi.org/10.1111/mono.12033>
- Bendetowicz D, Urbanski M, Garcin B et al (2018) Two critical brain networks for generation and combination of remote associations. *Brain* 141:217–233. <https://doi.org/10.1093/brain/awx294>
- Benson NC, Butt OH, Datta R et al (2012) The retinotopic organization of striate cortex is well predicted by surface topology. *Curr Biol* 22:2081–2085. <https://doi.org/10.1016/j.cub.2012.09.014>
- Bilker WB, Hansen JA, Brensinger CM et al (2012) Development of abbreviated nine-item forms of the Raven's standard progressive matrices test. *Assessment* 19:354–369. <https://doi.org/10.1177/1073191112446655>
- Blumenfeld RS, Ranganath C (2019) Chapter 12 - The lateral prefrontal cortex and human long-term memory. In: D'Esposito M, Grafman JH (eds) *Handbook of Clinical Neurology*. Elsevier, pp 221–235
- Boling W, Olivier A, Bittar RG, Reutens D (1999) Localization of hand motor activation in Broca's pli de passage moyen. *J Neurosurg* 91:903–910. <https://doi.org/10.3171/jns.1999.91.6.0903>
- Borst G, Cachia A, Vidal J et al (2014) Folding of the anterior cingulate cortex partially explains inhibitory control during

- childhood: a longitudinal study. *Dev Cogn Neurosci* 9:126–135. <https://doi.org/10.1016/j.dcn.2014.02.006>
- Botvinick M, Nystrom LE, Fissell K et al (1999) Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402:179–181. <https://doi.org/10.1038/46035>
- Bowie CR, Harvey PD (2006) Cognitive deficits and functional outcome in schizophrenia. *Neuropsychiatr Dis Treat* 2:531–536. <https://doi.org/10.2147/ndt.2006.2.4.531>
- Brown TT, Kuperman JM, Chung Y et al (2012) Neuroanatomical assessment of biological maturity. *Curr Biol* 22:1693–1698. <https://doi.org/10.1016/j.cub.2012.07.002>
- Buda M, Fornito A, Bergström ZM, Simons JS (2011) A specific brain structural basis for individual differences in reality monitoring. *J Neurosci* 31:14308–14313. <https://doi.org/10.1523/JNEUROSCI.3595-11.2011>
- Bunge SA, Wendelken C, Badre D, Wagner AD (2005) Analogical reasoning and prefrontal cortex: evidence for separable retrieval and integration mechanisms. *Cereb Cortex* 15:239–249. <https://doi.org/10.1093/cercor/bhh126>
- Burgess PW (2000) Strategy application disorder: the role of the frontal lobes in human multitasking. *Psychol Res* 63:279–288. <https://doi.org/10.1007/s004269900006>
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304. <https://doi.org/10.1177/0049124104268644>
- Cachia A, Roell M, Mangin J-F et al (2018) How interindividual differences in brain anatomy shape reading accuracy. *Brain Struct Funct* 223:701–712. <https://doi.org/10.1007/s00429-017-1516-x>
- Cachia A, Borst G, Jardri R et al (2021) Towards deciphering the fetal foundation of normal cognition and cognitive symptoms from sulcation of the cortex. *Front Neuroanat* 15:712862. <https://doi.org/10.3389/fnana.2021.712862>
- Carlozzi NE, Tulskey DS, Chiaravalloti ND et al (2014) NIH toolbox cognitive battery (NIHTB-CB): the NIHTB pattern comparison processing speed test. *J Int Neuropsychol Soc* 20:630–641. <https://doi.org/10.1017/S1355617714000319>
- Carlozzi NE, Beaumont JL, Tulskey DS, Gershon RC (2015) The NIH toolbox pattern comparison processing speed test: normative data. *Arch Clin Neuropsychol* 30:359–368. <https://doi.org/10.1093/arclin/acv031>
- Carpenter PA, Just MA, Shell P (1990) What one intelligence test measures: a theoretical account of the processing in the raven progressive matrices test. *Psychol Rev* 97:404–431. <https://doi.org/10.1037/0033-295X.97.3.404>
- Cattell RB (1943) The measurement of adult intelligence. *Psychol Bull* 40:153–193. <https://doi.org/10.1037/h0059973>
- Christoff K, Prabhakaran V, Dorfman J et al (2001) Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage* 14:1136–1149. <https://doi.org/10.1006/nimg.2001.0922>
- Clark GM, Mackay CE, Davidson ME et al (2010) Paracingulate sulcus asymmetry; sex difference, correlation with semantic fluency and change over time in adolescent onset psychosis. *Psychiatry Res* 184:10–15. <https://doi.org/10.1016/j.psycyehresns.2010.06.012>
- Cottaar M, Bastiani M, Boddu N et al (2021) Modelling white matter in gyral blades as a continuous vector field. *Neuroimage* 227:117693. <https://doi.org/10.1016/j.neuroimage.2020.117693>
- Crone EA, Wendelken C, van Leijenhorst L et al (2009) Neurocognitive development of relational reasoning. *Dev Sci* 12:55–66. <https://doi.org/10.1111/j.1467-7687.2008.00743.x>
- Cykowski MD, Coulon O, Kochunov PV et al (2008) The central sulcus: an observer-independent characterization of sulcal landmarks and depth asymmetry. *Cereb Cortex* 18:1999–2009. <https://doi.org/10.1093/cercor/bhm224>
- Dale AM, Fischl B, Sereno MI (1999) Cortical surface-based analysis I. Segmentation and surface reconstruction. *Neuroimage* 9:179–194. <https://doi.org/10.1006/nimg.1998.0395>
- Dumontheil I, Houlton R, Christoff K, Blakemore S-J (2010) Development of relational reasoning during adolescence. *Dev Sci* 13:F15–24. <https://doi.org/10.1111/j.1467-7687.2010.01014.x>
- Eriksen BA, Eriksen CW (1974) Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept Psychophys* 16:143–149. <https://doi.org/10.3758/BF03203267>
- Ezekiel F, Bosma R, Morton JB (2013) Dimensional change card sort performance associated with age-related differences in functional connectivity of lateral prefrontal cortex. *Dev Cogn Neurosci* 5:40–50. <https://doi.org/10.1016/j.dcn.2012.12.001>
- Ferrer E, Whitaker KJ, Steele JS et al (2013) White matter maturation supports the development of reasoning ability through its influence on processing speed. *Dev Sci* 16:941–951. <https://doi.org/10.1111/desc.12088>
- Fischl B, Dale AM (2000) Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proc Natl Acad Sci USA* 97:11050–11055. <https://doi.org/10.1073/pnas.200033797>
- Fischl B, Sereno MI, Dale AM (1999) Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *Neuroimage* 9:195–207. <https://doi.org/10.1006/nimg.1998.0396>
- Fornito A, Yücel M, Wood S et al (2004) Individual differences in anterior cingulate/paracingulate morphology are related to executive functions in healthy males. *Cereb Cortex* 14:424–431. <https://doi.org/10.1093/cercor/bhh004>
- Fornito A, Yücel M, Wood SJ et al (2006) Morphology of the paracingulate sulcus and executive cognition in schizophrenia. *Schizophr Res* 88:192–197. <https://doi.org/10.1016/j.schres.2006.06.034>
- Fornito A, Malhi GS, Lagopoulos J et al (2008) Anatomical abnormalities of the anterior cingulate and paracingulate cortex in patients with bipolar I disorder. *Psychiatry Res* 162:123–132
- Fry AF, Hale S (2000) Relationships among processing speed, working memory, and fluid intelligence in children. *Biol Psychol* 54:1–34. [https://doi.org/10.1016/s0301-0511\(00\)00051-x](https://doi.org/10.1016/s0301-0511(00)00051-x)
- Garcia KE, Kroenke CD, Bayly PV (2018) Mechanics of cortical folding: stress, growth and stability. *Philos Trans R Soc Lond B Biol Sci* 373:20170321. <https://doi.org/10.1098/rstb.2017.0321>
- Garrison JR, Fernyhough C, McCarthy-Jones S et al (2015) Paracingulate sulcus morphology is associated with hallucinations in the human brain. *Nat Commun* 6:8956. <https://doi.org/10.1038/ncomms9956>
- Gay O, Plaze M, Oppenheim C et al (2017) Cognitive control deficit in patients with first-episode schizophrenia is associated with complex deviations of early brain development. *J Psychiatry Neurosci* 42:87–94
- Glasser MF, Sotiropoulos SN, Wilson JA et al (2013) The minimal preprocessing pipelines for the Human Connectome Project. *Neuroimage* 80:105–124. <https://doi.org/10.1016/j.neuroimage.2013.04.127>
- Gratton C, Nelson SM, Gordon EM (2022) Brain-behavior correlations: two paths toward reliability. *Neuron* 110:1446–1449
- Grill-Spector K, Weiner KS (2014) The functional architecture of the ventral temporal cortex and its role in categorization. *Nat Rev Neurosci* 15:536–548. <https://doi.org/10.1038/nrn3747>
- Halford GS, Wilson WH, Phillips S (1998) Processing capacity defined by relational complexity: implications for comparative, developmental, and cognitive psychology. *Behav Brain Sci* 21:803–831. <https://doi.org/10.1017/s0140525x98001769>
- Harper L, Lindberg O, Bocchetta M et al (2022) Prenatal gyrification pattern affects age at onset in frontotemporal dementia. *Cereb Cortex*. <https://doi.org/10.1093/cercor/bhab457>
- Hartogsveld B, Bramson B, Vijayakumar S et al (2018) Lateral frontal pole and relational processing: activation patterns and

- connectivity profile. *Behav Brain Res* 355:2–11. <https://doi.org/10.1016/j.bbr.2017.08.003>
- Hathaway CB, Voorhies WI, Sathishkumar N et al (2023) Defining putative tertiary sulci in lateral prefrontal cortex in chimpanzees using human predictions. *Brain Struct Funct*. <https://doi.org/10.1007/s00429-023-02638-7>
- Hathaway CB, Voorhies WI, Sathishkumar N, et al (2022) Defining tertiary sulci in lateral prefrontal cortex in chimpanzees using human predictions. *bioRxiv* 2022.04.12.488091
- Hinds OP, Rajendran N, Polimeni JR et al (2008) Accurate prediction of V1 location from cortical folds in a surface coordinate system. *Neuroimage* 39:1585–1599. <https://doi.org/10.1016/j.neuroimage.2007.10.033>
- Hobeika L, Diard-Detoef C, Garcin B et al (2016) General and specialized brain correlates for analogical reasoning: a meta-analysis of functional imaging studies. *Hum Brain Mapp* 37:1953–1969. <https://doi.org/10.1002/hbm.23149>
- Holland M, Budday S, Goriely A, Kuhl E (2018) Symmetry breaking in wrinkling patterns: gyri are universally thicker than sulci. *Phys Rev Lett* 121:228002. <https://doi.org/10.1103/PhysRevLett.121.228002>
- Holyoak KJ, Monti MM (2021) Relational integration in the human brain: a review and synthesis. *J Cogn Neurosci* 33:341–356
- Hopkins WD, Procyk E, Petrides M et al (2021) Sulcal morphology in cingulate cortex is associated with voluntary oro-facial motor control and gestural communication in chimpanzees (*Pan troglodytes*). *Cereb Cortex* 31:2845–2854. <https://doi.org/10.1093/cercor/bhaa392>
- Huster RJ, Wolters C, Wollbrink A et al (2009) Effects of anterior cingulate fissurization on cognitive control during stroop interference. *Hum Brain Mapp* 30:1279–1289. <https://doi.org/10.1002/hbm.20594>
- James W (1890a) The principles of psychology, Vol I
- James W (1890b) The principles of psychology volume II By William James (1890)
- Kail R, Salthouse TA (1994) Processing speed as a mental capacity. *Acta Psychol* 86:199–225. [https://doi.org/10.1016/0001-6918\(94\)90003-5](https://doi.org/10.1016/0001-6918(94)90003-5)
- Kail RV, Lervåg A, Hulme C (2016) Longitudinal evidence linking processing speed to the development of reasoning. *Dev Sci* 19:1067–1074. <https://doi.org/10.1111/desc.12352>
- Kang SS, MacDonald AW 3rd, Chafee MV et al (2018) Abnormal cortical neural synchrony during working memory in schizophrenia. *Clin Neurophysiol* 129:210–221. <https://doi.org/10.1016/j.clinph.2017.10.024>
- Kaplan CM, Saha D, Molina JL et al (2016) Estimating changing contexts in schizophrenia. *Brain* 139:2082–2095. <https://doi.org/10.1093/brain/aww095>
- Keefe RSE, Harvey PD (2012) Cognitive Impairment in Schizophrenia. In: Geyer MA, Gross G (eds) *Novel antischizophrenia treatments*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp 11–37
- Kelava I, Lewitus E, Huttner WB (2013) The secondary loss of gyrencephaly as an example of evolutionary phenotypical reversal. *Front Neuroanat* 7:16. <https://doi.org/10.3389/fnana.2013.00016>
- Krawczyk DC (2012) The cognition and neuroscience of relational reasoning. *Brain Res* 1428:13–23. <https://doi.org/10.1016/j.brainres.2010.11.080>
- Kriegstein A, Noctor S, Martínez-Cerdeño V (2006) Patterns of neural stem and progenitor cell division may underlie evolutionary cortical expansion. *Nat Rev Neurosci* 7:883–890. <https://doi.org/10.1038/nrn2008>
- Kroger JK, Sabb FW, Fales CL et al (2002) Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. *Cereb Cortex* 12:477–485. <https://doi.org/10.1093/cercor/12.5.477>
- Le Provost J-B, Bartres-Faz D, Paillere-Martinot M-L et al (2003) Paracingulate sulcus morphology in men with early-onset schizophrenia. *Br J Psychiatry* 182:228–232. <https://doi.org/10.1192/bjp.182.3.228>
- Li S, Han Y, Wang D et al (2010) Mapping surface variability of the central sulcus in musicians. *Cereb Cortex* 20:25–33. <https://doi.org/10.1093/cercor/bhp074>
- Lopez-Persem A, Verhagen L, Amiez C et al (2019) The human ventromedial prefrontal cortex: sulcal morphology and its influence on functional organization. *J Neurosci* 39:3627–3639. <https://doi.org/10.1523/JNEUROSCI.2060-18.2019>
- Marek S, Tervo-Clemmens B, Calabro FJ et al (2022) Reproducible brain-wide association studies require thousands of individuals. *Nature* 603:654–660. <https://doi.org/10.1038/s41586-022-04492-9>
- McArdle JJ, Ferrer-Caja E, Hamagami F, Woodcock RW (2002) Comparative longitudinal structural analyses of the growth and decline of multiple intellectual abilities over the life span. *Dev Psychol* 38:115–142. <https://doi.org/10.1037/0012-1649.38.1.115>
- McCutcheon RA, Keefe RSE, McGuire PK (2023) Cognitive impairment in schizophrenia: aetiology, pathophysiology, and treatment. *Mol Psychiatry*. <https://doi.org/10.1038/s41380-023-01949-9>
- Meredith SM, Whyler NCA, Stanfield AC et al (2012) Anterior cingulate morphology in people at genetic high-risk of schizophrenia. *Eur Psychiatry* 27:377–385. <https://doi.org/10.1016/j.eurpsy.2011.11.004>
- Miller JA, Weiner KS (2022) Unfolding the evolution of human cognition. *Trends Cogn Sci* 26:735–737. <https://doi.org/10.1016/j.tics.2022.06.008>
- Miller JA, Voorhies WI, Li X et al (2020) Sulcal morphology of ventral temporal cortex is shared between humans and other hominoids. *Sci Rep* 10:17132. <https://doi.org/10.1038/s41598-020-73213-x>
- Miller JA, D'Esposito M, Weiner KS (2021a) Using tertiary sulci to map the “cognitive globe” of prefrontal cortex. *J Cogn Neurosci*. https://doi.org/10.1162/jocn_a_01696
- Miller JA, Voorhies WI, Lurie DJ et al (2021b) Overlooked tertiary sulci serve as a meso-scale link between microstructural and functional properties of human lateral prefrontal cortex. *J Neurosci* 41:2229–2244. <https://doi.org/10.1523/JNEUROSCI.2362-20.2021>
- Milner B (1963) Effects of different brain lesions on card sorting: the role of the frontal lobes. *Arch Neurol* 9:90–100. <https://doi.org/10.1001/archneur.1963.00460070100010>
- Ming K, Rosenbaum PR (2000) Substantial gains in bias reduction from matching with a variable number of controls. *Biometrics* 56:118–124. <https://doi.org/10.1111/j.0006-341x.2000.00118.x>
- Nakamura M, Nestor PG, Shenton ME (2020) Orbitofrontal sulcogyral pattern as a transdiagnostic trait marker of early neurodevelopment in the social brain. *Clin EEG Neurosci* 51:275–284. <https://doi.org/10.1177/1550059420904180>
- Nazli ŞB, Koçak OM, Kirkici B et al (2020) Investigation of the processing of noun and verb words with fMRI in patients with schizophrenia. *Noro Psikiyatırs Ars* 57:9–14. <https://doi.org/10.29399/npa.23521>
- Palomero-Gallagher N, Mohlberg H, Zilles K, Vogt B (2008) Cytology and receptor architecture of human anterior cingulate cortex. *J Comp Neurol* 508:906–926. <https://doi.org/10.1002/cne.21684>
- Paus T, Tomaiuolo F, Otaky N et al (1996) Human cingulate and paracingulate sulci: pattern, variability, asymmetry, and probabilistic map. *Cereb Cortex* 6:207–214
- Petrides M (2013) *Neuroanatomy of language regions of the human brain*. Academic Press
- Petrides M (2019) *Atlas of the morphology of the human cerebral cortex on the average MNI brain*. Academic Press

- Pillinger T, Rogdaki M, McCutcheon RA et al (2019) Altered glutamatergic response and functional connectivity in treatment resistant schizophrenia: the effect of riluzole and therapeutic implications. *Psychopharmacology* 236:1985–1997. <https://doi.org/10.1007/s00213-019-5188-5>
- Posner MI, Petersen SE, Fox PT, Raichle ME (1988) Localization of cognitive operations in the human brain. *Science* 240:1627–1631. <https://doi.org/10.1126/science.3289116>
- Raven JC (1941) Standardization of progressive matrices, 1938. *Br J Med Psychol* 19:137–150. <https://doi.org/10.1111/j.2044-8341.1941.tb00316.x>
- Revely C, Seth AK, Pierpaoli C et al (2015) Superficial white matter fiber systems impede detection of long-range cortical connections in diffusion MR tractography. *Proc Natl Acad Sci USA* 112:E2820–E2828. <https://doi.org/10.1073/pnas.1418198112>
- Richman DP, Stewart RM, Hutchinson JW, Caviness VS Jr (1975) Mechanical model of brain convolutional development. *Science* 189:18–21. <https://doi.org/10.1126/science.1135626>
- Rollins CPE, Garrison JR, Arribas M et al (2020) Evidence in cortical folding patterns for prenatal predispositions to hallucinations in schizophrenia. *Transl Psychiatry* 10:387. <https://doi.org/10.1038/s41398-020-01075-y>
- Sanides F (1962) Besprechung. In: Sanides F (ed) *Die Architektonik des Menschlichen Stirnhirns: Zugleich eine Darstellung der Prinzipien Seiner Gestaltung als Spiegel der Stammesgeschichtlichen Differenzierung der Grosshirnrinde*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp 176–190
- Sanides F (1964) Structure and function of the human frontal lobe. *Neuropsychologia* 2:209–219. [https://doi.org/10.1016/0028-3932\(64\)90005-3](https://doi.org/10.1016/0028-3932(64)90005-3)
- Semendeferi K, Armstrong E, Schleicher A et al (2001) Prefrontal cortex in humans and apes: a comparative study of area 10. *Am J Phys Anthropol* 114:224–241. [https://doi.org/10.1002/1096-8644\(200103\)114:3<224::AID-AJPA1022%3e3.0.CO;2-I](https://doi.org/10.1002/1096-8644(200103)114:3<224::AID-AJPA1022%3e3.0.CO;2-I)
- Shim G, Jung WH, Choi J-S et al (2009) Reduced cortical folding of the anterior cingulate cortex in obsessive-compulsive disorder. *J Psychiatry Neurosci* 34:443–449
- Shimamura AP, Janowsky JS, Squire LR (1990) Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia* 28:803–813. [https://doi.org/10.1016/0028-3932\(90\)90004-8](https://doi.org/10.1016/0028-3932(90)90004-8)
- Shinba T, Kariya N, Matsuda S et al (2022) Near-infrared time-resolved spectroscopy shows anterior prefrontal blood volume reduction in schizophrenia but not in major depressive disorder. *Sensors*. <https://doi.org/10.3390/s22041594>
- Sun ZY, Klöppel S, Rivi  re D et al (2012) The effect of handedness on the shape of the central sulcus. *Neuroimage* 60:332–339. <https://doi.org/10.1016/j.neuroimage.2011.12.050>
- Tranel D, Manzel K, Anderson SW (2008) Is the prefrontal cortex important for fluid intelligence? A neuropsychological study using Matrix Reasoning. *Clin Neuropsychol* 22:242–261. <https://doi.org/10.1080/13854040701218410>
- Tu P-C, Hsieh J-C, Li C-T et al (2012) Cortico-striatal disconnection within the cingulo-opercular network in schizophrenia revealed by intrinsic functional connectivity analysis: a resting fMRI study. *Neuroimage* 59:238–247. <https://doi.org/10.1016/j.neuroimage.2011.07.086>
- Tulsky DS, Carlozzi N, Chiaravalloti ND et al (2014) NIH Toolbox Cognition Battery (NIHTB-CB): list sorting test to measure working memory. *J Int Neuropsychol Soc* 20:599–610. <https://doi.org/10.1017/S135561771400040X>
- Urbanski M, Br  chemier M-L, Garcin B et al (2016) Reasoning by analogy requires the left frontal pole: lesion-deficit mapping and clinical implications. *Brain* 139:1783–1799. <https://doi.org/10.1093/brain/aww072>
- Van Essen DC (1997) A tension-based theory of morphogenesis and compact wiring in the central nervous system. *Nature* 385:313–318. <https://doi.org/10.1038/385313a0>
- Van Essen DC (2007) 4.16 - Cerebral cortical folding patterns in primates: why they vary and what they signify. In: Kaas JH (ed) *Evolution of Nervous Systems*. Academic Press, Oxford, pp 267–276
- Van Essen DC (2020) A 2020 view of tension-based cortical morphogenesis. *Proc Natl Acad Sci USA*. <https://doi.org/10.1073/pnas.2016830117>
- Van Essen DC, Jbabdi S, Sotiropoulos SN et al (2014) Mapping connections in humans and non-human primates. *Diffusion MRI*. Elsevier, Amsterdam, pp 337–358
- Vendetti MS, Bunge SA (2014) Evolutionary and developmental changes in the lateral frontoparietal network: a little goes a long way for higher-level cognition. *Neuron* 84:906–917. <https://doi.org/10.1016/j.neuron.2014.09.035>
- Vogt BA, Nimchinsky EA, Vogt LJ, Hof PR (1995) Human cingulate cortex: surface features, flat maps, and cytoarchitecture. *J Comp Neurol* 359:490–506. <https://doi.org/10.1002/cne.903590310>
- Voorhies WI, Miller JA, Yao JK et al (2021) Cognitive insights from tertiary sulci in prefrontal cortex. *Nat Commun* 12:5122. <https://doi.org/10.1038/s41467-021-25162-w>
- Waechter RL, Goel V, Raymond V et al (2013) Transitive inference reasoning is impaired by focal lesions in parietal cortex rather than rostralateral prefrontal cortex. *Neuropsychologia* 51:464–471. <https://doi.org/10.1016/j.neuropsychologia.2012.11.026>
- Wagenmakers E-J, Farrell S (2004) AIC model selection using Akaike weights. *Psychon Bull Rev* 11:192–196. <https://doi.org/10.3758/bf03206482>
- Wagner AD, Shannon BJ, Kahn I, Buckner RL (2005) Parietal lobe contributions to episodic memory retrieval. *Trends Cogn Sci* 9:445–453. <https://doi.org/10.1016/j.tics.2005.07.001>
- Wandell BA, Winawer J (2011) Imaging retinotopic maps in the human brain. *Vision Res* 51:718–737. <https://doi.org/10.1016/j.visres.2010.08.004>
- Wang S, Saito K, Kawasaki H, Holland MA (2022) Orchestrated neuronal migration and cortical folding: A computational and experimental study. *PLoS Comput Biol* 18:e1010190. <https://doi.org/10.1371/journal.pcbi.1010190>
- Wechsler D (1949) Wechsler intelligence scale for children; manual. 113
- Wei X, Yin Y, Rong M et al (2017) Paracingulate sulcus asymmetry in the human brain: effects of sex, handedness, and race. *Sci Rep* 7:42033. <https://doi.org/10.1038/srep42033>
- Weickert TW, Goldberg TE, Gold JM et al (2000) Cognitive impairments in patients with schizophrenia displaying preserved and compromised intellect. *Arch Gen Psychiatry* 57:907–913. <https://doi.org/10.1001/archpsyc.57.9.907>
- Weiner KS, Golarai G, Caspers J et al (2014) The mid-fusiform sulcus: a landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex. *Neuroimage* 84:453–465. <https://doi.org/10.1016/j.neuroimage.2013.08.068>
- Wendelken C, Bunge SA (2010) Transitive inference: distinct contributions of rostralateral prefrontal cortex and the hippocampus. *J Cogn Neurosci* 22:837–847. <https://doi.org/10.1162/jocn.2009.21226>
- Wendelken C, Bunge SA, Carter CS (2008a) Maintaining structured information: an investigation into functions of parietal and lateral prefrontal cortices. *Neuropsychologia* 46:665–678. <https://doi.org/10.1016/j.neuropsychologia.2007.09.015>
- Wendelken C, Nakhachenko D, Donohue SE et al (2008b) “Brain is to thought as stomach is to ???”: investigating the role of rostralateral prefrontal cortex in relational reasoning. *J Cogn Neurosci* 20:682–693. <https://doi.org/10.1162/jocn.2008.20055>

- Wendelken C, Ferrer E, Ghetti S et al (2017) Frontoparietal structural connectivity in childhood predicts development of functional connectivity and reasoning ability: a large-scale longitudinal investigation. *J Neurosci* 37:8549–8558. <https://doi.org/10.1523/JNEUROSCI.3726-16.2017>
- Westlin C, Theriault JE, Katsumi Y et al (2023) Improving the study of brain-behavior relationships by revisiting basic assumptions. *Trends Cogn Sci*. <https://doi.org/10.1016/j.tics.2022.12.015>
- White T, Su S, Schmidt M et al (2010) The development of gyrification in childhood and adolescence. *Brain Cogn* 72:36–45. <https://doi.org/10.1016/j.bandc.2009.10.009>
- Whittle S, Allen NB, Fornito A et al (2009) Variations in cortical folding patterns are related to individual differences in temperament. *Psychiatry Res* 172:68–74
- Willbrand EH, Parker BJ, Voorhies WI et al (2022a) Uncovering a tripartite landmark in posterior cingulate cortex. *Sci Adv* 8:eabn9516. <https://doi.org/10.1126/sciadv.abn9516>
- Willbrand EH, Voorhies WI, Yao JK et al (2022b) Presence or absence of a prefrontal sulcus is linked to reasoning performance during child development. *Brain Struct Funct* 227:2543–2551. <https://doi.org/10.1007/s00429-022-02539-1>
- Willbrand EH, Bunge SA, Weiner KS (2023a) Neuroanatomical and functional dissociations between variably present anterior lateral prefrontal sulci. *J Cogn Neurosci* 35:1846–1867. https://doi.org/10.1162/jocn_a_02049
- Willbrand EH, Bunge SA, Weiner KS (2023b) Neuroanatomical and functional dissociations between variably present anterior lateral prefrontal sulci. *bioRxiv* 2023.05.25.542301
- Willbrand EH, Ferrer E, Bunge SA, Weiner KS (2023c) Development of human lateral prefrontal sulcal morphology and its relation to reasoning performance. *J Neurosci*. <https://doi.org/10.1523/JNEUROSCI.1745-22.2023>
- Willbrand EH, Maboudian SA, Kelly JP et al (2023d) Sulcal morphology of posteromedial cortex substantially differs between humans and chimpanzees. *Communications Biol* 6:1–14. <https://doi.org/10.1038/s42003-023-04953-5>
- Willbrand EH, Tsai Y-H, Gagnant T, Weiner KS (2023e) Updating the sulcal landscape of the human lateral parieto-occipital junction provides anatomical, functional, and cognitive insights. *eLife*
- Yao JK, Voorhies WI, Miller JA et al (2022) Sulcal depth in prefrontal cortex: a novel predictor of working memory performance. *Cereb Cortex*. <https://doi.org/10.1093/cercor/bhac173>
- Yarkoni T, Poldrack RA, Nichols TE et al (2011) Large-scale automated synthesis of human functional neuroimaging data. *Nat Methods* 8:665–670. <https://doi.org/10.1038/nmeth.1635>
- Yousry TA, Schmid UD, Alkadhi H et al (1997) Localization of the motor hand area to a knob on the precentral gyrus. A New Landmark. *Brain* 120(Pt 1):141–157. <https://doi.org/10.1093/brain/120.1.141>
- Yücel M, Stuart GW, Maruff P et al (2002) Paracingulate morphologic differences in males with established schizophrenia: a magnetic resonance imaging morphometric study. *Biol Psychiatry* 52:15–23. [https://doi.org/10.1016/s0006-3223\(02\)01312-4](https://doi.org/10.1016/s0006-3223(02)01312-4)
- Yücel M, Wood SJ, Phillips LJ et al (2003) Morphology of the anterior cingulate cortex in young men at ultra-high risk of developing a psychotic illness. *Br J Psychiatry* 182:518–524. <https://doi.org/10.1192/bjp.182.6.518>
- Zelazo PD (2006) The Dimensional Change Card Sort (DCCS): a method of assessing executive function in children. *Nat Protoc* 1:297–301. <https://doi.org/10.1038/nprot.2006.46>
- Zelazo PD, Anderson JE, Richler J et al (2013) II. NIH Toolbox Cognition Battery (CB): measuring executive function and attention. *Monogr Soc Res Child Dev* 78:16–33. <https://doi.org/10.1111/mono.12032>
- Zelazo PD, Anderson JE, Richler J et al (2014) NIH toolbox cognition battery (CB): validation of executive function measures in adults. *J Int Neuropsychol Soc* 20:620–629. <https://doi.org/10.1017/S13555617714000472>
- Zhang B, Han M, Tan S et al (2017) Gender differences measured by the MATRICS consensus cognitive battery in chronic schizophrenia patients. *Sci Rep* 7:11821. <https://doi.org/10.1038/s41598-017-12027-w>
- Zilles K, Armstrong E, Schleicher A, Kretschmann H-J (1988) The human pattern of gyrification in the cerebral cortex. *Anat Embryol* 179:173–179
- Zilles K, Palomero-Gallagher N, Amunts K (2013) Development of cortical folding during evolution and ontogeny. *Trends Neurosci* 36:275–284. <https://doi.org/10.1016/j.tins.2013.01.006>
- Zlatkina V, Amiez C, Petrides M (2016) The postcentral sulcal complex and the transverse postcentral sulcus and their relation to sensorimotor functional organization. *Eur J Neurosci* 43:1268–1283. <https://doi.org/10.1111/ejn.13049>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.