Trends in Cognitive Sciences

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Forum

Unfolding the evolution of human cognition

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Recent findings spanning fields, from braincases in paleoneurobiology to *in vivo* measurements in cognitive neuroscience, provide insights into the evolution of cognition. Here, we integrate these findings and propose that studying small, evolutionarily new cortical structures has significant implications for identifying new links between neuroanatomical substrates and human-specific aspects of cognition.

When 'skull' is paired with 'cognition', many *TiCS* readers likely think of phrenology, not endocasts, paleoneurobiology, or tertiary sulci. In this Forum, we integrate findings from two parallel (anthropology and neuroanatomy) tracks that propose novel insights into the evolution of human cognition across millions of years. The first track reveals that the evolutionary trajectory of cortical expansion and sulcal morphology in the human brain is different than previously thought [1–5]. The second track shows that individual variation in cognition and functional brain networks is linked to variation in sulcal anatomy [6–10]. Building on work integrating these tracks in paleoneurobiology, we propose that small, tertiary sulci (which emerge late during gestation, continue to develop after birth, and are largely hominoid specific) have significant implications for the history of our own brains and understanding the evolution of human cognition.

Evolutionary insights into human cognition from endocasts

The size, shape, scale, ratio, or combinations therein of brain structures provide insights into the evolution of human cognition from the brain itself or from endocasts (e.g., 'brain cases' [1–5]). Endocasts either occur naturally during fossilization as the neurocranium is filled with sediment or can be artificially reconstructed. These records serve as important tools for evolutionary perspectives because we cannot invite our ancient human ancestors to lay down in an MRI scanner. For instance, since the morphology of sulci tracks with evolutionary complexity among primates, with more folding in the human brain, the presence and prominence of sulci on endocasts can be linked to the emergence of behaviors or cognitive skills in a particular species [3]. Critically, recent studies showed that the appearance, shape, and prominence of sulci in different parts of the brain on endocasts correlate with the emergent complexity of cognition.

Here, we consider five types of morphological insight: globular, lobular, ratial, combinatorial, and sulcal. At the globular level (globular refers to a modern human brain shape with a steep frontal lobe and a bulging parietal lobe, as well as an enlarged and rounded cerebellum), using shape analyses of endocasts from fossil skulls integrated with DNA analyses, recent research showed that genetic expression contributes to endocranial globularity. Specifically, two genes (*UBR4* and *PHLPP1*) are related to neurogenesis and myelination, further supporting that developmental mechanisms likely contribute to the shape of the human endocranium, which has implications for neural architecture and efficiency of cognition [3]. At the lobular level (lobular refers to primary sulci demarcating the frontal, parietal, temporal, and occipital lobes), recent research identifying primary sulci on endocasts and performing geometric morphometrics analyses across 11 genera and 17 species showed an inverse relationship between parietal and occipital lobes across species: the more evolutionarily recent, the larger the parietal lobe and the smaller the occipital lobe [5]. At the ratial level, considering an infant:adult ratio of endocranial volumes from a hominin species more than 3 million years ago indicates a protracted brain growth, which is likely critical of a long period of childhood learning in hominins [2]. At the sulcal level, new tools reveal variability in sulcal patterns in human endocasts that match descriptions from postmortem atlases [4], mainly for larger primary and secondary sulci. At a combinatorial level of lobes and sulci, recent analyses showed that reorganization and relative expansion of the frontal lobes associated with complex cognitive tasks, such as language, tool use, and social cognition, likely occurred much later than presently thought [1]. Complementing these anthropological findings, additional neuroimaging findings show that morphological features of tertiary sulci are functionally and cognitively relevant, which we consider in the next section.

Cognitive and functional utility of evolutionarily new (tertiary) sulci

Cortical thickness and gray matter volume are common anatomical features of the cortical ribbon to measure and consider for functional or cognitive relevance, or even differences across species. However, recent evidence also points to morphological features of sulci, such as depth and length, as additional features. Specifically, recent studies focused on tertiary sulci, which emerge last in gestation (compared with the earlier emerging primary and secondary sulci), are small and shallow, and exhibit extensive individual differences in their morphology. Historically, tertiary sulci have been overlooked for methodological reasons, yet recent studies show that their morphology is related to cortical network function and cognition. For example, tertiary sulcal depth predicts reasoning skills in children [6], while tertiary sulcal length is related to whether individuals with schizophrenia will hallucinate or not [11]. The latter finding is also related to additional evidence that the same sulcus (paracingulate) has more similar histological

and functional network connectivity with chimpanzees than was previously thought [8]. Mechanistically, morphological features of these sulci are hypothesized to reflect features of underlying white matter and, in turn, network communication.

Consistent with this idea, features of tertiary sulci, which are located within association cortices that have expanded the most through evolution and perform computations related to human-specific aspects of cognition, may hold important understanding in tracking when cognitive abilities emerged during human brain evolution. Furthermore, heritability and cross-species comparisons suggest these smaller, later-to-develop tertiary sulci are under less genetic control compared with earlier developing, larger structures [12,13]. Intriguingly, recent findings also show that the presence or absence of tertiary sulci in one part of the brain influences the presence or absence of functional regions in other parts of the brain [10]. Additionally, simply identifying these often-overlooked tertiary sulci provides network-level insight (Figure 1), as well as insight into the evolution of association cortices. For example, some tertiary sulci are hominoid specific, while others are human specific [9].

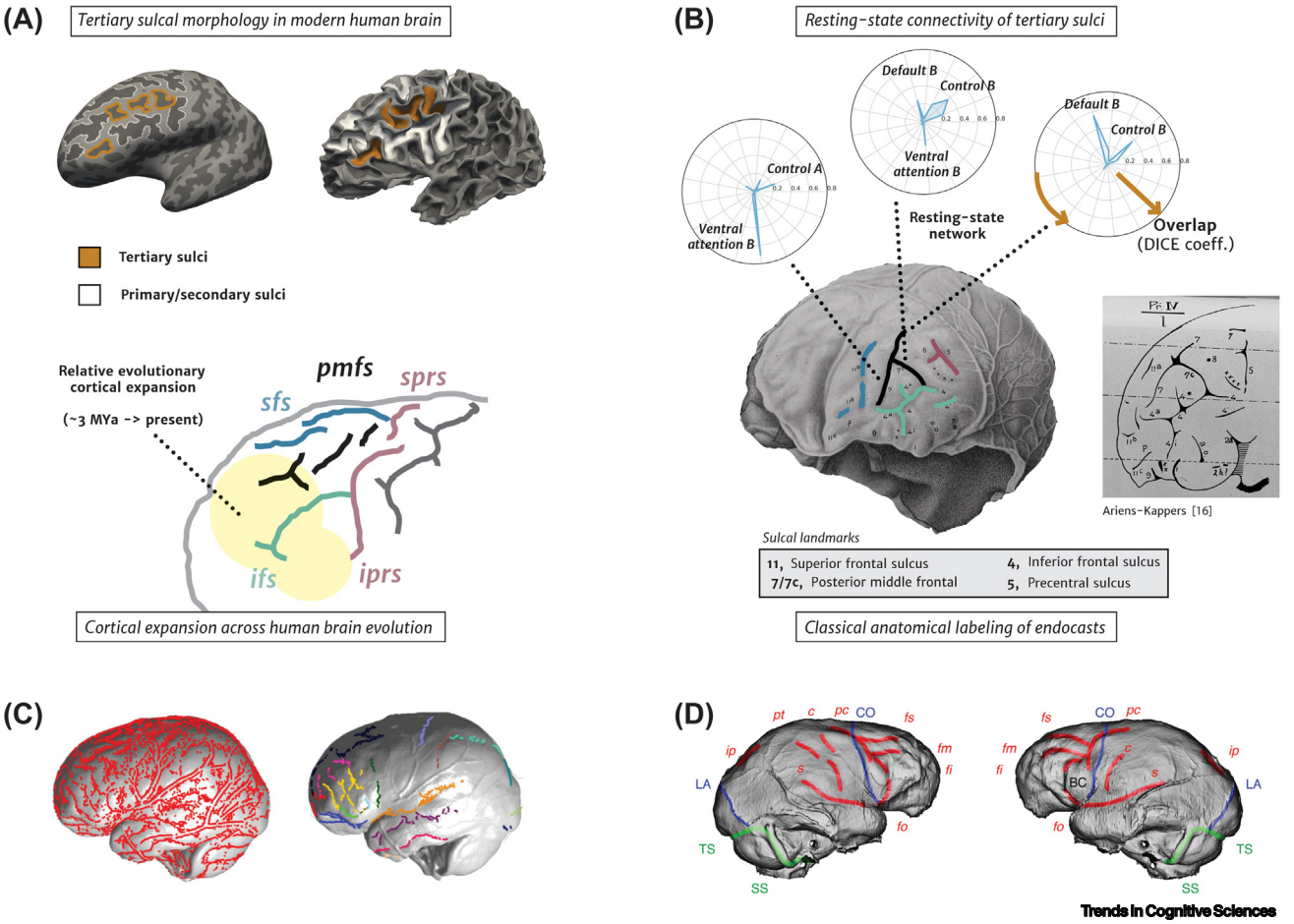

Figure 1. Tertiary sulci: from classic and modern endocasts to functional connectivity fingerprints. (A) Top: tertiary (orange) and non-tertiary (white) sulci defined on example inflated (left) and pial (right) cortical surface reconstructions from the same hemisphere. Bottom: schematic of cortical area expansion in lateral prefrontal cortex (LPFC) across ~3 million years (adapted from [1]). Blue, superior frontal sulcus (SFS); black, posterior middle frontal sulcus (PMFS); green, inferior frontal sulcus (IFS); pink, superior (SPRS) and inferior (IPRS) precentral sulci. (B) Top: resting-state functional connectivity fingerprints for three components of the PMFS [7]. Bottom: the three PMFS components can be identified on endocasts in classic [16] (see Box 1 in the main text) and modern images (C,D). (C) Left: automatic identification of crest lines (red) on a mesh reconstruction of an endocast. Right: sulci (colors) are identifiable on the mesh reconstruction of the endocast. Magenta indicates that tertiary sulci within the middle frontal gyrus are identifiable on modern endocasts. Images reproduced under Copyright Clearance (License ID: 1246802-1). (D) Endocranial structures of Dmanisi cranium D4500 from [1]. 'fm' indicates that tertiary sulci within the middle frontal gyrus are identifiable on endocasts from 1.85–1.77 million years ago. Across fields, these findings suggest that tertiary sulci can provide functional and cognitive insights with evolutionary implications across samples, from modern *in vivo* or postmortem measurements of human brains to braincases that are millions of years old. Images reproduced under Copyright Clearance (License ID: 1100386-2). Abbreviations: c, central; CO, coronal suture; fi, inferior frontal; fm, middle frontal; fo, fronto-orbital; fs, superior frontal; ip, intraparietal; pc, precentral; pt, postcentral; SS, sigmoid sinus; TS, transverse sinus.

Box 1. Identifying tertiary sulci on endocasts: methodological and mechanistic considerations

Recent findings show that endocasts match biological variability for many major sulci across the human brain when comparing sulcal identifications on endocasts and the brain from the same individuals [14]. Yet, studies often do not consider tertiary sulci, which brings us to a major methodological consideration for future studies: are tertiary sulci identifiable on endocasts and, if so, at what time point are they identifiable in our evolutionary history? In terms of feasibility, both modern and classical anatomical studies show that tertiary sulci can be detected from endocasts. For example, in lateral frontal cortex, tertiary sulcal indentations are identifiable both in modern human [4] and ancient *Australopithecus* fossils [15] (see Figure 1 in the main text). However, tertiary sulci in inferior frontal cortex near Broca's area are not detectable on endocasts [15], meaning that future investigations should carefully consider what structures can be detected at all before making inferences on their emergence over time in new samples. As discussed by Ponce de León *et al.* [1], absence of evidence is not evidence of absence. For example, many tertiary sulci likely will not leave endocranial imprints, but it is important to know which ones do cast endocranial imprints to help us understand the evolution of human cognition. Interestingly, classic findings from Ariëns-Kappers [16] show that lateral prefrontal cortex (LPFC) tertiary sulci are identifiable as early as 700 000–1 million years ago (see Figure 1 in the main text). The latter finding led Ariëns-Kappers to propose that the breaking up of the posterior middle frontal sulcus (PMFS) was phylogenetically relevant. Specifically, he wrote: 'it may be that [the PMFS] being broken up in pieces in most recent brains is indeed a result of further development of the cortex in the foot of the midfrontal convolution, which apparently increases phylogenetically just as much as the inferior frontal convolution.' ([16], p. 308). Thus, it appears likely that at least some tertiary sulci are identifiable on endocasts, which opens the door for exciting future studies at the intersection among cognitive science, neuroanatomy, and paleoneurobiology.

Tertiary sulci likely inform the evolution of human cognition: emergence and quantification

Given recent findings from each of these separate research tracks, we propose that small, tertiary sulci can likely inform the relationship between cortical folding and the evolution of human cognition in two main ways: emergence and quantification. First, while there is a long history of analyzing endocasts, tertiary sulci have been largely overlooked, as is also the case in neuroimaging studies [6–11]. Thus, identifying when tertiary sulci first appeared during our evolutionary history in association cortices will likely provide critical insight into the evolution of the human brain and cognition.

Specifically, since tertiary sulci are evolutionarily new, a logical hypothesis is that evolutionarily new cognitive abilities may emerge with these structures. Second, future and ongoing neuroimaging studies can pinpoint which tertiary sulci are human or hominoid specific, which would further inform future paleoneurobiology studies regarding which sulci could be identifiable on endocasts of specific species. However, we must carefully consider potential methodological constraints; for example, is it even possible to identify tertiary sulci on endocasts (Box 1)? Historical and modern data begin to answer this question and show that tertiary sulci are identifiable at least 700 000–1 million years ago (Figure 1 and Box 1). Finally, the generation of quantitative tools that computationally integrate the two tracks would greatly improve the crosstalk between these different fields and likely expedite future insights into the evolution of human cognition [1,4,14]. Box 1 proposes additional promising questions and potential methodological limitations.

Concluding remarks

Evidence from sulcal indentations on endocasts not only show big changes from our early human ancestors, but also hint that smaller sulcal structures may hold large implications for the history of our own brains. Considering when smaller sulci emerged in our evolutionary history builds on present work and offers a promising new application bridging studies of cognition, neuroanatomy, and paleoneurobiology.

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Declaration of interests

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