Precision estimates of network organization from functional connectivity MRI in the human and tract-tracing data in the marmoset monkey converge to reveal an orderly macroscale gradient of sequential networks across the cerebral cortex. Parallel networks begin with a sequence of multiple nested sensory-motor networks in both species progressing to more distributed association networks in rostral prefrontal and temporal association zones, which are expanded and differentiated in the human. From this perspective, the spatially distributed motif encountered in association networks appears to be on a continuum with primary sensory-motor networks. Network motifs supporting sophisticated forms of human cognition may arise from specializations of distributed anatomical networks formed in an ancestor at least 45 million years ago.

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**Introduction**

The cerebral cortex is populated by multiple distributed networks [1**,2**,3,4–6]. In addition to the long-standing goal of understanding in detail the connectivity and functional properties of areas within a network, there is growing appreciation that anatomical motifs are shared across distinct networks and also that a semi-ordery sequence describes how multiple networks are spatially localized in relation to one another across the cortex [7**,8–10]. As one radiates outward from primary sensory zones, there exists a sequence of networks that progressively support higher-order domains of cognition [7**,11]. Each of these networks possesses a similar spatial arrangement with network regions in each of the main anterior and posterior zones of cortex, suggesting the same anatomical motif might be emerging again and again across differentially specialized distributed networks.

Moreover, the detailed organization in the human is echoed in anatomical gradients that have been observed in both the macaque and marmoset as estimated by direct anatomical connectivity [12,13**,14] and functional connectivity [15**] including nested sensory-motor networks that have been underappreciated in the human. In an important analysis, Averbeck, Caminiti and colleagues explored extensive macaque anatomical data to describe a parieto-frontal network archetype that is duplicated multiple times [16,17**]. Their analyses revealed sequential, progressively more distributed networks as one moved outward from the primary motor network (see Figure 5 in Ref. [17]).

An open question is how the nested sensory-motor networks that have been the focus of anatomical work on the monkey relate to the macroscale organization of higher-order association networks that have been the focus in the human. Recent work using precision estimates within individuals provides evidence that sequential networks form a macroscale gradient across all of human cortex paralleling observations in the monkey and supporting the possibility that a basic anatomical motif is repeatedly duplicated across the cortex in support of lower-level sensory-motor networks through to the highest-order association networks that, in the human, are differentially expanded and specialized.

**Precision neuroimaging allows novel spatial details to be appreciated**

Precision estimates of network organization in the human provide novel information about the macroscale organization of cortical networks and, in their details, create the opportunity to appreciate correspondences between human and monkey. Specifically, within-individual analyses allow fine-grained details of cortical organization to reveal close juxtaposition of networks and regions that are
What is also observed in the detailed analysis of human network organization are separations among multiple sensory-motor networks that are spatially compressed into a relatively small zone of frontal cortex in the human (Figure 1). Note that in the present context, relative refers to the disproportionate expansion of zones that are occupied by higher-order networks linked to advanced cognitive functions and compression of zones that are occupied by putative motor networks [27,28]. In examining the details of these networks—including both networks within and close to sensory-motor cortex and those that populate the distant rostral association zones—further support is found for a broad macroscale organization of cortical networks that connects the parieto-frontal network archetype described on the monkey [16,17**] with the macroscale organization observed in the human [7**,11,29].

Macroscale organization of sequential networks in the human and monkey

The broad macroscale gradient of networks observed within the human brain, when examined in detail, parallels anatomical observations in the small New World marmoset monkey. We select the marmoset for illustration here because of the open availability of retrograde tracer injection maps that include the individual cell labels from numerous cortical injection sites [14,30**]. Anatomical findings in the macaque suggest that similar networks and correspondences are also present (e.g. see analyses in Refs. [12,15**]). Thus the patterns discussed here are proposed to be conserved across New World and Old World monkeys and humans (see also Ref. [17**]).

Figure 2 shows candidate network correspondences between marmosets and humans identified with injection sites and seed regions along a caudal to rostral sequence in frontal cortex. The human data are two subjects from Braga and Buckner [8] replotted to highlight networks associated with seed regions extending outward from primary motor cortex to progressively higher-order association regions: (A) primary motor cortex (at or near BA4), (B) caudal premotor cortex (BA6), (C) rostral premotor cortex (BA6), (D) rostral BA8 at or near the frontal eye fields, (E) dorsolateral prefrontal cortex (BA 44/46), (F) frontal pole on the medial surface (BA10). The marmoset data [13**] are culled from the open-source repository of the Marmoset Brain Connectivity Atlas [14,30**]. Candidate homologous networks are hypothesized based on the relative positions of the cortical zones involved in the networks and the spatial arrangement of the networks in the brain.

otherwise blurred in group-average data [8,18–25]. Emerging from these newer methods is the finding that higher-order association networks, often conceived of as large monolithic networks, are actually comprised of multiple, parallel networks with distinct regions often laying side-by-side with one another (e.g. see Refs. [8,22,26**]).

Relative positions of areas in the human and marmoset.
In order to appreciate candidate homologous networks between the marmoset and human it is useful to orient using area landmarks. (Top) A lateral view of the human brain illustrates several classical Brodmann areas (BA) [43]. Acknowledging more modern specification of areas in these zones is possible (V2 and V3 only partially correspond to Brodmann’s 18/19), the relative positions of these areas compared to marmoset are informative. Zones of frontal cortex that are occupied by motor and premotor regions are marked by (o). The vast expanse of frontal cortex in the human is rostral to motor zones (l). (Bottom) A lateral view of the marmoset brain illustrates areas using distinct (more modern) criteria. The V1/V2/V3 label does not include V3a. What this comparison illustrates is that the relative positions of areas are conserved between species but also that the extensive frontal association zones in the human fall within a relatively compressed zone in the marmoset, while visual areas are disproportionately expanded in the marmoset as contrast to the human (note the position of MT). Both humans and marmosets possess rostral prefrontal areas that are likely homologous (BA10 and A10) but expanded and differentiated in the human [9]. Comparisons of networks must consider the relative expansion and compression of cortical zones between the two primate species. The human cortex labels are based on Ref. [43] with MT labelled based on Ref. [44]. The marmoset areas reference the Paxinos et al. [45] atlas. See also Ref. [27].
Direct contrast of human and marmoset network candidates. (Example 1) The left columns display networks in the human based on functional connectivity MRI with seed regions in frontal cortex (white circles) next to candidate homologous networks in the marmoset based on retrograde label patterns from tracer injections in frontal cortex (blue arrows). (Example 2) The right columns display independent data replicating the human networks (in a second participant) and convergent retrograde label patterns for similarly localized injections in additional marmosets. The networks reveal a macroscale gradient in both the human and marmoset that progresses from a primarily local network to more distributed networks. Labels A–F illustrate the major gradient as the network estimates progress from motor (top) to frontal pole (bottom) seed regions. Tracer injections are plotted as if they are within the left hemisphere but variably come from individual cases with some right injections. Human functional connectivity MRI is from the left hemisphere and shows correlation using z values after r-to-z transform with a threshold for z > 0.2. Marmoset data show individually labelled cell bodies with black dots. F* denotes a predicted region near OPt that has minimal tracer label. As shown in Figure 3 this region does possess the predicted projections to frontopolar cortex, as revealed when injections are combined (see Ref. [13**]). The tracer injection cases are labelled in the bottom right as annotated in the Marmoset Brain Connectivity Atlas [14,30**]. Area labels reference the Paxinos et al. [45] atlas. The human participants are two separate individuals from Ref. [8].
The macroscale sequence of networks is evident in both species beginning with a motor network (Figure 2). The motor network (A) illustrates a motor and adjacent somatosensory component in both species. A significant feature of this first network is its preferential local property. As the sequence progresses, the networks that involve more rostral positions are coupled (neuroimaging data) or receive projections (tracer injections) from progressively more caudal and distributed zones, illustrating the nested hierarchy described by Averbeck, Caminiti and colleagues [16,17]. The beginnings of this distributed pattern are also evident in the progression to the caudal and rostral premotor networks in the human. That is, the progressively more distributed network motif does not emerge within association cortex but rather begins in motor systems. As the sequence progresses to the human candidate of the frontal eye field (FEF) and one of the possible homologues of FEF (or perhaps PEF) in the marmoset (A8aV), the distributed pattern prominently includes occipitotemporal cortex (at or near the MT+ complex). As the sequence continues the temporal regions involve more rostral zones until the final apex network includes regions at or near the temporal pole in both species. Analysis of the apex network, often referred to as the default network in the human, shows detailed correspondences between species across at least five and potentially many more distributed cortical regions [9,13,31].

A notable detail in the sequence of human networks that emphasizes the importance of within-individual precision estimates is the specific spatial juxtaposition of nested networks radiating outward from primary somatosensory and motor cortex. The networks can be seen in Figure 2 as the motor (A), caudal premotor (B), and rostral premotor (C) networks. While these networks occupy a large relative portion of the marmoset brain, in humans the hypothesized (candidate) homologous networks are compressed within a relatively small zone of caudal frontal cortex. Further exploration in the human will be needed to verify and explore in detail the organization of these networks, but their preliminary identification illustrates the need for individualized data analysis. They are closely juxtaposed and easily missed in blurred group-averaged data.

Most broadly the sequence of networks that radiate outwards from sensory-motor cortex is consistent with the emerging idea that the cerebral cortex is organized as a series of macroscale gradients [7,11,13]. The networks can be visualized here with quite distinct methods (functional MRI and tracer injection) in two distantly related primate species (human and marmoset), supports the possibility that these core macroscale gradients reflect ancient organizing motifs present in an early primate ancestor. As will be described in the next section, several of the higher-order association networks that have been the focus of human neuroscience have candidate homologues in the marmoset with their relative spatial positions conserved.

Topographic relations among major association networks

In examining correspondence between human and monkey, details of the macroscale gradient can be appreciated by focusing on three major networks that have been extensively studied in the human: the dorsal attention, frontoparietal control, and default networks [4,5,32–34]. Multiple injections in the candidate prefrontal homologues associated with these three networks are well represented in the open-source marmoset tracer injections [14,30] making provisional comparisons between the two species possible.

Figure 3 shows pooled frontal tracer injections for each network as well as a merged estimate allowing topographic relations to be resolved in posterior zones of cortex including parietal association cortex and temporal association cortex. For this visualization, seven published [14,30], see also Ref. 15] injections were summed for A10 and A9 (as a candidate region within the putative homologue of the default network), five within A8aV (dorsal attention), and four within A47L (frontoparietal control). To estimate the distinct

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6 The most rostral network involves frontopolar cortex and the temporal pole in both marmoset and human. We have referred to this network as the apex transmodal network in relation to marmoset anatomical connectivity and have hypothesized that it is homologous to the default network described in the human literature [13]. But homologies are not fully resolved. In a thorough analysis of marmoset network organization, Liu et al. proposed an alternative candidate for the human default network anchored from functional neuroimaging in both species [31]. We suspect that, paradoxically, functional neuroimaging in both species creates ambiguity about homologies because marmoset rostral prefrontal cortex is sufficiently small [see Figure 1] that the coupled network may be difficult to detect even with the best MRI currently available. By contrast anatomical connectivity in the marmoset, which possesses cellular resolution, can detect the full distributed extent of the apex association network including the frontopolar (A10) component.

8 Data were replotted into a 3D format and merged using openly available tools. Specifically, the 3D midthickness model, available as a polygonal mesh in vtk format, was obtained from http://r.marmosetbrain.org/marmoset_brain_template.zip. The datasets containing the M-L, A-P, and D-V stereotaxic locations of the individual cells labelled by the injections were downloaded from https://analysis.marmosetbrain.org/. The locations of the individual cells for the injections were extracted and merged together as a union set, and then projected onto the stereotaxic space generated by the midthickness surface using ParaView (version 5.8.0; https://www.paraview.org/).
Figure 3

Canonical networks reveal homologous topography in temporal and parietal cortex.
(I) Projection patterns from three groupings of frontal tracer injections reveal candidate homologues of the dorsal attention network (green), the frontoparietal control network (blue), and the default network (red) in the marmoset (also referred to as the apex transmodal network [13]). The surface is rotated to visualize temporal and parietal association cortex. White lines are positioned in the same locations across images radiating outward from area MT to aide visualization, with areas MT, AIP, OPT, LIP, TPO and TE3 indicated for reference. Additional lines point to areas A8aV, A47L, and A10 in frontal cortex. Labels D through E illustrate the caudal to rostral macroscale gradient that corresponds to the labels in Figure 1. Four of the seven injections in frontopolar cortex appear on both the lateral and medial views. (II) Human functional connectivity MRI estimates of the candidate homologous networks are illustrated within the two separate individuals using similar network colors to the marmoset.
anatomical connectivity pattern in frontal cortex, we utilized posterior injections including three within TPO and TE3 (default network), three within MT (dorsal attention), and two injections within AIP (frontoparietal control).

For the candidate homologue of the dorsal attention network, the posterior projections are dense at or around parietal area LIP and also in area MT extending rostrally in the temporal lobe. For the candidate homologue of the frontoparietal control network the dense parietal projections fall rostrally in the region of weak projections within the candidate dorsal attention homologue. The rostral temporal projections spare area MT. The candidate homologue of the default network reveals parietal projections that overlap the ventral portion of the candidate frontoparietal network at or near OpT and extensive projections in the most rostral regions of temporal association cortex extending into the temporal pole. These features match the broad topographic organization present in the human, in particular the clear caudal to rostral progression in temporal cortex as well as the general dorsal to ventral topographic pattern in parietal association cortex.

Figure 4 illustrates the topography of the three networks in frontal cortex when tracer injections in posterior zones of cortex are pooled. Recapitulating the candidate dorsal attention network, injections in area MT associate with projections from a focal region at and around A8aV, as well as the parietal region extending at and around LIP. Posterior injections linked to the candidate frontoparietal control network reveal projections that extend rostrally into prefrontal cortex including A47L as well as regions at or near A6Va/A6Vb. Distinguishing the projection pattern from that of the candidate dorsal attention network, the projections largely spare A8aV. Temporal projections also spare MT and include extensive regions of midtemporal association cortex at and around the caudal portion of TE3. Injections in rostral temporal cortex reveal projections in frontopolar cortex extending onto the midline and prominently including A10, as well as a parietal zone near OpT. Thus, consistent with a macroscale gradient, the posterior injections yield a caudal to rostral progression in frontal cortex all the way through to frontopolar cortex as seen in the human.

Implications of a conserved macroscale organization of cortical networks
Explanations of distributed network patterns have noted similarities between the human and monkey for networks that have been the focus of neuroimaging research [12,13**,**15**,31,35,36]. The work by Margulies and colleagues [7**,10] and our own work within individuals [8] provides evidence that the networks form a macroscale gradient. What has been underappreciated previously is that the multiple nested motor networks, involving a relatively large proportion of cortex in the monkey, are also present in the human, but in a relatively compressed portion of the cortex given the expansion of higher-order association cortex. This feature is easily missed in group-averaged data in the human. Detailed within-individual precision estimates illustrate that the hierarchy begins with an anterior-to-posterior motif in sensory-motor cortex that becomes more elaborated as one progresses rostrally in frontal cortex and caudally in parietal cortex (Figure 2).

Given the similarities between the macroscale organization in humans and the marmoset — which is one of the smallest living monkey species — it is important to consider differences. In this context, there are two separate points to raise. First, the present discussion highlights broad similarities in topographic patterns as a means to draw attention to conserved features of macroscale organization. Careful examination of the images in the figures also reveals differences, some of which are surely the result of making comparisons across radically different data types (group-averaged and individual retrograde tracer injection patterns in the marmoset and within-individual functional MRI connectivity patterns in the human). Other differences may reflect true species differences that are not captured by our present focus on the conserved broad macroscale organization. In the future it will also be possible to explore the differences in greater detail utilizing comprehensive estimates of connectational anatomy. Several efforts are underway to characterize the non-human primate connectome at an increasing level of detail and depth [14,30**,37–40] including focus on direct comparison of functional connectivity to anatomical tract tracing data [31,41]. Large sets of injections using traditional and next-generation anatomical tracing techniques will soon be available providing a basis to explore similarities and differences more extensively.

Second, the human cortex is vastly expanded in absolute size relative to living monkey species with disproportionated expansion of the distributed association zones (Figure 1; see also Refs. [27,28]). This disproportionate expansion, in light of the observed macroscale organization, may provide insight into one of the most challenging and interesting questions of human neuroscience.
Canonical networks reveal homologous topography in frontal cortex.

(I) Projection patterns from three groupings of temporal and parietal tracer injections reveal candidate homologues of the dorsal attention network (green), the frontoparietal control network (blue), and the default network (red) in the marmoset. Posterior injections allow visualization of the relations between networks in frontal cortex. White lines are positioned in the same locations in frontal cortex across images to aide visualization.

(II) Human functional connectivity MRI estimates of the candidate homologous networks are illustrated within the two separate individuals using similar network colors to the marmoset. Temporal cortex seed regions are displayed in white circles. Human functional connectivity MRI shows correlation using z values after r-to-z transform with a threshold for z > 0.2. Labels D–F highlight the caudal-to-rostral gradient of networks in prefrontal association cortex with an apex prefrontal network prominently including midline frontal regions in both species. An asterisk labels the posterior parietal region at or near Opt in the marmoset and the candidate corresponding default network component in the human.
Namely, how do especially advanced forms of human cognition — including language, social inference, and remembering — arise given the strong similarities in anatomical network organization that are shared across primates? As the hierarchy of nested networks progresses rostrally in prefrontal and temporal association cortices and caudally in parietal association cortex, the networks come to occupy the zones of cortex that show the greatest disproportionate expansion between the two species. In addition to shifting the relative positions of regions, the expansion of association zones may have allowed the archetype network to fractionate and specialize into multiple domain-preferential networks in the human [42]. Thus a critical divergence between species may have arisen from the opportunity of expanding cortical zones to allow for greater functional specialization.

**Conflict of interest statement**
Nothing declared.

**CRediT authorship contribution statement**

**Jingnan Du:** Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Randy L. Buckner:** Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Supervision.

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