Humans can reason about other minds, comprehend language and imagine. These abilities depend on association regions that exhibit evolutionary expansion and prolonged postnatal development. Precision maps within individuals reveal these expanded zones are populated by multiple specialized networks that each possess a spatially distributed motif but remain anatomically separated throughout the cortex for language, social, and mnemonic/spatial functions. Rather than converge on multi-domain regions or hubs, these networks include distinct regions within rostral prefrontal, temporal, and midline association zones. To account for these observations, we propose the expansion-fractionation-specialization (EFS) hypothesis: evolutionary expansion of human association cortex may have allowed for an archetype distributed network to fractionate into multiple specialized networks. Human development may recapitulate fractionation and specialization when these abilities emerge.

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**Introduction**

Our abilities to re-experience past events, make inferences about others’ thoughts, and communicate through language are hallmarks of human cognition. Tasks targeting these functions have linked all three — autobiographical memory, social inference and language comprehension — to nearby or overlapping regions of association cortex [1–5]. Fueling further interest, these same distributed association zones are disproportionately expanded in the brains of large primates [6–8] and show prolonged postnatal development in humans [8–10] (see Figure 1). A foundational question for the field concerns how networks supporting advanced cognitive abilities are organized in these expanded association zones.

A barrier to unravelling the organization of association networks has been that multiple networks often have component regions juxtaposed next to one another in the same zones, causing blurring between networks and sometimes the impression of convergence. Precision mapping within the individual provides insight into the detailed organization of networks by reducing spatial blurring and allowing functional specialization to be examined within the idiosyncratic anatomy of a given individual [e.g. Refs. 3,11].

What has been discovered using precision mapping is a high degree of anatomical separation and functional specialization between networks, not just within a single zone of cortex, but across the entire distributed extents of multiple distinct higher-order networks. Each specialized network includes regions distributed across rostral (anterior) prefrontal and temporal association cortical zones. The similar spatial motif — with network regions often side-by-side across cortex — raises the possibility that the multiple networks originated from a singular archetype that has fractionated and specialized to support advanced human cognitive abilities.

**Distributed regions of human association cortex exhibit disproportionate expansion**

Comparing the human cortex to that of a monkey reveals a non-uniform expansion pattern, with disproportionately greater expansion in association zones that include prefrontal, posterior parietal, and temporal cortex [6,8,12]. Figure 1a shows an estimate of the macaque-to-human expansion map [8]. Note how red regions, representing high relative expansion, appear widely distributed — not in a single zone, such as prefrontal cortex, but in multiple, separate zones.

What’s more, a similar pattern appears when examining human cerebral cortical expansion from infancy to adulthood (Figure 1b). Hill et al. [8] characterized human evolutionary and developmental expansion ratios and plotted correlations between these values (see also Ref. [9]). Regions showing markedly similar expansion were...
Distributed regions of human association cortex exhibit disproportionate evolutionary and developmental expansion. Estimates of cortical surface expansion (a) between macaque and humans and (b) between human infants and adults both exhibit disproportionate expansion across distributed association zones, including in prefrontal cortex (PFC), posterior parietal cortex (PPC) and anterior (rostral) lateral temporal cortex (aLTC). Similarities between evolutionary and developmental expansion are summarized in (c), where warm colors indicate positive correlations and cool colors negative correlations. Both evolutionary estimates and those from development highlight association zones distributed across posterior those distributed across association cortex, including zones in prefrontal cortex (‘PFC’ in Figure 1c), posterior parietal cortex (‘PPC’) and anterior lateral temporal cortex (‘aLTC’) [8].

These observations motivate examination of how these expanded and developmentally neotenous zones are organized.

**Association cortex comprises large-scale, distributed networks across primate species**

Unlike early sensory systems, where areas have predominantly (but not exclusively) local connectivity to adjacent and nearby areas, higher-order association cortex is characterized by connectivity to association zones located in widely distributed positions throughout the cortex. Association regions in one zone of cortex (e.g. the inferior parietal lobule) will receive and send projections to zones of temporal, prefrontal, and midline association cortex. This anatomical motif has been well-characterized in macaques [13,14] and marmosets [15–17], and is also consistent with network estimates in the human [18–20]. Moreover, there is evidence for anatomical specialization even within prefrontal zones such that adjacent regions in parietal association cortex and adjacent regions in temporal association cortex will form parallel networks with distinct prefrontal regions [13,21; see also Refs. 14,22]. This anatomical organization is informative because it suggests a circuit motif that, via its multiple parallel instances, could support functional specialization.

Direct comparisons of human to monkey estimates of network organization reveal considerable homology, including for networks involving the rostral temporal and prefrontal association zones that are disproportionately expanded in humans [2,23–25,26**,27]. Given that old world and new world primate lineages share a common ancestor about 45 million years ago, these homologies suggest the prototypical distributed association network was fully represented in a relatively small-brained primate ancestor many tens of millions of years ago. What is intriguing to consider is how disproportionate expansion of human association cortex might build upon this anatomical archetype and contribute to especially advanced cognitive abilities.

**Multiple parallel distributed networks occupy association cortex**

A barrier to fully unraveling details of network organization has been reliance on group-averaged estimates. Regions within the evolutionarily expanded association zones show marked variability between individuals as measured by parietal, temporal, and prefrontal zones that are disproportionately larger in humans and late to develop. A central question in human neuroscience is how networks are organized in these expanded zones of association cortex in support of higher-level functions. Data adapted from Ref. [8].
functional connectivity MRI (fcMRI) [28,29,30] as well as through direct anatomical approaches [31–33]. Until recently, fcMRI estimates of whole-brain network organization (or ‘parcellations’) provided insight into general patterns [18–20], but blurred across individual variation. Broad swaths of association cortex at or near apex zones (i.e. far from sensorimotor hierarchies), for example, were commonly attributed to monolithic, multiple function networks (e.g. the canonical default network – DN) [24,34] or proposed to contain hubs of convergence [35].

Explorations of network organization leveraging within-individual approaches reveal finer-grained details (e.g. Refs. [30**,36**,37–42]). Networks originally thought to support multiple functional domains or share regions of convergence (including ‘hubs’) have been revealed to possess anatomical separation and specialization. Such separation applies to many distinct networks, some hypothesized to contribute to domain-general aspects of cognitive control and others supporting more specialized domains of information processing.

Here we focus on emerging evidence that reveals at least three distinct domain-specialized networks within the expanded association zones that differentially support language, social, and mnemonic/spatial functions [43,44**]. While each of these three networks preserves the anatomical motif observed in other primates [13,26*], all exhibit parallel nodes, side-by-side but spatially distinct, across distributed association regions (see Figure 2). In the first decades of exploration of these networks, we and others believed that they converged on shared functional regions [18,35]; we have recently appreciated that much of the focus on convergence may arise from a technical artifact of between-individual averaging (spatial blurring) [e.g. Refs. 11,40**]. As precision estimation methods have improved, the multiple networks have been revealed to rely on largely — if not entirely — anatomically distinct, adjacent regions contributing to specialized processing domains [37,43,44**,45].

Two of the domain-specialized networks, termed DN-A and DN-B for convenience, were identified as interdigitated within the expanded association zones, including lateral and medial PFC (IPFC and mPFC), PPC, LTC, and posteromedial cortex (PMC) [36**]. Certain features of these two networks align with previously reported region-specific dissociations. For example, a more rostral (anterior) region, along the temporoparietal junction (TPJ), is active during tasks targeting theory of mind, in contrast to an adjacent, caudal PPC region active during autobiographical memory retrieval tasks [1,34,46]. What was unexpected is that the networks are anatomically separate throughout their entire distributed extents including tight interdigitation within midline zones that were previously difficult to parse [36**]; see Ref. 35. mPFC and PMC both feature juxtaposed but spatially separate regions of DN-A and DN-B [36**,37,47]. In PMC in particular, DN-A features a reliable triad of regions that surround a region of DN-B, mirroring task differences observed in high-resolution individualized analyses [48**,49]. Precision estimates of the two networks reveal that previously noted dissociations in local cortical zones are components of parallel distributed networks that are largely (or entirely) anatomically distinct throughout their cortical extents.

The third, fully distinct network putatively labelled a language network (LANG) because of its anatomical positioning and lateralization, exhibits a similarly distributed pattern, as well as tight juxtaposition to DN-A and DN-B across association zones (Figure 2) [43]. This network includes regions in inferior frontal gyrus (IFG), posterior superior temporal cortex (pSTC) and the temporal pole (TP), included in clinical [50–52] and task-based fMRI studies [11] of language. Of historical note, this network was underappreciated in several well-referenced estimates of network organization that used group-averaging approaches (e.g. blurred, including within the DN, in Refs. [18,19]; but see Refs. [53–55]).

Evidence for these multiple separate but interdigitated networks has now been found within over two dozen unique individuals [36**,37,43,44**], including those extensively sampled (i.e. featuring more than 6 hours of fixation data each) and those scanned with high field strength (7T), reinforcing that these networks appear spatially separate, sometimes even within the same sulcus (see Figure 9 in Ref. [37]). Parcellations from other within-individual data collection efforts (e.g. analyses of Human Connectome Project and Midnight Scan Club data) also show evidence for separate, interdigitated networks, particularly within subsets of individuals. For example, in one study, features of ‘Default A’, ‘Default B’ and ‘Temporal Parietal’ networks correspond to those in DN-A, DN-B and LANG (see Figure 4 in Ref. [30**]), and in another, midline solutions for the ‘Context’ network relate to DN-A and ‘Default’ to DN-B (particularly within MSC04, MSC05, MSC09, MSC10) and solutions for the ‘Ventral Attention’ network relate to LANG (across subjects; see Figure 3 in Ref. [38]).
Within an individual, parallel distributed networks differentially support remembering, theory-of-mind and language task contrasts. (Top) Within an individual, DN-A, DN-B and LANG networks exhibit distributed regions that are side-by-side across association zones, including prefrontal cortex (PFC), posterior parietal cortex (PPC), anterior lateral temporal cortex (aLTC), posteromedical cortex (PMC) and medial prefrontal cortex (mPFC). Of note, within this individual, DN-A included regions in aLTC in the right hemisphere (not shown), but many subjects have representation in both hemispheres (see Refs. [43]). (Bottom) Each of these networks exhibits preferential recruitment by task contrasts from distinct functional domains: DN-A for remembering, DN-B for theory of mind and LANG for language. This remembering task contrasted questions about personal past events to those targeting current feelings and beliefs (see Refs. [35,44**]). This theory-of-mind task contrasted consideration of others’ emotional to physical pain (see Refs. [44**,59,90]). The language task contrasted reading sentences comprising words to pronounceable nonwords (see Refs. [11,43]). Domain-preferential responses are a property of the entire distributed networks including rostral temporal, prefrontal and midline regions. Data adapted from Ref. [43] (Subject 13), 44** (Subject 12).

To reiterate, these networks occupy association zones that exhibit disproportionate expansion across human evolution and postnatal development. For example, compare the labelled zones in the parcellation estimate of a single individual in Figure 2 [43,44**] to corresponding zones in the correlation map from Figure 1c [8]. That these networks feature a common parallel, distributed motif suggests the possibility that such an organization might result from fractionation of a less-differentiated proto-organization, perhaps early in development (discussed further below; see also Ref. [56]).

**Parallel distributed association networks support domain-specialized higher-order functions**

Anatomically separate networks within the expanded zones of association cortex participate in specialized functional domains. Recent evidence for network specialization has been obtained by identifying the networks within individuals and then exploring functional dissociations in task-based activation studies targeting (i) mnemonic/spatial, (ii) social and (iii) language functions [43,44**]. Figure 2 summarizes a key set of dissociations in a single individual: DN-A is preferentially recruited for remembering, DN-B for social inference and LANG for language. Such evidence for specialization is striking, given the tight interdigitation of these networks, as well as prior group-based work suggesting potential convergence [1, but see Refs. 57,58]. Figure 2 shows data from one person, but task-based dissociations were independently replicated across most individuals tested to date [43,44**]. Distinct network recruitment was also not limited to specific regions, but appeared across multiple zones [44**], often including small distributed regions that might otherwise go unnoticed [43]. These findings collectively suggest that functional specialization — in relation to a task domain — is a property of the network as a whole, not just subregions.
For example, in a series of recent studies, we contrasted tasks involving remembering past and imagining future events, to a distinct set of task contrasts designed to probe theory of mind [44**]. The theory-of-mind tasks were developed by Saxe et al. to isolate regions recruited within-individuals when considering others’ mental states [59,60, see also Refs. 63,90]. We found evidence for a functional double dissociation, with DN-A preferentially recruited for remembering the past and imagining the future and DN-B for theory of mind. Evidence for functional dissociation was obtained for the network as a whole and across each of the five distributed regions labelled in Figure 2 (with the strongest results in subsets of participants) [44**]. Using another task contrast developed by Fedorenko et al. to isolate language-relevant regions (e.g. from nearby ‘multiple demand’ regions) [61**,62, see also Ref. 11], we explored recruitment of the LANG network. Task recruitment was highly selective for the LANG network as compared to the immediately adjacent association networks [43]. Of further interest, while the LANG network was left-lateralized in most individuals, one individual was right lateralized. The response to the language task contrast was specific and selective to the right-lateralized network regions in this individual, demonstrating that network organization predicts functional specialization even in instances of unusual organization.

Collectively, these results strengthen evidence that the three parallel networks — DN-A, DN-B and LANG — can be consistently identified as separate and functionally dissociated within individuals. While questions remain about network processes and the extent of specialization,4 these distributed networks occupy juxtaposed zones of association cortex and are differentially recruited by tasks from distinct, higher-order cognitive domains [43,44**]. Probing specialized regions, or groups of regions, differentially supporting such functions is not novel [e.g. Refs. 1,3,34,57,63,64; see also Ref. 88]. What has newly emerged is that functional dissociation is present across the entire distributed networks for these domains, including rostral temporal and prefrontal associations regions, as well as regions along the midline, and with juxtapositions between networks mirrored in many locations throughout the cortex, as if a common originating archetype is fractionated and specialized to support diverse functions. In the next section we will speculate on how such specialization might emerge during development.

Proposed role of hierarchical development in network organization

The expanded association zones of human cortex are populated by separate but intertwined networks. How might such an organization arise? The development of specialized functional areas and patches in visual extrastriate cortex provides insight into how distributed higher-order associations networks might fractionate and specialize [65]. Early in postnatal development, primate extrastriate regions (or ‘patches’ in monkeys) do not show the fully formed category-specific specialization (i.e. for faces or scenes) observed in adults [65–67]. Rather, extrastriate cortex is visually responsive and has a coarse retinotopic organization, featuring adjacent mapping of central-to-peripheral parts of the retina [68,71]. By one model, this proto-organization is hypothesized to scaffold further refinement of specialized zones that emerge via experience, with face-responsive patches forming within extrastriate zones aligned to the central portion of the retinotopic map and scene-responsive patches within the peripheral portion [68,69]. The broad, early retinotopic organization may thus influence how extrastriate patches fractionate and specialize early in postnatal development [68]. Recently, evidence for biased connectivity (e.g. between central V1 and a proposed face-selective cortical region and peripheral V1 and proposed scene-selective regions) was also observed in newborn human infants, further suggesting that connectivity may influence the development of network-specific functions, likely concurrently with top-down or other influences [70**].

Specialization of parallel networks within association cortex might similarly proceed hierarchically. An early proto-organization (perhaps reflecting broad, DN-like properties in apex zones) may fractionate and specialize through developmental processes that are biased by distinct features of network connectivity [44**,56]. A distinguishing feature of DN-A, for example, is connectivity to posterior parahippocampal cortex (PHC) [36**]. This feature, perhaps reflecting a hippocampal gradient of projections to association cortex, might bias network fractionation and specialization, with DN-A ultimately providing support for mnemonic and spatial processes [see also Ref. 56]. Similarly, Silson et al. [49] proposed that the development of category-preferences in ventral temporal cortex may impact specialization of such association regions as PMC. As another example, the association regions that form the canonical language network are

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1. By proposing that early, bottom-up connectivity differences might bias network specialization, we do not imply that specialization of extrastriate cortex emerges only from a retinotopic proto-organization. It could be a major, but not exclusive, developmental constraint. A retinotopic proto-organization, for example, leaves open why humans (and other primates) foveate faces [86, see also Ref. 87]. Bottom-up self-organization and top-down biases may together lead to strong developmental constraints that cause convergent anatomical and functional organization to emerge when expressed in the typical developmental environment (see also Ref. 91).

2. There is a tricky, unresolved issue that concerns the functional neuroanatomy of the hippocampal formation along its anterior-to-posterior axis. DN-A shows strong coupling to posterior PHC [36**] and can be linked to regions within the hippocampus proper at or near the subiculum [37]. However, MRI measures based on typically used methods have poor signal properties in anterior hippocampal regions, including a large extent of entorhinal cortex. Thus, we do not know yet whether DN-B, or other networks, are coupled to distinct regions of the anterior hippocampal formation.
not randomly positioned across the cortex. Prefrontal zones near what has historically been called ‘Broca’s area’ are close to the motor representations of the orofacial structures critical to speech. The temporal association zones are near to secondary auditory regions important to speech perception [e.g. Ref. 43]. Anatomical adjacencies might reflect early developmental anchors that bias or constrain which specific association regions emerge as components of each higher-order network.

This proposal also allows for the networks, like extrastriate patches, to display both similar modes of processing and distinct specialization [66,72]. DN-A and DN-B, for example, may share a broad processing mode (i.e. for internally constructed representations) and also specialization (i.e. preferentially supporting specific functional domains; see also Ref. [56]).

Proposing the expansion-fractionation-specialization (EFS) hypothesis
To account for the described network observations, we propose the expansion-fractionation-specialization (EFS) hypothesis (see also Refs. [22,73]). The evolutionary expansion of hominin association cortex might have created an opportunity for network specialization by providing large zones of cortex that share in common a distributed anatomical-connectivity motif (Figure 3). Comparative analysis with monkey species suggests this core motif is at least 45 millions years old [15,26**,27,74]. In modern humans this anatomical motif is expressed on a cerebral surface that is vastly expanded relative to the estimated primate ancestor. At birth, human association cortex may exhibit a proto-organization that reflects this ancient network motif but with poorly differentiated anatomical connectivity across the broad association zones. Fractionation and specialization may then occur during early development, through competitive activity-dependent processes, producing finer-grained networks that, as a property, have close juxtapositions across the cortex [56]. Connectivity differences may also bias specialization, evidenced by the networks’ distinct features and differential recruitment for mnemonic/spatial, social and language domains [43,44**]. In this way, fine-grained networks may develop in expanded association zones, with those farthest from sensorimotor hierarchies crucial to uniquely flexible human functions [22,75].

A note on the relation between domain-specialized networks and multiple-domain networks
While we have focused here on parallel networks that participate in domain-specialized functions, networks linked to domain-general cognitive and attentional control (e.g. ‘frontoparietal control’ network [23]) also occupy expanded association zones, including regions showing marked individual variability [28,29,76]. In this context, it is important to note that the presence of multiple specialized networks, with juxtaposed nodes within prefrontal cortex, challenges the notion that domain-general prefrontal regions exclusively control posterior domain-specialized regions. As far as we have been able to estimate, the association networks most specialized for domain-specific processing all include rostral (anterior) prefrontal and temporal association regions.

By some views, this observation may be surprising given the expectation that anatomical integration might lead to more and more abstracted, domain-flexible representations in rostral portions of frontal cortex [e.g. see Ref. 89]. The collective recent results argue that this is not the case for all prefrontal regions. Rather, domain-specialized networks include prefrontal and temporal regions as anticipated by the seminal work of Goldman-Rakic [13]. And while there is also clear evidence for distinct domain-general networks that participate in cognitive control, these networks are anatomically distinct throughout the cerebral cortex, including prefrontal cortex (see also Ref. [61**]). Without the detailed estimates of more precise locations of these functionally distinct regions, it would be easy to miss their full level of specialization and heterogeneity.

The detailed anatomical features identified in recent years via precision estimates of organization thus provide a view of specialization that includes considerably more modularity in certain zones of prefrontal cortex than might have been predicted, with domain-specialized prefrontal regions as components of widely distributed specialized networks. Interactions between these and other networks are an open topic for future investigation. For example, domain-specialized networks may be under the control of other networks. That is, rather than prefrontal regions acting as domain-general top-down control structures sending signals that bias processing in posterior regions, it may be that certain distributed networks control other distributed networks, with each network possessing its own anatomically distinct prefrontal component.

Most broadly, it will be interesting for the field to revisit notions of modularity, domain specialization, and interactions with domain-general processing functions from a network perspective informed by precision anatomy [see also Ref. 76].

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7 While our paper focusses on specialization between networks, one should not expect the multiple regions within a domain-specialized network to make the same computational contribution to the network’s overall functions. It is likely that anterior and posterior cortical regions possess their own local circuit motifs that are being used over and over across the multiple specialized networks in ways that are not revealed by our emphasis on domain specialization between the distributed networks.
Considerations for future research

Though we hypothesize that multiple networks may emerge from an early developmental proto-organization that fractionates and specializes, these ideas require testing. We predict that such fractionation may occur in the first years of life (i.e. coinciding with rapid surface area expansion [77]). Fractionation may occur by age 3, for example, given evidence that brain regions typically active during theory-of-mind tasks (e.g. overlapping with DN-B) respond preferentially to consideration of others’ thoughts by this age [78**]. Infant work also shows evidence of long-distance connectivity even earlier in postnatal development (e.g. see Figure 2 in Ref. [79]). Increasing efforts to examine infant cortical organization, prenatally or within days to weeks after birth (e.g. Refs. [70**,80,81]) highlight exciting opportunities for future research.

A crucial and related question pertains to how disruptions to proposed network fractionation and specialization processes might have diverse clinical implications. Considerable research, for example, has explored whether differences in brain regions supporting social and language functions could inform understanding of autism spectrum disorder (ASD) [82–84]. As described, networks supporting social inference and language may be tightly interwoven across the cortical mantle within neurotypical adults, raising the possibility that atypical fractionation and/or specialization contribute to the development of ASD symptoms. Exploring network trajectories during the first year of life, even before symptom emergence [85], could inform a potential role of network development.

Conclusions

We present recent evidence from precision mapping within individuals that parallel and distributed networks occupy regions of association cortex that exhibit disproportionate expansion during human evolution and development. Several of these networks appear to differentially support distinct higher-order functions including remembering, social inference and language [36*,43,44**]. To account for these findings, we propose the expansion-fractionation-specialization (EFS) hypothesis: the expansion of human association cortex might have allowed distributed association networks to fractionate and specialize, perhaps early in development, within zones farthest from (and least tethered to) sensorimotor hierarchies exhibiting links to advanced, sensory-independent functions [22,56].

Conflict of interest statement

Nothing declared.

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