

Chapter 16

Socially entwined memories and their neuroanatomical basis

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Autobiographical memory refers to the storage of information about one's past experiences. However, natural selection has not refined the human autobiographical neurocognitive system over generations merely for the purpose of reminiscing, but rather to guide adaptive behaviors that enhance survival and fitness. Thus the scientific study of autobiographical memory is incomplete without considering its adaptive function(s) (Klein, 2013; Morales-Calva & Leal, 2024; Nairne & Pandeirada, 2016).

Perhaps the greatest challenge humans encounter in everyday life is navigating the social world. That is because social interactions are uniquely complex and nuanced, often involving subtle or conflicting cues, unspoken rules, and a high risk of misunderstandings or social missteps. Yet, humans have a fundamental need to establish social bonds, and when these needs go unfulfilled, it has severe negative consequences for physical and mental well-being (Beutel et al., 2017; Mann et al., 2022; Ong et al., 2015; Park, Majeed, et al., 2020; Tilvis et al., 2011). Perhaps unsurprisingly, this basic need for social connection is accompanied by preferential processing of social information, evident in biased allocation of attentional resources (End & Gamer, 2017, 2019), enhanced recognition memory (Gomez et al., 2020), associative memory (Stewardson et al., 2023), and lexical-semantic processing (Diveica et al., 2024), as well as neural pathways specialized for social perception (Downing et al., 2001; Isik et al., 2017; Kanwisher & Yovel, 2006).

Compared to other primates, human sociality is marked by larger social networks (Dunbar, 2016), as well as higher levels of cooperation and collective decision-making (Tomasello, 2014b; Tomasello et al., 2012). The resulting challenges of navigating complex sociocultural environments are thought to have driven the evolution of our advanced cognitive abilities (Tomasello, 2009, 2014a), along with a significant increase in brain size to meet these computational demands (Dunbar, 1998). This line of reasoning, therefore, suggests that the primary function of the autobiographical memory system

might be to guide social cognition and behavior. Indeed, among the various functions autobiographical memory is thought to fulfill in everyday life (Bluck, 2003; Dean Webster, 2003), social functions have been proffered as the fundamental driver of the development of autobiographical memory in childhood (Nelson, 1993), and people most commonly report social motivations for their everyday memory recollections (Harris et al., 2014).

In this chapter, we will discuss the importance of autobiographical memories in social cognition and behavior, arguing for a key role of the brain's extended default network in facilitating information exchange between the autobiographical memory and social brain systems. In Part I, we will expand on the various functions that autobiographical memory fulfills in social contexts, including its role in forming and maintaining social bonds, enhancing empathy and pro-sociality, enabling adaptive social decisions such as approach and avoidance, and guiding our understanding of others' behaviors. In doing so, we will highlight the complementary contributions of semantic and episodic aspects of autobiographical memory. Next, we will present empirical evidence highlighting the importance of the brain's memory system in social contexts. In Part II, we will synthesize existing findings on the neural correlates of three types of prior knowledge that we acquire through personal life experiences and use flexibly in the service of social cognition, including the role of the anterior temporal lobe (ATL) in person-specific knowledge and abstract social concepts, the medial temporal lobe (MTL) in mapping social networks, and the medial prefrontal cortex (mPFC) in social event scripts and person schemas. In Part III, we will present novel findings demonstrating that the integration of information between these regions, as well as the wider autobiographical, semantic, and social systems, is enabled by a distributed set of brain regions that largely overlaps with the brain's default network. We will discuss how this network is preferentially modulated by sociality and the prior knowledge available about social targets, and we will examine its functional organization.

Part I. The functions of autobiographical memories in social interactions

Social bonding

People self-report that they share autobiographical memories with others to form new relationships and to maintain and strengthen existing bonds (Alea & Bluck, 2003; Bluck et al., 2005). Indeed, disclosure of autobiographical information has been linked to increased interpersonal closeness and liking (Aron et al., 1997; Collins & Miller, 1994; Lin & Utz, 2017). When we share personal facts or narrate past events to someone who was not present, we reveal something about who we are (Sprecher et al., 2013). The increased familiarity following self-disclosure plays a crucial role in fostering intimacy

in interpersonal relationships (Alea & Bluck, 2007; Laurenceau & Kleinman, 2006). Likewise, reminiscing over shared experiences creates a sense of shared history, whereas recounting experiences from one's own life that mirror or relate to another's self-disclosure fosters a sense of feeling understood, thereby enhancing social connection (Bazzini et al., 2007; Pilon et al., 2023; Reis et al., 2017). Reflecting the central role of self-disclosure in human sociality, opportunities to share personal experiences with others are intrinsically rewarding, strongly engaging the brain's reward system, and sometimes even surpassing the allure of financial incentives (Tamir & Mitchell, 2012).

Empathy and pro-sociality

Autobiographical memory has been strongly linked to the ability to share others' emotions and pain and to act pro-socially (Gaesser, 2020). For example, recalling similar past experiences when observing someone in distress enhances empathic feelings (Bluck et al., 2013), while remembering past instances of helping others increases the willingness to help (Gaesser & Schacter, 2014). Relatedly, pro-social intentions and behaviors are heightened after imagining oneself helping the person in need (Gaesser & Schacter, 2014; Gaesser et al., 2015; Gaesser et al., 2017; Gaesser et al., 2018; Gaesser et al., 2020), a process that relies on the same neurocognitive system as autobiographical recollection (Wilson & Ross, 2003).

In addition, autobiographical memory influences pro-social behavior through its intrinsic connection to self-identity (Tulving, 1985; Wilson & Ross, 2003). Individuals who perceive their memory efficacy as low—believing they are less able to recall current experiences in the future—tend to perceive their actions as less consequential for their self-concept and are therefore less likely to make pro-social choices (Touré-Tillery & Kouchaki, 2021). Likewise, recalling childhood memories enhances one's sense of moral purity, leading to more pro-social behavior toward others (Gino & Desai, 2012).

Adaptive social decision-making

Autobiographical memory informs adaptive social decisions (FeldmanHall et al., 2021; Murty et al., 2016; Schaper et al., 2019). In the context of a monetary game with fair and unfair partners, participants chose to re-engage with fair partners and rejected unfair ones only when they could remember the nature of their previous encounters (Murty et al., 2016). Such adaptive decisions were dependent on veridic episodic memories of the behavior exhibited by the previous partners, rather than stereotype-based guessing (Schaper et al., 2019). These findings suggest that adaptive social decisions following single-shot learning critically depend on autobiographical memory.

The importance of memory for adaptive social decision-making extends to future-oriented cognition, as prospective memory—remembering to act in a

specific way at some point in the future—is enhanced when encountering individuals who have previously shown cooperative or cheating behavior, compared to those with neutral behaviors (Schaper et al., 2022). This prospective memory bias likely supports the maintenance of reciprocal relationships and the avoidance of cheaters. Therefore successfully navigating the complexities of the social world may require excellent autobiographical memory. In line with this possibility, individuals who remember a higher percentage of previous social encounters tend to have larger social networks (Winke & Stevens, 2017).

Social inferences

When perceiving another person, we can infer both their stable attributes, like social group membership and personality traits, and their temporary mental states, such as their emotions, intentions, goals, and beliefs (Frith & Frith, 2012; Lieberman, 2007). These attributes are often inferred spontaneously and instantaneously (De Freitas & Hafri, 2024; Macrae & Bodenhausen, 2000), and are crucial for predicting people’s behaviors and guiding our responses—we might approach an older woman who appears to need help on the street but avoid crossing paths with an angry protester during a riot.

Social inferences are directly informed by prior knowledge (Binney & Ramsey, 2020; Freeman & Johnson, 2016; Spreng, 2013; Amodio, 2025). Our personal past experiences form the foundation of our social expertise—our understanding of when, where, why, and how people, or groups of people, behave in certain ways. This knowledge guides our flexible and context-sensitive appraisal of the social world. For instance, the more details one remembers about another person’s history of romantic failures, the more empathetic they feel toward that person when experiencing rejection in a romantic context, but not in a career-related one (Ciarumelli et al., 2013).

Over time, autobiographical memories become semanticized, shifting from unique events held in episodic memory (e.g., “When I met Laura last Thursday, she was happy”) to gist and autobiographical facts abstracted from repeated experiences (“Laura is a happy person”), to abstract semantic concepts and categories (that happiness is a desirable positive emotion expressed through behaviors like smiling and laughter) (Renoult et al., 2012; Renoult et al., 2019). Semantic knowledge can be acquired not only from the extraction of statistical regularities across repeated first-hand experiences but also through gossip and explicit instruction, such as a parent teaching their child about the various ways friendship manifests.

Episodic and semanticized autobiographical memories play complementary roles in shaping social cognition (Almeida, 2007; Amodio, 2019; Klein et al., 2002; Klein et al., 2009). Episodic memories are particularly useful in the absence of repeated prior experiences, like when you have interacted with someone just once before. They also ensure contextually relevant guidance

when encountering situations that closely resemble the perceptual, spatial, or temporal details of specific memories. However, retrieving detailed episodic memories is computationally demanding. By reducing information to a lower-dimensional representation, semantic knowledge offers a cognitively efficient alternative that enables generalization across perceptually dissimilar contexts (Hackel et al., 2024; Tamir & Thornton, 2018). Although semanticized memories facilitate inferences about others' behavior when the environment aligns with preexisting concepts, they can lead to errors when the environment contradicts those concepts. In such cases, concurrent retrieval of episodic instances that deviate from the generalization can establish valuable boundary conditions (Klein et al., 2002). Therefore, flexible context-appropriate social cognition and behavior depend on the dynamic interplay between social environmental cues and our socially-relevant episodic and semantic autobiographical memories.

A comprehensive, empirically derived ontology of socially-relevant prior knowledge is currently lacking. While much of the literature has focused on episodic memories of past experiences, several other types of socially-relevant prior knowledge have also been studied. These include person-specific knowledge, social network maps, abstract social concepts, social event scripts, and person schemas. In the next section, we explore specific brain regions that emerge as key centers for these latter types of prior knowledge, drawing on convergent evidence from multiple neuroscientific methods.

Part II. The neurocognitive underpinnings of socially-relevant prior knowledge

Person-specific knowledge and abstract social concepts in the anterior temporal lobe

The ATL has been implicated in a variety of social cognitive abilities (Binney & Ramsey, 2020; Diveica et al., 2021). Several lines of research demonstrate that the ATL contributes to social cognition via a key role in semantic memory.

The cooccurrence of socio-affective and semantic deficits following relatively focal ATL damage highlights its dual role in semantic and social cognition. This has been recognized for over a century, with comparative neurological studies showing that full ATL resection in nonhuman primates leads to a constellation of impairments that includes semantic deficits like visual associative agnosia (difficulty retrieving the meaning of objects) and hyperorality (a tendency to orally inspect objects), as well as dysregulated social behaviors, such as emotional blunting and hypersexuality (Brown & Schafer, 1888; Klüver & Bucy, 1939). These symptoms, collectively termed Klüver-Bucy syndrome, were later replicated in humans following surgical ATL resection for temporal lobe epilepsy (Terzian & Dalle Ore, 1955) and

observed in other ATL-related pathologies (Gerstenbrand et al., 1983). Notably, the syndrome is present even when the neighboring hippocampus is spared, implicating damage to the polar and/or inferolateral ATL as a likely cause (Ridley et al., 2001). The joint impairment of semantic and social abilities is mirrored in semantic dementia, a neurodegenerative disorder characterized by progressive ATL atrophy. Semantic dementia patients exhibit a pattern of impairments indicative of loss of semantic knowledge, including person-specific knowledge, accompanied by reduced capacity for face recognition, mental state inference, and empathy (Binney et al., 2016; Borghesani et al., 2019; Ding et al., 2020; Irish et al., 2014; Lindquist et al., 2014; Snowden et al., 2012; Rouse et al., 2024).

The increased spatial precision of functional MRI studies confirmed that semantic and social tasks activate overlapping portions of the polar and ventrolateral ATL (Balgova et al., 2022; Balgova et al., 2024; Deen et al., 2024; Rice et al., 2018), in line with the view that the ATL supports the retrieval of socially-relevant semantic knowledge in the service of social cognition (Binney & Ramsey, 2020; Olson et al., 2013). Two types of social knowledge—person-specific knowledge and abstract social concepts—have been linked to the ATL (Olson et al., 2013).

Person-specific knowledge encompasses memory of individuals, including their face, voice, biographical details, and emotional associations. Person-specific knowledge is essential for everyday social interactions, as we often engage with the same people. ATL supports person recognition via the storage of abstract identity information (Anzellotti & Caramazza, 2014; Collins & Olson, 2014; Kovács, 2020). ATL's local activity patterns can distinguish between the faces of different individuals (Kriegeskorte et al., 2007) and, unlike more posterior occipitotemporal regions, generalize across identity-irrelevant visual properties such as rotation, contrast reversal, partial views, and emotional expression (Anzellotti & Caramazza, 2016; Anzellotti et al., 2014; Nasr & Tootell, 2012; Nestor et al., 2011; Yang et al., 2016). However, the face-responsive ATL is engaged not only in face recognition but also when retrieving biographical knowledge about a person and imagining them in novel scenarios (Deen et al., 2024), reflecting a broader role in person-specific knowledge.

Indeed, as familiarity increases, perceptual identity representations become enriched by semantic and episodic details, as evidenced by ATL's sensitivity to mnemonic manipulations. The modulation of ATL activation by changes in a face's identity increases with familiarity (Rotshtein et al., 2005), and personally-familiar and famous faces elicit greater ATL responses than unfamiliar ones (Gorno-Tempini et al., 1998; Von Der Heide et al., 2013). This familiarity effect extends beyond faces to voices (Bethmann et al., 2012; Blank et al., 2015; Maguinness et al., 2018; Sun et al., 2023) and proper names (Gorno-Tempini et al., 1998), and increases with the amount of prior knowledge about a person (Desai et al., 2023). Notably, ATL activity patterns encoding a person's identity

remain consistent across different cues, such as their face, voice, name, a picture of their house, or an object associated with their career (Abel et al., 2015; Wang et al., 2017). This indicates that the ATL integrates diverse information about individuals into cohesive, person-specific representations. This process is supported by ATL's capacity to rapidly encode associative pairings involving person identities (Collins et al., 2016; Eifuku et al., 2010) and its broader role as the hub of a “spoked” neural architecture that integrates modality-specific information from distributed cortical “spokes” into coherent, generalizable concepts (Lambon Ralph et al., 2017; Wang et al., 2017).

Given its role as a semantic hub, the ATL also supports the retrieval of socially-relevant abstract concepts and categories, like those denoting emotions, personality traits, and social roles (Diveica, Pexman, et al., 2023; Pexman et al., 2023). Abstract concepts offer crucial insights into the workings of the social world—for example, one can only infer that someone is being dishonest given an understanding of what “honesty” means (e.g., Moll et al., 2008; Spunt & Adolphs, 2019). Social concept processing elicits reliable ATL activation (Arioli et al., 2021; Rice et al., 2015) and is disrupted following stimulation of this region (Catricalà et al., 2020; Pobric et al., 2016) or its atrophy in semantic dementia (Rouse et al., 2024). While its ventrolateral portions respond to social and nonsocial concepts alike, its dorsopolar portions are preferentially engaged by social concepts (Binney, Hoffman, et al., 2016), reflecting their special status within the semantic system (Pexman et al., 2023). The additional involvement of the dorsopolar ATL in social concept processing might be driven by a greater need to integrate affective information (Binney, Hoffman, et al., 2016; Rijpma et al., 2023; Wang et al., 2019), facilitated by its strong connections to orbitofrontal and limbic regions (Herlin et al., 2021; Papinutto et al., 2016). In line with this, the dorsopolar ATL responds more strongly to emotionally valenced social concepts than to emotionally neutral ones, which, in turn, elicit stronger responses than concepts lacking social significance (Mellem et al., 2016).

Social network maps in the medial temporal lobe

The hippocampus and adjacent MTL structures are crucial for both episodic (Dickerson & Eichenbaum, 2010) and autobiographical memory (Eslinger, 1998; Herfurth et al., 2010). Neuroimaging and neuropsychological studies also link these regions to social abilities, often interpreted as reflecting retrieval of autobiographical memories in support of social cognition (Davidson et al., 2012; Laurita & Spreng, 2017; Rubin et al., 2014; Spreng, 2013). For instance, judging others' emotional states elicits hippocampal activation, but the magnitude of this activation matches self-judgments only when the others are perceived as similar to oneself (Perry et al., 2011). This suggests that the hippocampus enables the retrieval of autobiographical self-knowledge to guide social inferences, especially when this knowledge is relevant. During dynamic

social interactions, hippocampal suppression is sensitive to the adaptiveness of approach/avoidance choices following single-shot learning, while hippocampal enhancement is associated with subsequent memory for the original social interaction (FeldmanHall et al., 2021). These findings suggest multifaceted autobiographical contributions of the hippocampus to adaptive learning during social interactions.

Emerging evidence also implicates the MTL in knowledge about social network structures, including who knows whom, how close they are, and their relative levels of social power (Li et al., 2021; Montagrin et al., 2018). Successfully navigating life in large interdependent social groups requires the ability to efficiently track such patterns of interpersonal relationships (Basyouni & Parkinson, 2022). For example, befriending a person well-liked by one's friend group versus a person they strongly dislike can have opposing social consequences.

The MTL plays a key role in both learning and retrieving social network knowledge. During learning, hippocampal and amygdala activation track the emergence of knowledge about the power hierarchy within an unfamiliar social group on a trial-by-trial basis (Kumaran et al., 2012; Kumaran et al., 2016). Similarly, the overall functional connectivity (degree centrality) of the hippocampus and parahippocampus reflects emerging knowledge about the community structure of the social network (Tompson et al., 2020). During retrieval, amygdala and hippocampus activation increases parametrically with the social rank of a perceived individual, even when hierarchy knowledge is irrelevant to the task—suggesting spontaneous retrieval (Kumaran et al., 2012; Kumaran et al., 2016). Likewise, for one's real-life social network, parahippocampal activity patterns spontaneously encode individuals' overall level of social contacts within the network (Parkinson et al., 2017), while the retrosplenial cortex encodes social distance (i.e., degrees of separation in the network) (Peer & Hayman, 2021).

The involvement of the hippocampus and affiliated MTL regions suggests that social network knowledge is organized into “cognitive maps,” similar to those used for navigating physical space (Eichenbaum, 2015; Schafer & Schiller, 2018). Cognitive maps integrate sparse observations from separate experiences into multidimensional spaces defined by continuous physical or abstract dimensions (Behrens et al., 2018). For example, in a role-playing social interaction game, left hippocampal activity tracked changes in participants' relationships with fictional characters within a two-dimensional social space defined by power and affiliation (Tavares et al., 2015; Zhang et al., 2022). While all relationships were embedded in this shared abstract space, the hippocampus also encoded the specific history of interactions with each character through unique neural state sequences (Schafer et al., 2024). This suggests that the hippocampus constructs abstract social maps and integrates these with episodic details of individual relationships. Importantly, hippocampal tracking of social cognitive maps was linked to lower self-reported

social avoidance tendencies and larger real-world social networks, highlighting its critical role in supporting everyday social functioning (Schafer et al., 2024; Tavares et al., 2015).

Cognitive maps enable flexible behavior by allowing inference of novel “routes” in the absence of direct experience (Behrens et al., 2018). For example, understanding the structure of a generic family tree allows inferring that if Emma is Liam’s aunt and Ava is Liam’s daughter, Ava must be Emma’s niece. People can easily make such novel social inferences. After learning the hierarchical organization of two separate social groups along two inferred dimensions, competence and popularity, participants used new information about the relative positions of pairs involving one individual from each group—the “bridges” between the two distinct hierarchies—to accurately infer the relative ranks of novel between-group pairs (Park, Miller, et al., 2020). This inferential process was linked to hippocampal reinstatement of activity patterns associated with the bridges (Park, Miller, et al., 2020). Neural pattern similarity in the hippocampus, entorhinal cortex, and affiliated regions (mPFC, orbitofrontal cortex, posterior cingulate, and retrosplenial cortices) reflected distances in the latent social space. Even though only one dimension was behaviorally relevant, pattern similarity was better explained by distances in the full two-dimensional space than along the single dimensions (Park et al., 2021), indicative of spontaneous construction of a unified relational structure. The representational geometry of this social space remained stable across tasks, indicating a generalizable knowledge structure (Park & Zolfaghar, 2023). Furthermore, during subsequent social decision-making, trajectories through the two-dimensional social space were associated with grid-like codes in the entorhinal cortex, mirroring how movement through physical space is tracked (Park et al., 2021). These findings demonstrate that the MTL contributes to social network knowledge by constructing and flexibly navigating cognitive maps of abstract social spaces.

Social schemas in the medial prefrontal cortex

The mPFC is central to neurobiological models of social cognition (Amodio & Frith, 2016; Mitchell, 2009; Van Overwalle, 2009). A large body of research also links the mPFC to schemas, which are superordinate relational structures that organize generalizable knowledge about entities, events, or situations. Schemas serve as reference templates against which incoming sensory signals are compared, thereby shaping how information is interpreted and remembered (Gilboa & Marlatte, 2017; Lieberman et al., 2019). Unlike conceptual knowledge, schemas are more easily updated and can preserve chronological information.

Two types of socially-relevant prior knowledge benefit from representation in the form of schemas, implicating the mPFC—social event scripts and person schemas (Krueger et al., 2009; Raykov et al., 2021). Social event scripts refer to knowledge about the typical behaviors encountered in specific situations and the

order in which they occur (Ghosh & Gilboa, 2014; Schank & Abelson, 2013). They can incorporate cultural norms, social rules, and expectations (Bicchieri & McNally, 2018). For example, a script for “restaurant dining” might include a sequence of events—being seated, ordering, eating, and paying—as well as the expected social roles and behaviors, like the waiter taking orders, the chef preparing food, and the diners paying the bills. Reasoning about the correct sequence of events in social situations reliably recruits the mPFC (Van Overwalle, 2009). During passive observation of naturalistic social interactions, the activity patterns in the mPFC and the affiliated posterior medial cortex can distinguish between different social situations, such as a café and a grocery store, in a way that generalizes across different storylines, specific locations, input modalities, and social agents involved, indicative of instantiation of schematic event knowledge (Baldassano et al., 2018; Reagh & Ranganath, 2023). The schema effects in the mPFC are disrupted when the sequence of events is random, highlighting this region’s sensitivity to the temporal structure of event scripts (Baldassano et al., 2018). Further, focal mPFC damage critically impairs the ability to make simple decisions on whether concepts, like “receptionist”, are associated with everyday situations, like a visit to the doctor (Ghosh & Moscovitch, Colella, et al., 2014), emphasizing the causal involvement of the mPFC in the retrieval of social event knowledge.

Person schemas refer to generalizable knowledge about mental states and personality traits, which are used to understand and predict others’ observable actions (Conway et al., 2020; Tamir & Thornton, 2024). These schemas can contain broadly applicable patterns, such as stable interrelationships between personality traits (Stolier et al., 2020), mental state associations and dynamics (Thornton & Tamir, 2017, 2020; Thornton et al., 2023; Weaverdyck et al., 2021), and stereotypes (Contreras et al., 2012; Garcia-Marques et al., 2006). Evidence for the involvement of mPFC in generic person schemas includes its reliable activation during mentalizing about others, even those we do not know personally (Diveica et al., 2021; Van Overwalle, 2009), and its encoding of multiple latent dimensions of mental state knowledge in local activity patterns (Tamir, Thornton, et al., 2016). Moreover, the mPFC is critical for stereotype-based social processing (Amodio, 2014). This is demonstrated by its increased activation during tasks probing stereotype knowledge (Contreras et al., 2012; Quadflieg et al., 2009), its encoding of individuals’ unique stereotyped associations between social categories in local activity patterns (Stolier & Freeman, 2016), and the disruption of implicit stereotyped attitudes following focal lesions or neurostimulation (Milne & Grafman, 2001; Sellaro et al., 2015).

With increased familiarity, person-specific schemas can emerge in the mPFC (Welborn & Lieberman, 2015). A schema for a well-known friend might encapsulate information about their likes, personality traits, and other behavioral tendencies, functioning as an individualized model of the mental states they habitually experience (Fleeson & Jayawickreme, 2015; Thornton, Weaverdyck, & Tamir, 2019). In line with a key role in the instantiation of

person-specific schemas, mPFC activation is greater when mentalizing with familiar compared to unfamiliar people (Ida Gobbini et al., 2004; Krienen et al., 2010). Moreover, after learning about individuals' behavioral tendencies across two orthogonal personality dimensions, mPFC activity patterns uniquely encoded the specific person being imagined in a novel situation (Hassabis et al., 2014). Similar person-specific neural codes in the mPFC are observed when imagining personally familiar people (Thornton & Mitchell, 2017). After familiarization with previously unfamiliar movie characters, mPFC activity patterns became more similar when viewing new clips of trained characters compared to untrained ones, with this effect persisting throughout the clips (Raykov et al., 2021). These findings implicate the mPFC in the activation and maintenance of person-specific schemas to support understanding of ongoing social interactions.

The ventral mPFC appears particularly sensitive to the degree to which generic person schemas must be tailored to specific individuals. During mental state inference, ventral mPFC activation increases with the idiosyncrasy of the mentalizing target, where a generic understanding of mental states is less applicable (Welborn & Lieberman, 2015). The mPFC not only encodes the identity of known individuals with distinct activity patterns, but these patterns become increasingly unique with greater social closeness, a contrast to posterior medial parietal regions, which show more normative patterns with closeness (Guthrie & Chavez, 2024). Additionally, because people know more about themselves than others, mPFC activation follows a gradient: ventral portions respond preferentially to self-reasoning, while dorsal portions respond more to others (D'Argembeau et al., 2007; Denny et al., 2012; Hu et al., 2016). The mPFC also encodes one's own mental states with more distinct patterns than those of others (Thornton, Weaverdyck, Mildner, & Tamir, 2019). Thus, it has been proposed that the ventral mPFC plays a crucial role in using individualized "theory of mind" schemas for social inferential processing (Welborn & Lieberman, 2015).

As described above, existing findings suggest that different types of social prior knowledge are underpinned by partially distinct neural systems. Perceptual and inferential processing of social cues engages yet another set of brain regions, particularly in the temporoparietal and medial parietal cortices (Quadflieg & Koldewyn, 2017; Saxe & Wexler, 2005). However, a comprehensive understanding of the social world requires the flexible integration of these distinct knowledge sources with incoming social signals (Sened et al., 2025; Tamir & Thornton, 2018). This coordination is likely facilitated by shared neural substrates across brain systems involved in autobiographical retrieval (Fig. 16.1A), semantic processing (Fig. 16.1C), and social cognition (Fig. 16.1B). Indeed, the MTL, ATL, mPFC, lateral temporal cortex (extending to the angular gyrus), and precuneus have all been shown to activate in response to at least two of these domains. This pattern of activation is evident in both metaanalytic comparisons of task activations consistently associated with each domain (Balgova et al., 2024; Diveica et al., 2021; Kim, 2016; Spreng et al., 2009), as well as in direct

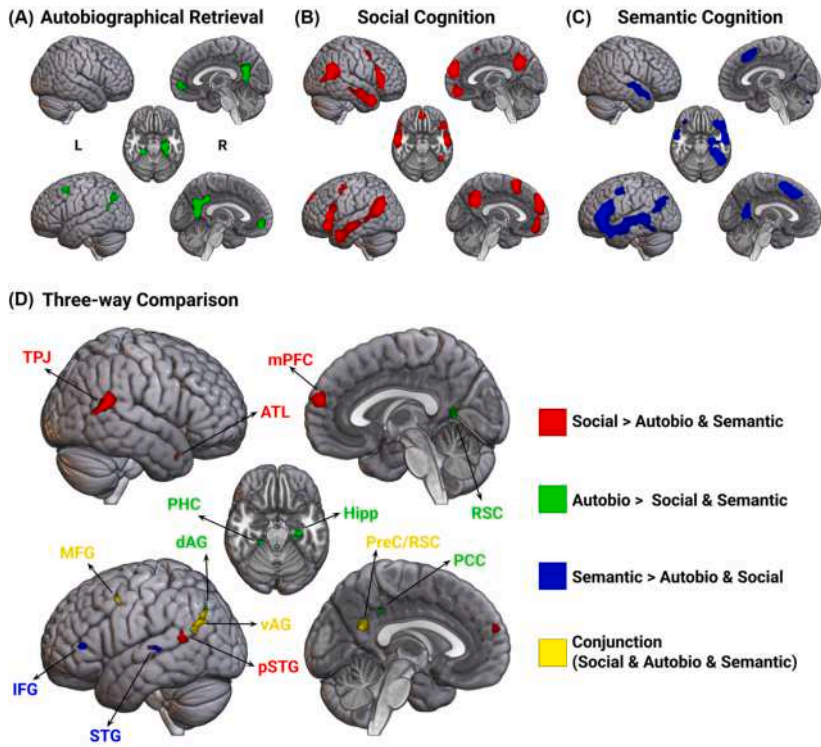


FIGURE 16.1 Common and distinct task-based activation patterns for autobiographical retrieval, semantic cognition, and mentalizing. Panels A-C: Reliable activation associated with (A) autobiographical retrieval, (B) mentalizing, and (C) semantic cognition as revealed by coordinate-based metaanalyses of tasks probing each cognitive domain. Peak coordinates were obtained from [Diveica et al. \(2021\)](#), [Fenerci et al. \(2022\)](#) and [Balgova et al. \(2024\)](#), respectively. Panel D: Conjunction and contrast analyses between the three cognitive domains reveal overlapping activation (yellow) as well as domain-specific activation: red regions are more reliably activated by mentalizing than the other two domains, green regions by autobiographical retrieval, and blue regions by semantic cognition. *Autbio* Autobiographical; *TPJ* temporoparietal junction; *mPFC* medial prefrontal cortex, *ATL* anterior temporal lobe, *PHC* para-hippocampal gyrus, *Hipp* hippocampus, *RSc* retrosplenial cortex; *MFG* middle frontal gyrus, *dAG* dorsal angular gyrus, *PreC* precuneus; *PCC* posterior cingulate cortex; *vAG* ventral angular gyrus, *IFG* inferior frontal gyrus, (*p*)*STG* (posterior) superior temporal gyrus.

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comparisons within individual studies probing each domain ([Balgova et al., 2022](#); [DuPre et al., 2016](#); [Hughes et al., 2024](#); [Spreng & Grady, 2010](#); [Tanguay et al., 2023](#)). However, whether all three cognitive domains elicit overlapping activations and whether they share a common neural substrate within the brain's intrinsic functional architecture remains unclear. In Part III, we present original findings that address these open questions.

Part III. The shared neural substrate of autobiographical, semantic, and social cognition

The methodological approach is described in detail at the end of the chapter. In short, we aimed to identify brain regions reliably activated by all three cognitive domains, as well as regions more consistently activated by one domain compared to the other two (henceforth referred to as domain-specific regions), via coordinate-based metaanalyses of functional magnetic resonance imaging (fMRI) studies probing autobiographical retrieval, semantic retrieval, and mentalizing. Next, to delineate the shared brain network that facilitates information exchange between the three cognitive domains, we conducted resting-state functional connectivity (RSFC) analyses using the domain-specific regions as seeds and computing the overlap between the resulting whole-brain functional connectivity (FC) maps. Then, we explored the relative importance of regions within the shared RSFC network by means of graph theory metrics. As a final step, we explored the similarity in the RSFC profiles of the domain-specific regions using hierarchical clustering. To understand the functional significance of the resulting clusters, we then identified the functional terms (e.g., “reward,” “language”) most reliably associated with the activation of each cluster through metaanalytic functional decoding.

The topography of the shared neural substrate

The three cognitive domains were reliably associated with overlapping activation in the left ventral angular gyrus, precuneus, and left middle frontal gyrus (Fig. 16.1). Reflecting the distinct cognitive demands imposed by each cognitive domain, 11 brain regions showed reliable activation for one domain but not the other two. Notably, regions within the right ATL and mPFC showed more consistent activation in response to social tasks, whereas the MTL showed more consistent activation in autobiographical retrieval.

Next, we assessed whether these domain-specific regions are functionally connected to an overlapping set of brain regions during task-free states. RSFC provides complementary insight into the brain’s functional architecture by capturing the tendency of regions to spontaneously coactivate (Raichle, 2010). Given their preferential engagement for one cognitive domain over the other two, there is no inherent reason to expect that the domain-specific regions are coupled with a common functional network. Indeed, not all pairs of domain-specific regions were functionally connected, with some displaying negative RSFC (Fig. 16.2A). Despite this, all domain-specific regions were functionally coupled with a shared network comprising the left angular gyrus and the bilateral MTL and ventral ATL (Fig. 16.2B). The existence of this shared functional network suggests that the brain is intrinsically wired to facilitate the integration of autobiographical, semantic, and social processes (cf. Spreng & Mar, 2012).

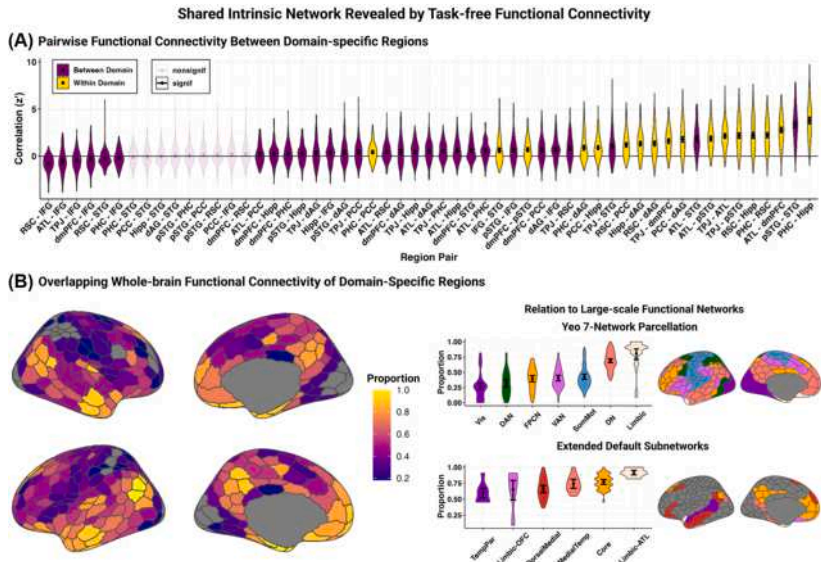


FIGURE 16.2 The functional network shared by autobiographical, semantic, and social cognitive processing. Panel A: Pairwise RSFC between domain-specific regions shows that some regions are not functionally coupled and that some regions exhibit negative FC. Panel B: A conjunction analysis of whole-brain RSFC patterns from the 11 domain-specific regions reveals a shared functional network. The brain map shows the proportion of domain-specific regions with which each parcel is functionally coupled. Only parcels that exhibit RSFC with at least two domain-specific regions are highlighted. This proportion is highest in the default and limbic networks, as defined by Yeo et al. (2011) and depicted on the right.

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The likelihood of FC with domain-specific regions is highest in the limbic and default networks (DN) (Fig. 16.2B). When using methods optimized for imaging the limbic network—including the orbitofrontal and anteroventral temporal cortices—the limbic and default networks are closely coupled, forming an “extended default” network (Girn et al., 2024). Maximally distant from unimodal sensorimotor cortices, the DN supports tasks involving multimodal integration, perceptual decoupling, and abstraction (Margulies et al., 2016; Smallwood et al., 2021). This functional profile makes it ideally suited to create evolving mental models of the environment by temporarily activating long-term memories and prior knowledge to interpret and predict sensory input (Fernandino & Binder, 2024; Menon, 2023; Yeshurun et al., 2021). Consistent with this, the extended DN plays a critical role in autobiographical retrieval, semantic processing, and social cognition (Andrews-Hanna, Smallwood, et al., 2014; Fernandino & Binder, 2024; Mars et al., 2012; Spreng et al., 2009). Moreover, while the ATL, MTL, and mPFC serve as hubs for retrieving distinct types of prior knowledge, multiple DN regions encode various aspects of retrieved knowledge, including self/other distinctions (Chiou et al., 2023), person identity and their stereotyped social roles

(Ron et al., 2022), abstract social concepts (Lin et al., 2018), social scripts and mental states (Thornton & Tamir, 2024), and social network structure (Peer & Hayman, 2021; Schwyck et al., 2023).

Despite its involvement in all three cognitive domains, DN activity appears particularly sensitive to social cognitive demands. Functional neuroimaging studies often contrast social tasks to nonsocial yet complex baseline conditions involving attention, decision-making, and inferential processing of meaning-imbued (semantic) stimuli. For example, a common mentalizing localizer contrasts inferences about others' mental states with those about the physical world (Saxe & Kanwisher, 2003). While both types of inferences rely on overlapping DN regions (Balgova et al., 2024; Saxe & Wexler, 2005), social tasks consistently show additional DN activation when subtracting the nonsocial baseline (Fig. 16.1B), indicative of greater demands imposed on shared cognitive resources. Even simple perceptual processing of social versus nonsocial scenes, or reading social compared to nonsocial literary passages, leads to increased activation throughout the DN (Tamir, Bricker, et al., 2016; Tso et al., 2018), suggestive of an all-encompassing sensitivity of the DN to the cognitive demands imposed by social information processing.

In line with a key role in enabling interaction between long-term memory and social cognition, DN activity during social tasks is modulated by familiarity with the social target. Thinking about personally-familiar people, for whom extensive person-specific knowledge is available, relative to strangers, for whom such knowledge is lacking, is associated with reliable activation of multiple DN regions (Bortolini et al., 2024), which increases with social closeness (Roseman-Shalem et al., 2024). Further, local activity patterns in both midline and temporoparietal DN regions distinguish between personally-familiar and unfamiliar people (Castro-Laguardia et al., 2024), as well as the identity of personally-familiar others (Thornton & Mitchell, 2017; Visconti di Oleggio Castello et al., 2021). Notably, midline, MTL, and temporoparietal DN regions are engaged similarly during autobiographical retrieval and mentalizing with a personally-familiar other but not a stranger, whereas mentalizing with a stranger recruits ventrolateral prefrontal DN regions associated with semantic processing instead (Rabin & Rosenbaum, 2012). This finding suggests that the DN flexibly supports the retrieval of either autobiographical or semantic knowledge in support of social cognition, depending on context. This aligns with a key role for DN regions in integrating these three cognitive domains.

In addition to its reliable recruitment by social cognitive tasks (Fig. 16.1A; also Spreng et al., 2009), the DN tends to increase its activation during task-free states when compared to a range of externally oriented tasks (Raichle et al., 2001; Shulman et al., 1997). This observation led to the proposal that the brain defaults to social cognitive processing in the absence of an explicit task (Mitchell, 2006; Schilbach et al., 2008). Indeed, people often think about other people when they mind wander (Andrews-Hanna et al., 2013; Mar et al., 2012). Recent evidence confirms that the spontaneous activity of DN regions during

task-free states fulfills social functions (Meyer, 2019; Geisler & Meyer, 2025). First, it primes the brain for social cognition—greater activation of the mPFC, a core DN region, during rest periods preceding a task was associated with faster decision times when the task required inferences about mental states or personality traits, but not perceptual decisions or math judgments (Meyer & Lieberman, 2018; Spunt et al., 2015). Second, DN prioritizes social memory consolidation. Greater functional coupling between two of its core regions, the mPFC and the AG, during rest periods following memory encoding is linked to improved memory for social—but not nonsocial—information (Meyer, Davachi, et al., 2019). Additionally, during rest periods after movie watching, a higher prevalence of reinstatements of activation patterns associated with social scenes in the dorsal mPFC was linked to better memory for social scenes, whereas this relationship did not hold for nonsocial scenes (Jimenez & Meyer, 2024). Critically, reinstatement of social scenes—unlike nonsocial ones—tended to occur earlier during rest, indicating prioritized replay for consolidation of social information.

However, the extended DN is not functionally homogeneous. Three main subnetworks (Fig. 16.2B) can be identified based on RSFC: the *medial temporal* subnetwork, associated with the MTL and engaged in episodic memory, the *dorsal medial* subnetwork, linked to the ATL and involved in semantic cognition, and the *core* midline subnetwork, which includes the mPFC and is highly correlated with both other subnetworks (Andrews-Hanna, Smallwood, et al., 2014). These subnetworks make dissociable contributions to social and autobiographical thought (Andrews-Hanna, Saxe, et al., 2014; Spreng & Andrews-Hanna, 2015). For example, the activity patterns in different DN regions encode different aspects of the same ongoing social interaction—the hippocampus encodes episodic details, the medial parietal cortex, angular gyrus, and para-hippocampal gyrus collectively encode the context, the ATL encodes person identity, whereas the mPFC encodes social event scripts (Reagh & Ranganath, 2023; also see Szpunar et al., 2014). Emerging evidence within-subjects has suggested dissociable yet interdigitated DN subnetworks (Braga et al., 2019), which show preferential engagement in mnemonic and spatial processes versus social processes (DiNicola et al., 2020; DiNicola & Buckner, 2021; Deen & Freiwald, 2025; but see Hughes et al., 2024). Despite progress in understanding the organization of the DN, the organization of the specific functional network that facilitates integration of autobiographical memory, semantic memory, and social cognition remains underexplored and is the focus of the next sections.

The centrality of regions within the shared functional network

To explore the relative importance of individual regions within the network's topology, we computed two centrality metrics: degree centrality, which quantifies the cumulative strength of a region's direct functional connections,

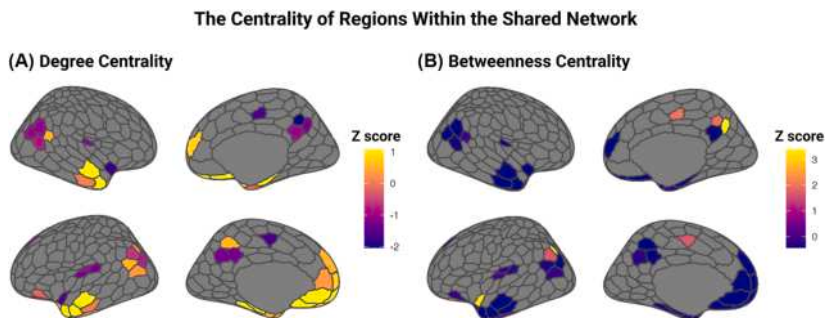


FIGURE 16.3 The relative importance of brain regions in the functional network shared by autobiographical memory, semantic cognition, and social cognition. Panel A: Degree centrality, which quantifies regions' overall strength of direct connections. Panel B: Betweenness centrality, which quantifies how often regions lie on the shortest paths that connect other regions in the network.
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and betweenness centrality, which quantifies how often a region lies on the shortest paths between other regions. The ATL, MTL, and ventral mPFC exhibited the highest degree centralities (Fig. 16.3A), indicating that they act as highly connected hubs within the network. This is consistent with the role of each of these regions in prior knowledge (see Part II), which involves binding information processed across distributed regions into coherent representations or relational structures (Gilboa & Marlatte, 2017; Opitz, 2010; Lambon Ralph et al., 2017). In contrast, the precuneus, left angular gyrus, and left superior ATL had the highest betweenness centralities (Fig. 16.3B), suggesting that they act as bridges or bottlenecks regulating information flow within the network. This may explain the reliable activation of the posterior cingulate and left inferior parietal lobule by all three cognitive domains and aligns with their established roles as functional hubs facilitating interactions across disparate brain regions at the whole-brain level (Buckner et al., 2009; Heuvel & Sporns, 2013; Tomasi & Volkow, 2011). The high betweenness centrality of the left superior temporal lobe aligns with its proposed role in tagging social conceptual knowledge with affective information (Rijpma et al., 2023) via connections with frontal limbic regions (Pascual et al., 2015) (see Fig. 16.3).

The hierarchical organization of domain-specific regions

To better understand the relationships among the domain-specific regions, we conducted data-driven clustering based on the similarity of their RSFC patterns. This revealed an intricate organization, with the regions forming two main clusters characterized by similarity in RSFC profiles (Fig. 16.4).

The regions associated with autobiographical retrieval clustered separately from those preferentially engaged by social cognition. Interestingly, the two semantic regions aligned with different clusters—one with the autobiographical

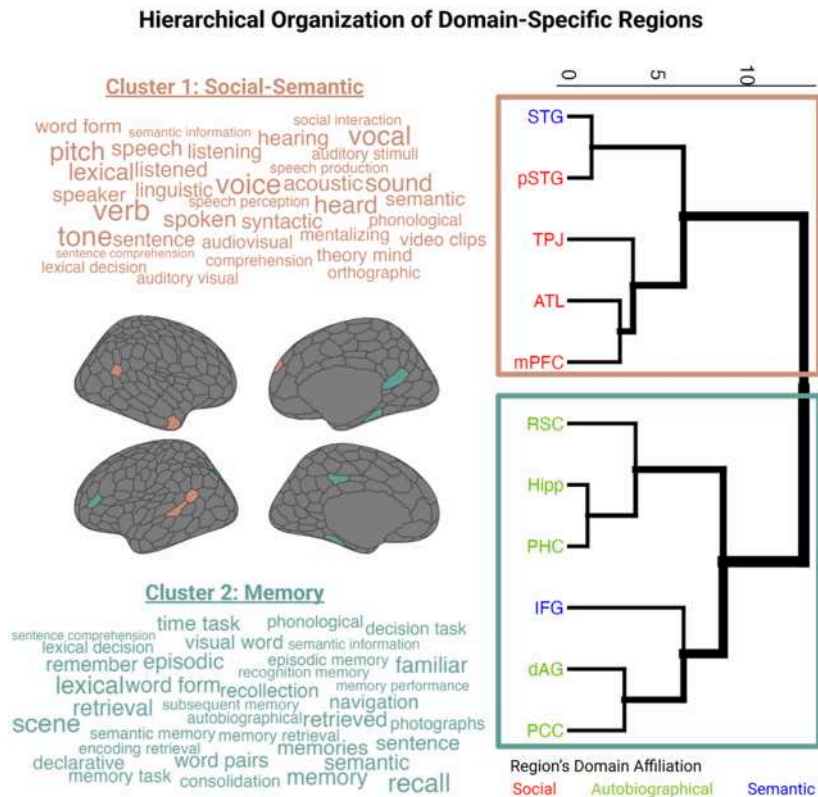


FIGURE 16.4 Hierarchical organization of domain-specific regions based on resting-state functional connectivity (RSFC) patterns. The dendrogram illustrates the similarity in RSFC patterns between the domain-specific regions. Label color indicates the cognitive domain each region preferentially supports (see Fig. 16.1). The two main clusters identified through hierarchical clustering are visualized on the brain surface. World clouds display the top 35 functional terms associated with activation in each cluster based on metaanalytic decoding.

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regions and the other with the social regions—suggesting functional heterogeneity within the semantic system. Specifically, the posterior superior temporal gyrus might be engaged in processes more relevant to social cognition, such as voice recognition and speech comprehension (Yi et al., 2019; Zhang et al., 2021). This social-semantic cluster was associated with functional terms related to hearing, language, in addition to social cognition. In contrast, the left inferior frontal gyrus might be engaged in processes more directly relevant to autobiographical memory, such as controlled memory retrieval processes (Diveica, Riedel, et al., 2023; Jackson, 2021; Vatansever et al., 2021; Wagner et al., 2001). In line with this interpretation, this cluster was associated with terms related to episodic, autobiographical, and semantic memory.

The finding that the primary distinction identified via clustering of RSFC patterns separates autobiographical and social regions suggests that semantic processes are more closely integrated with both autobiographical memory and social cognition than autobiographical memory is with social cognition. This supports the idea that semantic knowledge provides a scaffold for autobiographical memory (Irish & Piguet, 2013), with memories being enriched by semantic content before integrating with social processes (see Fig. 16.4).

Conclusions

From birth to old age, our lives unfold within a dynamic social environment. Consequently, our past experiences are imbued with social significance, making them a vital source of knowledge that we draw upon in the present moment to understand social cues, make adaptive social decisions, empathize with others, and strengthen (or weaken) our social bonds. Our findings reveal that the brain's intrinsic architecture includes functional pathways, anchored in the extended default network, for integrating memories with social information, underscoring the possibility that the autobiographical memory system may have evolved, at least in part, to address the complex cognitive demands of social life. Within the shared network, MTL, ATL, and mPFC emerge as critical hubs involved in retrieving and integrating diverse forms of socially-relevant prior knowledge, creating a cohesive framework through which autobiographical memories guide social inferences, decision-making, and behavior. Crucially, this relationship is multidirectional: social experiences, in turn, can enrich our autobiographical and semantic memories (Katsumi et al., 2024; Leichtman et al., 2003; Pexman et al., 2023), and personal significance is woven into the fabric of our semantic knowledge (Westbury & Wurm, 2022; Westmacott & Moscovitch, 2003). These bidirectional interactions between memory and social cognition, facilitated by their integrated neural basis, allow us to continually refine and adapt our understanding of the social world.

Methods

Step 1. Identifying brain regions activated by each cognitive domain

The neural correlates of autobiographical, semantic, and social processing were identified via coordinate-based metaanalyses. For autobiographical memory retrieval, we included peak coordinates from 28 experiments originally compiled by Spreng et al. (2009) and updated by Fenerci et al. (2022), which included tasks requiring the explicit retrieval of autobiographical memories. For social cognition, we included 136 experiments involving tasks that required inferring others' mental states, originally collected by Molenberghs et al. (2016) and updated by Diveica et al. (2021). Mentalizing was used as a proxy for social cognition because its neural correlates

significantly overlap with regions critical to a range of other social abilities, such as affective empathy, trait inference, and moral reasoning (Diveica et al., 2021). For semantic knowledge retrieval, we included 190 experiments contrasting meaning-imbued versus meaningless stimuli and/or semantic versus nonsemantic/perceptual control tasks. This dataset was collected by Jackson (2021) and curated by Balgova et al. (2024) to exclude tasks that were primarily social in nature.

Each dataset was independently analyzed using the activation likelihood estimation algorithm (Eickhoff et al., 2012) as implemented in the Python package Neuroimaging Meta-Analysis Research Environment (NiMARE) (Salo et al., 2022). The statistical significance of the independent maps was assessed via 1000 permutations, and the maps were thresholded at $P < .05$ following cluster-size familywise error correction (cluster-forming threshold: $P < .001$). A three-way overlay conjunction of the independent maps was used to identify brain regions consistently activated across all three domains. To identify brain regions more consistently activated by one domain compared to the other two, we first performed pairwise metaanalytic subtraction analyses (Laird et al., 2005). The statistical significance of the resulting contrast maps was assessed using 10,000 permutations, with maps thresholded at $P < .001$ (uncorrected) and masked with the corresponding independent maps. Finally, to identify brain regions more consistently activated in one cognitive domain relative to both other two (i.e., regions showing domain-specific activation), we computed conjunctions of contrast maps.

Step 2. Assessing overlap in the RSFC patterns of domain-specific regions

Resting-state fMRI data were collected from 154 healthy young adults (mean age 22.29, SD: 3.12; range: 18–34 years; 86 women) across two 10-min runs. A detailed description of the dataset is provided by Spreng et al. (2022). Notably, the blood-oxygen level dependent (BOLD) MRI scans were acquired using a multiecho echo-planar imaging sequence and were preprocessed using multiecho independent component analysis (ME-ICA), a method that ensures a superior signal-to-noise ratio across the whole brain, and attenuation of signal drop-out in typically problematic regions along the anteroventral surface of the brain, including the ATL and orbitofrontal cortex (Kundu et al., 2012). The denoised resting-state fMRI data were projected onto the cortical surface and parcellated into 400 regions based on the cortical atlas from Schaefer et al. (2018) using group prior individual parcellation, a method accounting for intersubject variability in brain functional architecture while enabling direct group comparisons (Chong et al., 2017).

We identified the parcels where each domain-specific activation cluster identified in Step 1 was located. Next, we computed the whole-brain RSFC for each of these parcels. To do this, we calculated the product-moment

correlation between each parcel and all other parcels within each participant. Given that we used multiecho data, FC was calculated using the product-moment correlation of the ME-ICA coefficients across parcels (parcel $\times$ coefficient vectors) rather than the traditional approach of correlating BOLD signal time series (parcel $\times$ time point vectors; see Kundu et al., 2012). To normalize the distribution of correlation values, we applied a Fisher's *r*-to-*z* transformation accounting for variations in BOLD ME-ICA components across participants (Kundu et al., 2012). To identify the RSFC patterns that were consistent across participants, we subjected the participant-specific connectivity maps to a one-sample *t*-test. The resulting standardized *Z* maps were thresholded for statistical significance using a false discovery rate (FDR) correction at $P < .05$. The thresholded connectivity maps of all domain-specific regions were binarized and combined into a conjoint probability map.

Step 3. Exploring the intrinsic organization of the shared brain network

The network of brain regions with >80% probability of connectivity to at least one domain-specific region was analyzed in two ways. First, the RSFC of each parcel in this network with all other parcels was computed using data from the second run, following the method described above. To assess the relative centrality of each region, we conducted a graph theory analysis. The graph was thresholded based on edge strength reliability using a bootstrapping approach with 10,000 iterations; edges whose 99% confidence intervals included 0 were assigned a value of 0. We then calculated the degree and betweenness centrality of each node (parcel) within the graph.

Step 4. Exploring the hierarchical organization of domain-specific regions

To understand how the domain-specific regions relate to each other based on their RSFC patterns, we applied Ward's hierarchical clustering algorithm to the parcel $\times$ parcel FC similarity matrix. This showed that their hierarchical relationship can be subsumed under two clusters of regions whose RSFC patterns are more similar within than between clusters. To understand the functional significance of the clusters, we identified the functional terms associated with each cluster through metaanalytic functional decoding. We used the NeuroSynth chi-square approach as implemented in NiMARE (Salo et al., 2022). For each term in the NeuroQuery database (Dockès et al., 2020), the consistency analysis (also known as forward inference) computes the likelihood of activation reported within the seed given presence of the term in the article's text, whereas the specificity analysis (also known as reverse inference) estimates the posterior probability of an article containing the term given activation reported inside the seed. The results of these analyses were thresholded at $P < .05$ using the Benjamini-Hochberg FDR correction, and

only terms with significant results in both the consistency and specificity analyses were retained. To aid the interpretability of the results, we further retained only the terms with at least 60% likelihood of being related to cognitive functions based on raters' annotations (Peraza et al., 2024).

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