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The default mode network: where the idiosyncratic self meets the shared social world

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Abstract

The default mode network (DMN) is classically considered an 'intrinsic' system, specializing in internally oriented cognitive processes such as daydreaming, reminiscing and future planning. In this Perspective, we suggest that the DMN is an active and dynamic 'sense-making' network that integrates incoming extrinsic information with prior intrinsic information to form rich, context-dependent models of situations as they unfold over time. We review studies that relied on naturalistic stimuli, such as stories and movies, to demonstrate how an individual's DMN neural responses are influenced both by external information accumulated as events unfold over time and by the individual's idiosyncratic past memories and knowledge. The integration of extrinsic and intrinsic information over long timescales provides a space for negotiating a shared neural code, which is necessary for establishing shared meaning, shared communication tools, shared narratives and, above all, shared communities and social networks.

Making sense of the world is a dynamic, ever-changing process requiring the integration of incoming information with prior knowledge about the situation over multiple timescales. For example, while listening to a debate, a listener must integrate their own prior thoughts and beliefs about the debate topics with the current and past statements of the speakers. Thus, our mindsets and our actions at each moment in time are shaped by at least three factors: what is happening now in the world (incoming sensory input); what happened in the world in the preceding moments (recent active memories that further contextualize and shape the present); and who we are and what we bring to the moment (that is, our long-term memories, conditional responses, beliefs and emotions that shape the way we process the

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incoming inputs). The ongoing integration of these three factors happens effortlessly in our brains, almost by default.

In this Perspective, we propose a key role for the default mode network (DMN) in dynamically integrating these three factors over extended timescales in order to make sense of a novel, constantly evolving situation. The DMN, which includes the posterior medial cortex, medial prefrontal cortex and temporoparietal junction[1–3], was classically viewed as an 'intrinsic' system, showing decreased activity during experimental tasks. Later work updated this view to suggest that the DMN is specialized for internally oriented or non-stimulus-induced tasks, such as 'mind-wandering', recall of past events and internal simulation of future events[4–7]. Although a recent review further divided the DMN into multiple interleaved networks[1], researchers have often made a distinction between this 'intrinsic' system and 'extrinsic' systems that process incoming sensory information or outgoing motor outputs[4,5,8–14] (see Box 1).

Here, we challenge the view of the DMN as an intrinsic system by pointing to the active and dynamic role of the DMN in synthesizing extrinsic and intrinsic information over long timescales. In a previous review, we argued that memory is an integral component of any processing act[15] and that the DMN resides at the top of this 'process–memory' hierarchy, playing a unique and central role in processing events as they dynamically unfold over time. Building on this model, we make three related arguments. First, we propose that activity in the DMN is modulated by incoming external information (top arrow in Fig. 1a), which is integrated over many seconds to many minutes (horizontal arrow in Fig. 1a). Therefore, the DMN should not be considered an intrinsic system active only during internally oriented or stimulus-independent processes. Second, we argue that activity in the DMN is nonetheless sensitive to intrinsic information (long-term memories, conditional responses, beliefs, emotions and so on), which influences and interacts with the interpretation and processing of incoming external information (bottom arrow in Fig. 1a). Therefore, the DMN should not be considered an extrinsic system, sensitive only to incoming sensory information. Last, we combine these points to propose that the DMN is an active and dynamic 'sense-making' network that integrates incoming extrinsic information with prior intrinsic information over long timescales to form rich, context-dependent, idiosyncratic models of the situation as it unfolds over time.

As the activity in the DMN is shaped by our unique history, it is by nature idiosyncratic. However, at the same time, our knowledge, memories and beliefs are shaped by the people we are connected to and the world in which we are immersed (Fig. 1b). Thus, in the last section of this Perspective, we argue that the DMN provides a space for social 'others' (the extrinsic people we interact with) to shape the self (our set of intrinsic memories and beliefs), which in turn can enable us to shape the memories and beliefs of others. This unique interplay between the extrinsic and intrinsic forces provides a mechanism for negotiating a shared neural code to facilitate learning and communication via shared common ground. Our view of the DMN is informed by numerous studies using naturalistic stimuli and inter-subject analyses that map shared neural responses across participants (Fig. 2).

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Extrinsic responses of the DMN

We begin by proposing that the DMN integrates moment-by-moment external information with prior information over seconds to minutes, as events unfold over time.

DMN activity is influenced by context and incoming inputs.

Research in visual and auditory perception has revealed the influence of context on neural activity even in early sensory areas. In the primary visual cortex of non-human primates, for example, the response of a simple cell to a vertical line will change as a function of lines in its extra-visual field, or its spatial context[16,17]. Regions in higher-order cortex then integrate these responses, resulting in sensitivity over larger spatial contexts[18,19]. This hierarchy of visual integration across the visual cortex is captured by spatial receptive fields: early visual areas process local parts of the visual field and so have small spatial receptive fields, whereas higher-order visual areas integrate information over larger parts of the visual field and thus have larger spatial receptive fields.

Analogously, temporal receptive windows (TRWs) capture the influence of context over time. The TRW is the window of time in which past information affects neural processing of new information. Studies using naturalistic stimuli have identified a topographical hierarchy of processing timescales extending from early sensory cortex to higher-order areas including the DMN[7,20–23]. TRWs are short in sensory areas and become gradually longer towards higher-order areas. The responses in early sensory areas such as the early auditory and visual cortex are influenced by the temporal structure over tens of milliseconds[20,21]. These findings are consistent with research[22] suggesting that early sensory areas process fast-changing, low-level stimulus features, such as sound amplitude or visual edges. By contrast, neural responses in mid-level areas, which include linguistic regions along temporal cortex, are affected by information integrated over a few seconds (for example, the preceding words in the sentence). At the apex of the processing hierarchy, the neural response of the DMN to each sentence is influenced by prior information accumulated over many minutes[15,20,21,23]. In addition to the modulation of DMN activity by information accumulated over many seconds, in the next section we discuss evidence for the modulation of DMN connectivity by information accumulated over many seconds.

DMN connectivity is influenced by context and incoming inputs.

To map DMN functional connectivity, analyses sample the temporal response in one node of the DMN and use this as a seed to search for co-varying fluctuations in neural activity across other nodes of the network within an individual brain (Fig. 3a). This analysis, although effective in outlining the anatomical boundaries of the DMN, is unable to distinguish subtle task-related fluctuations in connectivity across various experimental conditions including, for example, lying at rest in a scanner, listening to a list of scrambled words and listening to an intact story several minutes long[24–26] (Fig. 3a). The stability of the averaged connectivity maps across numerous conditions has frequently been used to support the claim of the intrinsic nature of the DMN[5,27]. Such interpretation, however, was called into question by the realization that within-brain functional connectivity patterns are heavily influenced by direct and indirect anatomical wiring, but are less sensitive for isolating spontaneous activity

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(for example, during rest) from stimulus-locked activity that propagates through the network as during processing of extrinsic information[26,28].

Task-related connectivity patterns can be isolated from spontaneous neural fluctuations by switching to a multi-brain perspective that characterizes the shared response across brains during the processing of temporally extended naturalistic stimuli. We recently developed such an approach: inter-subject functional correlation analysis[26]. Inter-subject functional correlation differs from standard functional connectivity analysis in one crucial way: it calculates the functional correlation across brains, as opposed to within brains (Fig. 2). Intrinsic neural dynamics during rest, as well as non-neuronal artefacts (such as those associated with respiration and head motion), can only influence the pattern of correlations within each brain, but cannot induce correlations between brains. By contrast, neural processes that are locked to the structure of the stimulus and shared across participants can be correlated across brains.

Using inter-subject functional correlation, we observed shared connectivity patterns within the DMN that are locked to the stimulus[26] (Fig. 3b). Crucially, we observed these stimulus-locked connectivity patterns only during processing of an intact, coherent and temporally extended spoken story. There are no shared connectivity patterns during rest or while participants listened to temporally incoherent stimuli such as scrambled words (Fig. 3b). The finding of stimulus-locked responses in the DMN only for intact, but not temporally scrambled, narratives highlights the importance of integration of information over long timescales in the DMN. This temporal dependency over long timescales makes the DMN more context-dependent than early sensory brain regions, in which responses are less affected by temporal structure of stimuli over such long timescales. These findings also highlight the importance of studying the brain's dynamics under temporally extended, ecological conditions[29].

Integration in the DMN depends on the content, not form, of external input.

DMN responses are locked to the content of the stimuli over long timescales. At the same time, they are relatively invariant to even dramatic changes in low-level stimulus properties that do not change the interpretation (meaning) of the stimuli. Despite substantial differences in low-level properties, the DMN shows similar temporal responses to the same narrative presented using: different modalities, such as written text versus speech[30,31] or audiovisual movies versus verbal descriptions[32–34]; different synonyms[35]; different languages, such as English versus Russian[36]; and different levels of abstraction, such as abstract Heidel and Simmel-like shape animation versus concrete verbal description of the same story[37]. A similar pattern of results was identified in the DMN using encoding models across written and spoken narratives[38]. In these studies, a model trained to predict neural responses to a narrative in one modality accurately predicted neural responses to the same narrative presented in a different modality. Other researchers have trained decoding models, showing that the specific story a participant is reading can be decoded from DMN neural responses, even across languages[39]. The DMN also has a role in integrating information across sensory modalities[40]; for example, the precuneus and bilateral temporoparietal junction have been shown to integrate sensory and motor information to represent word concepts[41].

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Nevertheless, a relatively small change to the stimulus can produce increasingly large differences in neural responses across the timescale hierarchy when it changes the interpretation of the stimulus. For example, manipulation of a small number of words in a spoken story (for example, changing 'laughing' to 'sobbing'), resulting in two very different stories[35], led to differences in the neural responses elicited by the two stories that correlated with the size of the TRW. As such, early auditory cortex showed relatively little difference in its response to the two stories, reflecting the relatively intact low-level acoustic properties of the stimuli. By contrast, DMN regions (which are on the top of the timescale hierarchy) showed large differences, reflecting the large difference in story meaning.

Integration in the DMN is modulated by attention.

Evidence suggests that the DMN is also modulated by attention. Stimuli that are more engaging elicit greater shared neural responses across participants in DMN regions such as the medial prefrontal cortex[42], and DMN regions of listeners who are more engaged and attentive show greater shared brain responses across participants[43,44]. Intriguingly, attention may facilitate propagation of information along the cortical processing timescale hierarchy. In one study[45], two unrelated narratives were presented simultaneously, with one in written form and one in spoken form. By manipulating attention to one or the other modality, processing of unattended stimuli was shown to be primarily restricted to sensory cortex, whereas attended stimuli went on to be processed by the DMN and dorsal attention networks.

Crucially, although attention can modulate responses in the DMN, it cannot, in isolation, account for the results described above. Between-subject multivoxel pattern analysis (Fig. 2) within each node of the DMN revealed that the multidimensional spatial patterns of responses are aligned across participants watching a movie[46]. Furthermore, using a shared response model, the same study reported at least 20 orthogonal dimensions in the DMN's spatial response patterns that are shared across participants, suggesting that no single univariate dimension, such as attention or arousal, can fully account for the complex multidimensional aligned responses in the DMN[46].

Intrinsic responses of the DMN

We next review research demonstrating how the activity in the DMN is affected not only by external events unfolding over many minutes but also by an individual's long-term memories, schemas and belief systems acquired over the years (Fig. 1a).

DMN responses are modulated by prior beliefs.

Context is not narrowly confined by the structure of the unfolding event. Information acquired prior to events can substantially change their interpretations. In one intriguing study[47], two groups of participants were presented with the same short story by J. D. Salinger, *Pretty Mouth and Green My Eyes*, in which a husband calls his friend at night asking for the whereabouts of his wife. Before listening to the story, the two groups were biased with different contextual information. One group was led to believe that the wife was unfaithful, whereas the other group was led to believe that the husband was paranoid and

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jealous. DMN regions showed stronger alignment of neural responses within a group that shared an interpretation than between groups with differing interpretations. This suggests that participants' prior beliefs (acquired just before the story started) changed the way the DMN processed the same story, which unfolded over many minutes. Similar findings have been observed following manipulations of perspective[48,49] or focus[50], as well as when context has led participants to interpret a situation as ironic[51], reflecting an attempt to 'save face'[52] or intentionally harmful[53]. Moreover, a recent study suggests that regions in the DMN are involved in reinstating the context of a storyline, which facilitates the convergence of the plot of two storylines into one[54]. Together, these findings suggest that DMN activity is influenced not only by the structure of the incoming events, but also by mindset and prior knowledge.

The DMN is sensitive to long-term memories.

Context extends to the days and even years before an event, as information gathered throughout a lifetime is used to contextualize an event. For example, an individual's experience of watching episode 5 in season 3 of the series *Game of Thrones* both depends on and is influenced by internally stored knowledge of events and characters in episodes that aired years ago. Indeed, researchers have exploited stimuli such as television shows or stories to demonstrate how the activity in the DMN is influenced by information acquired over days.

For example, one study[55] used functional MRI (fMRI) to scan participants as they watched the second half of an episode of the *Twilight Zone*. One group of participants watched the first half of the episode a day before they watched the second part (long-term context); a second group watched the entire episode without a break (short-term context); and a third group watched only the second half of the episode (no context). Inter-subject correlation in the DMN was greater among participants who had the background knowledge to interpret the clip than among participants who did not. Crucially, responses in the DMN were similar across the short-term context and the long-term context groups (although DMN regions showed increased connectivity to the hippocampus in the long-term context group compared with in the short-term context group). This result suggests that the responses in the DMN can be shaped by information accumulated across many minutes during uninterrupted viewing (short-term context) as well as by information gathered over days (as in the long-term context group) — and, conceivably, even years.

The ability of the DMN to use long-term context is probably related to its anatomical and functional connections to the medial temporal lobe and hippocampus, which are central to learning and memory[56–59]. At the same time, the ability of the DMN to accumulate information over many minutes (short-term context) may explain why individuals with amnesia can often sustain coherent conversations over a few minutes[60] or recall coherent narratives[61] during uninterrupted conversations, while showing profound impairments in tasks that require the retrieval of long-term memories[60]. Consistent with such behavioural results, a recent neuroimaging study involving an individual with hippocampal amnesia suggests that integration of information over several minutes in the DMN can be sustained even after hippocampal lesion[62]. In this study, the participant with amnesia showed typical

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response patterns in the DMN while listening to an intact narrative, as seen in neurotypical controls. Moreover, as in neurotypical controls, the DMN activity of the participant with amnesia was disrupted by temporally scrambling the paragraphs of the narrative, suggesting that the DMN otherwise successfully integrated information over windows of at least 10–30 s. Further research is needed to better characterize the role of the hippocampus in supporting the integration of information over long timescales in the DMN.

The DMN represents acquired schemas.

The ability to integrate information over days is necessary for building schemas, a mental codification of experience. Neuroimaging studies suggest that instantiation and reinstatement of schemas are mediated by the interaction among regions within the DMN — namely, the ventromedial prefrontal cortex, precuneus, bilateral temporoparietal junction and hippocampus[63]. One study demonstrated the involvement of the DMN in schema representation by measuring brain responses to different schemas (‘eating at a restaurant’ or ‘going through the airport’) presented as stories that varied widely in terms of their characters and storylines, and in terms of format (audiovisual clips or spoken narration)[64]. Regions including the posterior medial cortex and medial prefrontal cortex exhibited schema-associated event patterns that generalized across stories, participants and modalities. Moreover, the DMN was found to be involved in updating schemas when events violated expectations or were inconsistent with the established schema[65,66], as in the case of surprising events during a movie (for example, an unexpected plot twist). A recent review highlights the role of the DMN in representing and reinstating schemas while processing narratives[67]. Thus, the DMN is involved in generating and retrieving schemas in order to dynamically interpret an external situation.

The DMN is sensitive to individual differences in interpretation.

The finding that responses in the DMN are shaped by our long-term memories and beliefs raises the intriguing possibility that individual differences in the way we perceive the world can account for individual differences in DMN responses. Indeed, several studies have linked similarities in spontaneous, idiosyncratic interpretations of narratives to neural similarities. In one study[37], participants were scanned using fMRI while watching an ambiguous animation that conveyed a complex social narrative using only the motion of simple geometric shapes, in the vein of work by Heider and Simmel[68]. Greater similarity in the interpretation of the ambiguous shape animation (as reported by each of the participants) was associated with greater similarity in neural response in DMN regions across participants. Similar studies have reported that increased alignment in neural response across subjects in the DMN is correlated with the similarity in interpretation of spoken narratives[69], similarity in emotional response over time during spoken narratives[70], similarity in humour perception over time[71], similarity in socio-sexual desire while watching erotic movies[72] and similarity in moral decision-making[73,74].

Individual differences in behaviour or interpretation of a narrative that are linked to differences in DMN activity have been shown to be associated with trait-level personality differences, demographic factors or cultural differences[75,76]. Several recent studies have shown that individual differences in personality traits, including levels of paranoia[77],

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memory load[75] and a tendency to hold an analytic versus holistic perspective[78], may modulate the level of shared responses in regions of the DMN. Several researchers have also identified correlations between neural similarity in regions of the DMN and measures of mental health in clinical populations, including depression[79,80] and schizophrenia[81].

An active sense-making network

The evidence reviewed in this Perspective suggests that activity in the DMN is neither solely intrinsic nor solely extrinsic. Rather, the activity in the DMN is shaped by both the unfolding dynamical structure of real-life events (including what other social agents say and do in those events) over long timescales as well as our idiosyncratic prior dispositions, including learned schemas, prior knowledge and beliefs that shape our responses to a given context (Fig. 1b). In other words, we suggest that the DMN is an active and dynamic sense-making network that integrates incoming extrinsic social information with prior intrinsic information to form rich, context-dependent models of the situation as they unfold over time.

Perhaps one of the most intriguing findings across these studies is the discovery of neural patterns in the DMN that are shared across participants and aligned to the abstract structure and interpretation of the external events. In other words, the results suggest that participants who understand the situation in the same way will have similar neural patterns in nodes of the DMN, irrespective of considerable differences in the low-level stimulus properties of the sensory input. At the same time, subtle differences in DMN neural response patterns across participants seem to correlate with subtle differences in their interpretation. Together, these studies suggest that, through the interaction between the intrinsic self and the extrinsic world, the DMN develops a shared neural code.

The DMN in social interaction

A fundamental question is why similar understandings or interpretations of high-level concepts produce shared neural activity across individuals in the DMN. It was recently suggested that a crucial aspect of interpersonal interactions is a sense of dyadic shared reality[82]. Here, we propose that the shared representation in the DMN arises from dynamical social interaction between the self and others. In other words, through reciprocal and dynamical social interaction, other people's brains can shape your brain responses and, at the same time, be shaped by your brain's responses to generate a shared reality (Fig. 1b). Indeed, many studies suggested an extensive overlap between the DMN and the 'social brain' — the brain regions involved in social cognition (Box 1).

Throughout the day, DMN neural responses are shaped by the actions and gestures of other social agents. Even when isolated at home or lying down in a dark fMRI scanner during experiments, an individual's brain responses are still shaped by the actions of others, as conveyed by audiovisual movies, spoken words or written text. The switch from a single-brain perspective to a multi-brain perspective[83] opens the way to studying how the responses of one brain (the sender) shape the responses of other brains (the receivers). Reciprocally, the verbal and non-verbal actions of receivers' brains can also shape the neural responses of the sender in a coupled dynamical system[84,85]. Although we review evidence supporting our

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claim that DMN response patterns are shaped by the actions of other social agents, we note that this notion does not preclude the possibility that additional genetic factors on longer evolutionary timescales also shape responses in the DMN.

Brain–brain coupling between speakers and listeners.

Brain–brain coupling was first reported in a study that correlated the responses in the speaker's brain recorded while telling a personal story in the fMRI scanner with the listeners' brain responses while listening to the story[86]. The speaker's neural responses were coupled (that is, correlated, with or without a short time lag; Fig. 2d) to the listeners' neural responses in brain regions at various levels of the timescale processing hierarchy. Speaker–listener coupling in early auditory regions reflected shared processing of low-level acoustic properties of the stimulus, such as the audio amplitude envelope. By contrast, in language areas and the DMN, the responses in the listeners' brains lagged behind the responses in the speaker's brain, suggesting that responses in the speaker's brain causally shaped the responses in the listeners' brains. Furthermore, speaker–listener neural coupling in higher-order areas, including the DMN, reflected communication and shared understanding of the narrative. This study along with further studies revealed that speaker–listener coupling in the DMN, but not early auditory regions, is disrupted when communication is disrupted by either speaking nonsense words[86,87], telling a story in a language that the listener does not understand[86] or temporally scrambling the stimulus[88]. Moreover, speaker–listener coupling in the DMN predicted the quality of communication: the better the listener understood the speaker, the closer their brain responses matched the speaker's brain responses[86–89]. The speaker–listener coupling was observed in the temporal fluctuations of the response time courses within each node of the DMN[86–89] (for example, the time course of neural responses in the speaker's precuneus was correlated with that of the listener) as well as in the within-area alignment of spatial patterns across participants (for example, the spatial voxel pattern in the speaker's precuneus was correlated with that of the listeners)[33].

These findings demonstrate that comprehension-based processes in a listener's brain are driven by, or shaped by, production-based processes in the speaker's brain. Speaker–listener coupling has been observed using various stimuli and imaging modalities, including fMRI[33,70,88,90,91], functional near-infrared spectroscopy (fNIRS)[92–94] and electroencephalography[95]. Sender–receiver coupling has also been reported during non-verbal communications such as gestures[96,97] and facial expressions[98].

The communication cycle.

The full circle of experience transmission from the speaker's brain to the listener's brain has also been demonstrated[33] (Fig. 4a). In this study, participants were scanned using fMRI while watching an episode of a television series. Participants were then scanned while describing the episode out loud in their own words. A second group of participants, who had never seen the television episode before, were then scanned while listening to one of the viewer participants' descriptions. Strikingly, participants who had never seen the episode before showed spatio-temporally similar DMN activity to the speaker both as the speaker recalled the episode and as the speaker watched the episode (Fig. 4b,c). Classification analysis showed that similarities in the DMN responses between the movie viewers, the

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speaker and the listeners were scene-specific and invariant to low-level sensory features (such as differences between the audiovisual movie and its spoken description), suggesting that these shared responses reflected the transmission of information. Moreover, listener comprehension was better predicted by the unique alignment between the listeners' and the speaker's response patterns as the speaker encoded the movie to memory, relative to the alignment to the responses of other participants who watched the movie but did not share their experience with the listeners. This tight alignment between the speaker and their audience may reveal the mechanism by which we share our idiosyncratic perspectives and memories with other brains who never directly experienced them.

One-way versus two-way communication.

Although unidirectional communication through television, movies, social media and even online learning is increasingly common (Fig. 1b), much of communication is bidirectional and requires mutual adaptation and coupling between individuals who act simultaneously as senders and receivers[84]. Investigating these dynamical processes requires a shift to simultaneous scanning of multiple brains, which is sometimes called hyperscanning[99]. Emerging work using hyperscanning is uncovering the bidirectional flow of information during free dialogue and other naturalistic, complex tasks. For example, fNIRS was used to simultaneously scan dyads engaged in free dialogue; this approach showed that face-to-face communication elicits greater brain–brain coupling than does back-to-back communication[100], suggesting a role of non-verbal signals in enhancing communication and neural alignment. A later study using fNIRS identified conversational 'leaders' that emerge naturally in group discussions and used Granger causality analysis to show that the leader's neural activity more strongly predicted the followers' neural activity than vice versa[101]. Other work has focused on groups of individuals completing complex, real-life tasks that require substantial goal-directed coordination among group members[102–106], finding increased neural alignment — both spatial and temporal — during periods of the task that required heightened coordination and communication. Another electroencephalography study tested neural alignment between romantic dyads and unacquainted dyads, and found elevated coupling in the DMN during mutual gaze and smiling[107]. It was suggested that rudimentary non-verbal social cues such as mutual gaze and smiling, which are used by caregivers to initially establish coupling with children, can be used later on to facilitate neural coupling routinely throughout life.

The emergence of shared understanding.

There is no period in life when our brain responses are more strongly shaped by others than during the early years of child development. This is especially apparent during the acquisition of a shared linguistic code in early childhood, which enables the sharing of semantic representations between a child and their caregivers. Emerging fNIRS studies in which caregivers and children were simultaneously scanned during communication and interactive play shows coupled neural responses between caregivers and children (ages 8–12 years[108]) and between caregivers and infants as young as 9–10 months old[1–3]. This coupling was evident in a few DMN regions, mainly in the prefrontal cortex. Infant–caregiver coupling was most strongly associated with mutual gaze (eye contact), infant smiling and joint attention to objects[109], supporting a mutual influence of neural dynamics. Together,

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these findings suggest that that caregiver–child DMN coupling emerges early in development and likely plays a role in learning and language acquisition.

The development of shared understanding of concepts is also the hallmark of teaching and learning in formal education. In such contexts, novel, sometimes jargonized, information must be transmitted from an expert's brain to novices' brains. Here, we conceptualize teaching as a process of building a shared understanding of new information, supported by new or changed neural representations. For example, taking a computer science class might lead to the development of a new understanding of computer-science concepts and terms such as 'recursion' or 'multiplexor', as well as the contextual adjustment and modification of already familiar concepts. It might also require flexibly changing the interpretation of words depending on the context: for example, 'string' in common parlance refers to a length of thread, whereas 'string' in computer science refers to a sequence of characters. Several recent studies have identified teacher–student DMN coupling during teaching and learning in both real-life classrooms[110,111] and simulated classrooms[88,112–116]. Notably, teacher–student neural coupling predicts student learning outcomes[88,110,113,114,116].

Social networks shape shared understanding.

An old proverb says "Tell me who your friends are, and I will tell you who you are". Emerging neuroscientific research provides evidence that neural alignment across subjects is influenced and shaped by the people with whom we are connected in our real and virtual social networks. A striking recent study[117,118] mapped the close-knit social network of a class of students at a business school and found that pairs of people who have closer social relationships have more similar neural responses to narratives than do pairs of people who are less close (Fig. 4d).

Moreover, recent work from the same group measured brain responses of participants from the same social network as they watched ambiguous movie clips[119]. The participants then gathered in groups to with the aim of coming to a consensus about the narrative interpretation of each movie clip. Consensus-building conversation changed the minds of the participants and led to the alignment of their subsequent DMN neural responses as they watched the clip again. The increase in neural alignment following the consensus-building task persisted over novel clips sampled from the same movie. Participants who were central in their real-world social networks played an outsized role in building group alignment. Group-level differences in neural responses between cultures have also been observed during processing of culturally relevant stimuli, such as stories describing protected collectivist values, that may be related to the degree of identification with the culture[120,121].

Conclusions

Our thoughts, feelings and actions are constantly being shaped by the actions, memories and stories of others. At the same time, our actions, memories and stories shape and influence the thoughts, feelings and actions of the people to whom we are connected. In this Perspective, we argue that we are able to shape and be shaped by others in part because activity in the DMN is capable of both shaping other brains' responses and being shaped by the actions of other brains during social interaction. Shared neural activity at the sensory

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level naturally arises from the tendency of these areas to align with the low-level perceptual properties of the external stimuli. Shared neural activity at the top of the processing hierarchy, in the DMN, naturally arises from the tendency of social brains to align thoughts and actions. The same situation can be described using spoken words, written text or abstract animated shapes. Thus, the DMN representation must be invariant to changes in low-level perceptual properties that are not associated with changes in meaning or action. Conversely, the same situation can have markedly different meanings associated with different actions across different contexts. Thus, DMN representations must differ between people who perceive and act differently in a given situation. Shared language, shared memories and shared schemas allow us to better align and couple our DMN responses. Sharing stories and building collaborations further enhance such coupling.

Developing shared ways to understand and act in the world is an evolving communal effort in which we synthesize our intrinsic idiosyncratic perspectives and actions with the extrinsic perspectives and actions of others. In a world that is more polarized by the day, the need for rebuilding a shared common ground is perhaps more urgent than ever. The Ubuntu expression states “I am because we are”. “Are” in this insightful expression can refer to ‘us but not them’ or to ‘us as all people’. The synthesis of different perspectives in the DMN depends primarily on the structure and nature of our social interactions and social connections. In this Perspective, we argue that the DMN is ‘default’ not because it is engaged when we are looking inward, nor because it is shaped by others. Rather, we suggest that the DMN is ‘default’ because it is central for integrating external and internal information, allowing for shared communication and alignment tools, shared meanings, shared narratives and, above all, shared communities and social networks. This is what people continuously and naturally do by default.

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Alternative accounts of default mode network function

The function of the default mode network (DMN) is a matter of substantial interest and debate. in this box, we aim to highlight several prominent lines of studies that expose the richness and diversity of functions associated with the DMN. Furthermore, we aim to outline how such diversity of functions can be unified by our theoretical perspective.

Baseline activation for healthy function

The DMN was initially conceptualized as a 'task-negative' network, active only when the brain is not occupied by a task[4,8,123,124]. Later, it was discovered that regions of the DMN show spontaneous fluctuations in activity that are highly correlated across regions, suggesting that the DMN forms a functional network[11]. these findings led to the hypothesis that the activity and connectivity of the DMN have an important role in the offline intrinsic activity that is required to maintain balanced and steady internal states during rest[2,125].

Mind-wandering

Follow-up studies aimed to further characterize the cognitive functions associated with periods of rest, or when the mind is disengaged from processing external information. as a result, researchers found that DMN activity is increased during periods of 'mind-wandering'[126–129] and that an individual's tendency to mind wander is correlated with the DMN response[130]. Moreover, the content of mind-wandering may modulate DMN activity[131] (for example, thinking about what one needs to advance their research project versus thinking about how one's bedroom looks) and the connectivity of the DMN is different for different components of mind-wandering (for example, memory, social cognition and planning)[132].

Autobiographical memory

The first study to detect DMN responses associated with internally generated autobiographical memories in the absence of external stimuli was exploring brain mechanisms underlying personal memory[133]. since then, various neuroimaging studies have demonstrated that DMN activity and connectivity are modulated by tasks that require the retrieval of past events and by spontaneous autobiographical memory[128,134–136]. it was suggested that autobiographical memory is one of the prominent processes that shows the involvement of the DMN in mental representations generated using intrinsic information, independent of extrinsic information[1].

Prospective memory

In addition to the retrieval of episodic memories, participants are often occupied with thinking about future events and planning ahead while resting in the Mri scanner[137]. intriguingly, memory 'for the future', like memory for the past, activates the DMN and shapes its connectivity[131,136,138,139].

Social cognition

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Many studies have found extensive overlap between the DMN and regions involved in social cognition that are collectively known as the 'social brain'[140–148]. in addition to being involved in self-referential processes such as thinking about self-mental states[149,150], the DMN is involved in thinking about other people's beliefs, intentions and motivations[53,136,151], and in priming the intentional stance[152]. importantly, thinking about other people is not confined to moments of disengagement but is also, and perhaps even primarily, evident as people are engaged with other social agents in the real world, for example during telling (speaking) and listening to (comprehending) real-life personal stories[33,46,153] as well as watching and listening to fictional stories[37,42,47].

Where intrinsic meets extrinsic

Taken together, the studies described here suggest that, on the one hand, the DMN is active during internal-related thoughts that are self-generated in the absence of external stimuli, as in the case of mind-wandering, and therefore can be considered intrinsic; and, on the other, the response of the DMN is locked to external stimuli, especially during social interactions, and thus can be considered extrinsic. thus, in this Perspective, we combine many of these findings to suggest that the DMN is at the nexus of the interaction between the external and internal worlds.

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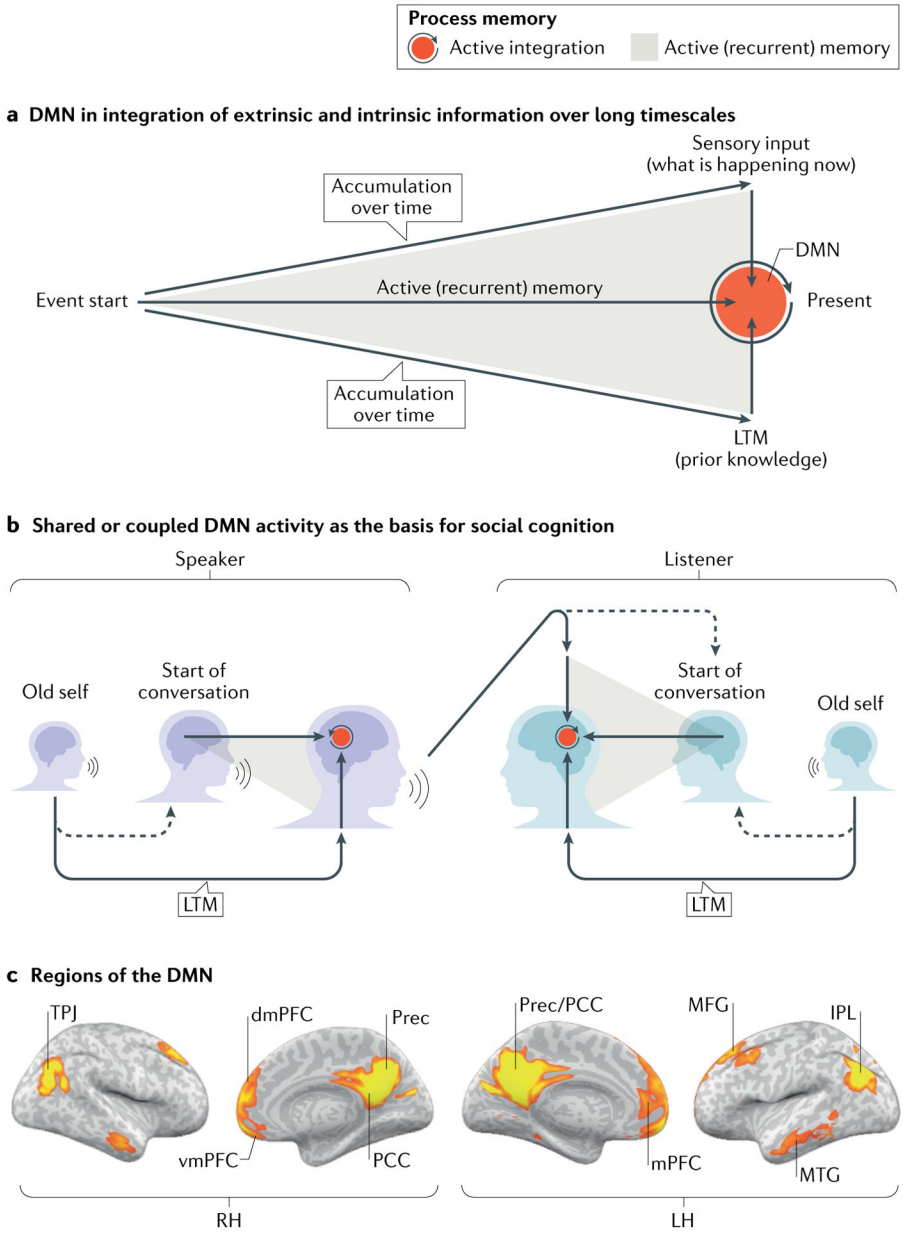

Fig. 1 |. A new view of the default mode network.

a | Activity in the default mode network (DMN) is modulated by incoming external information (top arrow), which is actively accumulated (grey expanding triangle) and integrated (red circle) over hundreds of seconds (horizontal arrow) with our intrinsic information (long-term memories (LTMs), conditional responses, beliefs and so on, represented by the bottom arrow) to form a rich, context-dependent, dynamic model of the unfolding situation. **b** | Our thoughts, feelings and actions are constantly being shaped by the actions, memories and stories of others. At the same time, our LTMs shape the way we process the external input. This unique interplay between the extrinsic and intrinsic forces provides a space for negotiating a shared neural code necessary for establishing shared meanings, shared communication tools, shared narratives and, importantly, shared

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communities and social networks. **c** | Regions of the DMN defined by functional connectivity analysis. These regions include the posterior cingulate cortex (PCC) and precuneus (Prec), the ventromedial prefrontal cortex (vmPFC) and dorsomedial prefrontal cortex (dmPFC), and the bilateral temporoparietal junction (TPJ). IPL, inferior parietal lobule; LH, left hemisphere; RH, right hemisphere; MFG, middle frontal gyrus; MTG, middle temporal gyrus. Part **c** adapted from REF.[26], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

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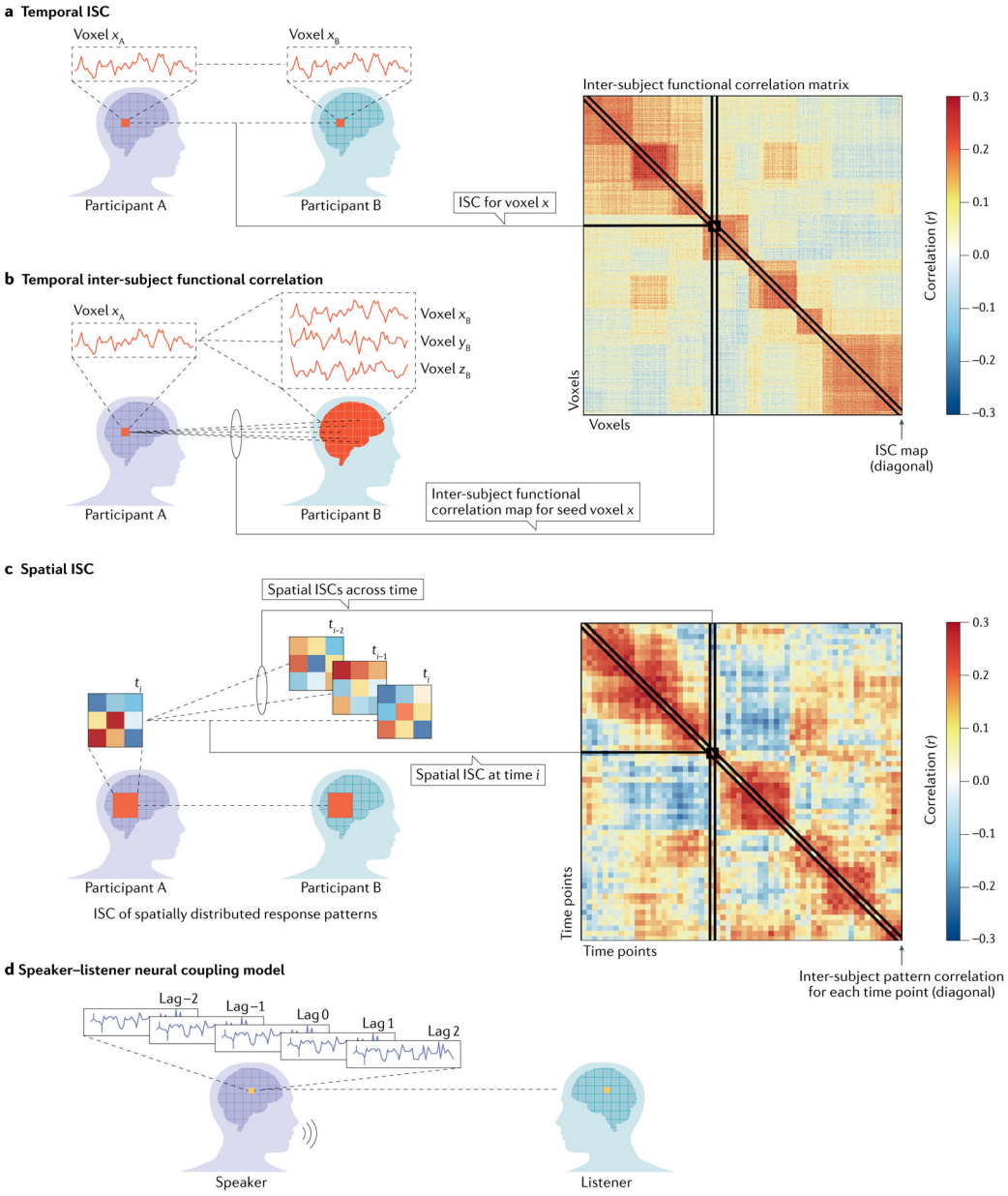

Fig. 2 |. Using inter-subject correlation analysis to map shared responses across subjects. Inter-subject correlation (ISC) analyses allow researchers to measure neural responses that are shared across participants and locked to the structure of the external input. ISC can be computed in the following ways (for more details, see REF.[122]). **a,b** | Temporal ISC within and between brain areas. In this basic form, the neural response to a continuous natural stimulus (as a story or a movie) in a given brain area is correlated with the responses in the same brain region in another participant (part **a**). This simple analysis allows us to measure the consistency of neural responses to complex naturalistic stimuli and to identify neural responses shared across individuals. The ISC method can be extended to correlate the response time course between each voxel in one participant's brain and all other voxels in another participant's brain to yield a voxel by a voxel inter-subject functional correlation

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matrix (part **b**). The diagonal values of this matrix reflect the conventional ISC map in which correlations are computed only between homologous targets in the participants' brains. A single value on the diagonal corresponds to the ISC for a given area. A single column (or row) of this matrix represents the functional connectivity map for one seed voxel. **c** | Inter-subject pattern correlation. ISCs can also be computed across spatially distributed response patterns. For a given region, the correlation between voxels' response patterns at a given moment (as illustrated by the coloured squares) is correlated across participants. Inter-subject pattern correlations can also be computed across time points to capture the evolution of response patterns over time (for example, if a particular pattern recurs at multiple time points). **d** | Speaker–listener neural coupling model. ISCs can also be extended to model the direct interaction between a speaker's brain and a listener's brain during communication (that is, not induced by shared external input). The speaker–listener coupling model uses the speaker's brain activity as a model for predicting the brain activity in each listener. To capture the temporal structure of the speaker–listener interaction, the speaker's time courses are shifted by time intervals backwards and forwards relative to the moment of vocalization. These shifted speaker time courses are combined with linear weights to build a predictive model for the listener brain dynamics. This method enabled investigation of whether the speaker's neural activity during speech production is coupled over time with the listener's neural activity during speech comprehension. Adapted with permission from REF.[122], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

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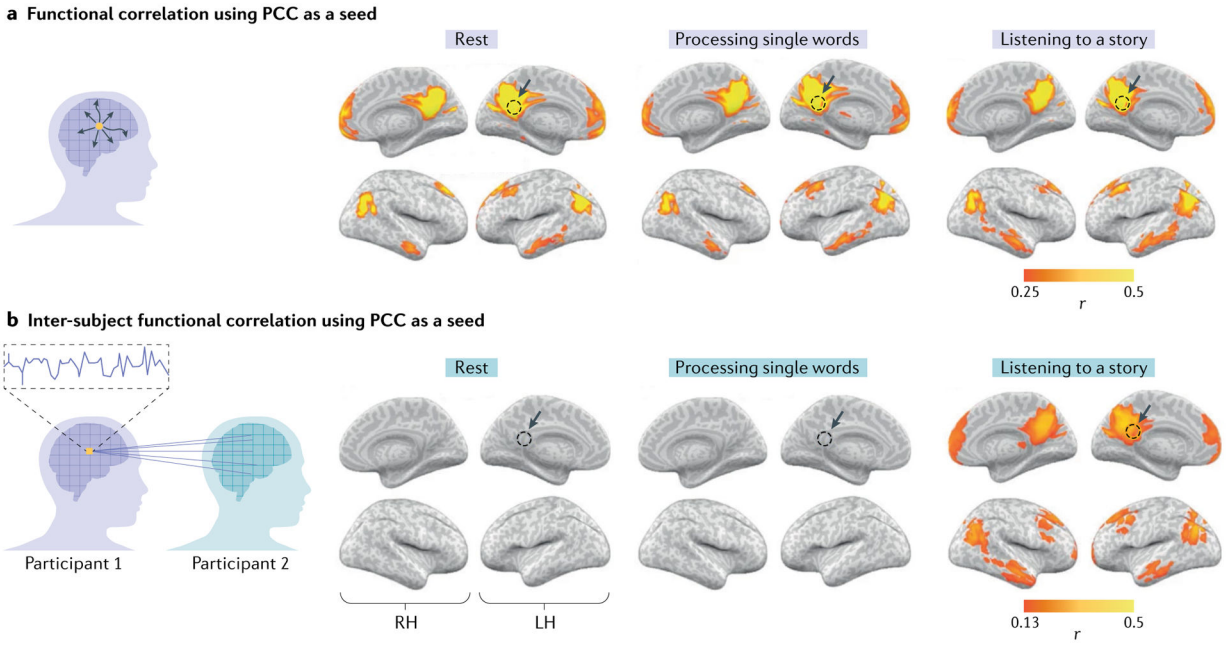

Fig. 3 |. Isolating stimulus-locked brain connectivity using inter-subject functional correlation. **a** | Within-participant functional correlation maps between the posterior cingulate cortex (PCC) seed (yellow voxel in the schematic; dashed circles in the brain maps) and the whole-brain neural activity. The functional correlation analysis delineates nodes of the default mode network (DMN) in which the activity fluctuates together (co-varies) in a given participant, owing to the direct or indirect anatomical connections during rest (left panel), processing of single words (middle panel) and listening to a coherent story (right panel). **b** | Inter-subject functional correlation maps between the PCC seed and the whole-brain neural activity observed in other participants. This analysis can filter out spontaneous intrinsic neural facilitation, and as such reveals no substantial stimulus-locked correlations in the DMN during rest (left panel) or during the processing of single words (middle panel). By contrast, however, inter-subject functional correlation exposed stimulus-locked shared responses across participants in the DMN as subjects listen to and process a spoken story minutes long (right panel). LH, left hemisphere; RH, right hemisphere. Adapted from REF. [26], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

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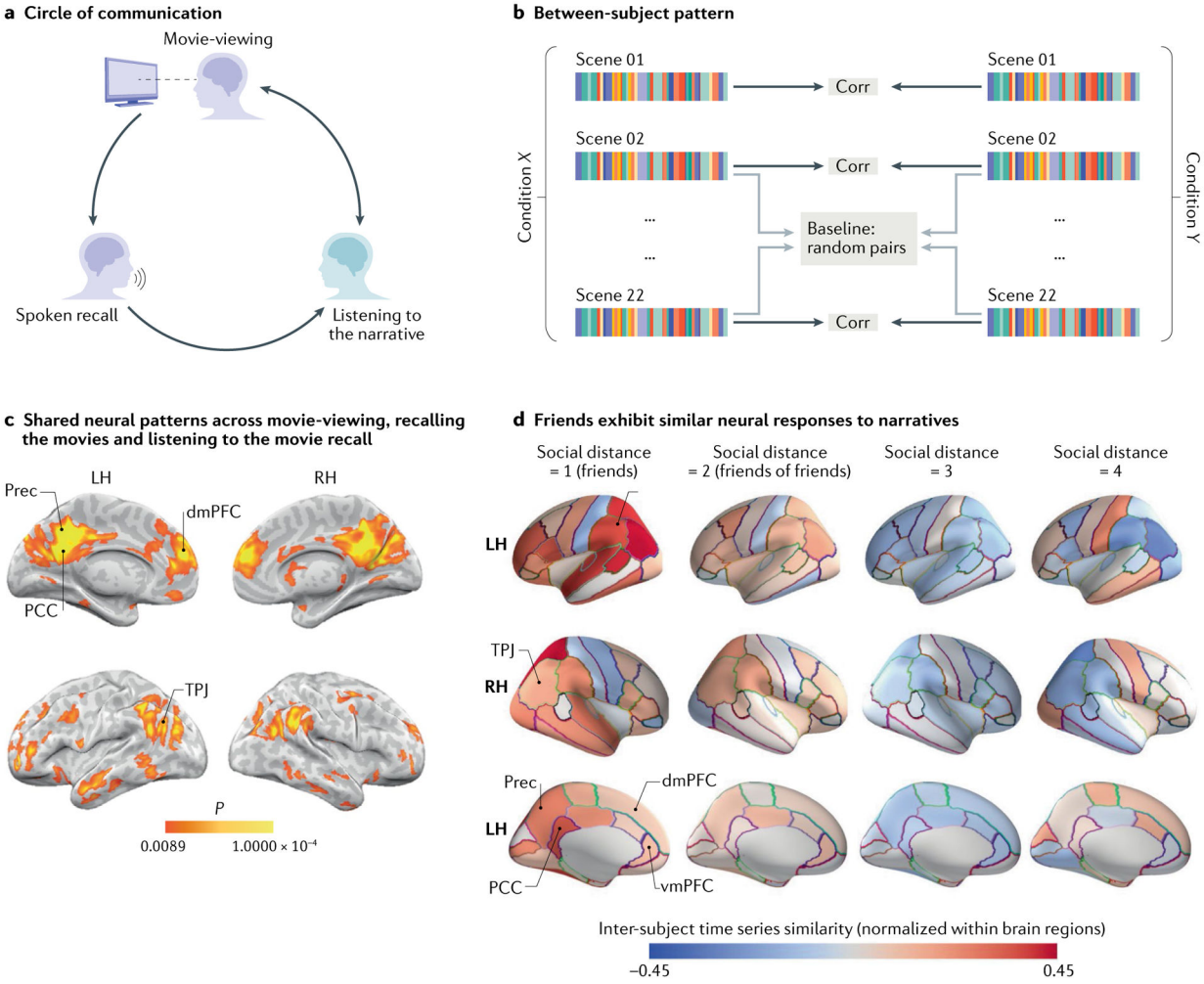

Fig. 4 |. Transmission of experience and the similarity of neural responses among friends.

a | An experimental paradigm for measuring how we share our memories with other brains. First, a participant was scanned while watching an episode of the television series *Merlin* (encoding information to memory). Next, the participant was scanned as they used words to recall and share their memories with a new group of participants who had never seen the television episode before. **b** | Neural coupling between groups was assessed using a between-subject pattern similarity spotlight analysis. An average spatial pattern of activity was calculated for each participant for each scene of the movie (coloured bars). Spatial patterns for each scene were then correlated (corr) across participants in different groups and averaged. **c** | Participants who had never seen the episode before and listened to the description of the episode had a similar pattern of neural response within the default mode network (DMN) to the participant who recounted the episode from memory. **d** | The social network of a cohort of students at a business school was reconstructed based on a survey of the students. From this network, 42 students participated in a functional MRI (fMRI) study and watched a collection of short movie clips while in the scanner. Similarities in fMRI response while watching these clips were calculated according to the social distance (defined by the social network) between a dyad. These were calculated by correlating the time series

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of response for each participant to that of every other participant in a given brain region and taking the mean of the resulting correlations. Warmer colours indicate relatively similar responses for a given brain region; cooler colours indicate relatively dissimilar responses for that brain region. Note the higher degree of inter-subject alignment of the neural responses in regions of the DMN (posterior cingulate cortex, PCC; precuneus, Prec; ventromedial prefrontal cortex, vmPFC; dorsomedial prefrontal cortex, dmPFC; and temporoparietal junction, TPJ) and nearby networks to the same movie clips among dyads that are social closer. LH, left hemisphere; RH, right hemisphere. Parts **a**–**c** adapted from REF.[33]. Part **d** adapted from REF.[117], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).