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What can narratives tell us about the neural bases of human memory?

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Narratives are increasingly used to study naturalistic human memory and its brain mechanisms. Narratives—audiovisual movies, spoken stories, and written stories—consist of multiple inter-related and temporally unfolding events which are rich in semantic and emotional content. These characteristics drive intersubject neural synchrony in the default mode network, where abstract situation models are represented and reinstated. Medial temporal lobe structures interact with the cortical subregions of the default mode network to support the encoding and recall of narrative events. Narrative memories are frequently communicated across individuals, resulting in the transmission of experiences and neural activity patterns between people. Recent advances in neuroimaging and naturalistic stimulus analysis provide valuable insights into narrative memory and the human memory system in general.

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Introduction

Recent years have seen increased interest in the use of narratives — movies, auditory stories, or written stories (Box 1) — in the neuroscientific study of human memory systems. The importance of narratives in human memory has long been recognized by psychologists, some of whom have gone so far as to propose that all of memory, or at least spoken memory, consists of stories [1]. This growing adoption of narratives in cognitive neuroscience studies of memory stands in contrast to the trial-based, randomized-order experimental approach which has long dominated the field. Advances in neuroimaging methods [2], together with mounting interest in hierarchical models of the brain and cognition [3] — and specifically, what nature of information might be carried at the top of these hierarchies [4] — have inspired more memory researchers to view narratives as a viable stimulus class for brain imaging studies.

What do narratives have to offer for studying memory and brain function? One benefit is ecological validity; movies and stories provide a more engaging and realistic experience than a random series of shapes or words. A second useful property of narratives, which initially captured the attention of the brain imaging community, is their ability to push the brain through a wider range of states relative to simpler static stimuli [5]. This characteristic potentially allows new discoveries of brain function and organization associated with naturalistic cognition. In particular, some high-order brain regions (e.g. default mode network; DMN; Box 2) respond in a markedly different manner (synchronizing across individuals) when the attended stimulus is narrative-like — semantically complex, coherent, and continuous over many minutes [3,6] — as opposed to punctate and random.

One might argue that these proposed benefits are false promises, because stories and movies do not represent real-world experience; that they are cleaned-up and more dramatic 'superstimulus' [7] versions of real life that elicit supernormal responses in our brains. However, stories are universal and ubiquitous in human life now and on the timescale of evolution. Anthropological work with hunter-gatherer communities links storytelling to reproductive success and group cooperation [8,9]: the ability to share warnings of danger, explain routes to resources, and exchange social information, in places and times beyond one's immediate experience, clearly would have enhanced survival outcomes. In modern society, people spend on average 20% of their awake time watching television or reading [10], and billions of dollars per year are poured into cinematic and novelistic pursuits, reflecting the high motivation of people across the globe to consume stories for pleasure. Thus, the ability to comprehend and produce narratives may be an ancient adaptation which has come to occupy a significant position in human daily experience, and the brain states elicited while encoding and retrieving stories could in fact have fundamental importance for understanding human neurobiology. As pointed out by Bower [11], consuming stories 'has strong face-validity as a task humans frequently perform with the goal of remembering. It is not the least bit 'artificial'.'

Box 1 What qualifies as a narrative?

In this review, we define a narrative as the verbal or nonverbal discourse of an event or a sequence of inter-related events, either fictional or nonfictional. Narratives are presented in various forms and modalities in memory research: written text [12], speech [13••], movies [14•,15], and animations [16•]. They also come in different lengths, from tens-of-seconds-long video clips [17•,18] to a two-hour-long film [19••], or from a paragraph-long story [20••] to a full novel [21]. Although varied in types and lengths, such narrative stimuli have common characteristics in that they typically consist of events involving agents and their goals and actions. Ryan [22] offers a more detailed list of eight conditions spanning spatial, temporal, mental, and pragmatic dimensions, which can be applied to determine the narrative-ness of a case on a spectrum. For example, the recipe 'Beat eggs until they form peaks; pour on fruits; bake 10 min until custard is set; cool and serve' may or may not be considered a narrative depending on who you ask, but most would agree that it becomes more like a narrative if one imagines the relationship between the chef and restaurant patrons, that the chef has a goal of acquiring a Michelin star, and that the events happened only once rather than being abstract instructions without a specific time or location [22].

Box 2 The brain's default mode network

The default mode network (DMN) is a set of inter-linked brain regions distributed throughout higher association areas, originally discovered as regions whose activity decreases during attention-demanding tasks compared to passive baseline (see Ref. [23] for a review). The subregions of the DMN include both medial and lateral parts of the prefrontal, parietal, and temporal cortices (Figure 1). These regions show high intrinsic functional connectivity, as their activation levels are correlated with each other both during tasks and rest (e.g. [24]). Despite the fact that the DMN is suppressed during externally oriented tasks, various internally oriented tasks (e.g. memory recall, mental simulation, scene construction, social inference, self-referential cognition) tend to activate common DMN areas ([25,26]; but see Ref. [23] for discussions on functional heterogeneity within the network). Thus, it is broadly recognized that the DMN performs high-level cognition involving abstract, trans-modal information, including complex event representations ([27]; see Section 'Studying narrative memory in the brain with inter-subject synchrony' for further discussions).

Here, we review recent studies on human memory using narratives as encoding material. We first provide an overview of the experimental paradigms and behavioral characteristics of narrative memory. We then discuss the brain mechanisms involved in narrative memory, focusing on neural synchrony across people in higher associative areas. Finally, we review the latest findings in terms of two major properties of narratives that distinguish them from other simpler types of stimuli: 1) narratives consist of one or more linked events that dynamically unfold over time, and 2) narratives are frequently shared between people through interpersonal communication.

Experimental paradigms and behavioral characteristics

Studies on narrative memory typically contain encoding periods and retrieval periods, similar to traditional trial-based memory experiments. During encoding periods, participants are instructed to watch, listen to, or read narratives as one would do in real life (e.g. 'sit down, relax and enjoy the movie,' [28••]) without performing any task other than attending to the stimuli [29] or sometimes trying also to remember them [17•,30••]. During retrieval periods, participants are tested on their memories for the overall plot or specific events of the narratives. While encoding tasks normally resemble naturalistic narrative consumption, retrieval tasks vary considerably both within and across studies in terms of the narrative-ness (see Box 1) of the responses they require: memory tests range from simple old/new recognition tests of still images from movies [31] to fully self-guided oral or written storytelling of all remembered plots and details [13••,16•,30••], with various other types of tests in between such as cued recall using multiple-choice or short answer questions [32,33]. Unconstrained, high-narrative responses are generally scored manually in terms of their accuracy and quality, including the quantity of details provided [18,34•]. Although not within the scope of this review, remembering one's own life experiences (as opposed to stimuli given as movies or stories) also frequently takes the form of high-narrative retrieval (Box 3). The narrative-ness spectrum of retrieval together with the narrative-ness of encoding material constitute two independent axes that different types of memory studies can be mapped onto (Figure 2).

Behavioral narrative memory performance shows characteristics that are both distinct from and similar to those observed in memories for simpler types of stimuli. Like memory for random syllables and words, narrative memory decays over time, but this decay seems slower relative to random stimuli; narrative details persist well for at least several months [28••], often in a reconstructed rather than verbatim form, as demonstrated in Bartlett's classic studies [35]. This robustness of narrative memory seems to benefit from the schema and prior knowledge on which narratives are based: narrative memory is enhanced when the narrative is congruent with one's prior experiences [17•] and when pre-existing situational contexts are provided [32], although very atypical or surprising events and details may also have mnemonic advantages [12,17•]. Narrative memory is also influenced by the hierarchical structure of story components, as central information crucial for the core plotline of a narrative (e.g. characters' goals and actions with significant outcomes) is better remembered than peripheral information such as perceptual details or incidental facts [33]. Relatedly, narrative stimuli typically contain rich perceptual, semantic, and emotional content, and events with certain types of content are more likely to be remembered than others. For example, a recent study [28••] generated extensive content annotations of movie shots and found that memory accuracy was higher for shots that elicit or depict emotions. Other features including the presence of

Box 3 Real-life experience as narrative

Psychologists have long argued that one's own life is experienced and described in the form of a narrative [36]: life consists of a stream of events involving characters, actions, and objects in spatiotemporal contexts, with the main protagonist being oneself. People also commonly tell stories of their own life experiences and events to themselves and others to build a meaningful and coherent 'self-narrative' that supports self-identity [37]. Spoken or written autobiographical memory recall can be conceptualized as such a narrativization of real-life experiences. In autobiographical memory experiments, participants are typically asked to provide detailed descriptions of their life events associated with various retrieval cues (e.g. words/phrases, specific life periods), and the produced memories are assessed in terms of the number and quality of episodic and semantic details [38]. Similar to memories for narrative stimuli, autobiographical memory recall is a reconstruction rather than an exact replay of the actual experience [39] and recruits a distributed set of brain regions including the DMN [25].

While autobiographical memory studies target life events that happened before the experiment, other types of studies induce and/or record real-life experiences during the experiment. For instance, participants may perform a series of planned activities while taking a walk following a specified route, and then verbally describe the details of the walk [40]. Portable devices such as smartphones or wearable cameras are often used to record these real-world experiences online, which in turn can be used as retrieval cues [41]. Unlike traditional autobiographical memory studies, these types of studies of real-life memory allow experimenters to at least partially access and control to-be-remembered events, making it easier to assess the objective accuracy of the memories and compare items across individuals.

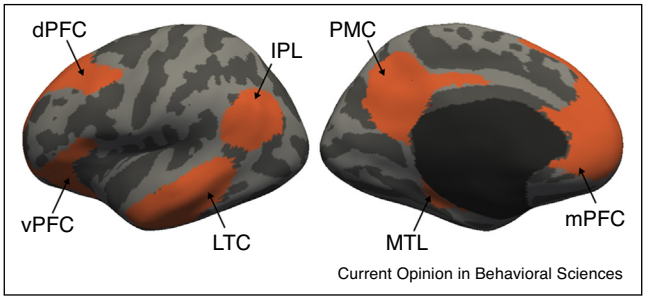
actions, sounds, and specific characters or objects also predicted subsequent memory.

Studying narrative memory in the brain with intersubject synchrony

A challenge of using naturalistic material, such as narratives, with brain imaging is that the complexity of the stimuli makes it difficult to specify a model for moment-by-moment brain responses. Even though the timing of individual words or images is known, these low-level elements cannot simply be summed to predict brain responses; there are numerous interactions between elements and intermediate levels of processing, likely different for different brain areas, which are unknown. Thus, brain responses to narrative stimuli are frequently studied using a technique known as intersubject similarity analysis [5,30••], which involves calculating correlations between the response timecourses or spatial patterns of neural activity across two or more subjects in a given voxel, sensor, or region of interest (Figure 3a; for a detailed primer, see Ref. [2]).

Intersubject similarity analysis was developed based on the observation that stories and movies drive shared response timecourses and spatial patterns *across* the brains of different individuals, that is, synchrony. Auditory stories and audiovisual movies ensure that the same sequence of information is relayed to the subjects at the same time,

Figure 1

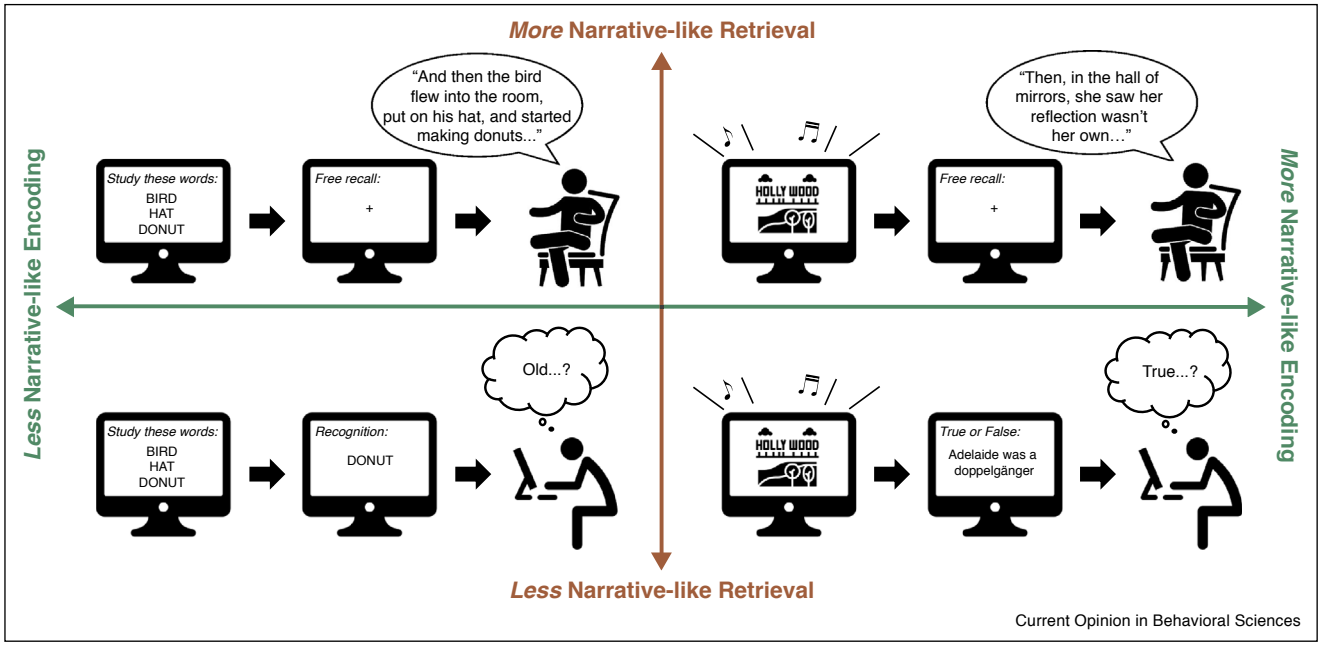


Subregions of the DMN based on intrinsic functional connectivity (from the 7-network cortical parcellation in Ref. [24]). The subregions are visualized on the inflated surface of a template brain (fsaverage). Left = lateral view, Right = medial view of the left hemisphere. Abbreviations: dPFC = dorsal prefrontal cortex, IPL = inferior parietal lobule, vPFC = ventral prefrontal cortex, LTC = lateral temporal cortex, PMC = posterior medial cortex, MTL = medial temporal lobe, mPFC = medial prefrontal cortex.

in terms of sensory input, amodal semantic features, and higher-level narrative content [43], allowing complex relationships between stimulus elements to build across minutes. Intersubject similarity analysis quantifies these brain responses that are shared across subjects and thus presumed to be elicited by the stimulus—in other words, another person's (or group's) brain response takes the place of predictions generated by a stimulus-based model. The shared component is by definition reliable signal, while the idiosyncratic component is a mixture of true individual signal and noise, in unknown proportions [44].

Intersubject similarity analysis has been especially important for elucidating the role of the DMN in narrative comprehension and recollection. A major finding from intersubject correlation (ISC) studies using narratives is that some high-order association cortices, including DMN regions, appear to synchronize strongly across individuals *only* when the stimulus is narrative-like. Specifically, ISC is observed strongly in DMN areas during a narrative, but is absent during resting state, during a video that lacks explicit narrative [5], and when the words or sentences in a story, or short segments of a movie, are randomly shuffled in time [3,6]. In other words, DMN regions only exhibit high ISC when participants engage with temporally coherent stories, leading to the proposal that they integrate information over long timescales (approximately 30 s) [3]. Short movies or story segments that elicit high intersubject synchrony in the DMN during encoding also tend to be better remembered [29,44], potentially reflecting higher engagement or a more canonical interpretation of the narrative. These findings are congruent with the broader literature which implicates the DMN in high-level cognition of transmodal information ([27]; see Box 2), and further specifies that

Figure 2



Two dimensions of narrative-ness in the study of human memory. Memory experiments typically contain encoding and retrieval periods, both of which can vary in the degree to which they emphasize narrative properties (see Box 1). For example, encoded stimuli may range from temporally isolated, decontextualized memoranda (i.e. less narrative-like) to full novels or professionally produced audiovisual movies (i.e. more narrative-like). Retrieval behavior can similarly vary from silent, two-alternative forced choice (i.e. less narrative-like) to fully self-guided narration (i.e. more narrative-like). We believe these two dimensions of narrative-ness are independent and provide a helpful four-quadrant framework for organizing how stories can be used to study memory. For example, studying a list of words and administering a recognition memory test does not emphasize narrative-ness during encoding or retrieval (i.e. bottom-left). However, we can emphasize narrative-ness at encoding by using audiovisual movies (i.e. bottom-right; see Ref. [28••]). The narrative aspects of encoding and retrieval can be emphasized simultaneously in a single paradigm by presenting participants with a narrative and allowing them to freely recount the episode (i.e. top-right; see Ref. [30••]). To our knowledge, experiments where participants *narrativize* non-narrative stimuli at retrieval (i.e. top-left) do not seem to exist yet, though it might be argued that some forms of autobiographical recall would qualify. (See Ref. [42] for an example of non-narrative stimuli narrativized at encoding.) Some of the images in this figure were purchased from The Noun Project, https://thenounproject.com.

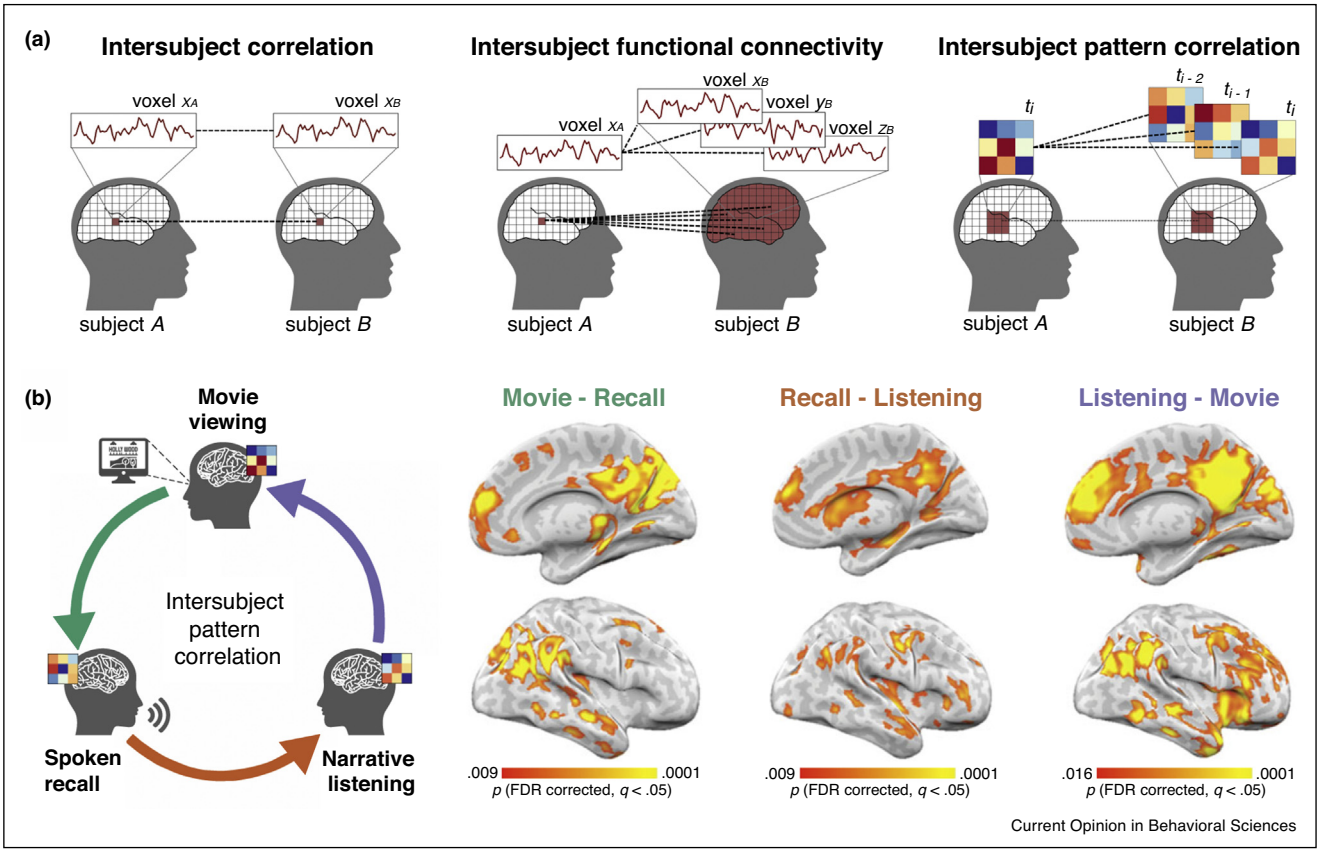
the DMN carries information with or about long-timescale dependencies within ongoing naturalistic (non-random) experience.

A related, increasingly popular viewpoint is that the DMN is involved in building a mental model of naturalistic situations, that is, a situation model [45]: 'a mental representation of the relationships between entities, actions and outcomes [. . .] a schema that specifies the gist of the spatial, temporal and causal relationships that apply within a particular context' [4]. Narratives are coming to play an important role in studies guided by this framework, as the purpose of a narrative is to simulate the unfolding story world in the minds of its audience as well as the speaker [46] — in other words, a continuous series of inter-related situation models. Indeed, when retrieval is conducted as a narrative, event-specific DMN activity patterns are reinstated scene-by-scene during unguided spoken recall [30••], echoing what has been observed in paradigms using cued silent recall of short movies [18,34•,47]. Further, these event-specific patterns were shown to be similar *across* individuals during recall, demonstrating a surprising level of stability in what are thought to be abstract event representations [18,30••]. It has also been suggested that cortical DMN subregions and the hippocampus work together in service of narrative comprehension and memory: ISC in DMN regions and coupling with the hippocampus is enhanced during movie-viewing when relevant prior context must be retrieved from long-term memory (e.g. 1 day earlier) [48,49].

Narratives unfold over time

A characteristic of narratives that distinguishes them from other simpler stimuli in trial-based experiments is that they are composed of connected elements that span a continuous, extended period of time, sometimes as long as an hour or more (e.g. [19••]). Thus, one experimental use of narratives has been to address the question of how the continuous stream of information arriving from the real world is perceived and remembered by humans as discrete events (for a review, see Ref. [50]). People detect

Figure 3



Intersubject synchronization during narrative processing. **(a)** Schematic descriptions of three common approaches to intersubject similarity analysis: intersubject correlation (ISC), intersubject functional connectivity (ISFC) and intersubject pattern correlation (pISC). ISC measures the temporal correlation between response timecourses of the same brain region across different subjects. ISFC measures inter-regional connectivity by correlating the response timecourse of a seed brain region from one subject and the response timecourses of different brain regions from other subjects. pISC measures the spatial correlation between activation patterns within the same brain region across different subjects (and sometimes across different time points). Figure adapted from Ref. [2], who provide a detailed primer on how presenting participants with a time-locked stimulus, such as a narrative, can make powerful intersubject analytic strategies possible. **(b)** An example use case of intersubject pattern correlation, showing that event-specific patterns of activity in higher-order association cortices, overlapping with the DMN, are shared between movie-viewing, spoken recall, and when naïve participants listen to the recalled story. Figure adapted from Ref. [13••].

discontinuities or boundaries between events in a narrative when there are changes in the situation (e.g. changes in the location or characters' goals) that make it difficult to predict the immediate future and thus require updating their current mental model of the situation (e.g. [51]). These perceived event boundaries are measurably consistent across individuals, and are tracked by shifts of fMRI activity patterns in the long-timescale DMN areas that represent situation models [52•]. Critically, detecting the completion of an event in a narrative promotes the registration or consolidation of the event into long-term memory as a cohesive unit: movie event boundaries trigger phasic activation in the hippocampus [19••,52•], whose magnitude is positively predictive of the subsequent gist memory of the event [53] and event-specific DMN neural pattern reactivation during recall [52•]. Event boundaries also drive the rapid reinstatement of a just-concluded event's EEG patterns, which is associated with later recall success [54••]. Thus, event representations are created and function as the organizational units of naturalistic long-term memory, supported both by the within-event accumulation of information and the online segmentation of continuous experiences following between-event transitions.

The continuous and temporally unfolding nature of narratives also makes them particularly suitable stimuli for studies on temporal memory and its neural mechanisms. A recent study [55•] demonstrated that retrieving the precise timing of an event is associated with anterolateral entorhinal and perirhinal activation by having participants watch a TV show and then indicate when each event (depicted by a still-frame) occurred on a continuous timeline. Lositsky *et al.* [56] targeted duration memory

and showed that the estimation of how much time has passed between a pair of audio clips from a radio drama depends on the amount of mental context change, measured as the dissimilarity between neural patterns in the entorhinal cortex. Other work focusing on temporal order memory has reported that retrieving which event happened earlier in a narrative activates DMN subregions including precuneus and angular gyrus [57]. Notably, the chronological order of events in a narrative does not necessarily follow the order in which they are presented (e.g. [14•]), and when the two types of temporal order do not match, chronological order judgments are biased toward the narrated order [58].

Narratives are communicated between people

Many psychologists have observed that communication between people frequently takes a narrative form, and that communication and memory are intimately linked [1,59]. Hirst and Echterhoff [60] take the view that remembering is most often an act of communication; Mahr and Csibra [61] propose that a primary function of episodic memory is to enable communication of the nature of our beliefs about past events. Questions about inter-person communication of memories necessarily involve multiple persons; here, the ISC approach is particularly appropriate, as it allows researchers to study inter-brain dynamics during naturalistic acts of communication.

Sharing of stories can be unidirectional—a speaker conveying ideas to one or more listeners—or bidirectional—a back-and-forth conversation about past events. The unidirectional case is simpler, as one person can be recorded while speaking and the audio played later to others, and thus most studies have focused on the relationship between storyteller (speaker) and listener(s). While simpler than bidirectional interaction, it should be noted that unidirectional communication is not an artifice of the laboratory; real-world storytelling often takes place without listener feedback, such as on a stage or in a classroom. These storyteller-listener studies generally agree that speaker-listener neural synchrony predicts comprehension, and that there are short and consistent delays (several seconds) in this coupling wherein the speaker brain signal precedes that of the listeners, or vice versa (interpreted as predictive listener behavior) [13••,62]. Synchrony is observed in sensory areas (speaker motor to listener auditory systems) as well as in higher-order areas (e.g. DMN). Notably, Zadbood [13••] (Figure 3b) went beyond speaker-listener coupling by examining both the speaker's speech and the original experience of the speaker (a movie). Brains of naive subjects (who had never seen the movie), listening to a speaker recount the movie's plot, significantly resembled the brain of the speaker as she watched the movie before retelling. This result demonstrates that listening to one person's spoken recollection can elicit brain activity patterns reminiscent of the original events that the speaker is trying to convey, that is, transmission of experience from one person to another.

The above studies focus on a single session or stage of communication, with one instance of storytelling; a new set of processes come into play when a group builds shared stories over multiple conversations, that is, oral tradition and collective memory [63,64]. The large number of persons and long timescales (days, weeks, years) involved in building such collective memories have made neuroscientific inquiry into the topic a daunting task, but the field seems poised for great advances. Recent behavioral work has applied graph methods to multi-stage communication in social networks. In lab-created social networks engaging in multiple rounds of conversation, researchers have shown that networks ultimately reach higher mnemonic convergence if individuals connected by bridge ties share memories earlier in the sequence [20••]; and a person's topological position in the social network affects their influence on the content of the group's collective memory [65]. In parallel, neuroimaging studies have emerged which examine the neural correlates of social network properties. For example, the hippocampus and posterior cingulate cortex encode social position of characters in an interactive game [66]; and widespread brain responses during movie-viewing are more similar between friends than between pairs of people more socially distant in the same network [67]. Studies such as these provide a tantalizing preview of how social network analysis and brain imaging may jointly contribute to a future neuroscience of collective memory.

Conclusion and future directions

The increasing use of narratives in memory research has delivered new insights as to how brain areas at the top of the information processing hierarchy encode and retrieve the stream of complex events which occur during intra-personal and inter-personal mentation. Further development in narrative memory research will be driven by methodological and conceptual advances which have already begun. Novel analysis approaches leverage artificial intelligence technologies, including natural language processing and computer vision, which allow quantification of vast quantities of dynamic, perceptually and semantically rich information in perceived or recalled narratives with unprecedented efficiency (e.g. [68]). Computational and theoretical modeling may address the mechanistic underpinnings of narrative memory, pushing the field beyond describing observed phenomena (e.g. [69]). Future studies may go beyond using narratives as encoding material to examine narrativization during retrieval, potentially relating memory to spontaneous and creative thinking [70]. Creating interdisciplinary links between cognitive psychology, neuroscience, linguistics, social psychology, anthropology, and even creative writing and cinematics, narratives provide

valuable insights into the understanding of the cognitive and neural mechanisms of naturalistic memory, not only as an imitation of real life but also as a unique class of human experience.

Conflict of interest statement

Nothing declared.

CRediT authorship contribution statement

Hongmi Lee: Conceptualization, Visualization, Writing - original draft, Writing - review & editing. **Buddhika Bellana:** Conceptualization, Visualization, Writing - original draft, Writing - review & editing. **Janice Chen:** Conceptualization, Writing - original draft, Writing - review & editing, Funding acquisition.

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- • of special interest
- •• of outstanding interest

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Zadbood *et al.* examined the neural bases of how we share our past experiences with others. In addition to replicating the finding that DMN activity patterns are shared across people when either viewing or recalling the same event [30], this study went further by playing the recall auditory recording to a group of naïve participants. In this way, the authors demonstrated that event-specific patterns of DMN activity from the original experiencer were elicited in a separate group of naive participants as they listened to the recall, completing the cycle of communication depicted in Figure 3.

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Kauttonen *et al.* leveraged the non-linear, reverse-chronological story-telling of the Christopher Nolan film 'Memento' to examine how the brain reinstates related past events to contextualize the present. This study exemplifies how researchers can use the particularities of stories and storytelling to bring interesting psychological phenomena into the laboratory.

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In this study, participants were scanned as they watched and recalled a short, ambiguous, nonverbal story told using animated geometric shapes. Using latent semantic analysis of the recall transcripts, Nguyen *et al.* were able to demonstrate that pairs of participants with similar interpretations of the narrative had higher ISC in regions of the DMN, relative to participants with differing interpretations. Higher ISC in DMN regions was also observed across subjects who listened to an audio version of the story if their recall was similar, further implicating the DMN in representations of high-level semantic meaning.

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In this study, Bonasia *et al.* scanned participants as they studied and recalled short (23 second) narrative film clips. Overall, they observed that a clip's typicality (i.e. congruence with prior knowledge) affected the neural substrate involved during both encoding and retrieval of these narrative clips: a bias towards DMN regions for typical clips and a bias toward medial temporal and early visual regions for atypical clips.

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Ben-Yakov and Henson used fMRI to examine hippocampal activity at event boundaries during film-viewing. With a large dataset of over 250 participants watching one of two movies, they provide evidence that the hippocampus responds to subjective event boundaries, with response amplitude increasing with boundary strength. This was true even after controlling for other perceptual changes.

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Momennejad *et al.* examined how memory for a written story can change across retellings, by placing participants into separate social groups and systematically manipulating when these groups interact. The authors observed that memory for the story is more likely to converge across social groups if across-group interactions (i.e. 'bridge ties') occur early in the conversation chain as opposed to later. By studying how narrative memory changes across multiple stages of communication, Momennejad *et al.* were able to gain invaluable insights into how insulated social groups can promote social polarization.

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