

Feature Review

From Knowing to Remembering: The Semantic–Episodic Distinction

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The distinction between episodic and semantic memory was first proposed in 1972 by Endel Tulving and is still of central importance in cognitive neuroscience. However, data obtained over the past 30 years or so support the idea that the frontiers between perception and knowledge and between episodic and semantic memory are not as clear cut as previously thought, prompting a rethink of the episodic–semantic distinction. Here, we review recent research on episodic and semantic memory, highlighting similarities between the two systems. Taken together, current behavioral, neuropsychological, and neuroimaging data are compatible with the idea that episodic and semantic memory are inextricably intertwined, yet retain a measure of distinctiveness, despite the fact that their neural correlates demonstrate considerable overlap.

The Episodic–Semantic Distinction in Contemporary Cognitive Neuroscience

Endel Tulving was the first to formally describe the distinction between **episodic** and **semantic memory** (see [Glossary](#)) in a book chapter published in 1972 [1], building on earlier philosophical (e.g., [2–4]) and psychological [5–7] writings. The episodic–semantic distinction remained central to Tulving’s thinking over subsequent years, while undergoing significant evolution (e.g., [8–12]), and the distinction retains its importance in contemporary cognitive neuroscience. With a few notable exceptions, however, research on the cognitive neuroscience of episodic and semantic memory has formed largely separate research traditions. Nonetheless, findings stemming from these two traditions show important points of convergence, and arguably have reached a stage where a synthesis might be possible. Here, we provide a selective review of these findings and discuss the extent to which they support Tulving’s original notion that episodic and semantic memory are distinct (albeit highly interactive) memory systems. Almost 50 years since Tulving’s original treatise, we reconsider the episodic–semantic distinction from the perspective of the modern era of cognitive neuroscience. Rather than emphasizing differences between these two forms of memory, we highlight their similarities at the cognitive and neural levels, focusing on the multifaceted ways in which they overlap and interact to support an array of sophisticated cognitive abilities.

Semantic Memory: Neural Underpinnings

Semantic memory refers to our repository of general world knowledge, and the term is often used interchangeably with that of conceptual knowledge. The semantic knowledge base is typically viewed as including general (encyclopedic) knowledge as well as schematic representations of events distilled from lifelong experiences, but that are retrieved independently from their original spatial or temporal context (e.g., 1984 was written by George Orwell; the definition of a birthday party) as well as personally relevant conceptual knowledge (i.e., personal semantics, e.g., ‘I have always been quite shy’). The neural underpinnings of semantic memory have been the topic of several recent reviews [13–15] and are discussed here in abbreviated form.

According to the highly influential sensorimotor (‘embodiment’) framework (e.g., [16–18] and [19] for an opposing viewpoint), a concrete concept is encoded as a specific combination of sensory, motor, and other modality-specific features, and is represented in the distributed pattern of neural activity that emerges when the neural elements representing these features are co-activated. Based partly on findings that neuropathology can result in seemingly category-selective impairments of conceptual knowledge (see [20] for discussion and critique), early proponents of the sensorimotor framework (e.g., [21,22]) argued that knowledge about different classes of object can be modality dependent. For example, whereas fruits are typically individuated by virtue of their constituent sensory

Highlights

Strong parallels exist between the theoretical frameworks underpinning retrieval of episodic and semantic information, including the proposal that both involve reinstatement or reactivation of neural representations of online experience.

Activity of some, or possibly all, regions belonging to the ‘core recollection’ network may support the reinstatement of semantic processes engaged during an experience, rather than processes linked to episodic retrieval more generally.

Mental time travel (the ability to re-experience the past and to ‘pre-experience’ the future) relies upon both episodic and semantic contributions

Studies of clinical populations converge to reveal considerable interdependencies between episodic and semantic representations during past- and future-oriented forms of memory.

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features (e.g., shape, taste, and color) rather than the actions that are associated with them (e.g., most fruits are eaten), tools can be individuated by their associated actions (e.g., twisting, in the case of a screwdriver, versus hitting, in the case of a hammer).

A sizeable body of functional neuroimaging evidence lends support to the idea that conceptual representations are distributed across modality-specific cortical regions. For example, in a study in which participants had to generate appropriate actions or color names in response to words denoting different objects, generating colors was associated with enhanced neural activity adjacent to color-sensitive cortical regions, whereas the opposite contrast identified enhanced activity in posterior temporal regions linked to action planning and motion processing [23] (reviewed in [17]). More generally, it has been argued that the neural activity elicited when a concrete concept is brought to mind overlaps with the activity elicited by the perception of, and interaction with, an exemplar of the concept [24], leading to a blurring of the boundary between perception and knowledge. That is, to bring the exemplar to mind is to reinstate ('simulate' [16]) the patterns of neural activity that would exist were the exemplar actually present in the environment (sometimes with an 'anterior shift', such that the activity linked with retrieval of conceptual knowledge is localized slightly anterior to the activity elicited during perception [25]; see also [24,26]). This idea finds a strong parallel in theoretical ideas about episodic memory retrieval (see 'Episodic Memory: Neural Underpinnings' section). Furthermore, as implied by the example given earlier, the set of features activated by a given concept is not invariant, but rather can differ according to task and contextual factors. Selection of the features most appropriate for a given behavioral goal, and the resolution of interference between potentially competing feature sets, depends on control processes supported by a brain network centered on left inferior prefrontal cortex (e.g., [27,28]).

It is widely held that conceptual representations limited to the sensorimotor level are insufficient to support the full gamut of human conceptual processing and need to be combined in complex ways to create multi- or supramodal representations. Notably, it is not obvious how a sensorimotor level of representation alone could support abstraction (e.g., the ability to categorize both roller skates and helicopters as modes of transport) or the representation of abstract concepts, such as 'pious' or 'liberty' (for recent discussion of this issue, see [29] and other papers in the same issue). These and related considerations have long motivated proposals for a mechanism that allows for not only the integration of sensorimotor information arising from different modalities in real-time, but also the encoding of covariances in this information that emerge over time. Such a mechanism could support the formation of higher-order representations that are abstracted away from modality-specific information (e.g., [30]). According to one prominent model [31], the mechanism takes the form of a computationally homogeneous 'hub' that receives input from activated sensorimotor feature sets and forms representations based on patterns of covariance across the different feature sets (this usage of 'hub', which encompasses specific integrative, computational, and representational functions, differs from its typical usage in network neuroscience, when no specific computational role is implied [32]). Largely on the basis of neuropathological evidence from the syndrome of semantic dementia (SD; see 'Episodic and Semantic Memory in Neurodegenerative Disorders' section), along with supporting evidence from transcranial magnetic stimulation and fMRI, the proponents of this 'hub and spoke' model have argued that the hub is localized to the bilateral anterior temporal lobe (ATL), centered on the anterior third or so of the fusiform gyrus [13]. This proposal has not gone unchallenged, with others arguing that amodal conceptual representations depend critically on more posterior regions of temporal cortex [33,34], or on multiple, heteromodal cortical 'convergence zones' [35,36]. Of particular relevance here, it has been proposed that a 'general semantic network' (Figure 1A) comprising, in addition to ATL, many of the same regions that are held to comprise the 'core recollection network' (see 'Episodic Memory: Neural Underpinnings' section) operate as a distributed convergence zone to support conceptual representations at varying levels of abstraction [36]. Consistent with its heteromodal characterization, neural activity in the regions belonging to this network covaries with amount of conceptual processing across a range of experimental tasks, materials, and manipulations [including lexicality (word versus pseudoword), word frequency, word concreteness, and number of thematic associations; reviewed in [36]]. Furthermore, multivoxel pattern analysis (MVPA) of fMRI data has revealed that the patterns of activity within these regions can support decoding of semantic and/or conceptual content [37].

Glossary

Episodic memory: recollection of personally experienced events situated within a unique spatial and temporal context (e.g., I remember reading *1984* in Hyde Park yesterday).

Familiarity: a collection of memory signals that support recognition memory in the absence of recollection (see Box 1 in the main text).

Gist: knowledge about a specific event or episode that encompasses its overall structure or central elements but without additional contextual, typically perceptual, details (e.g., what in general transpired at a particular birthday party [110]).

Recollection: retrieval of consciously accessible, qualitative information about a past episode (see 'Episodic memory').

Remote memory: memories corresponding to events in the relatively distant past, usually a year or more ago. Although no definite passage of time defines remoteness, such memories typically date from relatively early in an individual's life, for example, childhood in the case of a young adult, or young adulthood in the case of a middle-aged or older individual. The term is descriptive and is neutral as to whether a particular memory is supported by episodic or semantic memory information or processes. Importantly, a remote memory need not depend on access to the memory trace encoded concurrently with the event it represents; rather, it could reflect the content of a more recently encoded ('re-encoded') trace dating from the last time the memory was retrieved.

Schema: a large-scale knowledge structure that is extracted over multiple experiences. Whereas gist refers to a memory for the central elements of a specific episode (e.g., a recent birthday party), a schema captures similarities across multiple episodes or memories (e.g., what happens at birthday parties in general).

Schemas are dynamic structures that evolve with new experiences, can influence how events are experienced, and how memories are encoded, retrieved and evaluated (see [83] for a fuller discussion).

In summary, there is some consensus that conceptual (semantic) knowledge depends upon a combination of neural activity distributed across cortical regions that support modality-specific information, and neural processing within heteromodal cortical regions that operate on these patterns of modality-dependent activity to create representations in rich, high-dimensional feature spaces.

Episodic Memory: Neural Underpinnings

Episodic memory refers both to a hypothetical 'episodic memory system', which encodes, stores, and allows access to 'episodic memories', and to the memories themselves, which are often held to have unique phenomenological attributes. The distinction between these two usages is usually signaled only by the context in which they are used. Episodic memory in the latter sense refers to recollection of personally experienced events situated within a unique spatial and temporal context (e.g., I remember reading *1984* in Hyde Park yesterday). In Tulving's original conception [9], episodic memory is tightly associated with awareness of the self-situated in subjective time (autonoetic awareness), which permits events to be re-experienced (episodic retrieval) or 'pre-experienced' (episodic future thought; see Box 2).

According to a long-standing framework (reviewed in [38]), episodic memories are a by-product of the processing engaged by an event as it is experienced. As the event unfolds, some of the cortical activity it elicits is encoded in the hippocampus as a content-addressable memory in which the patterns of cortical activity that represent the features are bound into a memory representation. Retrieval of an episodic memory (recollection) occurs when a retrieval cue activates a stored hippocampal representation sufficiently to cause 'pattern completion', restoring the representation to an active state. In turn, this leads to reactivation of the encoded pattern of cortical activity and, hence, access to mnemonic content (see [38] for a discussion of the preconditions for successful episodic retrieval).

Findings from functional neuroimaging studies provide compelling support for this general framework. Relative to unsuccessful recollection, successful recollection is associated with not only hippocampal activation, but also reinstatement of some of the cortical activity that was elicited when the recollected event was initially experienced. Retrieval-related 'reinstatement effects' were first identified through univariate analyses of positron emission tomography (PET) and, subsequently, fMRI blood oxygen-level-dependent (BOLD) signal changes [38,39], when they take the form of overlap between regions demonstrating differential activity between two or more study conditions, and regions demonstrating study condition-dependent differences in recollection-related activity (see Figure 2 for an example). Retrieval-related reinstatement has also been demonstrated with MVPA of fMRI data. Such findings have been reported for linear classifiers trained on study data and used to classify corresponding test trials (e.g., [40]), and for analyses of the similarity of patterns of activity elicited during the encoding and subsequent retrieval of specific episodes (e.g., [41]).

As is illustrated in Figure 1B, recollection-related enhancement of BOLD activity is found not only in content-sensitive cortical regions, but also in regions that, along with the hippocampus, have been proposed to comprise a general or 'core' recollection network [42]; a similar, if not identical, network is active during autobiographical memory retrieval and 'episodic future thought' [43]. The network was so named because it is engaged during successful recollection seemingly regardless of the nature of the recollected content or the memory test used to elicit recollection. The cortical components of the network include parahippocampal, medial prefrontal (mPFC), and posterior cingulate/retrosplenial cortex, along with left angular gyrus and left middle temporal gyrus. Importantly, while activity within the network is enhanced in a generic manner when recollection is successful, studies using MVPA reported that retrieved content can be 'decoded' from most, if not all, of its members [41,44]. These findings indicate that the sensitivity of the network to successful recollection goes beyond a simple elevation of global activity, and that retrieval-related reinstatement is not confined to cortical regions, such as 'the fusiform face area' or auditory cortex (Figure 2), that are specialized for information belonging to a specific modality or perceptual category.

Semantic memory: general (encyclopedic) knowledge as well as schematic representations of events distilled from lifelong experiences, retrieved independently from their original spatial or temporal context (e.g., *1984* was written by George Orwell; the definition of a birthday party, or knowledge of events that typically happen during birthday parties).

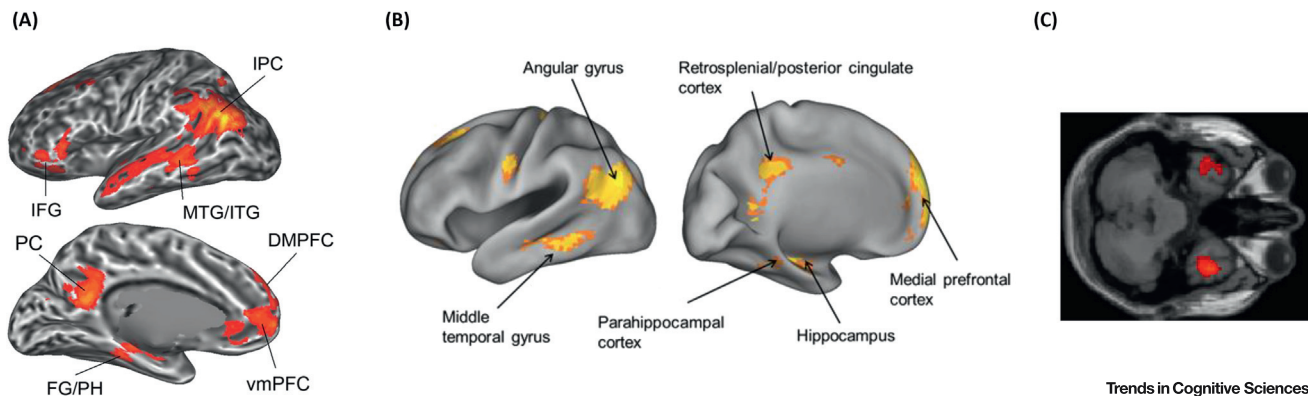


Figure 1. Overlap between the General Semantic Network (A) and the Episodic Core Recollection Network (B).

The two networks share essentially the same parahippocampal, middle temporal, ventral parietal, and midline frontal and posterior regions. By contrast, the hippocampus is present in the core recollection network (B) but not in its semantic counterpart (A) (see main text for discussion). Although the anterior temporal lobe (ATL) is absent from both depicted networks (likely due to the degradation of signal quality in this region), fMRI studies using sequences optimized to detect blood oxygen-level-dependent (BOLD) signals from the ATL reported increased activity in this brain region during conceptual processing, especially in the anterior fusiform gyrus [51,52]. Although it has yet to be established whether the ATL consistently demonstrates equivalent episodic retrieval effects with optimized fMRI, the outcome of the contrast between accurate and inaccurate associative recognition memory judgments on word pairs shown in (C) suggests that this is a distinct possibility. (A) The general semantic network as revealed by fMRI meta-analysis [36]. (B) The core recollection network [42]. (C) Recollection-related enhancement of fMRI BOLD signal in bilateral anterior ventral temporal cortex [thresholded at $P < 0.001$, with family-wise error correction ($P < 0.05$) at the cluster level]. The figure depicts the outcome of the contrast between accurate and inaccurate associative recognition memory judgments on word pairs, a contrast assumed to permit identification of neural correlates of successful recollection. These findings were originally reported in [195], but did not include a depiction of the ventral temporal effects illustrated here. The data were obtained from a sample of 136 participants ranging in age from 18 to 76 years. For further details, see [195]. Adapted, with permission, from [36] (A) and [42] (B). Abbreviations: DMPFC, dorsomedial prefrontal cortex; FG/PH, fusiform gyrus/parahippocampal cortex; IFG, inferior frontal gyrus; IPC, inferior parietal cortex; PC, posterior cingulate/precuneus; vmPFC, ventromedial prefrontal cortex.

The network depicted in Figure 1B represents the outcome of a contrast between retrieval cues that elicited recollection- versus familiarity-driven (Box 1) recognition memory judgments. Whereas such contrasts allow the neural correlates of successful recollection to be identified while holding stimulus and task factors constant, they cannot identify neural regions that are sensitive to the cognitive demands of episodic retrieval independently of the outcome of the retrieval attempt. However, consistent with the notion that the left inferior prefrontal cortex supports semantic control processes (see previous section), it has been reported that the region is more active during episodic memory tests that place high, as opposed to low, demands on the processing of retrieval cues (e.g., tests of source memory vs simple item recognition [45,46]). Additionally, it has been reported that members of the core recollection network demonstrate not only enhanced activity during successful recollection, but also enhanced functional connectivity with parietal and dorsolateral/dorsomedial frontal regions comprising the ‘frontoparietal’ and ‘cingulo-opercular’ control networks ([47], see also [48]). Regions belonging to these networks are held to act as ‘flexible hubs’ that couple with different functional networks depending on task demands [49]. Thus, enhanced functional connectivity with the core recollection network likely reflects the engagement of domain-general control processes in support of post-retrieval operations, such as selection of an appropriate behavioral response on the basis of recollected content. Perhaps not coincidentally (see following section), in one study [50], increased demands on semantic processing were reported to result in enhanced functional connectivity between members of the general semantic network and networks implicated in domain-general cognitive control.

Episodic and Semantic Memory Retrieval: Overlapping Neural Correlates

As is evident from Figure 1, the core recollection network overlaps strongly with the general semantic network. Specifically, the two networks share essentially the same parahippocampal, middle temporal, ventral parietal, and midline frontal and posterior regions. Conspicuous by its absence in

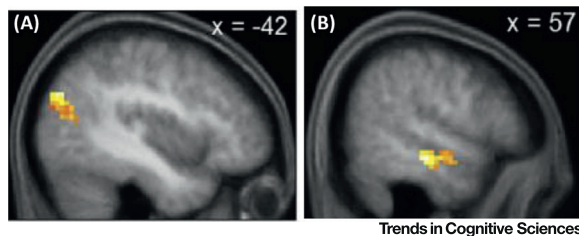


Figure 2. Examples of Episodic Reinstatement Effects.

This figure displays two examples of episodic reinstatement effects [(A) visual and (B) auditory], when cortical activity elicited when a recollected event was initially experienced is reactivated during successful recollection [196]. Subjects studied pictures in association with their visually or auditorily presented names. At test, they discriminated studied pictures according to the modality of the associated name. Yellow clusters indicate where modality-selective source recollection effects (high > low confidence judgments) overlapped with modality effects at study (visual > auditory and vice-versa). Adapted, with permission, from [196].

Figure 1A,B is the ventrolateral ATL, the putative ‘semantic hub’ with a central role in the ‘hub and spoke’ model of semantic cognition described in the section ‘Semantic Memory: Neural Underpinnings’. As has been noted previously (e.g., [51,52]), the seeming absence of the ATL from the semantic network likely reflects the degradation of signal quality in the region caused by magnetic susceptibility artefacts in the vicinity of the sphenoid sinus. Consistent with this possibility, fMRI studies using sequences optimized to detect BOLD signals from ATL have reported that its activity, especially in anterior fusiform gyrus, is enhanced during conceptual processing [52,53]. Although it has yet to be established whether the ATL consistently demonstrates episodic retrieval effects with optimized fMRI, Figure 1C, which illustrates findings from a single large-scale study, suggests that this is a distinct possibility.

Also evident in Figure 1 is the presence of the hippocampus in the core recollection network but not in its semantic counterpart. The greater prominence of the hippocampus in the recollection network is perhaps unsurprising in light of its key role in both the encoding and reinstatement of the patterns of cortical activity set in train by episodes as they are experienced (see previous section). Indeed, the hippocampus may act as a hub that supports integration of information distributed across the recollection network, and helps distinguish it from the semantic one, despite the substantial overlap between the two networks. However, although the hippocampus might ordinarily have only a limited role in the retrieval of conceptual information (see not only the following section, but also Box 3, and [54,55] for evidence that the hippocampus supports performance on certain semantic fluency tasks), it likely does have a role in its acquisition, at least for some kinds of information. This role is evident in numerous studies that report a marked impairment in the ability of patients with hippocampal damage to acquire new factual (encyclopedic) knowledge, even after intensive, repeated training ([56,57], although see [58] for a discussion of possible exceptions to these findings in cases of hippocampal damage in early childhood, and see [59,60] for discussion of the possibility of ‘fast mapping’ in adults). Additional evidence possibly implicating the hippocampus in semantic cognition comes from single-unit studies of the human hippocampus. These studies identified cells that responded to specific individuals, places, or objects (and to stimuli associated with these concepts) whether the entity was presented as an image, or as a written or spoken word (reviewed in [61,62]). Dubbed ‘concept cells’, they have been interpreted as coding semantic representations that ‘constitute the building blocks for declarative memory functions’ ([61, p. 592]). However, these responses to specific individuals, places, or objects may only represent one form (and perhaps not the canonical form) of semantic memory. Semantics frequently requires extraction of statistical regularities over different exemplars of a category (e.g., we develop a representation of the concepts of cats through learning about many different cats, typically not through a single individual, but see [63] for a recent example of an exemplar-memory model of category learning). An alternative, although not mutually exclusive, interpretation is that concept cells are experiential, episodic cells that link a specific entity to other aspects of an experienced event involving the entity [64,65].

Box 1. The Concept of Familiarity in Episodic and Semantic Memory

The essence of episodic memory lies in the process of recollection, by which one can not only reinstate the contextual details of an event, but can also mentally re-experience it. Nevertheless, it is widely held that, in tests of recognition memory, judging whether an item is old or new can also be achieved by evaluating its 'familiarity', a sense of prior experience bereft of contextual details. However, familiarity, is 'not a well-grounded theoretical concept' [145]; it is defined by exclusion (recognition memory in the absence of recollection) and is likely based on multiple sources of information that can each support a judgment that a stimulus event has been recently experienced. A celebrated example of such information is the enhanced 'perceptual fluency' of recently studied objects and words that, under appropriate circumstances, can lead to a positive recognition memory judgment and a subjective sense of familiarity [146,147]. More recently, it has been claimed that high levels of 'conceptual' fluency can likewise support familiarity-based recognition (e.g., [148,149], see also [150,151]).

A popular behavioral method (the 'Remember/Know procedure') for segregating recognition memory judgments according to whether they are based on recollection or familiarity was proposed by Tulving [9] not with the aim of supporting 'dual-process' models of recognition memory, but rather, to separate memory judgments supported by episodic (associated with auto-noetic consciousness or 'remembering') as opposed to semantic (associated with noetic consciousness; 'knowing') memory. Whereas relatively few of the many researchers who currently use the Remember/Know procedure do so on the assumption that they are dissociating episodic and semantic memory (as noted earlier, familiarity is a catch-all term for a variety of memory signals), to the extent that conceptual processes have a role in familiarity-based recognition [148–152], 'know' judgments may indeed sometimes fulfill the role Tulving attributed to them.

As noted in the main text, the semantic network overlaps closely with the recollection network and 'recollection success effects' in the core recollection network may reflect reinstatement of conceptual processing. From this perspective, familiarity arising from conceptual fluency might involve weak (and, hence, undetectable) reactivation effects in the core recollection network. Indirect support for this possibility comes from the finding that study content can be decoded from core recollection regions almost as accurately for 'Know' as for 'Remember' judgments, despite the absence of an effect on fMRI BOLD signal magnitude [44].

What underlies the overlap between the semantic and recollection networks? We propose that the answer lies in the fact that the content of an episodic memory typically comprises a conjunction of familiar concepts and episode-specific information (such as sensory and spatial context), much as the episodic interpretation of concept cells suggests. Thus, recollection of a prior episode entails the reinstatement not only of contextual information unique to the episode, but also of the conceptual processing that was engaged when the recollected event was experienced (see also [66]). From this perspective, 'recollection success effects' in cortical members of the core recollection network do not reflect processing that supports episodic memory *per se*, but rather, the reinstatement of the conceptual processing that invariably underpins our interactions with the world in real-time (e.g., [10,67,68]). The importance of such processing for episodic memory is well illustrated by the syndrome of SD (see 'Episodic and Semantic Memory in Neurodegenerative Disorders' section), when recollection of meaningful information is selectively impaired (e.g., [69,70] but see [71]). Of importance, if the foregoing proposal (a similar proposal was advanced in [68]) is correct, then, from the standpoint of episodic memory, regions belonging to the core recollection network deserve no more privileged a position theoretically than any other cortical region in which retrieval-related reinstatement can be identified.

We note that the foregoing proposal leaves open the important question of the specific roles of these different regions in semantic (and, by implication, episodic) memory (see [72] for recent discussion of this question). This question is far from resolved, although numerous and sometimes conflicting proposals have been advanced. Interestingly, several brain regions have been proposed to serve as an interface between semantic and episodic memory, such as the parahippocampal cortex and the posterior cingulate cortex [14] or the perirhinal cortex [73]. As for the parahippocampal cortex, it has variously been proposed that it may have a role in semantic associative processing [74–76], while others have discussed its importance in processing scenes [64,77] and objects that evoke an

awareness of surrounding space [78]. In the case of the angular gyrus, proposals have ranged from the idea that the region contributes to combinatorial processes (online construction of concepts such as ‘fast truck’, or ‘plaid jacket’, etc. [79,80]) to the proposal that it does not have a specialized role in semantic cognition at all, but instead supports a domain-general ‘buffer’ [81]. Similarly diverse proposals have been put forward regarding the roles of other members of the core network in semantic cognition. For example, in the case of the middle temporal gyrus, proposals range from a role in the conceptual representation of concrete objects [72] to semantic control [82]. In addition, the ventromedial (vm)PFC has been proposed to support processing of the affective significance of concepts [14], to be a critical brain region for the encoding and storing of cognitive **schemas** supporting the extraction of commonalities between events [83–86], and to have a role in memory consolidation [87,88].

Although the proposal that recollection success effects in the core network reflect the reinstatement of conceptual processing is both parsimonious and, we contend, consistent with the available evidence, it lacks direct support. fMRI studies examining the neural correlates of successful recollection have invariably used meaningful experimental items, such as concrete words, or pictures of objects, and have typically done so in the context of study tasks that require or encourage semantic elaboration. To our knowledge, with the exception of [89], there are no published studies in which recollection effects were contrasted according to the amount of semantic or conceptual processing engaged during encoding (although see [90] for a study in which encoding was manipulated but the subsequent memory test did not allow identification of items recognized on the basis of recollection rather than on familiarity). In [89], the memory test required a discrimination between unstudied items and items subjected to semantic or nonsemantic study. Retrieval effects in the core network were not fully explored, but intriguingly, one member of the network (left parahippocampal cortex) was reported to demonstrate a greater recollection effect (operationalized as greater activity for correct than incorrect source judgments) for semantically than nonsemantically studied items. This finding is consistent with the present proposal, but it remains to be established whether, as predicted by the proposal, recollection-related activity within the core network as a whole covaries with the amount of semantic processing accorded a recollected episode when it was first experienced.

Evolution and Transformation of Episodic and Semantic Memories over Time

Thus far, we have discussed episodic and semantic memories without reference to the possibility that their content and neural underpinnings might vary over time. However, there is a long-standing literature documenting that memory representations can be highly dynamic, shifting their dependence from the hippocampus and adjacent regions of the medial temporal lobe (MTL) to other neocortical regions, a phenomenon often referred to as ‘systems consolidation’ [64,65,91–93]. In recent years, systems consolidation has become increasingly intertwined with the construct of memory ‘semantization’ and schematization, processes by which semantic knowledge and schemas [83] emerge from episodic memory or assimilate aspects of it.

Early studies and theories of memory consolidation, beginning with Ribot and reiterated for almost a century, typically did not distinguish between episodic and semantic memory [65,94–96]. Among the first to realize the importance of the episodic–semantic distinction for theories of memory consolidation were Kinsbourne and Wood [97]. They proposed that traumatic amnesia affected only episodic memory, regardless of the age of the memory, and left semantic and schematic memory relatively preserved. Cases in which remote episodic memories appeared to be preserved were attributed to semantization or schematization through repeated re-encoding (see **remote memory**), allowing them to achieve the status of personal facts [98,99].

In an important development of the ‘standard’ model of consolidation, McClelland *et al.* proposed that the hippocampus maintains episodic representations of an event while communicating with (‘instructing’) the neocortical system to incorporate information about the event into its knowledge structure [100]. It was argued that, to protect the cortical network from catastrophic interference,

learning had to be slow, thus providing a principled explanation for the extended time period that systems consolidation was assumed to take. Of importance, the model proposes that, in the process of incorporating an episodic memory into a semantic network, the episodic component, initially dependent on the hippocampus, is lost. This represents an important point of divergence from the standard model, in which episodic information is retained in the neocortex along with semantic information (see later).

Incorporating the original idea of Kinsbourne and Wood [97] and the complementary learning perspective [100], 'multiple trace theory' (MTT) [101] proposed that the hippocampus supports episodic memories for as long as they exist. By contrast, the theory proposed that semantic memories depend upon the neocortex, which extracts statistical regularities across distinct episodes. Thus, hippocampal damage should have a profound effect on retention and retrieval of episodic memories of any vintage, while leaving semanticized and schematized memories relatively intact.

While receiving empirical support [64,102] (see also [65,103,104] for examples of convergent findings from studies of experimental animals), MTT has also been subjected to several critiques (e.g., [93,105–108]). However, the essence of the theory resonates with the recurring theme of the present review that episodic and semantic memory are intertwined, yet retain a measure of functional and neural distinctiveness. Since its inception, MTT has been extended [65,104,109] to propose that episodic memories can become transformed to more semantic or schematic versions with time and experience (see 'Episodic and Semantic Memory in Neurodegenerative Disorders' section); indeed, in some cases, both the original and the semanticized or schematic version of a memory coexist and engage in dynamic interaction with one another. According to this Trace Transformation Theory, the specific neocortical regions supporting transformed memories differ depending on the kind of information that is retained and retrieved. Correspondingly, for complex events, the transformed memories might depend either on event schemas, or on the **gist** of the event [110–113]. Increased activation of the vmPFC, believed to be implicated in processing schemas [83], and decreased hippocampal activation have both been reported as details are lost and memories become more gist-like and schematic [83,102,110,113], particularly for memories that are congruent with existing schemas [114,115]. Even when details of remote memories are retained, along with continuing hippocampal activation, there is increased vmPFC activation over time [116,117]. Which memory of an event (e.g., its semanticized or schematic version or the detailed episodic memory of the original event) predominates at retrieval will depend on a variety of factors, such as contextual factors and processing demands (see 'Semantic memory: Neural Underpinnings' and 'Episodic Memory: Neural Underpinnings' sections), in addition to the availability of one or the other type of information (see also [118]). Thus, retrieval of complex memories depends on the coordinated activation of different combinations of regions ('process-specific assemblies' [64,119,120]) belonging to neural networks underlying episodic and semantic memory.

The neuroimaging evidence reviewed to date strongly suggests that successful recollection necessitates the reinstatement not only of sensory-perceptual contextual information characteristic of the original experience, but also the semantic representations and conceptual processing that occurred during that experience. Rather than viewing episodic and semantic memory as dichotomous or mutually exclusive entities, the marked neural overlap between these forms of memory suggests that we must move towards considering the dynamic interplay of sensory-perceptual and conceptual elements during reinstatement of a recollected experience. One way in which we could test this proposal is to examine how progressive neural insult of key structures implicated in episodic and semantic memory impacts related putative functions, including event recollection and event construction. We next consider how studies of these processes in the dementias have provided important insights into the brain regions that not only are implicated in, but also essential for, successful recollection.

Episodic and Semantic Memory in Neurodegenerative Disorders

In recent years in particular, the study of neurodegenerative disorders has provided important insights into the neurocognitive architecture of the episodic and semantic memory systems, as well

as their respective interactions. Alzheimer's disease (AD), characterized by relatively selective MTL degeneration in its early stages, is often invoked as a lesion model for episodic memory, given the prominent deficits in episodic memory for visual and verbal information that are characteristic of this condition [121,122]. Early studies of autobiographical memory revealed negative temporal gradients in AD by which retrieval of recent, presumably episodic, memories was compromised compared with relatively preserved remote retrieval, assumed to reflect semanticized memory representations [123,124]. Notably, however, more fine-grained assessment of autobiographical memory that focuses on episodic (e.g., 'internal') content [125,126] has suggested the presence of deficits in episodic memory that extend across the lifespan in AD, manifesting as flat retrieval gradients. Moreover, examination of the 'external' content (commonly assumed to reflect semantic or nonepisodic details) of autobiographical narratives reveals a confection of perceptual and conceptual information that ranges in specificity from well-defined episodes to decontextualized semantics [127]. This amalgam of episodic and semantic representations enmeshed within the autobiographical narrative resonates with continuum-based accounts of personal semantics [128] and suggests that episodic-semantic interdependencies are critical for autobiographical retrieval, irrespective of the age of the memory [129].

The fuzziness of the boundaries between the episodic and semantic memory systems (see 'Episodic and Semantic Memory Retrieval: Overlapping Neural Correlates' section) is accentuated when considering converging evidence from SD, a younger-onset neurodegenerative disorder typified by an amodal loss of conceptual knowledge associated with progressive degeneration typically starting in the ATL and spreading to posterior temporal and prefrontal regions. Although predominantly a disorder of semantic processing, SD has illuminated our understanding of complex cognitive processes traditionally labelled as 'episodic'. Despite profound semantic impairments, these patients present with relatively spared episodic memory for recent experiences and intact visuospatial processing, at least during the early stages of the disease [130]. Studies of autobiographical memory in SD regularly document a step function whereby recent memories remain relatively intact in the context of impoverished remote recall [125,131]. This relative sparing of recent episodic memory in SD has been suggested to reflect intact perceptual and visuospatial processing, crucial for episodic memory likely mediated by relatively preserved posterior temporoparietal regions [122,132], at least during early stages of the disease. The retrieval of recent experiences tends to rely more heavily on sensory-perceptual representations in healthy individuals [133,134]. Therefore, it is not surprising that the recent event narratives of patients with SD tend to be more heavily weighted towards the provision of perceptually rich contextual details, in conjunction with whatever residual conceptual information remains available, some of which may be unrelated to the main event being described [127]. By contrast, the well-documented remote memory impairments in SD mesh well with the observation of a shift towards more semanticized accounts, even in healthy adults, thus taxing the semantic processing system disproportionately [135].

Episodic–Semantic Interactions during Event Construction

The harnessing of intact sensory-perceptual contextual details to support recent episodic retrieval is of particular interest when considered in the context of episodic construction. Current theoretical frameworks hold that the capacity to construct imagined future events, termed 'episodic future thinking' (Box 2), hinges upon the extraction of contextual details from episodic memory, which are recombined in a flexible manner to construct new and novel event representations [136]. While episodic representations remain available and accessible to patients with SD, these representations do not appear sufficient to support the construction of novel future events [137]. A consistent finding in the literature is of marked future thinking impairments in SD despite intact episodic memory for perceptual and sensory information [138,139], with most future events recapitulated from past experiences. These findings lend compelling support for the semantic scaffolding hypothesis [118,140], which views semantic representations as imparting the essential organizational framework to guide (re)construction of the past, simulation of the future, and the realization of spatially coherent scenes (Box 3). With the appropriate schematic framework in place, relevant sensory-perceptual details can be co-opted into the simulation to form a coherent mental representation. Note that

Box 2. Mental Time Travel

Relevant to the distinction between episodic and semantic memory is the unresolved question of temporality, or 'mental time travel' [9,11,153,154]. In his later formulations, Tulving placed increasing emphasis on the conjunction of self, agency, ownership, and subjective temporality in promoting a sense of self-knowing or auto-noetic consciousness [11,155]. By this view, a defining feature of episodic memory is a first-person subjectivity involving the experience of mentally reliving the original event [156]. By contrast, semantic memory was associated with noetic (knowing) consciousness, by which one would simply 'know' that events had transpired in the absence of a feeling of re-experiencing [156]. As noted elsewhere (see Box 1), such phenomenological distinctions were argued by Tulving as amenable to systematic empirical study via the 'Remember/Know' procedure. Subsequently, several related procedures have been developed that permit rememberers to classify different subjective experiences accompanying memory retrieval (e.g., [157–160]).

As noted earlier, Tulving accorded episodic memory a unique status in conferring the phenomenological sense of mentally reliving the past. By this view, merely retrieving the conjunction of 'what, where, and when' is not sufficient to qualify as an episodic memory, a proposal that elevated human episodic memory above that of the rudimentary 'episodic-like' retrieval displayed by corvids and other nonhuman animals ([161], but see [162]). Therefore, a critical question is whether the contemporary empirical focus on the products of episodic and semantic memory (i.e., their representational content) downplays the importance of phenomenally based distinctions between the two types of memory. Moreover, if auto-noetic experience is an inherent part of episodic retrieval, how do we reconcile this with current neurobiological models of memory that seemingly have no place for subjective experience? Some recent proposals dissociate memory traces from related subjective experiences (i.e., from auto-noesis [156] or from the capacity to travel mentally in time [163]), acknowledging that there may be no clear dividing line between episodic and semantic memory traces in the brain, and leaving open the question of the neural bases of auto-noesis and mental time travel (see Outstanding Questions in the main text). Several brain regions have been proposed to have a role in mental time travel, including prefrontal (e.g., [164]) and parietal cortex (e.g., [165]), and the hippocampus (e.g., [162]). In the case of the hippocampus, its involvement in mental time travel would be consistent with its stronger association with episodic than with semantic retrieval (see 'Episodic and Semantic Memory Retrieval: Overlapping Neural Correlates' section in the main text). However, evidence implicating the hippocampus in mental time travel remains inconclusive [166].

this proposal is similar to the one made above (see 'Episodic and Semantic Memory Retrieval: Overlapping Neural Correlates' section), that recollection of a prior episode entails the reinstatement not only of contextual information unique to the episode, but also of the conceptual processing that was engaged when the recollected event was experienced. Interestingly, however, examination of the 'nonepisodic' content of such simulations in SD suggests an inflation of 'external' (seemingly nonepisodic) details [141], a somewhat counterintuitive finding in a population characterized by stark semantic impairments (see Outstanding Questions). However, closer inspection of the narratives provided by SD patients reveals that a large proportion of these external details relate to temporally extended episodes, which in turn are negatively associated with semantic processing capacity [141]. As such, with progressive deterioration of the conceptual knowledge base, patients with SD shift towards a predominantly episodic narrative, most likely reflecting a compensatory strategy whereby content is salvaged from the least-compromised memory system. This pattern is also evident for the mental construction of static scenes with no temporal constraints (i.e., scene construction; Box 3), with patients with SD effectively repurposing previously experienced episodes in their entirety [142].

The asymmetrical impairments during future, relative to past, (re)construction in SD highlight the central role for conceptual representations in knowledge manipulation and generalization during the construction of new experiences. Rather than viewing complex constructive processing as the sole remit of episodic memory, contemporary theories of memory function must consider the intricate interdependencies between these representational systems. Irrespective of whether we remember the past or envisage the future, episodic and semantic elements are inextricably intertwined, with the relative weightings of these representations in the resultant construction hinging upon task demands and the integrity of the underlying memory system [118,143]. This proposal

Box 3. Declarative Memory and Spatial Cognition

The distinction between episodic and semantic memory has been applied to the domain of spatial cognition. In everyday situations, having a general conceptual outline of our spatial environment, as opposed to remembering specific instances of travelling somewhere, is often sufficient to navigate successfully from A to B. However, when visiting new places, taking a detour from a well-worn path, or attempting to remember a particular route one once took, a fine-grained representation more closely resembling contextually rich episodic retrieval is required [167]. The hippocampus is thought to be essential for representing spatial details at high resolution, providing the essential spatial context during episodic retrieval, but less so for the schematic or conceptual representation of space [109,168,169]. In line with this view, patients with hippocampal amnesia have been reported to show an impaired capacity to imagine coherent scenes in rich detail (such as lying on a beach on a sunny day [170]). While the descriptions produced by patients with amnesia contain the requisite semantic information, their overall constructions are spatially fragmented. Conversely, scene construction appears to be relatively well preserved in patients with SD, who, despite marked deterioration of the conceptual knowledge base, can nevertheless imagine and describe scenes in rich detail, at least during early stages of the disease [142]. This pattern of preservation may reflect the relative sparing of the right hippocampus (see also [171]) or integrity of posterior parietal brain structures, such as the retrosplenial cortex [172]. Thus, while the hippocampus has been ascribed a central role in constructing the requisite spatial context across past, future, and hypothetical scenarios [173–176], it may be important to consider the role of other structures and laterality effects in this context.

Although preferentially responsive to the retrieval of episodic memories, mounting evidence suggests significant involvement of the hippocampus in semantic processing tasks, particularly those containing spatial information ('furniture in a living room') (e.g., [55,177]). Furthermore, patients with amnesia and MTL damage display selective deficits on semantic fluency tasks involving spatial as opposed to nonspatial categories [54]. Together, these findings can be interpreted in light of the idea that the hippocampus provides a domain-general form of scene construction or 'spatial scaffolding'; for example, thinking about a conceptual category such as 'kitchen' often instantiates a related scene in the mind's eye. In a study that varied spatial content while comparing hippocampal activation during episodic and semantic memory tasks, researchers identified significant hippocampal activation for all instances of memory retrieval (episodic or semantic) in which a spatial context was evoked [178]. Moreover, spatial retrieval, irrespective of memory type, was associated with activation of posterior brain structures typically implicated in visuospatial processing. The authors interpreted their findings as evidence for the hippocampus supporting spatial, rather than relational, content during retrieval, and serving as a key interface between the episodic and semantic memory systems.

resonates with the prescient observations of Ingvar, who posited that semantic memory is 'mainly involved in the cognitive or future consequences and meaning of events' ([144], p. 129). Thus, semantic memory provides the necessary organizational framework from which detailed events can be constructed. As such, interactions between the episodic and semantic memory systems, both being declarative (i.e., conscious, but see Box 4) and subject to control processes, provides us with optimal flexibility to complete an array of complex computations. Just as an episode can be described in terms of its gist, or its specific sensory-perceptual details, so too can we focus on different aspects of a semantic concept and relate it to higher- or lower-order concepts (e.g., a dog can be viewed as a mammal or a specific breed). This confers an impressive flexibility enabling us to dynamically shift between different representations at varying levels of specificity according to task demands, contextual factors, and integrity of the underlying memory systems (see also [118]).

Concluding Remarks

When Endel Tulving first proposed that a distinction be drawn between semantic and episodic memory, he considered it to be a 'pre-theoretical position' that did not imply they were necessarily functionally distinct in any deep sense [1]. Over time, he came to view the two forms of memory as being both functionally and neurally dissociable [8–11], while never failing to emphasize that normal cognition depends on their intimate interaction. Here, we have reviewed diverse evidence that suggests that, although episodic and semantic memory represent the expression of different memory systems as Tulving proposed, the boundaries between them, whether anatomically or functionally defined, are not as distinct as Tulving's proposal may have led one to believe. Behavioral,

Box 4. Episodic and Semantic Memory: Both Implicit and Explicit?

Recently, data have accumulated that suggest that simple dichotomies, such as explicit/implicit or declarative/nondeclarative, may have to be revised, and that the presence or absence of conscious awareness may not always be the best way to categorize memory systems [179–182]. For instance, in the domain of episodic memory, it has become clear that episodic memories can implicitly influence performance on a variety of tasks (e.g., [183–185]). Indeed, Moscovitch and colleagues proposed that episodic retrieval has two stages. The first stage is fast and nonconscious and involves an interaction between a retrieval cue and a memory representation (or ‘ecphory’ [186]) that makes episodic information available to ongoing cognition, whereas a second, slower, stage is required for the retrieved information to be re-experienced [64,185,187]. The first stage involves the hippocampus, while the second depends on interactions between the hippocampus and prefrontal and parietal cortices.

Turning to semantic memory, although it is typically referred to as explicit/declarative, the notion that it can be expressed either implicitly or explicitly is not new [100,188,189]. For example, there is evidence that meaningful stimuli, such as words, automatically activate their meanings to bias a subsequent behavioral judgment even under presentation conditions that seemingly preclude their conscious identification (reviewed in [190]). Moreover, brain regions thought to have a role in semantic processing, such as temporal and inferior parietal cortex, appear to be sensitive to semantic priming manipulations regardless of whether the prime was processed implicitly or explicitly ([191–193], see also [194]). Thus, taken together, recent evidence suggests that episodic and semantic memory involve both implicit and explicit processes.

neuropsychological, and neuroimaging data converge to indicate that episodic and semantic memory are inextricably intertwined and that their neural correlates largely overlap. Yet, current evidence also suggests that the relative weightings of episodic and semantic representations of the same event vary with time and with task demands, and that the neural correlates of episodic and semantic memory maintain a degree of distinctiveness. It will be of considerable interest to see whether future research leads to a clearer delineation of these boundaries accompanied by a better understanding of how the systems interact, or to the further dissolution of these boundaries and their replacement with a different perspective on Remembering and Knowing.

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Outstanding Questions

Are there differences in the content or format of the elementary sensorimotor features that are reinstated in semantic versus episodic retrieval?

Given the apparent overlap in the ‘core’ networks associated with episodic and semantic memory retrieval, where should we look to identify the neural substrates of mental time travel?

Can the hippocampus (and related structures) and anterior temporal lobes be considered episodic and semantic hubs, respectively and is there a way to differentiate between their integrative functions? Does the anterior temporal lobe consistently demonstrate episodic retrieval effects with fMRI methods optimized to detect signal in this region?

Are emotions represented differently when expressed in semantic and episodic memories?

To what extent is the preserved performance of patients with SD in ‘episodic’ memory tests, such as recognition memory, supported by familiarity rather than recollection? How accurately do current autobiographical scoring practices (e.g., internal versus external details) map onto the neural substrates of episodic and semantic memory, respectively? How can we best code the information provided during autobiographical narratives to capture the interdependencies between episodic and semantic elements?

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