a0005 # Episodic Memory

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p0005 Of all human capabilities, the one central to our development of a unique sense of personal identity is episodic memory. The ability to form and retrieve memories of our life experiences provides an opportunity to identify those events as our own and embed the memories in a malleable framework of related experiences. This process in turn influences our interpretation, and therefore learning, of new experiences. Indeed, people who have lost the ability to access their past episodic memories have sometimes reported feeling a loss of self identity. Over the past 50 years, significant advances in the philosophical, theoretical, and empirical study of memory have begun to shed light on the nature of memory and the intricate cognitive and neural mechanisms involved in remembering past episodes.

s0005 ## What Is Episodic Memory?

p0010 Episodic memories are consciously perceived memories of personal events or episodes. One defining feature of episodic memories is that they are the personal memories. Among other types of information, they include where you were, what you were doing, who you were with, what you saw, how you felt, and what you were thinking during a particular event. A second defining feature is that episodic memories are accompanied by a conscious awareness of the temporal context in which the events occurred. In bringing to mind events from childhood, there is an awareness that the events occurred before the present time, and perhaps an awareness of precisely when they occurred.

p0015 Episodic memories represent one type of declarative memory – memories which are accessible to consciousness and which can be readily communicated or declared to others. Nondeclarative memories, such as learned skills, are memories that are not directly available to consciousness but nevertheless influence behavior. Semantic memories are memories of factual knowledge and represent a second type of declarative memory. Declarative memory is dependent upon the integrity of medial temporal lobe (MTL) structures including hippocampus, entorhinal and perirhinal cortex, and parahippocampal gyrus, and also on the fornix and anterior and mediodorsal nuclei in the thalamus. Significant damage to these structures produces amnesia and consequently an impaired ability to form and retrieve declarative memories. By some accounts, episodic and semantic memories arise from different memory, and by extension, brain systems. These accounts are supported in part by behavioral dissociations and in part by evidence that some patients are impaired on tests of episodic but not semantic memory while other patients are impaired on tests of semantic but not episodic memory. Further support for different memory systems has come from neuroimaging studies which demonstrate dissociations among brain regions associated with episodic and semantic memory tasks. By other accounts, episodic and semantic memories differ according to the presence or absence of personal spatial and temporal context, but are otherwise similar. When the initial context has been lost or is inaccessible, or the current situation does not encourage conscious recollection, the result is retrieval of semantic knowledge. By this account, the difference is due to the different processing demands of a given situation rather than differences in the underlying memory systems. These accounts are not necessarily mutually exclusive.

p0020 A distinction is often drawn between memories of personal events accompanied by subjective awareness, and memories of personal facts related to those events. For example, you may remember purchasing your first car, bringing back to mind where you found it, how it appeared, and how the seller talked. However, some of these remembered details can also be retrieved as facts. You know that you bought your car from an individual rather than a dealer. You know that it was blue. And you know that the seller was a man. Another distinction is sometimes made between episodic memories pertaining to a single event (recollections) and those pertaining to repeated similar episodes (generic personal memories). Autobiographical memory is often used synonymously with episodic memory. However, in some instances, the two terms are used to denote memories of life experiences and laboratory events, respectively.

Reconstructing Memories Using Retrieval Cues s0010

p0025 Prevailing frameworks of episodic memory describe remembering as a dynamic process during which an active model or simulation of an event is constructed from memory traces. A memory trace, also called an engram, is a neural change reflecting the thoughts, emotions, and sensory experiences of the original experience. The construction account of remembering rejects the proposition that memory traces are replayed like a song or a movie. Instead, memory cues are used to create a mental simulation of an event by drawing upon available memories and filling in the missing pieces with educated guesses. Ulric Neisser compares this process to that of assembling a dinosaur from mere bone chips. The reconstruction process begins with a retrieval cue, and subsequent retrieval is influenced by an individual's past experiences, his or her current state of mind, and the contextual demands in which remembering occurs. For example, accessing the same memory trace on two different occasions may produce qualitatively different recollections if the first occasion is immediately following a transcontinental flight and the second is after a full night of rest. The German biologist Richard Semon created the term ecphory to describe this synergistic interaction of the original memory trace and the current retrieval cue to form the episodic memory experience. Because of an inherent dependence on the retrieval cue, memories entering consciousness need not be veridical representations of the mnemonic content of a stored engram. By this view, only the products of the interpretive interaction of current intent and past experience are available to awareness.

p0030 The effectiveness of a retrieval cue depends in large part upon the degree of similarity between the cue and the original event. The more similar the relationship, the more likely it is that the retrieval cue will lead to ecphory. Therefore, the way in which events are interpreted at encoding influences how they can later be accessed and reconstructed. Endel Tulving refers to this relationship as the encoding specificity principle. Daniel Schacter provides a memorable example of this principle by describing an experiment carried out by the artist Sophie Calle at The Museum of Modern Art. In the experiment, museum staff were asked to recollect as much detail as they could about various paintings. The level of detail provided by the staff differed widely, from just a few words to detailed sentences. Calle found that the degree and quality of detail was related to the type of work carried out by the staff member. Staff in charge of art placement provided structural descriptions of the paintings, while those in charge of procuring the art provided more detailed accounts and interpretations of the artwork. The differing experiences of the museum staff influenced how they thought about the artwork, and this in turn influenced the types of memory they were later able to retrieve. According to the encoding specificity principle, the cues that will best evoke episodic memories of the paintings will be those that most closely match the initial processing.

Components of Remembering s0015

Episodic remembering is typically perceived as a unitary phenomenon. A memory comes to mind, sometimes easily and sometimes after some effort, but the details of the process are often unavailable to superficial introspection. There is an abundance of research demonstrating, however, that remembering depends on a variety of memory-specific and domain-general cognitive abilities, including among others, formation of search strategies, memory-based decision making, and postretrieval assessment. The most convincing evidence for separable components in human episodic memory has come from studies that produce a dissociation, either by identifying patients in whom lesions to different parts of the brain produce different types of memory deficit, or by identifying brain areas in which neural activity modulates according to variations in one component differently than the other components. p0035

Strategic Processing s0020

At times, memories of past events come to mind rather easily, seeming to pop into awareness after an encounter with a retrieval cue. At other times, a feeling of knowing can lead to a more strategic search through memory for the appropriate information. Strategic search involves generating retrieval cues from memory and using those cues to guide further searches. Models of strategic processing in remembering typically describe three basic stages, including initial identification of the desired information (target), a search for information and a matching process in which retrieved information is compared with the target, and an assessment or monitoring of the degree of accuracy. Neuropsychological studies of patients with lesions in the prefrontal cortex (PFC) have provided valuable insight into the role of frontal cortex in memory. Frontal patients are readily able to encode and retrieve memories. In fact, they tend to perform at levels approaching that of control subjects on simple item recognition tests that can be accomplished using nonrecollective memory (i.e., familiarity). However, patients with prefrontal damage perform significantly more poorly than control subjects on memory tests that require strategic processing, such as source memory tests of cued recall, free recall, and recognition. Source memory tests require the ability to identify the appropriate learning context, such as the time (was this item studied in the first or second study session?), place (was this item studied in the laboratory or in the classroom?), or feature (was this item presented in a male or female voice?). In these frontal patients, memory deficits are due not p0040 to problems forming memories (as in amnesia) but instead are related to impairments of organization of new memories, strategic access to memory contexts, and the supervisory control required to maintain information in working memory and assess retrieval effectiveness. As a result, frontal patients can experience difficulty under situations that require flexible processing, such those required by source memory tasks. This difficulty is sometimes observed in the form of confabulations – the generation of false and contradictory statements.

p0045 Results from neuroimaging studies are consistent with the neuropsychological findings. Because the need for strategic search typically increases as retrieval difficulty increases, retrieval difficulty can be manipulated in order to examine the neural substrates of strategic processing in memory. For example, difficulty can be manipulated by varying encoding strength so that weakly encoded items are more difficult to retrieve than strongly encoded items, or by varying the amount of detail required so that retrieving more detail is more difficult. These studies demonstrate that frontal lobe regions near the anterior extent of the left inferior frontal gyrus (aIFG), left anterior prefrontal cortex (aPFC), and bilateral posterior middle frontal gyrus (pMFG) consistently increase activity as retrieval difficulty increases. There is also evidence for functional specialization within this set of regions. Posterior MFG activity tends to also modulate according to the type of information retrieved, with a preference toward processing of verbal stimuli in the left hemisphere and nonverbal stimuli in the right. Other brain regions also appear to play an important role in strategic processing. Bilateral anterior insula/frontal operculum (AI/FO), the anterior cingulate gyrus
Au2 (ACC), and basal ganglia (bilateral caudate nucleus, putamen) also tend to increase activity as retrieval difficulty increases. While there has been relatively little attention given to the role of AI/FO and basal ganglia in these studies, the ACC has received quite a bit of attention. Current models suggest that ACC is involved in reward-based decisions, motor control, error detection, emotional self-control, problem solving, and/or conflict monitoring. The demand for all of these functions conceivably increases as retrieval difficulty increases, and therefore often it is a particular challenge to clearly identify the source of signal modulations.

s0025 Contents of Remembering

p0050 There is a host of evidence from neuropsychological, single-unit physiology, event-related potential (ERP), and neuroimaging studies supporting the view that regions of the nervous system that initially process an event (i.e., data-processing regions) are reactivated when the event is later remembered. For example, recalling your car's seller involves the coordinated recruitment of regions of the brain that initially processed the appearance of his face, the color of the car, the sound of his voice, and your thoughts about the situation. Work on human and nonhuman primates is particularly relevant to episodic remembering and mental imagery, but extends also to semantic knowledge. The findings indicate that memory traces are distributed in the nervous system as a function of the type of material encoded. For example, patients with focal lesions can exhibit impaired memory for visual objects, yet show preserved memory for spatial relationships. Neuroimaging experiments have shown that data-processing regions that are active during initial encoding of stimuli are, to some extent, reactivated during later remembering. It is yet to be determined how such a coordinated reactivation is organized and controlled, but prominent theories propose an interaction of frontoparietal attentional control processes and a medial temporal associational mechanism that provides an index of stored memory traces.

An unresolved issue concerning how memory contents are reconstructed is related to the degree to which p0055
data-processing centers are reactivated. In the visual system, for example, the most basic aspects of visual stimuli are processed in early stages, with complexity and receptive field size increasing as information is transmitted to later stages. Thus, while fundamental stimulus features such as line segments located in discrete parts of the visual field are processed in early stages of the visual processing hierarchy, more complex features that are less dependent upon location in the visual field, such as object form, are processed in later stages. Evidence that visual memories are reconstructed from the bottom up arises from studies that show involvement of early and late regions during visual retrieval. By this view, remembering the appearance of your car involves reconstructing the visual image from basic featural components up to the whole object. Other studies, however, indicate that visual memories are reconstructed by recruiting the levels most specialized to process the desired information. That is, remembering the general appearance of your car is accomplished by recruitment of higher-level object-processing regions, while remembering the color is accomplished by recruitment of color-processing regions.

Retrieval Success (Ecphory) s0030

Episodic memory retrieval is associated with a con- p0060
scious awareness of re-experiencing an event that

occurred in the past. As noted previously, it has been convincingly demonstrated that the MTL plays a critical role in retrieval success. Recent studies using ERP and neuroimaging techniques have identified a set of neo- and subcortical areas that also play a role in retrieval success. ERP studies of recognition memory were the first to note a distinct set of frontal and parietal signals related to the successful identification of previously studied items. This old/new, or retrieval-success effect, has been further studied in studies using ERP, positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). The ubiquitous finding across studies is that recognizing old versus new items modulates activity in left PFC, as well as lateral and medial posterior parietal cortex. In PET and fMRI studies, frontal activations have been identified in bilateral dorsolateral PFC, medial PFC, and frontal polar cortex. Parietal activations have been consistently found in the anterior intraparietal sulcus and lateral parietal cortex near the supramarginal gyrus. While the findings are significant because they guide future research, the functional role of each of these regions has not been elucidated by the old/new manipulation.

p0065 In dual-process accounts of memory, recognition can arise from the fundamentally different memory processes of recollection and familiarity. Recollection is the ability to retrieve episodic memories, whereas familiarity is a strength-based signal that information is old. Familiarity is not supported by recollective evidence. Source memory tests, and the remember/know test developed by Endel Tulving, have been used to successfully dissociate these processes and further characterize the role of retrieval-success regions. Importantly, activity in the hippocampus has been consistently tied to memory decisions based on recollection, but not to those based on familiarity/knowing in the absence of recollection. In contrast, a related region of MTL near the rhinal cortex has been associated more with familiarity-based decisions. The neuroimaging results are consistent with an extensive animal literature that supports a role of hippocampus in recollection, and perirhinal cortex in nonrecollective recognition decisions. However, as there is also evidence that patients with lesions restricted to hippocampus proper are impaired on recognition memory, it is not currently known precisely how different MTL structures contribute to memory.

p0070 Somewhat surprisingly, ERP and fMRI studies suggest that parietal regions involved in old/new decisions are differentially related to whether those decisions were based on recollection or familiarity/knowing. ERP studies tend to indicate that parietal signals are related to recollection rather than familiarity. This general finding is supported by fMRI such that lateral parietal cortex near the supramarginal gyrus has been shown to respond preferentially to decisions based on recollection. The supramarginal regions have also been reported in studies evaluating temporal judgments and temporal orienting of attention, suggesting that they could be involved in providing temporal context during remembering, allowing us to mentally travel through time. Functional MRI studies also suggest that slightly more medial parietal cortex, near the anterior intraparietal sulcus (particularly in the left hemisphere), is similarly responsive to decisions based on recollection and familiarity. Interestingly, the literature on patients with posterior parietal lesions offers no supporting evidence for parietal involvement in long-term memory processes. Instead, parietal lesions tend to disrupt visuospatial and visuomotor abilities. There is evidence, however, that lesions affecting the angular gyrus in the left hemisphere impair short-term memory. In addition, studies of epileptic patients indicate that seizures originating in posterior parietal cortex can be associated with déjà vu or a disturbance in consciousness. This observation is broadly consistent with neuroimaging experiments that have found posterior parietal activity related to temporal attention. Thus, posterior parietal cortex may play a role in establishing temporal context during remembering.

Retrieval Mode s0035

p0075 What would life be like if every stimulus evoked a memory of a past experience? As noted previously, ecphory occurs when there is an interaction between a retrieval cue and a stored memory trace. A retrieval cue can be any stimulus in the internal or external environment, including a word spoken by a companion, the sight of a flower, or a thought about an aching joint. Most stimuli we encounter, however, do not evoke episodic memories. In fact, because there would be little opportunity to adequately process and interpret relevant stimuli, it could be quite detrimental to basic survival if every stimulus cued an episodic memory.

p0080 At the same time, it is possible to allow stimuli to serve as cues to remember past events. One could freely associate by allowing each thought entering awareness serve as a cue to remember a past experience. Or one could look at items in the room and think about how they were obtained. In both cases, the thoughts and objects do not typically evoke episodic memories. However, this simple suggestion could have suddenly turned an object on your desk into a cue that sparked a memory about where you purchased it. The all-or-none state in which stimulus cues serve to evoke memories is known as retrieval mode.

p0085 Studies using neuroimaging, ERPs, and neuropsychological techniques suggest that the most anterior portions of the PFC are important for engaging in retrieval mode. A large number of neuroimaging studies using PET have consistently found right aPFC activity during episodic memory tests. aPFC was not found to modulate depending upon whether retrieval is successful or unsuccessful, indicating that it is not important for retrieving individual items from memory. Recent studies using fMRI and ERP add some insight into the role of aPFC by showing that right aPFC is active in a sustained manner, throughout the testing session and independently of the transient trial responses. aPFC could therefore be important for maintaining task-level rather than trial-level processes, playing a role in maintaining retrieval mode.

s0040 Associative Nature of Memory

p0090 Some theories of episodic memory consider the connections between the facts of the memory and the context in which they were encoded (i.e., time, place, emotional state), as well as the connections between items presented simultaneously. Since we are constantly presented with many items at once, it may not be the case that each memory trace is completely separate from the others; it is possible that each memory item can be related to many other items for organizational and efficiency reasons. Imagine if each chapter in this encyclopedia had to describe each piece of the brain it references and how certain processes work. This would add length and complexity to every chapter. Instead, the use of linking each chapter to related items allows each chapter to describe a specific piece while the reader can reference related pieces as necessary to form a whole. In this way, each related memory item can potentially serve as a recollective cue for the others in the organized group. While this can be true for the network of declarative facts alone, it can also connect declarative facts to the contextual items that allow for episodic memory. For instance, in the first car example given above, perhaps you remember that the salesperson was nervous because he had a very clammy handshake. This would be an example of the connection between a declarative fact (the seller was nervous) and a contextual fact (your disgust at his handshake) to form an episodic memory.

p0095 Several computational models attempt to use an associative system to represent the process of memory. One example is Lynne Reder's source activation confusion (SAC) model of memory, which suggests that people create different nodes of information at the time of encoding. One type of node contains the basic semantic knowledge of the item, while another type contains the contextual elements of the encoding episode. A memory within the SAC model can have many nodes and associations between these nodes, as well as common nodes that are associated with many memories (e.g., all the words studied during in an experiment might be connected to a context node encompassing the experiment room, computer, lighting, etc). A person experiences an episodic recollection when not only the item node is reinstated during recall, but also nodes containing information about the context. It is the activation of the association between the item and context nodes that makes the difference between remembering an event episodically versus simply a feeling of familiarity. It has also been suggested that a lack of association, or binding, of elements into memory can cause a lack of episodic experience at a later time. Other models that focus on the interconnected nature of memory include the search of associative memory (SAM) model and versions based on parallel distributed processing (PDP).

p0100 Neuroimaging studies have sought to investigate the neural mechanisms behind the creation of associations among items to be remembered. These studies involve presentation of multiple stimuli at one time and participants either study the items singly or as a group. The hypothesis is that studying each item singly does not prompt the creation of associations with the other items, while studying the items as a group does. These studies have shown that the hippocampus and parahippocampal gyrus (particularly on the right) is more active during associative encoding than single item encoding. Other neuroimaging studies have focused on the encoding and retrieval of contextual information about the remembered items. A variety of paradigms can be used to test recollection of contextual information, and often include a question at test regarding the temporal order of items, list membership, or color/font/spatial location at study. These studies have also found activation in the hippocampus and parahippocampal gyrus. Other areas of interest include bilateral dorsolateral PFC and parts of parietal cortex, which may be involved in the more specific contextual memories of spatial locations.

See also: Functional amnesia (00764); Animal Models (00483); Computational models (00768); Systems (00770); Cerebral cortex (00771); Amnesia: Declarative and Nondeclarative Memory (00548); Anatomy (00755); Functional imaging of memory (00765); Semantic Memory (00786).

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Abstract:

Episodic memories are consciously recollected memories related to personally experienced events. Episodic remembering is a dynamic process that draws upon mnemonic and nonmnemonic cognitive abilities in order to mentally reconstruct past experiences from retrieval cues. The neural substrates of these abilities represent a distributed set of functionally specific nervous system structures that operate in concert. The profound anterograde amnesia observed in patient HM demonstrated that the medial temporal lobes are critically involved in the formation of episodic memories, while more recent research highlights the role of other brain regions, including prefrontal and parietal cortex, in episodic memory.

Keywords: Associative; Declarative; Engram; Episodic; Memory; Recollection; Remember

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