Provided for non-commercial research and educational use only. Not for reproduction, distribution or commercial use.

This article was originally published in *Encyclopedia of Behavioral Neuroscience*, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, distribution to specific colleagues, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

http://www.elsevier.com/locate/permissionusematerial

Dobbins I G and Raposo A (2010) Episodic and Autobiographical Memory: Psychological and Neural Aspects. In: Koob G.F., Le Moal M. and Thompson R.F. (eds.) *Encyclopedia of Behavioral Neuroscience*, volume 1, pp. 493–501 Oxford: Academic Press.

© 2010 Elsevier Ltd.. All rights reserved.

Author's personal copy

Episodic and Autobiographical Memory: Psychological and Neural Aspects

I G Dobbins, Washington University in St. Louis, St. Louis, MO, USA

A Raposo, University of Lisbon, Lisboa, Portugal

© 2010 Elsevier Ltd. All rights reserved.

Glossary

Phenomenology – It is the subjective mental experiences of observers during cognition or perception. These experiences are assumed reportable, although the nature of the experiences may be influenced by the requirement to report them, and the veracity and reliability of reporting is often of concern.
Semantic knowledge – It is the long-term knowledge about the properties of objects and canonical features of events. This form of memory is typically spared by damage to medial temporal lobe and midline diencephalic brain regions that support the memory for specific events and experiences.

Conceptualizations of Episodic and Autobiographical Memory

The ability to recover information about unique prior experiences in order to guide current choices is a cornerstone of human adaptive behavior. When memories are temporally remote, personally significant, and encompass extended events (e.g., one's high school graduation), this skill is referred to as autobiographical memory. In contrast, when the remembered events are highly controlled laboratory experiences with verifiable characteristics (e.g., retrieval of newly learned word associations), the skill is typically referred to as episodic memory. The distinction between autobiographical and episodic memory is largely quantitative and not qualitative. In general, autobiographical memories contain considerably more emotional content and visual imagery than episodic remembrances, although it is sometimes unclear the degree to which autobiographical reports rest, not on specific remembrances, but on the observer's knowledge of the typical characteristics of the targeted experiences. For example, when asked to describe one's high school graduation, one can rely on the features common to all high school graduations when attempting to report the event. To control for this, autobiographical designs typically score reports for their specificity and degree of idiosyncratic content, in hopes of attributing the report to a genuine remembrance. This reconstruction problem is typically less of a concern for episodic memory designs, which often test for the remembrance of arbitrary associations or contextual associations, for example, the ability to remember that the word 'cabbage' was previously part of an animacy rating task as opposed to a subjective pleasantness rating task (**Figure 1**). This type of mini-event is not associated with a routine experience and therefore observers are limited in their ability to reconstruct the event from semantic knowledge stores. Regardless of these differences, episodic and autobiographical memory are generally considered highly overlapping memory capacities, and the term episodic memory will be taken here to refer collectively to both.

Contrasts with Other Forms of Memory

The distinction between episodic memory and other kinds of memory has been conceptualized along many dimensions, such as phenomenology, content, persistence, behavioral control, and, most recently, neural substrate. Phenomenology was perhaps the earliest characteristic used to parse putative types of memory, dating back to the Ancient Greeks, and it contributes to modern conceptualizations as well. For example, one fundamental modern distinction is between declarative memory (making declarations about the past, or 'knowing that') and procedural memory (carrying out actions based on past learning, or 'knowing how'). The latter encompasses a broad range of skills and abilities that rely upon processes observers are often unable to describe or characterize, such as motor skills like riding a bike and tying one's shoes. In contrast, knowledge that is accessible to conscious awareness falls under the category of declarative memory. Within declarative memory, an important distinction arises between episodic and semantic memory. One's general knowledge of the world, such as knowing that lions have manes or that breakfast occurs in the morning, constitutes one's semantic memory. In contrast, it is also possible to report the details of a particular episode in which say a lion was viewed, or a specific breakfast was consumed. Critically, accessing semantic memory does not require retrieval of the original time or place of learning, as opposed to episodic retrieval. As a particular type of episode recurs across the lifespan, it is

494 Episodic and Autobiographical Memory: Psychological and Neural Aspects

(a)

(b)

Study phase - Please remember items for future memory test



Test phase - Indicate whether item was shown on prior list



(c)



Study phase - Perform indicated task



Test phase - Indicate whether item was shown on prior list



Test phase - Retrieve a personal memory for each item



Figure 1 Examples of experimental episodic- and autobiographical-memory tasks. (a) Item recognition. Participants are asked to remember presented words for an unspecified number of memory tasks. During testing they are prompted with studied or novel items and asked to indicate whether items originated from the study list. (b) Context/source task. Participants encounter words during two different encoding tasks. During testing they are required to identify items from the study phase and further to distinguish between items originating from each context task. (c) Autobiographical Crovitz-Galton word-cueing task. Participants are asked to generate memories from their own life in response to word cues.

generally assumed that its canonical features are incorporated into the semantic knowledge store.

Episodic and semantic memory reflect examples of long-term memory, since retention lasts more than several seconds and survives intervening experiences. In contrast, the concept of working memory describes a collection of temporary memory processes in which information is maintained and manipulated in an active or labile state for a short period of time. It is an essential part of current conscious awareness, with important connections to attention and mental ability. Workingmemory tasks usually require one to maintain and transform information, keep track of changes, divide attention, and make comparative judgments. Originally thought to function independently of episodic representations, recent conceptualizations of working memory have introduced an episodic buffer which enables the integration of information from perceptual and linguistic operations and long-term memory. The component is episodic because it is assumed to bind different features of an event into a unitary episodic representation; however, it differs from episodic memory in that the episodic buffer is a temporary store.

As is clear from the above, the clarity of the theoretical boundaries between episodic memory and other kinds of memory vary. In most instances, experimental tests of memory cannot be assumed to be 'process pure' in that they likely recruit several partially or fully independent memory processes. Nonetheless, through behavioral experimental dissociations, animal lesion studies, the examination of special populations, and, most recently, functional imaging of the brain, psychologists and neuroscientists have amassed evidence for an episodic memory system that is at least partially dissociable from other forms of memory.

Neuroanatomical Frameworks of Episodic Memory

The Amnesic Syndrome

The strongest evidence for a unique episodic memory capacity arose from neuropsychological research examining the patterns of spared versus disrupted memory capacities following neurological insult. In the late 1950s, seminal case-study research examining a 27-year-old patient undergoing experimental surgical treatment for intractable epilepsy demonstrated that bilateral damage to the hippocampus and surrounding cortical structures resulted in a global amnesic syndrome characterized by severely impaired memory for events occurring up to 3 years before the surgery (retrograde amnesia) and a virtually complete inability to remember new experiences following the surgery (anterograde amnesia) (Figure 2). The severity of the syndrome is easy to underestimate and such patients often demonstrate complete forgetting of to-be-remembered material when distracted for mere seconds with a secondary task. Despite this profound memory impairment for episodes, other intellectual domains appear spared and this has been used as a defining characteristic of the amnesic syndrome, namely, an abnormally low standardized memory score in relation to a preserved estimate of general intelligence. Subsequent animal research and lesions of opportunity in human subjects have also implicated other medial brain structures outside of the medial temporal lobes (MTLs) as critical, including the thalamus, mamillary bodies, fornix, basal forebrain, and retrosplenial areas. Damage to any of these regions can result in a profound global amnesia with preserved intellectual functioning in other domains, such as reasoning, the expression of general semantic knowledge about the world, and the learning of new motor skills.

Perception and Short-Term Visual Memory

Although global amnesia is defined as gross episodic memory impairment in concert with preserved intellectual functioning in other domains, closer examination of patients with damage to MTL regions suggests that not all nonepisodic functions may be fully preserved. Both animal and human neuropsychological studies indicate that the ability to discriminate perceptually similar visual exemplars over short periods may be compromised by damage to MTL regions. During these paradigms, subjects are typically shown a visual sample, required to wait for a brief unfilled delay (e.g., 4-8s), and then asked to identify the target probe among visually similar lures. Such tasks were thought to fall fully within the realm of working-memory maintenance, that is, the form of memory supporting the maintenance of items in the mind during brief unfilled delays, such as when one holds a phone number in mind before dialing. Previous extensive work with amnesic patients suggested that visual and verbal short-term working memory was spared; however, these designs typically did not use highly visually confusable stimuli. Nonetheless, damage to the MTLs does yield impairment on such tasks, although the cause of the impairment remains controversial. From one viewpoint the compromised short-term working memory suggests a link between working memory and the MTL regions. In contrast, the deficit may reflect the fact that control subjects may occasionally rely upon episodic memory to overcome occasional lapses or disruptions of working-



Figure 2 Schematic rendering of regions of the medial temporal lobes (MTLs) critical for episodic memory. Green regions approximate the hippocampus. Red regions encompass the parahippocampal gyrus, the anterior extent of which is often referred to as perirhinal cortex. Blue regions illustrate the entorhinal area. The filled yellow area on the three cardinal views indicates the range from which the partially overlaid slices originated.

memory maintenance. This latter account fits with the observation that even brief attentional distraction in global amnesic subjects is sufficient to cause complete forgetting, which in turn suggests that hippocampally supported retrieval processes are important for bridging even brief delays when attention has been captured or otherwise diverted.

Transitive Inference and Flexible Reasoning

Episodic memory is a vital contributor to flexible, adaptive behavior. For example, determining the correct course of action can be facilitated by remembering that alternative courses of action previously led to undesirable outcomes in similar situations. Here episodic memory does not directly inform the most adaptive behavioral choice, but it can be used to inform reasoning about the relative merit of options. The simplest tests capturing this type of flexibility are known as transitive inference problems. During such problems, observers are selectively reinforced for responses to pairs of stimuli. For example, the bolded items in the following set would lead to reinforcement when selected (A–B; B–C; C–D; D–E). Critically, the redundancy of the pairs means that the reinforcement status of B, C, and D items is entirely contextually dependent; thus, the acquisition of the appropriate response requires configural-level knowledge. Furthermore, these designs allow testing with critical probes (e.g., B–D) that have never been reinforced, but which should lead to a preference (B) if a hierarchical episodic representation has been encoded (A > B > C > D)or if observers can inductively construct such a representation given the individual learning of the pairs. Animal, neuropsychological, and functional imaging research implicates the hippocampus as important during both the acquisition and critical probe periods of transitive inference problems. However, despite this convergence of evidence, the level of conscious awareness required to solve such problems remains in dispute. Although episodic memory is often considered to pertain to conscious recollection of prior events (or reasoning based on conscious recollection), and is known to require the hippocampus, this does not logically require that all hippocampal-dependent tasks be accompanied by conscious recollection. This argument is bolstered by findings in repeated visual search and visualinspection paradigms, where hippocampally dependent improvements in detecting target stimuli enmeshed in visual arrays may occur outside of observer awareness that the arrays have been repeated.

Developmental Trends and Dependencies

At both ends of the developmental spectrum, episodic memory is less efficient when compared with that of young adults. In the case of early development, the study of episodic memory has been challenging since instruction and verbal report measures are inappropriate. However, mimicry paradigms that can be accomplished by pre-verbal children suggest that episodic remembering occurs in children as early as 2 years of age. Although such research has demonstrated that episodic-memory functioning occurs earlier than once thought, it nonetheless remains the case that a major portion of early childhood experience, up until approximately age 3 or 4 years is later either wholly inaccessible to most adults, or when available is quite fragmentary and impoverished. This phenomenon, termed infantile or childhood amnesia, suggests that the co-development of semantic knowledge and other representational systems may be critical for adult levels of episodic memory capabilities. Although widely debated, one current hypothesis is that prior to age 3 or 4 years, children often do not actively construct larger more distinctive representations of ongoing experiences and for the same reason also do not adopt reconstructive strategies during attempted retrieval. The ability to precisely encode the relationships between event elements and to situate events into larger experiences likely relies upon the prefrontal cortex (PFC) function and is conceptually linked to the idea of an episodic buffer within working memory. This hypothesis receives further support from functional brain imaging research demonstrating PFC recruitment during both initial encoding and later retrieval in the kinds of memory tasks with which young children experience the most difficulty. For example, although children below the age of four are rapidly acquiring large amounts of semantic information, behavioral experiments demonstrate they are impaired in the ability to later remember where and under what circumstances this information was acquired, a phenomenon known as source amnesia. The demonstration, using functional imaging, that PFC regions are heavily involved in source memory tasks (Figure 3), and the known late developmental maturation of PFC cortex in humans, jointly suggest that in this region may underlie the emerging ability to distinctively encode and selectively recover extended events and experiences in childhood.

At the other end of the developmental continuum, impairments in episodic remembering are also prominent. Indeed, even during healthy aging, lapses in episodic memory are one of the most prominent complaints of older adults. As with early childhood, a portion of the impairment likely reflects impairments in organization or processing of information during the encoding of experiences. For example, although older adults experience relative decline in memory performance for even basic item-recognition tasks compared to young adult controls, a large portion of this decline is eliminated when participants are provided explicit strategies that encourage reflecting upon the semantic and unique characteristics of each stimulus during initial study. This has led to one



Figure 3 An example of the network implicated in context/source–memory retrieval relative to simple item recognition. Source–memory retrieval increasingly activates left lateral parietal (A), dorsolateral PFC (B), and ventrolateral PFC (C and D) regions along with midline areas.

major theoretical account of age-related memory decline that stresses the role of self-initiated distinctive processing in creating durable episodic memories. Although the root cause for the failure of older adults to spontaneously process materials and events in a distinctive manner remains debated, as with the relative episodic impairment in children, it has been linked to PFC. Consistent with a common PFC locus, older adults, as with children, demonstrate considerable difficulty in source-memory paradigms that require recovery of the contextual specifics of prior encounters and experiences. Despite the evidence for a gross role of PFC in the memory impairments observed at both ends of the developmental spectrum, the precise neurological causes for the failure to recruit PFC, while unknown, presumably arise from different root causes.

Functional Magnetic Resonance Imaging Data

Subsequent Memory and Episodic Encoding

Forming a new memory depends upon the neural mechanisms set in motion at the moment the event is experienced. An influential approach to the study of memory formation or encoding is the subsequent memory paradigm. Neural activity is recorded while participants study a sequence of items, after which memory for the items is tested. The neural responses elicited during prior study are retrospectively coded according to whether the items were later remembered or forgotten, with differences between cortical responses for later remembered versus forgotten items taken as correlates of successful memory encoding. Data from electrophysiological event-related potentials (ERPs) and functional magnetic resonance imaging (fMRI) suggest that the neural mechanisms that mediate encoding depend upon several factors including the nature of the stimulus, the goals or tasks during encoding, and individual differences in the tendency to adopt particular processing strategies. For example, successful word encoding is associated with activation in the left ventrolateral PFC, MTL, and fusiform gyrus. In contrast, successful encoding of complex visual scenes has been associated with right inferior PFC and bilateral MTL. Aside from these simple stimulus differences, the specific PFC-MTL circuits that covary with successful encoding depend on the particular task and the subject's goals during learning. Subsequent memory designs in which the semantic features of study materials are processed have implicated bilateral PFC and left MTL regions, but when the same items are studied in a perceptual manner, only a subset of these regions is activated and predictive of later memory. Differences in the degree to which these regions are spontaneously activated also vary considerably across subjects and populations. For example, when the encoding tasks are largely unconstrained and participants are simply instructed to memorize meaningful materials, there are considerable individual differences later reported in terms of adopted strategies, with some participants reporting perceptual or imagery strategies, and others reporting adopting complex semantic judgments and construction of sentences or stories, for example. Critically, these differences are reflected in the pattern of activity seen during encoding and in the later level of success during memory judgments; the left ventrolateral PFC, in particular, appears associated with adopting semantic analysis strategies during encoding. The degree to which these strategies facilitate later memory is dependent upon the form of the later memory task, and tasks that require the recovery of context associations, as opposed to the simple identification of familiar stimuli, appear to benefit considerably from recruitment of PFC during encoding.

Aside from individual differences in encoding strategy, recruitment of left ventrolateral PFC during encoding also varies across age cohorts with elderly participants often demonstrating reduced recruitment compared to vounger controls. Requiring all subjects to render semantic level judgments for each to-be-encoded item, in part, eliminates these age-based differences. Thus, when considering both differences across individuals and across age populations, it appears to be critical to consider the degree to which the encoding environment controls the approach to the task, since this will necessarily constrain the types of information later available for retrieval. Nonetheless, recruitment of left ventrolateral PFC and MTL regions during the initial encoding of meaningful events is associated with increased episodic memory for those experiences during later retrieval.

Retrieval Success

Along with a role in memory formation, MTL structures are associated with successful retrieval. Neuroimaging research suggests that distinct subregions of the MTL support dissociable retrieval processes with the hippocampus proper involved in the contextual recollection of past event features and extra-hippocampal regions supporting judgments based on item familiarity. Hippocampal activation is consistently reported during successful source-memory judgments, when subjects correctly retrieve the prior context of a previously encountered item, relative to correctly identifying new unstudied items or correctly identifying items as studied but failing to retrieve context information. In contrast, the surrounding perirhinal and parahippocampal cortices of the MTL region appear to show a different pattern, with the former hypothesized to support familiarity-based recognition for individual objects, independent of whether contextual retrieval is possible or required. This characterization is largely based on reports demonstrating that although the region displays increased fMRI activation for correctly identified and studied materials relative to novel materials, the level of activation for studied materials does not further differ as a function of contextual retrieval outcomes. Anatomical projection

studies in animals complement these findings by demonstrating that the perirhinal cortex receives considerable information about the properties of items to be remembered whereas the parahippocampal gyrus receives inputs about the spatial context in which the items are encountered. This coarse 'what' versus 'where' distinction is itself undergoing refinement in the literature; however, it nonetheless suggests that different regions of the extrahippocampal portions of the MTL process different information about events. These two regions then converge in the hippocampus, potentially supporting the ability to situate objects into larger episodes at retrieval. Human neuropsychological investigations further support this two-retrieval-process interpretation with reports linking damage of the hippocampus proper to marked declines in the behavioral estimates of contextual recollection with relatively preserved scores of item-familiarity discrimination. Despite the convergent evidence suggesting separable familiarity and recollection-retrieval processes in the MTLs, the utility of this dichotomous characterization of the MTL processes has been questioned and this remains a highly active area of investigation.

Although research continues to focus on the role of MTL in successful retrieval, an emerging body of literature has also begun to focus on the putative role of left lateral parietal cortex during successful episodic retrieval (Figures 3(A) and 4(B)). The earliest findings suggesting a role for this region were based on ERP research, and subsequent fMRI studies have documented increased left lateral parietal responses when subjects correctly detect previously encountered items compared to the correct identification of new items. Furthermore, the inferior extent of this lateral parietal activation often extends into the region of the angular gyrus, and demonstrates activation properties consistent with a role specifically in contextual recollection. For example, the activation tracks phenomenological reports of recollection, is present for the autobiographical recall of distant prior events, distinguishes successful from unsuccessful sourcememory judgments, and tracks the amount of episodic detail that can be reported about a prior event. Nonetheless, the hypothesis that left lateral parietal cortex supports a core element of recollection faces opposition. This opposition primarily arises from the fact that damage to the left lateral parietal region is not linked with a global amnesic syndrome in the neuropsychological literature. This conspicuous absence may reflect the fact that the contralateral region is capable of assuming a mnemonic role following damage to the left hemisphere, and the possibility that language and comprehension dysfunction due to damage in proximal regions may mask a more subtle memory impairment in patients. Nonetheless, the historic failure to observe striking deficits such as those that occur following insult to the MTL and midline diencephalic regions, continues to

challenge the idea that lateral parietal cortex plays a direct or critical role in recollection.

Retrieval Strategies and Decision Operations

The products of an episodic retrieval attempt are usually not immediately available. For example, in autobiographical-memory tasks, participants often take 6-8s to recover the first piece of relevant memory content. The dependence of these types of memories on volitional and sustained retrieval attempts, and the frequent correlation between tests of episodic retrieval and general intelligence, suggest that successful episodic retrieval often depends upon effective memory search and evaluation processes. Recent functional imaging research supports this assumption, demonstrating considerable PFC activation for memory judgments that require recollection of contextual information. Critically, this activation is robust even when participants ultimately fail at the task, which further suggests that PFC supports retrieval search and evaluation processes that are recruited even when sufficient memory evidence ultimately fails to be recovered. Currently, it is assumed that distinct ventrolateral (Figures 3(C) and 3(D)), dorsolateral (Figure 3(B), and rostrolateral (Figure 4(A) regions of the PFC contribute to different search or evaluative processes, although there is considerable variety in the functional characterizations ascribed to these regions. Furthermore, because these regions are also active during a host of tasks other than episodic retrieval, any successful functional characterization must accommodate a large range of decision-making and reasoning tasks. To this end, current characterizations of the role of left ventrolateral PFC during retrieval are perhaps the most successful. Recruitment of this region during context relative to item memory judgments has been interpreted as reflecting controlled semantic operations that facilitate the recollection of contextual information by foregrounding or selecting the semantic features of retrieval probes that are potentially central to an episodic representation of the event. Consistent with



Figure 4 An example of regions implicated in simple item recognition for the contrast of correct responses to studied items (hits) vs. correct responses to new items (correct rejections). Left rostrolateral PFC (A) is frequently implicated in this contrast.

well-documented cognitive models, this is thought to improve the match between active search cues and the original event, increasing the likelihood of recollection when appropriate. Buttressing this view, activation in this region has been reported in tasks in which subjects must retrieve contextual memories about prior object encounters that are linked to the semantic properties of the memory probes (e.g., remembering having made a pleasant/unpleasant or a living/nonliving judgment at encoding for each test probe - Figure 1(b). In contrast, when the to-be-remembered information is perceptual in nature (e.g., whether the object had appeared in a large or small size during prior encoding), the left ventrolateral region is not recruited, presumably reflecting the reduced relevance of the semantic or conceptual features of the memory probes during memory search. Thus activation in the left ventrolateral region potentially signifies a proactive strategy enabling the maintenance of semantic information that serves as a cue to retrieval during memory search. This characterization fits well with research directly examining semantic processing, and with research on self-initiated semantic encoding strategies, with both research domains implicating the same left ventrolateral PFC region.

In contrast to the selection or foregrounding of semantic information during memory search, dorsolateral PFC activation during retrieval instead appears to reflect the monitoring or evaluation of the products of retrieval with respect to decision standards. Thus the region is thought to underlie the ability to evaluate the products of memory retrieval with respect to their task relevance. Direct comparisons between inclusion tasks (wherein subjects must respond 'yes' to studied words regardless of their specific prior context) and exclusion tasks (in which subjects are asked to respond 'yes' only to words that are familiar and from a specific source) reveal increased dorsolateral PFC activity, during the latter. Similarly, memory tasks that require a greater number of intermediate judgments about recovered episodic information elicit greater activation than simpler tasks with matched materials requiring fewer intermediate memory judgments. Thus, activation in dorsolateral PFC appears to index either the number of judgments rendered during retrieval attempt or the complexity of the decision standard adopted by the participants when evaluating memories. From either perspective, extended retrieval tasks that require successful recovery of convergent aspects of a prior event are predicted to be the most compromised following damage to dorsolateral PFC.

The least-understood PFC region that is routinely activated during episodic retrieval tasks is rostrolateral PFC. Neuropsychologically, the most prominent behavioral impairment following damage to rostrolateral PFC is one of flexible planning and multitasking, not memory retrieval. Despite this, the region is frequently implicated in the functional imaging of simple item-recognition memory, demonstrating greater activation for correctly recognized old items versus correctly rejected new items, typically lateralized to the left hemisphere (Figure 4(A)). However, this differential activation is sensitive to subjects' beliefs regarding the relative frequency of old and new items in the test list, with the differential response amplified when subjects believe old items to be relatively infrequent, even if objective frequency remains constant. Furthermore, the region has been shown to demonstrate complex temporal profiles of activation during retrieval. For example, in the right rostrolateral PFC there is an increase in tonic or sustained activation across recognition trials under conditions of low discriminability during item recognition, whereas the region demonstrates an increased trial-based anticipatory response when subjects are forewarned of an upcoming context-memory demand compared to when they are forewarned of an upcoming simple recognition demand. Given the temporal complexity of the responses, combined with the dependence upon subjects' beliefs about the list structure, a consensus of the region's contribution to retrieval will likely require considerable future research. As with ventrolateral and dorsolateral PFC regions, a major challenge will be to ensure that retrieval characterizations accommodate the role of the region in nonepisodic tasks as well. For example, fMRI studies of analogical and complex reasoning also frequently implicate rostrolateral PFC. At present, the only firm conclusion that can be drawn with respect to episodic memory is that activation in the region represents a complex combination of global beliefs regarding the structure or properties of the test list and the recovery of episodic information for individual items within the list.

Event Reconstruction and Forecasting

Cognitive and computational models of episodic memory have long assumed that efficient retrieval requires reconstructive processing, in which observers fill in aspects of a to-be-remembered event with semantic knowledge of its most likely components. For example, when attempting to retrieve a memory about a given breakfast, observers will often fill in details based on their semantic knowledge of the typical components of the meal, in addition to refining these components if additional constraints are also available. For example, if one is trying to remember a particular breakfast that occurred when one was in a hurry, then candidate meal items and event characteristics can be further constrained. This reconstructive process not only serves as a best guess of the likely event elements should retrieval ultimately fail, but a large body of cognitive behavioral research demonstrates that it also facilitates actual recovery of episodic information by improving the overlap between the retrieval cues actively held in working memory, and the actual event. Based on this framework, pioneering memory researchers speculated that anticipating the future should recruit many of the same mechanisms engaged when reconstructing the past. In short, thinking about the likely constituents of a prior event should recruit much of the same processing as trying to predict the characteristics of an event that has not yet occurred.

Recent functional imaging work has supported this hypothesis by directly comparing the networks activated during autobiographical retrieval tasks to those in which subjects are instructed to imagine specific future scenarios (e.g., imagine yourself in a future beach holiday). The networks activated by these two tasks are virtually identical with both the tasks implicating left dorsal PFC, medial prefrontal and anterior cingulate areas, posterior cingulate and restrosplenial areas, and parahippocampal gyrus. Critically, this network is engaged above and beyond conditions that attempt to control for simple visual imagery. At present there are multiple ways of interpreting the high degree of similarity between the network activated during future simulation or forecasting, and that typically observed during autobiographical memory retrieval. Much of this overlap could be due to the voluntary or involuntary retrieval of episodic content when attempting to construct a future scenario. Although subjects are encouraged to create entirely new episodes this need not mean that every element is new, since the task merely requires the configuration of elements to be novel. Thus the overlap could largely result from the fact the both tasks encourage retrieval of episodic content. Somewhat similarly, both tasks have a constructive component whereupon initial descriptions are incrementally enhanced across an extended time period and this requirement would likely recruit working memory operations. Finally, both tasks may require mechanisms for overcoming episodic interference with the autobiographical task triggering multiple candidate events competing for selection and the future simulation tasks triggering episodic remembrances that potentially interfere with the goal of creating novel future scenarios. Current research is investigating these possibilities, and given the importance of accurate prediction and simulation in higherorder reasoning, this new line of research is quite important.

Acknowledgment

This work has been supported by NIH grant MH073982 to IGD.

See also: Cogintve Decline in Laboratory Animals: Models, Measures, and Validity.

Further Reading

- Cabeza R, Prince SE, Daselaar SM, LaBar KS, and Rubin DC (2004) Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience* 16(9): 1583–1594.
- Cohen NJ and Eichenbaum H (1993) *Memory, Amnesia, and the Hippocampal System*. Cambridge, MA: MIT Press.
- Davachi L, Mitchell JP, and Wagner AD (2003) Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences, USA* 100(4): 2157–2162.
- Dobbins IG, Foley H, Schacter DL, and Wagner AD (2002) Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron* 35(5): 989–996.
- Grady CL and Craik FIM (2000) Changes in memory processing with age. *Current Opinion in Neurobiology* 10(2): 224–231.
- Henson RN, Rugg MD, Shallice T, Josephs O, and Dolan RJ (1999) Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience* 19(10): 3962–3972.
- Johnson MK, Hashtroudi S, and Lindsay DS (1993) Source monitoring. Psychological Bulletin 114(1): 3–28.
- Moscovitch M, Winocur G, Stuss DT, and Knight RT (2002) The frontal cortex and working with memory. In: Stuss DT and Knight RT (eds.) *Principles of Frontal Lobe Function*, pp. 188–209. New York: Oxford University Press.

- Murray EA, Bussey TJ, and Saksida LM (2007) Visual perception and memory: A new view of medial temporal lobe function in primates and rodents. *Annual Review of Neuroscience* 30: 99–122.
- Schacter DL, Kaszniak AW, Kihlstrom JF, and Valdiserri M (1991) The relation between source memory and aging. *Psychology and Aging* 6(4): 559–568.
- Scoville WB and Milner B (1957) Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery and Psychiatry* 20: 11–21.
- Squire LR, Stark CE, and Clark RE (2004) The medial temporal lobe. Annual Review of Neuroscience 27: 279–306.
- Szpunar KK, Watson JM, and McDermott KB (2007) Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences, USA* 104(2): 642–647.
- Tulving E (1983) *Elements of Episodic Memory*. Oxford [Oxfordshire]: Oxford University Press; New York: Clarendon Press.
- Velanova K, Jacoby LL, Wheeler ME, et al. (2003) Functional-anatomic correlates of sustained and transient processing components engaged during controlled retrieval. *Journal of Neuroscience* 23(24): 8460–8470.
- Wagner AD, Schacter DL, Rotte M, et al. (1998) Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. Science 281(5380): 1188–1191.
- Yonelinas AP, Widaman K, Mungas D, et al. (2007) Memory in the aging brain: Doubly dissociating the contribution of the hippocampus and entorhinal cortex. *Hippocampus* 17(11): 1134–1140.