memory systems, neural basis of

rest on assumptions about the relation between the two types of processes. Curran and Hintzman (1997) as well as others have been critical of the independence assumption that underlies the PDP. Against that assumption, they argue that consciously controlled and automatic influences of memory are correlated. Jacoby et al. (2007) discuss possible alternative assumptions regarding the relation between conscious and unconscious influences, and provide strong evidence for their independence assumption. They argue that separating the contributions of different forms or uses of memory is important for applied purposes as well as for theory. As an example, distinguishing between consciously-controlled and automatic influences of memory is important for both diagnosis and treatment of memory disorders.

LARRY L. JACOBY


different types of memory may be associated with distinct forms of consciousness. Yet the general consensus favouring a non-unitary view of memory is not matched by a corresponding consensus concerning the nature and identity of the different systems of memory. Many different kinds of memory have been proposed, and there is—at best—modest agreement among extant proposals. Indeed, it is sometimes difficult for researchers even to agree on how they define a 'memory system' or a 'form of memory'.

1. Historical development of ideas concerning memory systems: a brief synopsis

2. Memory systems: definitions and criteria

3. The major memory systems: some proposals

memory systems, neural basis of

The analysis of consciousness is closely linked with the analysis of memory. On the one hand, memory depends critically on consciousness: the contents of memory reflect, with varying degrees of accuracy, aspects of previous conscious experiences. On the other hand, the nature and content of conscious experience depend on, and are shaped by, knowledge and experience that is stored in memory. It therefore seems safe to conclude that progress in understanding consciousness will likely depend on progress in understanding memory.

Achieving that goal, however, is complicated by the fact that during the past few decades, there has been a growing consensus among researchers that memory is not a unitary entity, but instead consists of different processes, forms, and systems. This basic insight has had numerous and important consequences for our understanding of memory (Schacter and Tulving 1994). At the same time, a non-unitary view of memory has implications for the analysis of consciousness, because different types of memory may be associated with distinct forms of consciousness. Yet the general consensus favouring a non-unitary view of memory is not matched by a corresponding consensus concerning the nature and identity of the different systems of memory. Many different kinds of memory have been proposed, and there is—at best—modest agreement among extant proposals. Indeed, it is sometimes difficult for researchers even to agree on how they define a 'memory system' or a 'form of memory'.

1. Historical development of ideas concerning memory systems: a brief synopsis

The idea that memory consists of multiple forms or systems is not new: it has been advanced by a variety of philosophers, psychologists, and neuroscientists during the past 200 years (for a detailed historical summary, see Schacter and Tulving 1994). This section summarizes some key developments during the past few decades concerning the notion of multiple memory systems.

Beginning in the 1960s and 1970s, there have been two distinct lines of research relevant to the issue of memory systems, one concerned with distinguishing between short-term and long-term memory, the other focusing on distinctions among types of long-term memory. Interestingly, research in both areas was sparked, at least in part, by observations concerning an interesting group of neurological patients who suffer from a condition known as the 'amnesic syndrome'. Amnesic patients exhibit severe difficulties remembering their recent experiences and acquiring new information, despite relatively intact perception, language, and other cognitive abilities that do not depend on remembering recent experiences. The amnesic syndrome typically results from damage to the hippocampus and related structures in the medial temporal lobe (Squire et al. 2004), which can occur following a variety of neurological insults, including encephalitis, anoxia (loss of oxygen to the brain), and head injury.

Early studies of the famous amnesic patient H. M., who became severely amnesic in 1953 after bilateral removal of the medial temporal lobe to relieve intractable epilepsy, revealed that he could remember small amounts of new information normally when tested immediately after studying the information (see Corkin 2002 for a summary of research with H. M.). This observation provided an important basis for drawing a distinction between short-term memory, which could hold a limited amount of information for a brief period of time, and long-term memory, which holds much
larger amount of information across much longer time periods. A debate raged during the 1960s and 1970s concerning whether it was necessary to distinguish between short- and long-term memory, or whether experimental results could be understood by postulating a single memory system. In the early 1970s, Baddeley and Hitch (1974) helped to settle the debate by conceptualizing short-term memory as *working memory*: a separate system from long-term memory whose main function is to hold information in mind while an individual works on other cognitive tasks.

At around the same time, a number of researchers were beginning to draw distinctions between different kinds of long-term memory. For example, Tulving (1972) put forward the influential distinction between *episodic memory*, which is involved in recollecting personal experiences that occurred in a particular time and place, and *semantic memory*, which handles general knowledge of the world, including facts and concepts. Researchers began to pay increasing attention to this distinction (and related ideas) in part because it was becoming clear that amnesic patients—who exhibited profoundly impaired long-term episodic memory—could nonetheless exhibit some forms of intact long-term retention. For example, research initially conducted during the 1960s with patient H. M., and pursued intensively during the 1970s and 1980s with many other amnesic patients, revealed that such patients can learn new perceptual and motor skills, and also that they can show normal *priming effects, where presentation of an item influences subsequent identification or production of that item on a test that does not require subjects to think back to the prior episode in which the item was presented. Such observations stimulated cognitive studies of healthy, non-amnesic individuals that began to document and characterize such phenomena as priming effects, and show that these effects could be dissociated experimentally from traditional measures of recall and recognition (for review of this early work, see Schacter 1987). Taken together, these studies of amnesic and healthy individuals led to spirited discussions and debates concerning what form or forms of long-term memory might underlie amnesic patients' preserved abilities for long-term retention, and also account for dissociations between forms of memory observed in healthy, non-amnesic individuals.

2. Memory systems: definitions and criteria

The scientific literature is replete with distinctions among forms of memory, which are often couched in terms of dichotomies. Visual vs auditory, short term vs long term, explicit vs implicit, associative vs item, recall vs recognition, and episodic vs semantic are just a few of the better-known distinctions. But do all of these distinctions reflect the operation of different memory systems? If not, how can we tell whether a proposed distinction among forms of memory reflects the existence of distinct memory systems?

To address this question, it is necessary to define what we mean by a 'memory system'. The general idea of a 'system' implies the operation of an ensemble or network of processes that function in conjunction with one another. More specifically, a memory system includes encoding, storage, and retrieval processes that operate together. By contrast, a form or type of memory need not involve a network of correlated processes; individual processes such as recall or recognition are often referred to loosely as different 'forms of memory'. Three criteria can be used to distinguish a 'memory system' from the weaker notion of a 'form of memory': class inclusion operations, properties and relation, and convergent dissociations (Schacter and Tulving 1994).

*Class inclusion operations* refers to the notion that a memory system allows one to carry out various tasks or functions within a class or domain. A memory system should not be identified with performance on only a single task, but instead operates across a range of tasks. Damage to the system, in turn, will affect performance to some degree on all tasks that tap that system. For this reason, the study of patient populations with brain damage that selectively affects neural structures associated with particular systems can be a highly productive research strategy: such patients should have difficulty performing various tasks subserved by a damaged system while performing well on tasks that depend on systems that are spared by brain damage.

*Properties and relations* refers to the idea that a memory system should be described by a list of properties that specifies features of the system and how they are related to those of other systems. Properties and relations include the types of information that the system handles, the neural networks that underlie the system, the rules according which the system operates, and functions that the system serves. Of course, developing an understanding of properties and relations constitutes a major goal of the research enterprise, so it is hardly surprising that, at the present time, hypotheses regarding properties and relations of memory systems are at a relatively early stage of development.

*Convergent dissociations* refers to evidence that reveals differences between classes of tasks that tap postulated memory systems. Convergent dissociations can take different forms: dissociations produced by manipulating cognitive features of behavioural tasks (e.g. manipulating how information is encoded affects tasks that tap system A but not system B), neuropsychological dissociations from brain-damaged patients (e.g. a particular patient population performs poorly on tasks that...
memory systems, neural basis of
tap system B while performing normally on tasks that
tap system A), or demonstrating different neural
characteristics (e.g., a region of the prefrontal cortex is
more active on tasks that tap system A than system B).
Without convergent dissociations, there would be
no reason in the first place to postulate multiple mem-
ory systems. However, different systems should not
be proposed based merely on dissociations between a
particular pair of tasks, because such dissociations are
easy to produce even within a particular system (Roedig-
ger et al. 1990).

As suggested earlier, the criteria of class inclusion
operations, properties and relations, and convergent
dissociations distinguish a 'memory system' from the
less constrained construct of a 'form of memory'
or 'type of memory'. Because the notion of 'form' or
'type' of memory is less constrained than that of a
memory system, forms of memory need not and often
do not satisfy all of the criteria. For example, one
commonly used distinction between forms of memory
is that between explicit memory, which involves con-
scious recollection of previous experiences, and implicit
memory, which involves non-conscious influences of
past experiences on current performance and behaviour
(Schacter 1987). Explicit and implicit memory were pro-
posed as descriptive terms to characterize an important
difference in the way that memory can be expressed
at the time of retrieval—not as different memory sys-
tems. While there are convergent dissociations to sup-
port the implicit/explicit distinction, it is more difficult
to satisfy the criteria of class inclusion operations or
properties and relations.

3. The major memory systems: some proposals
Numerous forms and systems of memory have been
proposed—more than can be reviewed in this brief
entry (for a comprehensive survey of memory systems,
see Schacter and Tulving 1994, Eichenbaum and Cohen
five major memory systems: (1) working memory, a short-
term or transient form of retention that supports the
online maintenance of internal representations for
use in ongoing cognitive tasks, and also supports the
controlled manipulation of these representations; (2)
episodic memory, which supports the encoding and re-
trieval of personal experiences that occur in a particular
time and place; (3) semantic memory, which refers to
a person's general knowledge about the world, contain-
ing a complex web of associated information, such as
facts, concepts, and vocabulary; (4) the perceptual repre-
sentation system, a collection of domain-specific subsys-
tems that operate on perceptual information about
the form and structure of words and objects; and (5)
procedural memory, which supports the acquisition and
retention of perceptual, motor, and cognitive skills,
and is involved in everyday tasks such as learning to
ride a bicycle or becoming skilled in cognitive domains
such as reading or motor domains such as athletics.

Much research has been done to elucidate the cog-
nitive and neural properties of these (and other) memory
systems. Working memory, episodic memory, and semi-
semantic memory are all thought to operate primarily
in the domain of conscious awareness, whereas the
perceptual representation system and procedural
memory are thought to rely on largely non-conscious
processes. For example, amnesic patients can show in-
tact procedural memory even though they lack any
conscious recollection of having engaged in procedural
learning. Similarly, amnesic patients can also show in-
tact priming effects that are thought to reflect modifica-
tion of the perceptual representation system, despite
lacking conscious memory for the stimuli that produced
priming. Given that amnesia is associated with damage
to the medial temporal lobe, including the hippocam-
pus, it is thought that the neural basis of the perceptual
representation system and procedural memory lie out-
side the medial temporal region. Posterior cortical
regions involved in visual and auditory processing have
been linked with the perceptual representation system
(Schacter et al. 2004), and subcortical structures such as
the basal ganglia have been linked with procedural
memory (Poldrack and Rodriguez 2004). The relation-
ship between semantic memory and the medial tem-
poral lobe has been the subject of debate: amnesic
patients are capable of adding new knowledge to semi-
semantic memory, but they typically do not show normal
semantic learning (Squire et al. 2004). Semantic memory
is thought to depend importantly on widely distributed
networks, involving regions with the lateral frontal
and temporal cortices (for review, see Schacter et al.
2000).

Because issues related to consciousness have been
most closely linked to working memory, episodic mem-
ory, and the perceptual representation system, let us
consider some of the basic properties of these systems
in a bit more detail. As mentioned earlier, working
memory was initially advanced as an extension of the
concept of short-term memory. Much of the pioneering
research on working memory was carried out by Alan
Baddeley and colleagues (for a recent review, see Bad-
deley 2002). According to the model initially proposed
by Baddeley's group, working memory can be fraction-
ated into three subsystems: a limited-capacity central
executive involved in controlling ongoing cognitive pro-
cesses, and two domain-specific 'slave subsystems'
that assist the central executive: a phonological loop
involved in temporary storage of speech-based informa-
tion, and a visuospatial sketch pad dedicated to the
temporary storage of information about objects and
their spatial locations. Information held in each subsystem is available online to conscious awareness.

Evidence supporting the fractionation of working memory into subsystems has come from multiple sources, including cognitive studies concerned with functional capacity of the subsystems and the types of informational codes they rely, studies of brain-damaged patients that reveal how selective damage to particular regions can disrupt each of the subsystems, and brain imaging studies that have delineated distinct neural correlates associated with each subsystem. For example, functional brain imaging studies suggest that regions within the lower left frontal lobe (i.e. Broca's area) and parts of the left parietal lobe are associated with the phonological loop, whereas other parietal and prefrontal regions are associated with the visuospatial sketchpad.

Much research on working memory has examined the two 'slave subsystems', but more recently increasing attention has been paid to the central executive. In fact, Baddeley (2002) argues that it is necessary to propose a fourth subsystem of working memory that he has called the episodic buffer, a limited-capacity system that provides temporary storage of information held in a general, multimodal code (as opposed to the unimodal codes relied on by the phonological loop and visuospatial sketchpad). According to Baddeley, the episodic buffer binds or links together information from the slave systems (and from long-term memory) into a unified, conscious representation of a current episode. There is as yet relatively little direct evidence concerning the cognitive and neural properties of the episodic buffer but in Baddeley's view it plays a key role in linking working memory with long-term memory, specifically the form of long-term memory referred to earlier as episodic memory.

Many of our ideas about the nature of the episodic memory system come from Tulving (1972, 2002), who has emphasized its role in providing us with the ability to store information about our personal pasts and to consciously re-experience aspects of what had happened to us. Indeed, Tulving views episodic memory more generally as allowing us to engage in 'mental time travel', entailing both re-experiencing of the past and projecting ourselves into the future (see AUTONOMIC CONSCIOUSNESS). When episodic memory is destroyed or seriously damaged, as in some cases of amnesia, the ability to engage in mental time travel is absent and patients' consciousness is temporarily restricted to the present. Much psychological and neuroscientific research has attempted to delineate the cognitive and neural properties of episodic memory by analysing episode encoding and retrieval processes. Cognitive psychologists have established that episodic memory is enhanced by deep or elaborative encoding processes that link incoming information to pre-existing knowledge structures. Episodic memory also depends heavily on encoding of contextual information that links an event to a particular time and place. Episodic retrieval, in turn, relies on retrieval cues that help to re-instate or re-activate aspects of episodic encoding.

Evidence from the analysis of both brain-damaged patients and neuroimaging studies indicates that both the medial temporal role and regions with the frontal lobe play an important role in episodic memory. When the hippocampus and related medial temporal lobe structures are damaged, episodic memory is severely impaired. When the frontal lobes are damaged, more subtle episodic memory problems are often observed: patients have difficulty recalling source or contextual information concerning when and where an episode occurred, and are sometimes prone to memory distortions (Schacter et al. 1998). In healthy adults, specific regions within the medial temporal and frontal lobes often show increased activity during episodic encoding and/or retrieval. Indeed, there is some evidence that hippocampal activity is sometimes related to the conscious re-experiencing of the details of a prior episode (Eldridge et al. 2000).

In contrast to the experience of conscious recollection that is a hallmark of episodic memory, research concerned with the perceptual representation system has focused on the phenomenon of priming, which is thought to reflect non-conscious changes in the perceptual representation system as a result of exposure to a stimulus. Neuroimaging studies suggest that such priming effects are associated with decreased activity in occipital, temporal, and frontal regions, perhaps reflecting sharpening of perceptual representations as a result of stimulus exposure (Schacter et al. 2004). One recent neuroimaging study has provided compelling evidence for a neural distinction between priming in the perceptual representation system and episodic memory by examining how brain activity during encoding is related to subsequent episodic memory or priming (Schott et al. 2006). Increased activity in the bilateral medial temporal lobe and left prefrontal cortex at the time of encoding predicted subsequent episodic remembering (i.e. greater activity at encoding for subsequently remembered than forgotten items). By contrast, decreased activity at the time of encoding in a variety of posterior regions thought to be involved in perceptual processing (i.e. extrastriate cortex, fusiform gyrus) predicted subsequent priming. These findings clearly point to distinct neural bases for episodic memory and the perceptual representation system that supports priming. As these latter results suggest, current research on memory systems is providing an ever more refined
analysis of the cognitive and neural constituents of each of the major systems considered here. Moreover, recent research has begun to attack the important issue of how memory systems interact with each other (Poldrack and Rodriguez 2004). It is now clear that memory systems do not operate independently of one another, so understanding the neural basis for their interactions constitutes a critical task for researchers. Studies concerning the nature of and interactions between memory systems will no doubt go a long way toward furthering our understanding of the nature of consciousness itself.

DANIEL L. SCHACTER


memory, visual short term When we have just looked away from a scene we can still see it in our mind's eye, but how much do we actually remember? Visual short-term memory (VSTM) is defined as short-lasting memory for visual properties of just-viewed objects or scenes. Whereas iconic memory lasts for less than 0.5 s under most conditions, is eliminated by new visual stimulation, is precategorical, and is highly detailed, VSTM lasts for several seconds, is more resistant to interference from new stimulation, is postcategorical, and is limited in how much information can be represented (Phillips 1983). Although VSTM is more abstract than perception in that the viewer does not mistake it for concurrent perception, it maintains information about many characteristics of visual perception, including spatial layout, shape, colour, and size.

By definition, contents in VSTM are currently available to conscious awareness. Just as selective attention ensures conscious access, the contents in VSTM are also gated by attention. A standard test of VSTM for an array or picture is to show a second array that may have a change, requiring the viewer to detect the change. Visual input that is not selectively attended is poorly remembered in VSTM. Once information is encoded in VSTM, continued attention is required for memory maintenance and consolidation. Dividing attention between a VSTM task and other cognitive tasks, including auditory choice reaction time (RT) tasks, impairs VSTM maintenance. During the retention interval, spatial attention tags the location of encoded items, and the distribution of spatial attention affects the durability of VSTM. Distributing attention to multiple items in VSTM leaves them vulnerable to new visual input, whereas orienting attention to one of these makes memory robust. On the other hand, contents in VSTM can also influence attentional allocation. Perceptual input that matches VSTM contents tends to receive attentional priority compared with other input.

The close link between VSTM and consciousness is also reflected in their shared neural substrates. In the primate brain, maintaining objects or locations in VSTM activates lateral prefrontal cortex, posterior parietal cortex, thalamus, and other dorsal brain areas. These areas are also considered the neural network for voluntary attention and consciousness.

Much research in VSTM has been devoted to characterizing its capacity limits (jiang et al. 2007). This capacity is often considered to be no more than three or four units, with the units being individual visual objects rather than visual features (Luck and Vogel 1997). There is apparently no limit to the number of visual features one can remember as long as they belong to a single object: a compound object of four features