Learning and Memory

Chapter · July 2003

DOI: 10.1038/npg.els.0000172

Yonatan Goshen-Gottstein
Tel Aviv University

Learning and Memory

Introductory article

Yonatan Goshen-Gottstein, *Tel-Aviv University, Tel Aviv, Israel*

Learning and memory describe the ability of organisms to benefit from prior experience. While different terms are designated to describe this ability, no clear boundary differentiates between the meanings of these terms. For historical reasons, however, the term learning has been primarily used to refer to the ability as it applies to nonhuman organisms, while memory is primarily used in the context of human remembering.

Article Contents

Introduction

The term 'memory' implies a single, unitary mechanism. Modern research, however, has uncovered numerous memory systems and subsystems that are interconnected in interesting ways. These systems, and their organization, will be described in this article. Although the focus will be on human memory, two learning mechanisms, readily found in any animal, will also be described.

While the main theme of this article will be that memory is not a unitary system, the different subsystems that will be described share common features that justify their common label as memory. Among other things, all forms of memory involve three discrete stages: encoding, storage and retrieval. First, the organism must encode the new information. Encoding refers to processes that are involved in allowing the new information to be perceived and adequately attended so that this information can form a neural trace that represents the information. Second, the organism must be able to store the memory trace. If a memory trace is formed, but the neural connections are too weak to sustain the information, then the lost information can obviously not be retrieved. Third, once the information is encoded and stored, the information must be retrieved for remembering to occur. Retrieval involves the process of locating and activating the neural trace that represents the required information, ostensibly by recapitulating the processes that were involved in the initial encoding of the information.

Beyond the commonalities of memory stand the differences that distinguish the different memory systems. The primary classification of memory is that of long-term memory and short-term memory, known also as working memory. At least two parameters distinguish between the two types of memory. The first parameter is the time frame in which the memories are expressed. Long-term memory can be exhibited for durations lasting anywhere between a few minutes and a lifetime. Working memory, however, is considered to affect performance only over time durations of seconds, and at most a minute or two. The capacity of information that can be stored is the second defining characteristic that distinguishes between the two forms of memory. Experimentally derived estimates suggest that only four to seven items can be maintained in working memory. In contrast, the only known limit on long-term memory is derived from the computational constraints of the finite number of neurons in the brain. However, no experimentally derived upper limit has ever been demonstrated for long-term memory. Thus, long-term memory is virtually unlimited in its capacity, thereby enabling us to remember an almost endless number of ideas, thoughts and concepts.

Both long-term memory and working memory can be further fractionalized. Two very fundamental long-term memory mechanisms, which are found in both animals and humans, are that of classical and operant conditioning. Under the heading, Basic Learning Mechanisms in Animals, the two types of conditioning will be described. Further subdivisions of long-term memory will be discussed under the heading, Human Memory Systems.

The empirical evidence in support of the biological reality of the classification of memory is derived, in part, from performance of memory-impaired patients. These disorders will be described under the heading, Disorders of Memory and Brain Localization. Finally, the processes that enable memory to remain stored for a long time to come will be considered. These processes will be described under the heading, Consolidation.

Basic Learning Mechanisms in Animals

Classical conditioning

Classical conditioning involves a stimulus that reliably elicits a characteristic response. An example of such a stimulus is meat, which reliably elicits a salivary response in dogs. The stimulus of this pair is called the unconditioned stimulus (US), and the response an unconditioned response (UR). The term 'unconditioned' is used to highlight the fact that the connection between the stimulus and the response it elicits is not conditioned on the learning episode.

Classical conditioning occurs when a new stimulus that prior to the experiment does not elicit the characteristic response of the unconditioned stimulus is paired many times with the unconditioned stimulus. Such frequent pairing transforms the new stimulus to a conditioned stimulus (CS) that due to the conditioning now elicits a conditioned response (CR) (i.e. the same response as that produced by the unconditioned stimulus). For example, if a dog is presented with frequent pairings of the sound of a bell with a bowl of meat, then the sound of the bell will be the conditioned stimulus that will by itself elicit a salivary response in the dog. Classical conditioning is also known as Pavlovian conditioning (after its discoverer, Ivan Pavlov).

Classical conditioning occurs in numerous animals in a wide variety of response systems. It has been demonstrated in muscular reflexes, such as the knee-jerk reflex and the pupillary reflex. It has also been demonstrated to affect reflexive responses of glands and organs.

A prominent model of classical conditioning, the Rescola–Wagner model, asserts that with repeated pairings of the US with the CS, animals learn to predict the appearance of the CR once they see the CS.

Several phenomena are typical of conditioning. Acquisition can be likened to the encoding stage of learning. During acquisition, many trials where the CS and US are paired are necessary for the CR to become fully developed. After the first few trials, only a small CR is elicited. Gradually, the CR increases in strength until it fully resembles the UR.

Extinction describes the processes of forgetting in classical conditioning. After the acquisition stage, the CS can elicit a CR even when presented alone. If, however, the CS is repeatedly presented alone, without subsequent presentation of the US and the UR, then the conditioning will be extinguished, and the CS will no longer elicit the CR. Supposedly, the animal will learn that the CS no longer predicts the UR, and so, will not produce the CR.

In terms of neural organization, the cerebellum is essential for classical conditioning of skeleton musculature, and the amygdala, for conditioned emotional responses. Also the neostriatum has been implicated as an important substrate for classical conditioning.

Operant conditioning

Operant conditioning, known also as instrumental conditioning, does not require a preexisting connection between a stimulus and a typical response that it produces. Instead, operant conditioning is directed at animals (or humans) that freely operate (hence the term 'operant') in their environment. If a particular action of the animal is reinforced, by following this action with a response that is pleasant for the animal, then the animal will more likely produce this action in the future.

This simple principle, the Thorndike law of effect, is the fundamental rule underlying operant conditioning. An animal's learning, according to the law of effect, is no more than a strengthening of responses as a result of the consequences of those responses. B. F. Skinner, the prominent American psychologist, systematically analysed many variables that are governed by the law of effect.

By applying this principle to the variability that is inherent to animals' ongoing operant behaviour, one can produce totally new behaviours in laboratory animals as well as in humans. Researchers, as well as animal trainers, use the procedure of shaping to produce novel behaviours by successive reinforcement of behaviours that are closer and closer to the desired new behaviour. Such systematic reinforcement of behaviours that are forever closer to the desired behaviour can lead to such extraordinary demonstrations as dogs climbing ladders and students paying attention to their teachers.

Operant conditioning, like classical conditioning, also involves an acquisition phase where the animal encodes new information to acquire the conditioned response. The principle of extinction can also be demonstrated, when an animal's desired behaviour is consistently not reinforced and the acquired behaviour is thus 'forgotten'.

Human Memory Systems

Declarative (explicit) versus procedural (implicit) memory

American neuropsychologist Larry Squire has argued that human long-term memory is biologically realized in two different subsystems. These subsystems are declarative memory and procedural memory. The two systems differ with regard to the type of information that is contained within them. Declarative memory is usually expressed in thought, and contains information that can be transmitted between individuals (hence 'declarative' – information that one can declare). Procedural memory, in contrast, can only be expressed in overt behaviour and can be acquired only through extensive practice. It is memory of how to perform an action to reach a goal.

The meaning of the word chair, for example, is registered in declarative memory. This meaning, in its entirety, can be passed verbally from one individual to another. Similarly, that the Toronto Blue Jays never won a world cup may also be a memory recorded in the declarative system, albeit a false memory. Personal memories such as remembering what one ate last night are declarative memories that can be fully communicated between individuals. Procedural memory, in contrast, includes skills such as learning to ride a bicycle. Such memories can only be acquired through practice. No matter how many classroom hours are spent trying to acquire this skill verbally, only by actually sitting down and turning the pedals will this skill be learnt.

Declarative and procedural memory also differ with regard to the type of encoding that information must undergo to be registered within them. For information to be registered in procedural memory, it must be acquired by a gradual accumulation of experience. Such accumulative learning, however, does not allow the organism to select one specific episode from the agglomeration of prior experience, as in declarative memory. For the organism to retrieve a specific episode, it must have a means of specifying that episode. The most likely mechanism for such a selection is via the use of context. Thus, for information to be registered in declarative memory, it is sufficient to rapidly form links between different stimuli that are experienced at the same time. Therefore, while single-trial learning is not uncommon in declarative memory, it is very rare to find examples of such procedural learning.

Finally, the rate at which information is forgotten also differs between the two systems. Information can be rapidly forgotten from declarative memory, as in the case of dates in a history exam. Procedural memories, in contrast, are rarely, if ever, forgotten. No one forgets how to ride a bicycle.

Declarative memory has been labelled by some researchers as explicit memory, and procedural memory as implicit memory. The idea behind this terminology is that the declarative memory system is primarily addressed by explicitly referring to it. Procedural memory, however, is tapped through overt behaviour. Thus, procedural memory is assessed implicitly through facilitated performance, without reference to past experience. Further subdivisions of the two memory systems are now described.

Declarative memory

Canadian psychologist Endel Tulving has argued that two biologically distinct subsystems can be identified within the declarative memory system,. These systems are the episodic and the semantic subsystems. Semantic memory represents a person's knowledge of the world. Among other things, this includes knowledge of the meanings of words and their relationship to one another, and knowledge of facts, including historical, geographical, scientific and familial facts. In contrast, episodic memory refers to personal memories, in which the rememberer can consciously refer back to a particular time and place in which the memories were created.

Procedural memory

Procedural memory is a general term that describes skill learning. This form of memory can also be fractionalized into many smaller subsystems. The subsystems differ in regard to the overt behaviours that are learned. The behaviours, and their corresponding neuronal subsystems, can be categorized as either perceptual, motor, or behaviours involving rule learning. In addition to the learning systems that will now be described, classical conditioning and operant conditioning (described above) are also forms of learning that are part of procedural memory. While the various forms of learning may employ different underlying neural structures, they have in common the fact that they are all acquired by a gradual accumulation of experience.

Perceptual learning

Perceptual learning refers to the mastery of new skills in perceiving visually presented displays. Perceptual learning occurs whenever a novel visual display is presented. With practice, visually similar displays are deciphered more quickly. Learners of languages such as Arabic or Hebrew, in which the written code (orthography) of written words is different from that of English, demonstrate that with practice they can read words in the new language with increasing ease. Thus, sensorimotor records or programmes are registered in memory and enable facilitated processing upon subsequent encounters.

Indeed, even the ability of normal readers to form perceptual representations of written words in their own language is part of the perceptual procedural-memory system. That is, the very act of translating visually presented written codes to their corresponding sounds and meaning is an act that involves the procedural memory system. The mnemonic consequence of this process is that when the identical written code is encountered again, reading is faster and with fewer errors. The better reading skills demonstrated by third graders over second graders is due, among other factors, to the enhanced perceptual learning that third graders have undergone. Other examples of perceptual learning include learning to see through prisms that transform the visual scene and learning to read mirror-inverted text.

Priming

Like perceptual learning, priming also involves facilitated perceptual processing. Priming, however, describes the benefit as it is incurred to the particular items that were previously learned. Thus, above and beyond the general mastery of the new skills (say, reading mirror-inverted text) priming describes the additional mnemonic benefit that can be shown for the particular words with which the skill was originally acquired (say, rereading, in mirror-inverted text, Shakespeare's first sonnet). Thus, if a perceptually degraded word is presented during test, subjects will be more likely to identify this word correctly if it was previously presented during study than if not. Similar effects of priming can be shown if a conceptually related cue is presented during test (rather than a perceptually degraded copy of a studied word) and subjects are asked to generate a target word related to the cue. Thus, subjects will more likely respond to the cue word 'leash' with 'cat', if 'cat' had previously been studied.

Motor learning

Motor learning is displayed when with practice, motor tasks are carried out with increasingly greater ease. The act of writing is probably the most prominent example of the workings of motor procedural memory. Beginning writers form their first words with considerable difficulty. With time, the motor sequences that are necessary for performing the act of writing become engraved, and writing becomes easier. This facilitation in performance exemplifies the affects of motor procedural memory.

Learning rules

One type of activity that humans are especially well designed to perform is the act of implicitly learning rules, in a ruled-based system in which the governing rules are very complex. The most incredible example of such learning is the ability of humans to learn the syntax of a language. Very heavy, densely written books are needed to detail all the rules governing the syntax of the English language. Yet young children are able to implicitly learn these rules by simply using the language. This demonstrates the rule-learning abilities that are part of the procedural memory system.

Learning of rules can have many more mundane applications than that of learning a language's syntax. Learning to navigate through a complex city, with many one-way streets and off-limit areas, is another activity we readily perform, without paying attention to the complexity inherent to such performance.

Working Memory

Working memory is a system that can store temporary information and at the same time manipulate information that is required for complex cognitive activities such as comprehension, learning and reasoning. Studies that required subjects to rehearse a sequence of digits while performing simultaneous cognitive tasks showed that the requirement to remember the digit sequences did not catastrophically impair performance on the cognitive tasks. This, together with studies that examined the performance of neurologically impaired patients, suggests that working memory is not a unitary entity, but instead (like long-term memory) is composed of a number of subsystems. Overseeing the actions of these subsystems is a postulated executive control system, which is in charge of coordinating the performance of the subsystems, by allocating attentional resources to the subsystems as needed for attaining good performance. According to some suggestions, this executive system is located in the frontal lobes (see below). The subsystems will now be described.

The phonological loop

The phonological loop stores speech-based information, which unless rehearsed, decays within approximately two seconds. Coupled with the speech-based store are control processes that feed the information into the store and keep the information in the store from decaying through subvocal rehearsal. These characteristics of the phonological loop explain the finding that the number of items that can be remembered after a single hearing is poorer for long words than for short words. To keep items from decaying, items must be rehearsed in real time. Since longer words take longer to rehearse than shorter words, more of them decay, resulting in shorter memory spans.

The functional role of the phonological loop is probably to facilitate long-term phonological learning, as is needed to acquire a second language. Indeed, phonological learning is probably a primary determinant for successful first language acquisition. Thus, repetition of nonwords, a measure of phonological storage, turns out to be the best predictor of vocabulary acquisition in young children.

The visuospatial sketchpad

The visuospatial sketchpad stores visuospatial information, which unless rehearsed, quickly decays. Control processes also form part of this system, and are responsible for registering the information into the store, and enabling rehearsal of this information. Storage in the store may be disrupted by either concurrent visual processing, as when patches of colour are presented, or by concurrent spatial processing, as when tracking a moving sound.

Recent evidence suggests that the pattern-based and space-based characteristics of the system represent separate anatomical and functional subsystems, with the pattern-based system being dependent on the occipital lobe, and the spatial system depending more on the parietal lobe. Work with monkeys indicates that the frontal lobes also contribute to the executive control of visual memory.

Disorders of Memory and Brain Localization

There are several neurological disorders that have devastating consequences on memory performance. Some disorders, like Alzheimer disease, show relatively diffuse effects on memory. Most disorders, however, can single out different memory systems, including declarative memory, procedural memory and working memory. These disorders will be categorized according to the memory system that is primarily affected.

The amnesic syndrome – automatic retrieval of episodic memory

The amnesic syndrome is a permanent global disorder of memory. Amnesia can be found in patients with damage to different brain structures resulting from different aetiologies. The most severe amnesia is found in patients with focal legions to the medial temporal lobes involving the hippocampus and surrounding cortex (and amygdala) that result from encephalitis, anoxia or surgery. An example of such amnesia is found in H.M., an epileptic patient who in 1956 underwent surgery in which the hippocampus and surrounding cortex were removed bilaterally.

Another form of amnesia is found in damage to midline thalamic structures, including the mamillary bodies, dorsomedial and anterior nuclei of the thalamus, and possibly the mamillo-thalamic tract, that results from alcoholism and thiamin deficiency (Korsakoff syndrome), infarcts, stab wounds and ventricular tumours. A third aetiology is damage to basal forebrain resulting from aneurysms of the anterior communicating artery, from anoxia, and from encephalitis.

Amnesia is a selective impairment of memory. Amnesic patients are unable to form new episodic memories, but have intact working memory and procedural memory. Their semantic memory system is also intact, and evidence exists that new semantic memories may sometimes be created. Thus, it seems that amnesic patients have a circumscribed impairment of the episodic memory system.

The frontal lobes – strategic retrieval of episodic memory

The prefrontal cortex is a large structure that consists of a number of distinct areas, each with its own projection to and from other brain regions. Together, these areas contribute to performance on episodic forms of memory that rely on strategic search and organization.

For some episodic memories retrieval is automatic (did you drink beer today?), while other episodic memories require strategic, deliberate retrieval (how did you celebrate your birthday four years ago?). The deficits that arise in amnesia are all failures at storage and retention. Thus, amnesic patients lack the ability to create or reactivate memory traces. Patients with damage to the frontal lobes, in contrast, are able to reactivate memory traces, but lack the ability to initiate strategic, deliberate search for information.

The frontal lobes are necessary for goal-directed memory activity under voluntary control. Often, appropriate memories do not emerge automatically, but must be ferreted out by systematic retrieval strategies. In this sense, the task of the frontal lobes is to organize the raw material made available by the hippocampal system so that this search is intelligent and well organized. In this sense, the frontal lobes are 'working with memory' structures that operate on the input to the hippocampal structures and to the output from these structures. Indeed, the frontal lobes are probably general central executive systems that operate on the input and output of more modular, specific brain processors.

Huntington disease and Parkinson disease – procedural memory

Huntington disease and Parkinson disease are degenerative disorders associated with damage to the basal ganglia and to structures that are part of the extrapyramidal motor system. Patients with these diseases show intact performance on declarative tests of memory, but are impaired on perceptual and motor implicit tests. The same patients, however, perform normally on priming tasks, which suggests that the memory impairment concerns only the formation of perceptual and motor records or programmes, and not the entirety of procedural memory.

The short-term memory syndrome

Although quite rare, this syndrome is found in patients with grossly defective short-term storage, together with intact long-term learning. Close examination of many such patients reveals damage that is circumscribed to affect only the phonological loop, leaving intact the visuospatial sketchpad and the central executive control system. Other patients, however, do show functional impairment to either the pattern-based or the space-based subsystems of the visuospatial sketchpad. Recent evidence suggests that patients with Alzheimer disease have particularly marked impairments of working-memory executive control processes.

Consolidation

Consolidation describes the resilience to forgetting of memory traces over time. Two consolidation processes have been identified. Short-term consolidation describes the process of converting short-term memories into long-term memories. This ability is often interrupted when people undergo head injuries. Following such injuries, memories of the events preceding the injury are invariably lost and cannot be recovered again. Presumably, these memories were only registered in working memory, and the process of gaining access into long-tem memory was interrupted. At the cellular level, the switch from short-term to long-term memory may be the result of switching from a process-based memory to a structural-based memory.

A second type of consolidation operates over time periods as long as years or decades. That is, some memory traces appear to become more resilient to loss with the passage of years. Thus, amnesic patients may show poor memories for events preceding the accident, yet show considerably better memory for memories from the distant past. A similar temporal gradient can be found in patients undergoing electroconvulsive therapy.

Converging evidence suggests that the hippocampus and related structures play a role in long-term memory consolidation for a limited time after the occurrence of the event. Subsequently, consolidation occurs within cortical areas, other than the hippocampus, with different cortical areas consolidating different kinds of information. Thus, damage to occipital areas may impair the consolidation for visual information and damage to parietal areas may impair consolidation for spatial information.

Further Reading

Baddeley AD (1992) Working memory. *Science* **255**: 556–559.

Moscovitch M, Vriezen E and Goshen-Gottstein Y (1993) Implicit tests of memory in patients with focal lesions or degenerative brain disorders. In: Spinnler H and Boller F (eds) *Handbook of Neuropsychology*, vol. 8 (F Boller and J Grafman, Volume Editors). Amsterdam: Elsevier.

Schacter DL (1996) *Searching for Memory: The Brain, the Mind, and the Past*. New York: Basic Books, HarperCollins.

Schacter DL and Tulving E (1994) *Memory Systems, 1994*. Cambridge, MA: MIT Press Bradford.

Squire LR (1987) *Memory and Brain*. New York: Oxford University Press.

Squire LR (1992) Memory and the hippocampus: A synthesis of findings with rats, monkeys, and humans. *Psychological Review* **99**: 195–231.

Squire LR and Butters N (1992) *Neuropsychology of Memory*. New York: Guilford Press.

Squire LR, Knowlton B and Musen G (1993) The structure and organization of memory. *Annual Review of Psychology* **44**: 453–495.

Tulving E (1983) *Elements of Episodic Memory*. Oxford: Clarendon Press.

Tulving E and Schacter DL (1990) Priming and human memory systems. *Science* **247**: 301–306.