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Memory: Why the engram is elusive

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Memory is a lasting, internal representation of a past event or experience (or some aspect of it) *that is reflected in thought or behavior*. It follows, therefore, that *memory does not exist until it is recovered*.

Many probably agree with the first part of the definition (especially if we include neural and neurochemical events as underlying representations, see Section 3 of this volume), but at least as many may disagree with the second. Evidence from subjective experience, and from the human and animal laboratory, has shown that memories may momentarily be inaccessible, or difficult to reveal, but that given enough time and the proper cues and testing conditions, those memories can be recovered and demonstrated in thought or behavior. Because memories were only temporarily absent, it is concluded that they had always existed. At a conceptual level, this kind of evidence has supported a concept of memory as a free-standing entity (R.L. Lockhart, personal communication 2005) which exists independently of the operations needed to recover it, and possibly to encode and retain it (see Sections 6, 9 and 10 of this volume).

The concept of memory as a free-standing entity fits the lay person's view nicely, though some dictionary definitions of memory take into account the operations needed to recover the past event or experience (e.g. *Webster's New World Dictionary* 1959; *The American Heritage Dictionary* 1979). It also fits well with most psychologists' and neuroscientists' conception of memory. Although almost everyone concedes that in order to study memory there has to be ultimately some demonstration of a change in behavior (or thought in the case of humans) from which we infer that memory exists, this condition is considered to be only a procedural necessity that may even be eliminated once we can find neural or molecular markers of memory. Indeed, we may already have reached that point. Quite a number of neuroscientists consider themselves as studying memory simply by examining lasting changes in neural activity [e.g. long-term potentiation (LTP)] in the synapse, or in intracellular molecular mechanisms and processes which are induced by a particular event.

The alternative view, that memory does not exist until it is revealed in behavior or thought, conceives of memory not as a free-standing entity, but as linked to a process of recovery and emerging from it. Memory is the product of a process of recovery (an act of memory) rather than an entity which exists independently of that process. This view is at least as old as Semon's (1904) conception of memory, and has a number of more recent incarnations in the work of Tulving (1983), Kolers and Roediger (1984), Whittlesea (2002) and Craik (2002*b*; Chapter 23, this volume), among others. This quote from Craik (2002*b*) captures this view well:

> Where is the percept when we are not perceiving? The question does not make much sense; clearly percepts are not micro-representations waiting patiently for 'their' specific combination of input patterns to activate them. Rather, perceiving is a dynamic process that occurs online in a given time period, and reflects the interaction of incoming sense data with pre-wired and learned processes; this interaction in turn drives behavior and subjective awareness. It is thus perhaps equally meaningless to ask Where is the memory trace when we are not remembering? Again the various behavioral and experiential aspects of remembering occur only during memorial processing, and the hunt for the engram [the physical manifestation of the memory trace that is independent of the operations needed to recover it] may prove as fruitless as the hunting of the Snark. To alter Lewis Carroll's mournful tale only slightly, those pursuing the memory trace may find 'in the midst of their laughter and glee' that the engram has 'softly and suddenly vanished away—for the Trace was a Boojum, you see'.

I agree with all that Craik says except his conclusion. Like many other psychologists and neuroscientists (see a recent paper by Schafe *et al.* 2005), he posits that the engram or memory trace and memory are conflated, whereas I believe, along with Semon (1904) and Tulving (1983), if I understand them correctly, that the two are separate. The engram or memory trace is the representation of an encoded event or experience. It is not yet a memory, but provides the necessary (physical) condition for memories to emerge, just as an external stimulus provides the occasion for a percept to emerge. Put another way, the engram is permissive or necessary for memory but does not suffice for its materialization. A memory emerges when the engram interacts with retrieval cues or information derived from particular environmental conditions, a process which Semon termed "ecphory". The product of this retrieval–engram interaction is a memory. Without retrieval, there is only the engram, and even its existence is inferred from memory's emergence.

The book in the library analogy

Let me illustrate this distinction, and the general point that a memory does not exist until it is recovered, with a simple analogy of looking for a book in a library. Suppose you think a particular book is in the library. You go to the

shelf where you believe it was located and it is not there. Does the book exist in the library or not? One possibility is that you looked in the wrong place. You now look up its call number but you discover that the book is not at the location the call number specified. There are now two possibilities: the book is somewhere in the library but you cannot find it, or the book has disappeared. For all intents and purposes, as long as you do not recover the book, you cannot know whether it exists. Saying it is there because there is a record that it possibly existed once (the call number) does not solve the problem, but begs the question.

There are a number of problems with that analogy, but far from undermining the conclusion that a memory does not exist until it is recovered, they only reinforce it. The first problem is that the engram is not like a book. Once written, a book is immutable. That is not true of an engram. Though the engram is the representation of an encoded event, it, too, is subject to change. Moreover, though the book is a bound entity existing in a single location, the engram may consist of information that is not tightly bound, if it is bound at all, and is distributed over many locations. Recovering a memory, therefore, is not like finding a book at a particular single location, but more like assembling the pages of a book which may be scattered in different locations in the library. Finally, unlike a call number which is distinct from the book itself, retrieval cues and processes interact with the engram and influence the memory which is recovered. Depending on the interaction, some 'pages' of the memory may be missing, others may be placed in the wrong sequence, still others may be imported from other books which are related in some way to the cues and the engrams, and some of the cues themselves may be incorporated into the memory that is recovered and change the engram on which it was based (Schacter 1996, 2002). These ideas, that memory is a product of a recovery process, rather than a free-standing entity awaiting discovery, and that it is distinguishable from an engram which itself may be mutable, have a number of implications for the science of memory.

Relevance to research and theory

There is little in this description of the nature of memory that should be surprising to psychologists who work on memory in humans (for reviews, see Schacter 1996, 2002). Though malleable, and sometimes fragile, human memory is sufficiently resilient to support everyday needs and provide an (imperfect) record of past events and experiences. Memory, though not perfect, is good enough. As Schacter rightly observes, memory's deficiencies or imperfections arise as a natural consequences of the operation of the processes and mechanisms on which it is based. Though Schacter did not go so far as to state

explicitly that memory does not exist until it is recovered, I believe it is a conclusion that is consistent with the evidence he reviews.

This conclusion applies not only to complex, clearly reconstructive memories, such as recalling a sequence of events that form part of an autobiographical episode, but also to such seemingly simple types of memory which are evident in tests of perceptual and conceptual priming, and even in Pavlovian or classical conditioning (see Section 2 of this volume). Let me give an example from a study on priming that Vriezen, Bellos and I conducted a few years ago (Vriezen *et al.* 1995). Working on the widely held assumption that viewing a stimulus alters its structural representation so that it can be recognized better the next time it is presented (priming), we asked participants to make an animacy judgment on the first presentation and a size judgment on the second, or an identical judgment on both presentations. We fully expected that performance would be better in the identical than the crossed conditions, but predicted that priming, though diminished, would still be observable in the crossed condition. To our surprise, it was completely abolished. These results have been replicated often, and confirmed that priming is altered because some aspect of the 'context' or response has changed (see Schacter *et al.* 2003). It is as if even the simple memory that supports priming did not exist until the retrieval conditions were appropriate for its recovery. As predicted by Vriezen *et al.* and others, viewing the stimulus does effect a change in the structural representation as is evident by alterations in activation in regions of occipital and inferior temporal cortex associated with object perception; nevertheless, these changes in activation in posterior sites are not correlated with priming in the crossed condition (see also Wig *et al.* 2005). The engram may be there, but the implicit memory is not.

As this example illustrates, the definition can accommodate different types of memory, from implicit to explicit, and has the advantage of calling attention to the process of recovery as crucial to our understanding what memory is and how it functions. It also accommodates easily a number of phenomena that are puzzling if we consider memory to be a free-standing entity awaiting discovery, but not if we consider it as being the product of the interaction between engram and retrieval. Among these phenomena are the misinformation effect (in which the cue alters the memory that is retrieved; Loftus *et al.* 1995), confabulation (in which people with damage to ventromedial prefrontal cortex distort past events almost beyond recognition; Gilboa and Moscovitch 2002), the mutability of memory with time, an aspect of which is captured by multiple trace theory of recent and remote memory (Nadel and Moscovitch 1997; Moscovitch *et al.* 2005; Chapter 31, this volume), and re-consolidation (in which memories which were thought to be fully consolidated are 'lost' if an

amnestic agent is applied shortly after they are recovered; Dudai 2004; Frankland and Bontempi 2005). The definition also encourages us to consider memory as a process that emerges from underlying representations, and in doing so can alter the representations themselves.

This definition also applies to studies of simpler organisms, such as *Aplysia*, simple preparations, such as hippocampal slices, or even to simple procedures in complex organisms, such as classical eyelid conditioning in mammals. Here, too, the role of retrieval in recovering a memory should not be overlooked. Great strides have been made in identifying the changes at the synaptic and intracellular level needed for engram formation and retention, but little is known about how those changes interact with conditions at retrieval to elicit a memory. Changes which are relatively permanent take a long time to form, and presumably to re-activate, yet they must lead to other changes which can be instantiated quickly to account for the almost instantaneous recovery of even very old memories (see Dudai 2004; and Section 10 of this volume). Conducting studies on retrieval–engram interactions at the synaptic or cellular level, which are analogous to those at the systems level, would be very illuminating in light of the definition we adopted.

Conclusion

The definition of memory for which I argued placed as much weight on retrieval processes as on storage. It follows from the definition that memory does not exist independently of its being retrieved. Such a definition forces us to think of memory as a representation which is created from the interaction of retrieval cues and processes with stored knowledge rather than as an entity awaiting discovery. The implication which this definition has for research and theory was noted.

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