Implicit Memory: How It Works and Why We Need It

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ABSTRACT

Since the discovery that amnesiacs retained certain forms of unconscious learning and memory, implicit memory research has grown immensely over the past several decades. This review discusses two of the most intriguing questions in implicit memory research: how we think it works and why it is important to human behaviour. Using priming as an example, this paper surveys how historic behavioural studies have revealed how implicit memory differs from explicit memory. More recent neuroimaging studies are also discussed. These studies explore the neural correlate of priming and have led to the formation of the sharpening, fatigue, and facilitation neural models of priming. The latter part of this review discusses why humans have evolved with highly flexible explicit memory systems while still retaining inflexible implicit memory systems. Traditionally, researchers have regarded the competitive interaction between implicit and explicit memory systems to be fundamental for essential behaviours like habit learning. However, recently documented collaborative interactions suggest that both implicit and explicit processes are potentially necessary for optimal memory and learning performance. The literature reviewed in this paper reveals how implicit memory research has and continues to challenge our understanding of learning, memory, and the brain systems that underlie them.

Keywords: implicit memory, priming, neural priming, habit learning

INTRODUCTION

Not until Scoville and Milner studied the amnesic patient H.M. in 1957 did investigations into the biological and neurological basis of memory begin in earnest. Among the many contributions to science that H.M. provided, one of the most important and fascinating was the first convincing evidence of multiple memory systems. Milner (1962) showed that in ten trials, H.M. was able to learn to trace a star only by using its mirror image. Impressively, he retained the skill across several days despite having no recollection of the learning trials. For a time it was believed that the acquisition of motor skills was the only type of learning H.M. was capable of (Corkin, 1968). It would take another decade until it was discovered that other non-motor skills could be learned as well. What was known about learning skills retained during amnesia was again broadened when it was demonstrated that amnesiacs had the ability to learn perceptual skills like mirror-reading (Cohen & Squire, 1980). These early investigations of H.M. and

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other amnesiacs formed the foundation for research involving the relationship between memory and awareness. This paper will look into the implicit memory research that has been conducted since then, with a focus on two key questions: how it works, and why we need it.

First, an examination of the behavioural and neuroimaging evidence of priming will lead to a discussion on neural models which attempt to explain how implicit memory may work. Historic behavioural priming studies of both amnesic and non-amnesic subjects provide convincing evidence that implicit memory and explicit memory systems are in fact distinct. More recent neuroimaging studies have discovered the neural correlate of priming, which has led to sharpening, fatigue, and facilitation neural models of priming. Secondly, interactions between implicit and explicit memory systems will be used as evidence in the discussion of the need for an implicit memory system for human behaviour. Behaviours like habit learning require a competitive interaction between implicit and explicit memory systems, but more recently theorized collaborative interactions may be necessary in producing optimal learning and memory.

Implicit memory encompasses a wide range of phenomena, including procedural and motor memory, habit learning, classical conditioning, and emotional memory (Squire, 2009b). Because of this, implicit memory research is important not only because it increases our basic understanding of the human brain, but also because of it role behind a wide range of behaviours. Such an understanding is not only be necessary in developing solutions where such behaviours become maladaptive—like

habit learning becoming addiction—but also in enhancing beneficial behaviours. For example, understanding motor memory may lead to the development of optimal strategies in skill acquisition. It may also lead to better teaching strategies for people who do not learn effectively with conventional teaching methods, like amnesiacs or Alzheimer's patients, or even an ill-behaved household pet.

MECHANISMS OF IMPLICIT MEMORY

The term implicit memory is a general label which refers to the observation that past experiences can modify subsequent task performance, despite the learner lacking conscious recollection of the learning episode (Schacter, Chiu & Ochsner, 1993). Many skills are acquired and maintained implicitly, for example typing. Most people do not remember when or how they learned to type, nor do they need to consciously monitor their typing. Implicit memory is thus expressed through performance as opposed to explicit memory, which is expressed through recollection (Squire, 2009a). While the previous example illustrated procedural memory, the most extensively studied implicit memory paradigm is priming. (Schacter et al., 1993).

Early Priming Studies

Priming refers to the phenomenon where a recent encounter with a stimulus creates an improvement in the ability to identify or process a related stimulus (Tulving & Schacter, 1990). One of the main differences between priming and other types of implicit skill learning is that priming takes only takes a single or a small number of learning trials, whereas skill learning requires numerous learning

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trials (Schacter et al. 1993). In the 1980s, visual word priming was the most widely studied form of priming. Some of the most popular experimental paradigms included stem or fragment completion, where subjects are given the first three letters or fragments of the word and choose between multiple possible completions (i.e., for___ or f_re_t (forest)); and word identification, where subjects are shown a word for a very brief duration (i.e., 35ms) and asked to identify it (Schacter et al. 1993).

The key principle that emerged from early studies of visual word priming was the fact that processes involved in priming are distinct from ones pertaining to explicit memory. Strong support for this principle came from studies of amnesic patients who had comparable levels of priming as non-amnesic subjects in stem completion tasks (Graf, Squire & Mandler, 1984), provided that the instructions did not suggest an explicit strategy. It was also shown that normal subjects had similar explicit/implicit dissociations. Manipulations to depth of encoding (i.e., semantic study tasks which focus on the meaning of a word, compared to non-semantic tasks which focus on the physical properties of a word) produced equal levels of priming despite large differences in explicit memory (Graf, Mandler & Hayden, 1982; Graf & Mandler, 1984). Post-experiment questionnaires revealed that subjects who were not aware of the relationship between the completion task and the learning task still showed equivalent priming effects as subjects who were aware (Bowers & Schacter, 1990). Amnesiacs provided the first piece of the puzzle that the implicit memory system was distinct from the explicit memory system, while studies on non-patient

samples began to paint a more detailed picture of how these systems differed.

One such difference revealed by early priming studies was the endurance of priming effects. Fragment completion tasks have been shown to persist from as long as one week (Tulving, Schacter, & Stark, 1982) to over a year (Sloman, Hayman, Ohta, Law, & Tulving, 1988). While initial studies of amnesic patients failed to find priming effects at long delays (Squire, Shimamura & Graf, 1987), it was later shown that the amnesiac K.C. retained priming effects over the course of a year (Tulving, Hayman & MacDonald, 1991). These long term effects are thought to be related to the fact that manipulations of interference that normally impair explicit memory exhibited no effect on performance on fragment and stem completion tasks (Graf & Schacter 1987; Sloman et al., 1988). The endurance of priming effects added to the growing picture of how implicit memory was different from explicit memory.

Lastly, visual word priming was established to be relatively specific. Priming has little cross-modality capabilities, a fact evident when priming was diminished with auditory—as opposed to visual—target stimuli in stem completion (Graf, Shimamura, & Squire, 1985), and word identification (Hashtroudi et al., 1988). When subjects studied mixed list of words and pictures in a word or a picture-fragment completion task, priming was nearly abolished in picture completion tasks despite free recall of the pictures being better than words (Weldon & Roediger, 1987). Bilingual subjects also showed little priming when they studied words in one language but were tested in another (Durgunoglu & Roediger, 1987). Even changing the

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typecase or font of the words can adversely affect priming (Jacoby & Hayman, 1987). The apparent finicky and inflexible nature of implicit memory was very unlike that of explicit memory.

These early visual word priming experiments all suggested that the processes behind implicit memory were physiologically and computationally different than the ones responsible for explicit memory. Contrary to explicit memory tasks, priming was uninfluenced by semantic processes in depth of encoding manipulations, has high specificity, and can produce long term effects due to its independence from interference. Furthermore, priming occurred in both non-amnesic and amnesic subjects. The dominant view which emerged suggested implicit memory was a function of an entirely different system, one which did not depend on crucial explicit memory structures in the medial temporal lobe (MTL) like the hippocampus (Schacter, 1992; Schacter et al., 1993; Squire, 1992; Tulving & Schacter, 1990).

Neural Correlates of Priming

With advances in neuroimaging technology, researchers are now able to look for the brain structures necessary for priming. An early positron emission tomography (PET) study by Squire et al. (1992) found significantly decreased blood flow in the area of the lingual gyrus of the posterior occipital lobe during a stem completion task. There was also an increase activity in the right hippocampus. However, the same authors suggested some explicit recognition of familiar word stems was possible, thus ruling out hippocampal activity as a contributor to priming performance. Subsequent PET studies (Buckner et al., 1995; Schacter, Alpert, Savage, Rauch & Albert, 1996), as well as functional magnetic resonance imaging (fMRI) studies (Demb et al., 1995; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997), all found decreases in activity in regions relevant to the task under consideration. For example, stem completion tasks decreased activity in posterior ventral occipital lobes (Squire et al., 1992), whereas semantic priming tasks would decrease activity in the left inferior prefrontal cortex (Demb et al., 1995). These neural activity reductions have been correlated with priming behaviour, such that greater reductions in prefrontal cortex activity were associated with faster performance in word classification tasks (Maccotta & Buckner, 2004). This effect is also robust, in that it has been shown to last even with intervening stimuli (Henson, Shallice, & Dolan, 2000) and across several days (Turennout, Bielamowicz, & Martin, 2003; Turennout, Ellmore, & Martin, 2000), mimicking the behavioural results of the early behavioural priming studies. Although neural activity reductions have not been shown to last for as long as behavioural priming effects, there appears to be an absence of studies examining such long-term effects. In any case, any memory traces would likely be altered and shifted with time, providing immensely challenging methodological problems for researchers with current neuroimaging techniques.

Neuroimaging studies all suggest one neural correlate for priming: anatomically-specific decreases in activation of brain regions responsible for any particular task, with lower-level areas showing smaller reductions than higher-level areas (Schacter & Buckner, 1998). This effect has been termed neural

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priming. Neural priming converges with a phenomenon called repetition suppression (RS), first discovered concurrently by Brown, Wilson, and Riches (1987) and Balyis and Rolls (1987) in single-cell recordings of monkey neurons. They found reduced responses to familiar stimuli compared to novel stimuli in 15-26% of neurons in the inferior temporal cortex. RS has subsequently been shown in other brain areas like the prefrontal cortex (Miller, Erickson, & Desimone, 1996), and provides a convincing mechanism for neural priming in human brain systems.
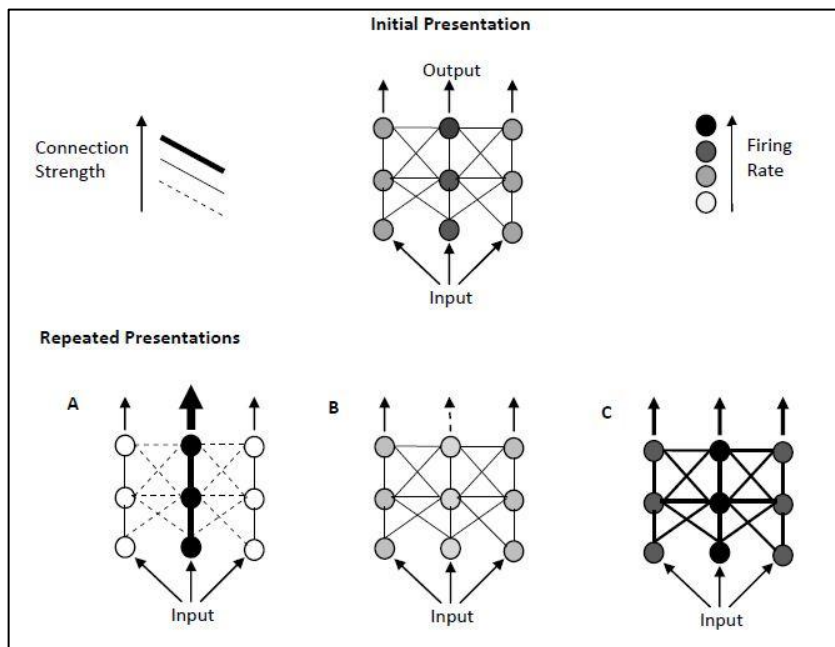

Figure 1. Models of neural priming are depicted. **(A)** The sharpening model predicts strengthening of initially optimally responding neurons and weakening of other neurons via lateral inhibition, resulting in less neurons responding overall. **(B)** The fatigue model predicts a global decrease in firing rate, with initially optimally responding neurons having a greater decrease in firing rate. Output from initially weak responding neurons are now relatively stronger than output from optimally responding neurons providing a mechanism for novelty detection. **(C)** The facilitation model predicts a global increase in firing rate, presumably through strengthened connections.

Neural Models of Priming

Three neural models have been proposed to explain neural priming (see Figure 1). The first, and perhaps most popular, is the sharpening or tuning model proposed by Desimone (1996) and Wiggs and Martin (1998). As a stimulus is repeatedly presented, neurons that code nonessential features for recognition of the stimulus decrease firing, thereby weakening and eventually eliminating connections to the rest of the neurons in the network representing the stimulus. As a result, the network becomes sparser, with a smaller neuronal population overall. This sharpening of the network is presumably advantageous because it reduces metabolic cost, and elicits increasingly efficient and rapid stimulus

identification in the remaining neurons. How the network is sharpened is thought to be due to competitive interactions and lateral inhibition of neurons in the network (Grill-Spector, Henson, & Martin, 2006). A computational neural network model of the MTL, developed by Norman and O'Reilly (2003), revealed that neurons which respond strongest initially increase their activity with subsequent repetitions while also inhibiting weaker neurons. Since the weak neurons outnumber strong ones, a global decrease in activation (i.e., neural priming) is observed despite quicker processing.

The second model of neural priming is termed the fatigue model (Grill-

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Specotr et al., 2006). In this model, all neurons which initially respond to the stimulus show proportional reductions in responding on subsequent exposures. Firing decreases in the highest proportion within neurons that respond optimally to the repeated stimulus, creating relatively enhanced sensitivity to different stimuli. This model provides a mechanism for novel detection since novel stimuli would create higher levels of activation in the inferior temporal cortex and prefrontal cortex (the areas most associated with neural priming), and via top-down feedback to attentional systems, would drive the organism to automatically seek novel items (Li, Miller, & Desimone, 1993). This model however, provides no suitable explanation as to how reduced firing can result in increased performance on priming tasks.

The last model of neural priming is the facilitation or accumulation model, which predicts shorter durations of neural firing causing faster processing of repeated stimuli (James & Gauthier, 2006). Because the temporal resolution of fMRI is over several seconds, shorter durations of firing would lead to smaller responses. While this model is consistent with evidence from fMRI and behavioural priming data, it cannot account for the decreases in firing rate found in single-cell recording studies – individual neurons should fire more under this model, not less.

While all three models may have their faults, they each offer unique insights into how the brain can potentially change itself due to experience. In other words, they are potential neuroplastic mechanisms of priming. It is unlikely that these models are mutually exclusive, but each model may operate in parallel or may

be dependent on different brain regions, time, or task conditions (Grill-Spector et al., 2006). While these neural models were developed to specifically explain priming, the principles underlying these models likely apply to other manifestations of implicit memory as well. Sharpening, fatigue, and facilitation are theorized principles which attempt to explain how the implicit memory system works, and more generally, how the brain can successfully adapt to its environment and modify behaviour based on prior experience.

WHY HAVE IMPLICIT MEMORY?

Priming is a potentially adaptive process because organisms evolved in an environment where stimuli encountered once are likely to be encountered again, so it would be beneficial for organisms to interact more quickly and more efficiently in familiar environments (Squire, 2009a). The neural priming models discussed above may provide satisfactory explanations as to how priming works, but they do not answer one of the most basic questions in implicit memory research: why should such processes be implicit? Why have such inflexible implicit memory systems at all? Is it simply an evolutionary spandrel serving little purpose in the human species with such developed forms of explicit memory? The fact that monkeys take several hundred trials to learn a simple pattern discrimination task (i.e., □ versus +) using medial temporal lobe (MTL) independent skill learning that humans can learn in a few trials using MTL dependent memorization reveals the power of human explicit memory (Zola-Morgan & Squire, 1984). In order to explore how implicit memory contributes to behaviour, the interactions between

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implicit and explicit memory systems must first be discussed.

Competitive Interactions between Implicit Memory and Explicit Memory

Interactions between implicit and explicit memory can be broadly viewed as either competitive or collaborative. Competitive interactions, as described by Poldrack and Packard (2003), stem largely from habit-learning tasks, which constitute a form of implicit memory. In another study, Packard and McGaugh (1996) trained rats in a cross maze to approach the west arm from the south arm for a food incentive. On days 8 and 16, the start location was changed to the opposite (north) arm and the rats were evaluated on whether they showed place learning (i.e., approach the same west arm where the food was in training), or response learning (i.e., make the same right turning response as during training). Normal rats showed place learning on day 8 but response learning on day 16. When place learning was destroyed early in training by lidocaine injections to the hippocampus, rats showed no preference for either arm. Interestingly, when lidocaine was injected into the caudate nucleus to destroy response learning, rats still demonstrated place learning. This study in particular yielded two important observations: (1) behaviour initially supported by the hippocampus in a task is later dominated by behaviour which did not require the hippocampus, and (2) even when behaviour was dominated by the caudate nucleus, hippocampal information about the place remained available. Support for competitive interactions between memory systems also comes from human fMRI studies. Poldrack et al. (2001) found that MTL activity early in a classification learning task, but as performance improved caudate activity increased and MTL activity decreased. The study also showed a negative correlation between the activation of the caudate and MTL, suggesting a competitive interaction.

The competitive interactions between caudate-dependent and MTL-dependent learning are regarded as the bases of habit learning, where dopaminergic inputs from substantia nigra and ventral tegmental area form a reward circuit with the striatum, which the caudate nucleus is a part of (Packard & Knowlton, 2002; Squire, 2009a). Such habit learning mechanisms, which are associated with extreme repetitive behaviours like addiction and obsessive-compulsive disorder, should not be seen as maladaptive. Sherry and Shacter (1987) suggest that multiple memory systems may have evolved due to the functional incompatibility of different demands for a single memory system. Once one learns how to drive a car, for example, the activity becomes automatic independent of whether it is day or night, rain or shine. When an organism encounters a predator, however, it suddenly becomes vital to remember whether it was day or night, rain or shine, in order to avoid future encounters. In habit learning, remembering the details of a situation may detract from task performance. But in explicit episodic memory, details may be essential for survival. Competitive memory systems may be required to arbitrate between the incompatible need to flexibly access detailed knowledge and the need for fast, automatic responses (Poldrack et al., 2001).

Collaborative Interactions between Implicit Memory and Explicit Memory

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An emerging view suggests implicit and explicit memory may collaborate—instead of compete—to produce behaviour. This view is endorsed by the component process model by Moscovitch (2008), which predicts that priming can be influenced by explicit memory processes dependent on the MTL at an unconscious level. At first it would seem that the priming evidence discussed previously would discount this view as they all suggested a distinct system independent of the MTL. However, implicit memory tasks were designed specifically to preclude any use of explicit memory strategies, creating an artificial situation in which any natural use of the MTL would never be seen.

Evidence for MTL activation during implicit tasks has begun to emerge. A study by Sheldon and Moscovitch (2010) found that performance on visual word priming tasks was higher when subjects were able to remember the details or context in which the words appeared during the study phase, compared to words for which they could not recollect any specific information. In a separate study, Alzheimer's patients with extensive MTL degeneration retained priming effects for a perceptually based visual priming task, but exhibited impaired performance compared to healthy controls (Koenig et al., 2008). Additionally, fMRI data has shown MTL activation in both perceptual (Koenig et al., 2008) and conceptual implicit learning tasks, particularly in the perirhinal cortex (Wang, Lazzara, Ranaganath, Knight, & Yonelinas, 2010). This new evidence suggests that the largely disregarded hippocampal activation discovered by Squire et al. (1992) could potentially have been due to MTL processes supporting implicit learning behaviour.

The implications of a collaborative interaction between implicit and explicit memory processes to produce optimal learning remain largely unknown. Did implicit and explicit memory systems evolve to serve fundamentally incompatible functions and were later co-opted to facilitate and improve each other's processing? Is such a collaborative interaction unique to humans? Do explicit memory tasks also employ resources traditionally observed for implicit memory processes? Recent fMRI (Turk-Browne, Yi, & Chun, 2006) and electroencephalographic studies suggest that they do (Voss & Paller, 2007, 2008). If both implicit and explicit systems share both implicit and explicit processes, the lines used to define and separate these systems begin to vanish. Bussey and Saksida (2005) have suggested that looking at brain regions in terms of what computations they perform or what representations they contain would be more useful than modularising areas based on their psychological function. Perhaps in a similar manner, dichotomizing memory systems based on conscious awareness may also be no longer useful. The findings of collaborative interactions certainly opens up numerous questions which will no doubt transform the way we think about memory systems and the human brain in general.

CONCLUSION AND FUTURE DIRECTIONS

Since H.M. and the early priming tasks used to investigate the newly discovered implicit memory system, research in implicit memory has expanded rapidly, benefiting immensely from new imaging techniques like fMRI. This paper analyzed evidence focused on the mechanism of implicit memory, and why

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such a system is needed. Several neural models for priming which attempt to explain both historic behavioural priming and neural priming evidence were discussed, and competitive and collaborative interactions between implicit and explicit memory systems showed how both systems contribute to behaviour. Competitive interactions form the basis for habit learning, while collaborative interactions have been found to produce optimal performance on memory tasks. It should be noted that this paper was necessarily selective, and major fields in which implicit memory processes have also had substantial contributions have been passed over. Fear conditioning in the amygdala (LeDoux, 2003), conditioned motor responses in the cerebellum (Thompson & Steinmetz, 2009), sleep (Stickgold, 2005), grammar learning (Reber, 1967), visual search (Chun & Jiang, 1998) and selective attention (Vuilleumier, Schwartz, Duhoux, Dolan, & Driver, 2005) are just some of the additional fields in which implicit memory has been implicated in.

As technology continues to improve, our knowledge of implicit memory processes will continue to grow. More powerful neuroimaging and computational modeling techniques will allow researchers to refine and distinguish between neural models of priming, increasing our knowledge of neuroplasticity and benefiting applications in machine learning and artificial intelligence. Further study of the interactions between implicit and explicit memory systems will certainly force us to rethink our theoretical conceptions of memory and consciousness. The future promises of new and exciting findings in implicit memory research.

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