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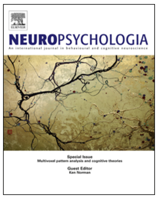

# The neural basis of implicit learning and memory: A review of neuropsychological and neuroimaging research

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ABSTRACT

Memory systems research has typically described the different types of long-term memory in the brain as either declarative versus non-declarative or implicit versus explicit. These descriptions reflect the difference between declarative, conscious, and explicit memory that is dependent on the medial temporal lobe (MTL) memory system, and all other expressions of learning and memory. The other type of memory is generally defined by an absence: either the lack of dependence on the MTL memory system (nondeclarative) or the lack of conscious awareness of the information acquired (implicit). However, definition by absence is inherently underspecified and leaves open questions of how this type of memory operates, its neural basis, and how it differs from explicit, declarative memory. Drawing on a variety of studies of implicit learning that have attempted to identify the neural correlates of implicit learning using functional neuroimaging and neuropsychology, a theory of implicit memory is presented that describes it as a form of general plasticity within processing networks that adaptively improve function via experience. Under this model, implicit memory will not appear as a single, coherent, alternative memory system but will instead be manifested as a principle of improvement from experience based on widespread mechanisms of cortical plasticity. The implications of this characterization for understanding the role of implicit learning in complex cognitive processes and the effects of interactions between types of memory will be discussed for examples within and outside the psychology laboratory.

## 1. Introduction

The seminal report of patient H.M. by Scoville and Milner (1957) deserves its place as perhaps the most important foundational finding for the field of cognitive neuroscience. The observation that selective damage to the medial temporal lobe (MTL) led to an isolated deficit in long-term memory provided the first evidence that a complex, high-level cognitive function operates in a localized region within the brain. By the end of the following decade, it had also become clear that the presentation of anterograde amnesia implied that memory was not a unitary function dependent solely on the MTL memory system damaged in H.M.'s surgery. The identification and characterization of forms of memory that are not dependent on the medial temporal lobe (MTL) cannot be traced to a single research report. The observation of some types of preserved learning in H.M. were first documented in (Corkin, 1968; see also Milner, Corkin, & Teuber, 1968). The establishment of a set of these types of learning phenomena (not dependent on the MTL) unfolded over the next 20 years of neuropsychological research in humans and parallel studies in animals (Squire, 1992) and was termed *nondeclarative memory*.

At around the same time, a separate field of research was documenting the curious ability of people to express acquired information via performance in the absence of conscious awareness of memory (Reber, 1967, 1989; Schacter, 1987), a phenomenon characterized as *implicit learning* or *implicit memory*. While the terminology and underlying definitions of these two research areas vary slightly, the phenomena largely but not perfectly overlap (Reber, 2008). The overlap suggests that types of memory that appear as implicit, defined as occurring without awareness, are supported by neural mechanisms that do not depend on the MTL memory system. However, both lines of research have evoked fairly significant controversy (e.g., Shanks & John, 1994) that is driven by the need to define this type of memory by an absence: either the absence of dependence on the MTL or the absence of conscious awareness. Difficulties with the impossibility of proving a negative have led to persistent concerns about how to characterize the memory systems. Definitions based on systems neuroscience are precise, e.g., declarative memory is whatever memory processes are accomplished by the MTL memory system and everything else is nondeclarative. But this does not offer direct insight into the differing operating characteristics and

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subjective experience of both types of memory. Definitions based on consciousness, e.g., implicit learning is what is learned outside awareness, require a precise definition of consciousness and are often confounded by the parallelism of the memory systems that lead to both types of memory being acquired simultaneously in healthy participants.

The difficulty of defining a type of memory based on conscious awareness and the variety of ways that implicit memory is observed in behavior have lead some authors to propose abandoning the term entirely (e.g., Willingham & Preuss, 1995). As an alternate approach, it has been suggested that a description of differing characteristics of a common set of memory representations might better account for differences between implicit and explicit memory (Cleeremans & Jiménez, 2001; Reder, Park, & Kieffaber, 2009). A common underlying memory representation set is difficult to reconcile with neuropsychological findings of memory dissociation in which explicit memory is observed to be selectively impaired leaving implicit learning intact. However, this idea may be valuable for understanding some recent reports of implicit learning impaired by MTL damage (e.g., Chun & Phelps, 1999), findings that suggest that even anatomical dissociations may not divide memory systems cleanly (Hannula & Greene, 2012). The goal of the current review is to expand the standard memory systems framework to provide a broad characterization of human memory that incorporates the known structure of the MTL memory system, and also describe how implicit learning is represented in the brain based on general principles of plasticity rather than a specific coherent parallel memory system. Within this framework the varied phenomena of implicit learning are reviewed to further identify consistent differences in the operating characteristics of these two types of memory that reflect their differing neural basis.

The core idea is that implicit memory reflects a general principle of plasticity within neural processing circuits that leads to adaptive reshaping of function to match experience. This approach provides a way of grouping the variety of phenomena described as implicit learning and identifying similarities across domains in the way that this type of learning proceeds. By framing implicit learning as a principle, it is made clear that there is no general "implicit learning system" in the brain that can provide a clear double dissociation with explicit/declarative memory. This framing aims to avoid the occasional misconception that memory systems theory implies the existence of an alternate implicit memory system that parallels the MTL memory system and acts as a unitary construct (e.g., Vidoni & Boyd, 2007; Danner, Hagemann, Schanking, Hager, & Funke, 2011; Ballesteros & Manual-Reales, 2004). The idea of general and pervasive plasticity fits well with the wide range of studies that have used neuroimaging, neuropsychological and behavioral empirical techniques to identify implicit learning as separate from explicit learning. Further, this framework provides hypotheses for understanding the handful of phenomena that do not fit neatly into the memory systems approach (e.g., implicit memory dependent on the MTL) and for developing new approaches to understand interactions between memory systems in complex cognitive functions that depend on both types of memory. Whereas many prior characterizations of implicit memory have focused on enumerating phenomena that meet the criteria of learning without awareness (or do not depend on the MTL memory system), understanding implicit learning as an emergent property of general plasticity means that we should expect implicit learning phenomena to be pervasive and universal. Rather than being confined to specific empirical laboratory tasks, implicit learning contributes in some way to all forms of behavior change that reflect the impact of prior experience on cognition.

## 2. Prior descriptions of memory system organization

Previous broad characterizations of implicit or nondeclarative memory have mainly focused on enumerating demonstrations of memory that does not depend on the MTL memory system (Squire, 1992, 2004; Squire, Knowlton, & Musen, 1993; Seger, 1994; Cleeremans, Destrebecqz, & Moyer, 1998). This taxonomy-based approach has been useful in demonstrating the wide variety of phenomena that appear to be learned implicitly but has generally stopped short of identifying any consistent operating principles (beyond awareness) or suggesting a learning mechanism across domains. Computational modeling of some specific memory phenomena has suggested that incremental, distributed changes in processing can account for some forms of implicit learning (Cleeremans & McClelland, 1991; Stark & McClelland, 2000). The computational model of memory described in the Complementary Learning Systems (CLS) model of O'Reilly et al. (2011) is based on separate mechanisms within the MTL and an external, slow, cortically-based mechanism. However, this slow, cortical mechanism has been primarily discussed with respect to the ongoing consolidation of explicit long-term memories rather than focusing on its potential applicability to understanding implicit learning.

Eichenbaum and Cohen (2001) in their excellent review of memory systems also advocated for the idea that memory is a fundamental property of the brain's information processing activities, which is the approach here. Their analysis of memory systems of the human brain focused partly on reviewing the operation of the MTL memory system and partly on clarifying the differences between this system and other specialized memory systems such as a procedural "memory system" supporting implicit learning. The somewhat different characterization used to frame this review is that it is specifically implicit learning that reflects plasticity within information-processing circuits and not that there is a coherent "implicit memory system." The current review further incorporates additional findings over the past decade that have used functional neuroimaging to examine the neural basis of implicit learning and connect these findings to the idea that this form of memory emerges from the pervasive plasticity mechanisms throughout the cortex. In contrast to this principle-based model of implicit learning, the operation of the MTL structures that support explicit, declarative memory can be usefully described as a system since damage leads to deficits across a range of related explicit memory phenomena. The specialized computations needed for explicit memory storage and retrieval do not fit simply into the idea of memory emerging from pervasive synaptic plasticity processes throughout the brain.

Other reviews have attempted to identify a specific information processing characteristic such as relational binding (Konkel & Cohen, 2009) or formation of associations (Reder et al., 2009) that might unify the categories of differing memory tasks without over-reliance on the difficulty of defining conscious awareness. Similarly, Henke (2010) argued for the laudable goal of identifying these key operating characteristics and differing processing modes of memory rather than consciousness. However, these approaches have not yet been successful at broadly bringing together implicit learning phenomena. Relational associations are critical to explicit memory, but associative learning also occurs in many implicit learning tasks (e.g., sequence learning, category learning). In addition, a very recent study (Verfaellie, LaRocque, & Keane, 2013) presented an example of preserved relational implicit memory following MTL damage. Perhaps another important characteristic, such as the flexible use of representations, can be incorporated into an information-processing definition that will eventually accurately describe the functional differences between types of memory. Pursuing this research program will require continuing to study and establish the differing operating characteristics of implicit and explicit memory. However, it should also be noted that since this area of research continues to identify novel tasks for examining the expression of implicit memory, there is risk of a certain circularity in the identification of operating characteristics for novel tasks. First, it will be necessary to establish that the task is an effective measure of implicit memory, a process that cannot depend on the not-yet-identified processing characteristic that fully distinguishes the systems. In practice, this means falling back on definitions based on subjective experience (consciousness) or the contribution of the MTL memory system in order to drive the subsequent studies that we hope will eventually identify reliably differential operating characteristics.

Organizing implicit learning as based on a general principle of pervasive plasticity, as done here, is not a radical departure from the taxonomy approach of enumerating specific learning circuitry. This approach is concordant with many of the ideas embedded in the memory systems description of Eichenbaum and Cohen (2001) and the computational approaches to memory (e.g., CLS; O'Reilly, Bhattacharyya, Howard, & Ketz, 2011). The current review and synthesis aims to facilitate connections among different areas of implicit learning research, provide a framework for extending this work to memory system interactions, and include a mechanistic hypothesis for recently described findings that report implicit memory dependent on the MTL memory system. The recent findings that highlight the discrepancy between the implicit/explicit and declarative/nondeclarative frameworks have led some to suggest that memory systems differences cannot be well-defined exclusively by MTL anatomy (Hannula & Greene, 2012) or subjective experience (Reder et al., 2009). As noted below, the idea of pervasive plasticity can be extended to allow for implicit learning operating on representations formed by the MTL memory system, capturing these intriguing new findings while still acknowledging the general utility of heuristics based on either anatomy or subjective experience.

## 3. Neural bases of learning and memory

Research on the cognitive neuroscience of human memory has focused to a great extent on the operation of the MTL memory system damaged in the surgery to alleviate H.M.'s seizures. Subsequent examinations of the brain regions implicated in this surgery indicated that the collection of structures defined as the hippocampus and surrounding cortical areas (entorhinal, perirhinal and parahippocampal cortex) together make up the medial temporal lobe (MTL) memory system (Corkin, Amaral, Gonzalez, Johnson, & Hyman, 1997). Effective functioning of this system further depends on the integrity of the basal forebrain, fornix, mammillary bodies and thalamic nuclei that are closely connected to these regions (Zola-Morgan & Squire, 1993). Numerous studies have investigated how this system supports acquisition and retrieval of memories, how facts and episodes are stored, and how the experience of familiarity may or may not be dissociable from the experience of “mental time travel” (the vivid imagination of a prior event used to define the subjective experience of episodic memory). These studies have illustrated the complexity of the MTL memory system and also its critical connections to other regions of the brain. Interactions between the MTL and prefrontal cortex are critical for successful memory (Simons & Spiers, 2003; Reber, Wong, & Buxton, 2002). Functional neuroimaging studies have also implicated the parietal lobes as playing an important role in long-term memory function (Wagner, Shannon, Kahn, & Buckner, 2005), reflecting interactions between these areas as part of the functioning of the MTL memory system. Through interconnections with these other cortical areas, the MTL acts as the central node in a coherent brain system specialized to support many forms of long-term memory like recognition and recall. Damage to this system leads to a selective deficit in these kinds of memory while leaving other cognitive functions (e.g., language, attention) intact.

Studies of the neurobiological basis of synaptic plasticity have frequently examined the underlying processes by which the neural circuitry of the MTL carry out the processes of long-term memory. However, it is also clear that many kinds of experience-dependent changes can occur without depending on the MTL memory system (e.g., Kirkwood, Rioult, & Bear, 1996). The fact that there is inherent plasticity among neurons that do not directly participate in the MTL memory system indicates that there are learning and memory processes operating elsewhere and by definition, these learning effects are nondeclarative because they do not depend materially on the MTL memory system. Since neuroplasticity is primarily studied in animal models, these findings cannot tell us about the subjective experience of this form of memory. It is hypothesized that the effect of these plasticity processes are reflected as implicit memory which affects behavior without supporting the conscious experience of memory retrieval.

To understand the operation of human memory broadly, where and when these other types of plasticity occur will be important for understanding how they affect general and complex cognitive operations. While neuropsychological studies have been critical to establishing the existence of implicit memory as separate from the MTL, they have not generally been helpful in identifying where in the brain it occurs or how implicit learning and memory work (with some notable exceptions described below). Intact learning in patients with MTL damage indicates only a lack of dependency on the MTL and not in which neural systems that learning has occurred. In addition, studies that simply report intact implicit/nondeclarative memory after MTL damage have sometimes described this as the result of an intact “implicit memory system” that suggests the existence of a coherent, specialized non-MTL memory system. However, this would imply the possibility of a double dissociation in which some selective neural dysfunction impairs all forms of implicit memory while leaving explicit memory intact, which has never been observed. The approach here characterizes implicit memory not as a separate system, but as a principle of plasticity inherent throughout the neural processing circuits of the brain, an idea also proposed by Eichenbaum and Cohen (2001) and here specifically applied to the wide range of implicit learning phenomena.

To describe this alternate idea, it is useful to consider the history of memory research prior to the observation of Scoville and Milner (1957). Prior to this observation, the conventional understanding was that learning and memory were reflected in *equipotentiality* across the brain (Lashley, 1929; see Tizard, 1959 for a review). The theory of equipotentiality was applied to all cognitive functions, not just memory, and implied that higher cognitive functions could not be precisely localized in the brain, but instead reflected broad action across a neural “field.” With respect to memory specifically, this approach implied that changes in the brain reflecting memory should not depend on a specific structure such as the hippocampus, but be embedded in synapses throughout the brain. A candidate neural mechanism for this was described by Hebb (1949) by which the synapses between any of two neurons of the brain could potentially change following experience and reflect the acquisition of new memories. The idea was that this mechanism would operate throughout the brain and support memory phenomena throughout the cortex.

The idea of equipotentiality of all forms of long-term memory was refuted by the observation of patient H.M. The fact that H.M's non-memory high level cognitive functions were largely intact while the ability to acquire new long-term conscious memories for facts and events was impaired provided unequivocal evidence for localization of memory acquisition. As an added consequence, this observation suggested that other high level cognitive functions might be similarly localized within the brain. While there were known brain regions clearly associated with sensory and motor function, the idea that complex cognition depended on a specific brain region seemed initially reminiscent of the discredited field of phrenology (but see Zola-Morgan, 1995 for a reappraisal of the underlying scientific ideas). We now know that high level brain functions are indeed often supported by specific brain regions or networks. Although the functionality of these regions is not exhibited through the bones of the skull, neuroimaging of the brain can even observe changes in size and structure associated with experience and expertise (Zatorre, Fields, & Johansen-Berg, 2012).

However, in the consideration of implicit memory phenomena that are not dependent on the localized MTL memory system, it is useful to return of the idea of equipotentiality in learning in neural systems outside of the MTL. It is not implied that equipotentiality applies to all high-level cognitive processing, but that the capacity for changes in functioning reflecting memory are embedded in every circuit and connection in the brain; that is, every neural connection (synapse) has the potential to be adjusted to reflect experience. Under this approach, we should expect to find implicit learning and memory phenomena whenever perception and/or actions are repeated so that processing comes to reflect the statistical structure of experience.

The core idea underlying learning and memory functions operating outside of the MTL memory systems is a natural one for neuroscientists coming to this question from studies of the cellular neuroplasticity mechanisms. Much of the seminal work in examining neurobiological mechanisms of learning and memory comes from invertebrate animal models (Carew & Sahley, 1986) examining changes in synapses that have nothing to do with the MTL. A core functional description of basic neuronal plasticity is the same mechanism first described by Hebb (1949) that has come to be known as Hebb's Law: neurons that fire together, wire together. The idea is that temporally synchronized firing leads to synaptic change and provides a basic mechanism for learning from experience. Two key mechanisms of this process are long-term potentiation (LTP) and long-term depression (LTD), which are thought to be possible at virtually every excitatory synapse in the brain (Malenka & Bear, 2004). While these mechanisms are extensively studied within the circuitry of the MTL, experience is known to change neural function elsewhere, for example in sensory cortex (e.g., Feldman & Brecht, 2005; Buonomano & Merzenich, 1998). The operation of these mechanisms within the MTL memory system is likely to be the neurobiological underpinnings of declarative (explicit) memory. When these types of synaptic change occur outside of and independent of the MTL, they meet our definition of nondeclarative memory.

Studies of perceptual learning indicate that changes occur within the visual system as a result of experience indicating that there is plasticity even in the regions such as sensory cortex that might be expected to be most stable in their general functioning (e.g., Li, Piech, & Gilbert, 2004). Following training, firing patterns in primary visual cortex neurons change so that they are tuned to be optimized for task processing. The same types of effects are observed in primary auditory cortex (e.g., Polley, Steinberg, & Merzenich, 2006) in which neuronal firing patterns change to reflect the statistical structure of frequently experienced input patterns. The changes in neural function occur as perceptual learning proceeds, indicating that the sensory processing changes are the neural substrate of these learning phenomena. The inherent plasticity in these systems is certainly critical for developmental processes but significant plasticity is retained in the adult brain that supports additional perceptual learning.

In addition to learning within sensory and somatosensory cortical areas, there are a number of known specialized circuits that have been used to study the neurobiology of learning processes. These include the conditioned eyeblink response (Kim & Thompson, 1997) which depends on cerebellar structures, fear conditioning in the amygdala (Rogan, Staubli, & LeDoux, 1997), and habit learning in the basal ganglia (Graybiel, 2005). Each of these systems has been extensively investigated in animal models in order to identify cellular and systems-level changes associated with experience.

While these specific systems have been particularly well-characterized, the more general principle is that plasticity in neuronal connections is generally retained in adults and can support a wide range of types of learning. Studies of cellular level changes in neural activity for higher level cognitive function are obviously not possible to perform in animal models, but the pervasive plasticity mechanisms within cortical and subcortical areas suggest we can expect experience-dependent change throughout the brain. In each of the model systems used to study the neurobiology of plasticity, the changes in function reflect processing shifts to improve performance for important or frequently encountered experiences. The value of retaining this ability to shape behavior to experience should also be clearly seen as a rational mechanism for improving the overall fitness of the human organism. Some computational approaches to human cognition have argued that a more parsimonious model of memory (e.g., single system) should be preferred as a theory (e.g., Shanks & John, 1994; Berry, Shanks, Speekenbrink, & Henson, 2012). The computational parsimony approach overlooks the fact that the brain is an evolved organ and a necessary question is therefore does the ability to reshape processing circuitry provide a functional advantage that would lead to it being retained in human high-level cognition.

## 4. The adaptive nature of adaptation

Changes that allow cortical processing to adjust and adapt to experience provide a mechanism for improving functioning in an adaptive manner. Plasticity within cortical processing circuits allows experience to shape, hone and improve the efficiency of information processing in a manner that increases the fitness of the organism. As an extreme example of adapting to the environment, plasticity within sensory cortical areas allows for remapping of function following loss of sensory input (Merzenich et al., 1983). The potential for changes in sensory cortical areas in the adult brain is notable given that it might be expected that these regions would not be malleable past normal development. However, retaining the ability to change processing and shape behavior can support changes that adaptively reflect experience, leading to improvements in functional utility such as increasing the efficiency of performance. At the same time, an excessively labile sensory cortex would seem to run the risk of losing important infrequently-used perceptual abilities as the system re-organized continuously to experience. Sensory cortex does exhibit some experience-driven change even in the adult brain, although the changes happen slowly. The observation that there is cortical plasticity even in regions where change might be least likely together with the utility of adapting processing to experience suggests that the ability to shape and improve processing is a basic principle of neural organization. At the same time, we should expect some limits on this plasticity to avoid creating dysfunction in sensory or motor systems. For this reason, these implicit learning effects might be expected to accrue slowly over practice and tend to be fairly inflexible (i.e., tied specifically to training conditions).

Because we expect these changes to be ubiquitous and frequently occurring directly within the brain regions that support task performance, dissociations between implicit learning and performance will be rare. In amnesic patients such as H.M., damage to the MTL produced a dissociation between acquiring new memories and high-level cognitive functions such as language and problem solving. In perceptual or motor learning, damage to the systems involved in learning will likely significantly impair task performance as well. From this model, we would also expect the learning-based changes to be specific to experience (e.g., the training stimuli) since the sensory, somatosensory and motor cortex areas in the brain are organized in ways that reflect the environment (as retinotopic or somatotopic maps). In these core processing areas, gradual changes would allow for extraction of statistical relationships present in the environment while also avoiding destabilizing, too-rapid re-organization.

The idea that the environment presents us with a somewhat statistically structured experience to which our cognitive functions adapt was conjectured in Anderson's (1990) theory of Rational Analysis. Across several examples from human memory performance and categorization processing, experiences were shown to contain sequential or associative structure that was reflected in characteristics of cognitive function. Embedded in this approach is the fact that our human ability to adapt to the structure of the world is limited by the costs in processing, e.g., the difficulty of keeping track of all possible relationships. A notable critique of this approach (Simon, 1991) pointed out that understanding these costs requires direct study of the human processing system (the brain) rather than the advocated position of studying the environment. Characterizing implicit learning as the cognitive consequence of a continuous neural process of adaption to the environment follows in this tradition. Studying the operation of implicit learning in the brain will indicate the constraints (costs) and characteristics of the process of adapting cognitive function to the structure of the external environment in which we operate in order to improve cognitive processing.

Adaptive plasticity within every neural circuit and processing system in the brain provides a mechanism behind the concept that implicit learning is reflected in a kind of equipotentiality for change throughout the brain. While these neuroplasticity mechanisms are generally studied in animal models, the hypothesis here is that extending this principle to high-order cognitive processing systems in the human brain leads to the prediction that there will be emergent expression of implicit learning in complex vision, attention, language and problem solving. To develop this hypothesis more concretely, it will be necessary to identify properties of implicit learning and operating characteristics that are general across phenomena and also to identify which characteristics are specific to certain tasks (and circuits). To accomplish this, empirical approaches that quantify behavioral change, identify changes in neural activity and examine impairments that result from neurological damage or dysfunction will need to be used in combination. Neuropsychological studies provide the strongest causal inferences about brain regions necessary for specific forms of learning, but can be complicated by cases in which learning occurs within a processing system thus making it impossible to dissociate learning from performance. These studies are also constrained by the facts that damage to the human brain is rarely circumscribed to specific regions and that compensatory strategies can emerge. Functional neuroimaging studies provide a unique opportunity to examine changes in processing throughout the brain and identify the neural correlates of implicit and explicit memory. However, the separate and parallel operation of multiple memory systems can create a difficult challenge for drawing inferences about changes in activity that are the basis of behavior change. For example, task performance in some implicit learning tasks may not depend on the MTL memory system, but that memory system may still be acquiring explicit information during practice and thus producing correlated changes in activity. Quantifying behavioral changes under controlled experimental manipulations has provided a great deal of data about the operating characteristics of implicit learning but without information about the underlying neural systems, persistent concerns about process-purity (i.e., whether the task relies solely on implicit learning processes) are difficult to completely address. Task strategies may change within an experimental session or across participants and the need to rely entirely on subjective reporting of awareness is sub-optimal.

The current review aims to draw a set of common principles from implicit learning phenomena and studies to frame a theory of implicit learning grounded in cognitive neuroscience. The review will focus primarily on tasks and domains for which neuropsychological and neuroimaging data are available to connect learning phenomena to the general principle of pervasive plasticity. Improving the efficiency of processing based on experience should lead to characteristic neural signatures for implicit learning that can be observed with functional neuroimaging. With practice, the increasing fluidity of task execution seen in expertise should be mirrored in brain activity as a reduction in the level of evoked activity associated with task performance. Reduced activity will not necessarily be a defining characteristic of implicit learning as in some cases, e.g., the learning of new categories, we might expect to see increased activity reflecting novel types of processing acquired as a result. In addition, changes within motor cortex (for example) have been found to be a complex cascade where increased activity is initially observed followed by activity reductions. In general, the review of neural activity associated with implicit learning and memory will not identify a single consistent neural correlate of implicit learning. Instead, the general plasticity framework will be used to provide an approach to interpreting the observed neural correlates of tasks that have been found to be learned implicitly based on intact learning in memory-disordered patients and/or learned without awareness of the underlying structure.

## 5. Implicit memory in sensory cortex: Repetition priming

The most studied phenomenon in research on implicit learning and memory is repetition priming. When a recently encountered stimulus is re-encountered, it is processed differently, usually more quickly, and recently encountered stimuli also show a tendency to “pop to mind” on partial cuing (Schacter, 1987). These behavioral effects reflect increased availability of previously seen items that is a memory trace dependent on sensory cortex and not the MTL memory system. Functional neuroimaging studies of priming have fairly consistently found that the neural signature of priming is a reduction in evoked activity for the re-encountered experience (Schacter & Buckner, 1998; Henson, 2003). Priming effects have been shown for both visual and auditory stimuli (e.g., Bergerbest, Ghahremani, & Gabrieli, 2004) and also extend to facilitating processing on conceptual tasks (e.g., Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000). The reduction effect is robust enough that it has been used to map component processes in visual object processing by creating partially overlapping repeated stimulus properties to identify regions involved in extracting object structure or features (Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2000)

Evoking less activity on a repeated presentation has been described as *repetition suppression* in single-cell studies of memory processing in monkeys (Desimone, 1996). When a stimulus is re-encountered, neural firing rates are lower than they were to the initial presentation in a manner analogous to the activity reductions observed with fMRI. Theories for how processing is changed to produce repetition suppression and behavioral priming effects have suggested that neural activity in sensory cortex should exhibit either faster (shorter duration) firing, sharpening of activity in a distributed representation (in which fewer active neurons are needed to represent the same information), or improved synchronization across areas that speeds processing (Wiggs & Martin, 1998; Grill-Spector, Henson, & Martin, 2006; Gotts, Chow, & Martin, 2012). Each of these models reflects relatively subtle changes in stimulus processing that increase the overall efficiency of the system. If experience with a particular stimulus is a signal that you are likely to re-encounter this same item again in the near future, then these changes are adaptive and will lead to general improvements in processing by shaping perception to match experience.

While initial studies of priming focused on changes in sensory processing for repeated presentation, subsequent research reported a significant contribution from response learning (Dobbins, Schnyer, Verfaellie, & Schacter, 2004). This finding challenged the conventional view of priming as a solely sensory processing phenomenon, but fits in well with the model here of plasticity throughout cortical processing areas. Repeatedly selecting the same response to repeated stimuli should produce efficient re-processing in prefrontal areas related to response selection in the same way that repeated processing of sensory input evokes less neural activity. Separate components of priming the overall behavioral response can be seen across the brain (Schacter, Wig, & Stevens, 2007; Horner & Henson, 2008; Race, Badre, & Wagner, 2010). These priming effects likely also reflect changes in interactions between these posterior and frontal areas (Ghuman, Bar, Dobbins, & Schnyer, 2008) where increasingly efficient processing leads to greater cross-regional neural synchrony. Notably, some of these cross-regional effects may depend on the MTL memory system (Schnyer, Dobbins, Nicholls, Schacter, & Verfaellie, 2006) which would reflect an interesting interaction between memory types. For example, it may be necessary for the MTL to create an associative memory binding together visual and response information before implicit response learning occurs and primes the response upon re-exposure to the visual stimulus. A handful of examples of this form of memory system interaction have now been identified (e.g., contextual cuing and priming for new associations) and these are discussed below with relation to this idea of how certain forms of implicit learning could require intact MTL function.

In addition, a small number of studies have reported increased activity with priming paradigms (Henson, Shallice, & Dolan, 2000; Schacter et al., 1995) that indicate the existence of a mechanism that does not produce repetition suppression. These cases may reflect the establishment of new representations for perceptual processing that is analogous to effects seen in some visual category learning experiments (see below). While improving perceptual processing most frequently produces changes in neural processing observed as reductions in evoked activity with fMRI, the adaptive shaping of perceptual processing may be reflected in other types of activity changes as well. A key theoretical question will be to identify the conditions in which repeated exposures lead to the development of new, implicit representations rather than improving efficiency in existing neural networks.

While priming is typically observed following a single exposure to a stimulus, this memory process is likely to be related to changes in perceptual processing that occur during extended training in studies of perceptual learning. In these studies, hours of practice with specific perceptual stimuli produce improvement in processing that are generally outside of awareness (of what exactly is learned, not the stimuli themselves) and are generally very specific to the training conditions and even the training stimuli. These effects depend on changes within sensory cortical areas and therefore meet the definition of nondeclarative memory phenomena in that they do not depend on the MTL memory system. The content of the perceptual knowledge acquired is not available to awareness which further supports the idea that this type of learning depends on implicit mechanisms (Sasaki, Nanez, & Watanabe, 2010). Changes in cortical areas supporting auditory processing also reflect tuning to adapt neural processing with increased efficiency for trained stimuli (Jäncke, Gaab, Wüstenberg, Scheich, & Heinze, 2001). One idea is that repetition priming effects reflect the first step in a perceptual shaping process that over increasing numbers of repetitions leads to the development of perceptual expertise (Reber, Gitelman, Parrish, & Mesulam, 2005). However, the acquisition of expertise in a visual domain has been also associated with the development of stimulus-specific regions in the brain that emerge following repetitive practice (Bukach, Gautheir, & Tarr, 2006), a process that does not appear to rely entirely on repetition suppression effects. The examination of implicit learning mechanisms involved in this type of visual expertise have typically been explored in studies of implicit category learning.

## 6. Implicit category learning

An important way that experts exhibit knowledge of their domain is the ability to quickly and easily recognize categories and subcategories of objects within that domain. Category learning processes have been the subject of a vast number of experimental studies in cognitive psychology and it is clear that learning to make category judgments can be supported by explicit strategies, either by knowledge of categorization rules or reference to consciously learned exemplars. In addition, categorical structure can be abstracted implicitly from examples based on experience, indicating that nondeclarative memory mechanisms can also support category learning. For visual categories, learning likely depends on experience-dependent shaping processes that adapt perceptual processes to be optimized for important visual categories in the environment. Changes in sensory processing observed in priming provide a comparative example of a related memory process, but category learning is notably different in that learning is based on identifying structure across stimuli and applying this to items not previously seen. Priming and perceptual learning effects are often found to be very specific to the perceptual characteristics of studied items but category judgments need to generalize to new stimuli.

Evidence that nondeclarative memory could support category abstraction was first provided by Knowlton & Squire (1993). Using a simple category of dot patterns based on distortions of an underlying prototype, patients with damage to the MTL memory system were shown to exhibit visual category learning at the same rate as cognitively healthy older adults. Functional neuroimaging studies subsequently identified changes in visual processing areas reminiscent of priming effects that occurred following this type of category learning (Reber, Stark, & Squire, 1998a,b). After learning the category, subsequent visual processing of category members elicits less activity than non-members indicating a priming-like fluent processing for even novel stimuli from the category. A similar fluency effect was reported by Aizenstein et al. (2000) and these reductions were also found to be dissociable from explicit stimulus memorization that depends on the MTL memory system (Reber, Gitelman, Parrish, & Mesulam, 2003). Gureckis, James, and Nosofsky (2011) replicated these effects but raised concerns about the strategic approach to stimulus processing that appears to modulate the finding of fluent processing. The differences in very early visual area activity observed in categorization and recognition tasks (Reber et al., 2002) support the idea that the strategic approach to the task affects whether fluency is observed in the early stages of visual stimulus processing. These findings imply that there is an important role of top-down attention processes that affects the expression of implicit memory and the neural basis of this top-down effect has not yet been identified.

In each of these studies, the type of category learning being examined is one where the category structure is incidentally extracted from experience without instruction or feedback. While this is likely an important part of shaping perceptual processes, many fine-grained categorical discriminations are also learned via feedback. The COVIS model (Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Ashby, Ennis, & Spiering, 2007) of category learning proposed that category learning dependent on feedback could be supported by either of two systems: verbal learning and application of conscious rules (depending on the MTL memory system and prefrontal cortex) or by an implicit system that would extract categorical structure outside of awareness. The implicit category learning system is hypothesized to depend on posterior cortical areas supported by cortico-striatal circuits connecting these to the basal ganglia, specifically the caudate. To isolate and study the implicit category learning system, Ashby and Maddox (2005) and their colleagues developed an elegant experimental paradigm in which category learning dependent on explicit rule-based (RB) processes could be discriminated from information-integration (II; implicit) processes. In this paradigm, the underlying category structure is changed so that the category boundary is either easily verbalizeable (leading to rule-based learning) or not (leading to implicit learning).

In COVIS, the basal ganglia are hypothesized to play a role in both implicit and explicit category learning via different cortico-striatal connections between the basal ganglia to either frontal or posterior cortex. The basal ganglia are connected to every region of the cortex via a complex multi-synaptic circuit through basal ganglia regions (caudate, putamen and globus pallidus) and the thalamus (Middleton & Strick, 2000). These connections form cortico-striatal loops that project from cortical regions, through this circuit, and back to the same cortical region. The structure of these loops may provide computational advantages (Houk et al., 2007) and connections within the basal ganglia regions exhibit plasticity based on a three-factor, dopamine dependent mechanism (Kerr & Wickens, 2001). These synapses strengthen like cortical connections following coincident firing but only when dopamine is also present. Since dopamine is released by positive feedback (Schultz, 2002), this provides a mechanism for feedback-based learning by which the basal ganglia can support cortical learning by rapidly strengthening connections when there is an external indication that the processing was correct. Activity in the basal ganglia during the learning of categorization rules was found by Seeger and Cincotta (2005,2006) indicating a key role for this system in category learning.

The involvement of the basal ganglia specifically in implicit category learning was shown via neuroimaging by Nomura et al. (2007). Successful categorization in an II task was found to be associated with increased activity in the posterior caudate. In contrast, RB categorization was associated with increased activity in the MTL. Additional analysis based on computational modeling of the underlying cognitive processes showed that these effects were associated with posterior cortical regions for II and prefrontal cortical regions for RB, as predicted by COVIS (Nomura, Maddox, & Reber, 2007; Nomura & Reber, 2012). These findings provided an important connection from the neurally-inspired COVIS theory to empirical observations based on functional neuroimaging and demonstrated how evoked activity measures provide insight into nonverbalizeable implicit learning processes.

The neural activity associated with implicit category learning in the II task was increased levels of activity for the learned category (or learning process, which may have been continuing). An important difference between this task and the category learning paradigms that produce fluent processing is that the II learning task requires discrimination between two well-formed categories (A versus B) which is learned by feedback rather than extracting a category structure from experience (A versus not-A). In A versus B discrimination tasks, it may be necessary to form new representations (or processing regions) for the items that cluster together within a category and separate these from other categories. These new representations can then exhibit increased activity when novel stimuli from that category are subsequently experienced, leading to increased activity patterns for the learned category.

This type of mechanism provides a model for how experts can develop specific regions of cortex that exhibit selective activity for the objects within the domain of expertise. The connection between findings examining neural activity associated with category learning and the development of object recognition perceptual abilities was reviewed by Palmeri and Gauthier (2004). These processes appear to depend on important underlying mechanisms that operate implicitly within the visual system and are supported by cortico-striatal connections. However, it is notable that the development of expertise rarely occurs completely in the absence of any explicit domain knowledge. The evolution of the knowledge state of a person acquiring expertise will likely require incorporating a model of interactions among explicit and implicit processes in addition to characterizing the mechanisms supporting each (e.g., Nomura & Reber, 2012).

## 7. Probabilistic classification

Category learning requires abstraction of the underlying structure of a set of stimuli and then associating a general label with that set. A similarly structured paradigm known as probabilistic classification requires learning associations between outcomes and combinations of stimuli. This task has been shown to be learned implicitly and also to depend on the basal ganglia. In this task, sets of cues are shown to participants who then predict one of two subsequent outcomes that are arbitrarily and probabilistically associated with the cues (typically presented as “weather prediction” with rain or sun as the weather outcomes based on a set of four cards containing geometric shapes). Knowlton, Squire, & Gluck (1994) found that amnesic patients exhibited normal learning rates on this task, indicating it depends on nondeclarative memory. Subsequently, patients with Parkinson's disease (PD) were found to be impaired at learning (Knowlton, Mangels, & Squire, 1996) suggesting a critical role for the basal ganglia in this form of implicit learning.

The role of the basal ganglia in probabilistic classification learning was also observed with neuroimaging by Poldrack et al. (2001). In this study, not only was increased activity observed during learning but evidence for a competitive interaction between the basal ganglia and the MTL memory system was observed. Increases in evoked activity in the caudate occurred simultaneously with decreased activity in the MTL, suggesting that when one system was driving task performance, the other system was actively inhibited. Competition between systems could be important in contexts where there are multiple strategies, e.g., explicit and implicit, but one would produce inferior performance and should be inhibited.

Probabilistic classification may evoke a more competitive relationship between memory systems because the structure of the task requires aggregation of outcomes over multiple trials. Since the task is probabilistic, on a low but notable percentage of trials, the outcome is the opposite of the most likely outcome predicted by the cues. Relying too heavily on explicit memory for specific instances could lead to over-weighting these events and impair performance (Shohamy, Myers, Kalanithi, & Gluck, 2008). The task is structured to require gradual accumulation of the statistical information about the cue-outcome relationships in order to make the best possible predictions about future outcomes. Statistical learning is a common element of implicit learning paradigms and many tasks are based on accumulating information over trials. In contrast, the MTL memory system is optimized for learning information about individual experiences and retrieving these consciously to allow them to be flexibly applied to cognitive processing.

Competition between types of memory might be particularly expected for tasks where there are competing outcomes and only one can be selected (as in probabilistic classification and 2AFC category learning tasks). With these task demands, relying on the most accurate memory system is the optimal strategy. However, if both systems have some relevant information about prior experience, being able to combine information across systems, e.g., for the types of memory to be used cooperatively, would seem to be most efficient. The observation of inter-system competition is therefore a particularly interesting finding that suggests architectural constraints on the way information is processed. If the two types of memory function as encapsulated processing streams (as in Nomura & Reber, 2012) then combining the sources of information could be hampered by the fact that implicit processing operates outside of awareness. The exploration of interactions between memory systems is a generally less studied area but one that is becoming increasingly important as theories of multiple systems are developed and applied to complex cognitive processes such as category learning and recognition memory.

## 8. Priming, fluency and implicit recognition

Measures of recognition memory have generally provided the most sensitive assessments of explicit, declarative memory traces. A patient with a mild memory impairment arising from subtle damage to the MTL memory system may have difficulty with recall, but still perform reasonably well at recognizing previously seen stimuli reflecting some spared explicit memory. An early question about memory systems interaction is whether this relative preservation of recognition memory reflects a contribution of implicit memory via priming or whether that recognition is simply a less demanding task. Hirst et al. (1986) reported relative sparing of recognition memory in amnesic patients and interpreted this result as reflecting a contribution of implicit memory to recognition judgments. However, Haist, Shimamura, and Squire (1992) sampled memory performance over a range of delays to better control for difficulty differences and found that recognition and recall were equivalently impaired. Giovanello and Verfaellie (2001) found that repeated presentation to match difficulty produced estimates of relatively spared recognition similar to Hirst et al. (1986) while lengthening the study-test delay produced matched impairments as reported by Haist et al. (1992). Thus, repeated presentation appeared to disproportionately improve recognition memory when recall performance was matched, possibly reflecting a contribution of the patients' intact implicit memory. In contrast, when recall performance was matched by lengthening study-test delay, recognition performance tracked closely with recall. These findings suggested that the possible influence of intact implicit memory on recognition might be curiously dependent on details of experimental procedure.

Questions about parallel impairments in recall and recognition after MTL damage had previously raised something of a puzzle about possible interactions between these two types of memory. Unlike opposing categorization strategies, implicit and explicit memory for previously seen stimuli reflect almost exactly the same information about prior experience. Therefore it would not appear adaptive to rely only on one source when the other is also available and it would seem to be optimal to integrate both sources of information whenever possible. In spite of this, Stark and Squire (2000) found no evidence for any contribution of implicit memory to recognition judgments in a severely amnesic patient, even when recognition memory judgments immediately followed successful word-stem priming. That result indicated that intact implicit memory did not contribute at all to explicit memory judgments in dense amnesia. However, with healthy participants, Johnston, Dark, and Jacoby (1985) showed that manipulating fluency does affect recognition judgments. Since priming produces fluency, this effect seems to provide a mechanism for cooperative interaction whereby priming contributes to recognition. Observing additional relationships between implicit and explicit memory, Sheldon and Moscovitch (2010) proposed a theory of recollection based on this idea that would operate in two stages with a rapid unconscious process followed by a more traditional conscious deliberate search of explicit memory.

In contrast, neuroimaging measures of priming effects and recognition memory have suggested that, as in the findings from amnesia, the two types of memory operate via distinct mechanisms. Repetition priming generally leads to activity reductions in sensory cortex, while recognition generally leads to increased activity in similar areas (Donaldson, Petersen, & Buckner, 2001). A way to reconcile these findings is provided by a recent study by Voss and Paller (2009) that reported the identification of a neural signature of a condition in which implicit memory influenced recognition judgments (implicit recognition). This phenomenon was most robustly seen when participants felt they were making guess responses and had little confidence that the test stimulus had been previously seen. It was further suggested that the strategic approach used by the participants making memory judgments is critical to whether implicit memory can affect recognition judgments (Voss & Paller, 2010). In typical experimental settings where participants attempt to make maximally accurate responses with high confidence, the role of implicit memory may therefore be reduced or inhibited. The effect of confidence and task instructions to adjust endorsement criteria suggest that top-down executive control processes influence the degree to which the types of memory interact during recognition. The importance of executive control does not fully explain the inability of severely amnesic patients to bring implicit memory to bear on supporting recognition judgments. An intriguing possibility is that this interaction between types of memory requires some residual function within the MTL memory system, raising the idea that some forms of implicit memory may operate on MTL-dependent memory traces. That is, only after initial acquisition of an MTL-dependent explicit memory trace can subsequent implicit memory mechanisms (i.e., priming) operate to guide behavior without awareness.

Evidence in support of this type of memory system interaction is observed in the impairment seen following MTL damage using the paradigm of priming for newly acquired verbal associations (Shimamura & Squire, 1989; Paller & Mayes, 1994; Verfaellie, Martin, Page, Parks, & Keane, 2006). In this paradigm, participants first learn a memorable sentence such as “the HAYSTACK was lucky because the PARACHUTE failed.” Subsequently, they are exposed to a word pair in a priming condition, “HAYSTACK-PAR” and when responding with the first word that comes to mind, tend to produce the primed word “parachute.” For this effect to occur, the initial sentence has to be learned explicitly and is thus dependent on the intact function of the MTL memory system.

However, once learned explicitly, it appears that priming of the word “parachute” can follow perception of “haystack” without needing the memory of the original sentence to come to mind consciously. Therefore this appears to reflect a priming effect based on implicit memory association occurring across elements of a recently acquired explicit memory representation. In these studies, the neuropsychological evidence has been difficult to interpret strongly due to lingering concerns that participants without MTL damage might have some weak explicit memory that leads to slightly better performance than amnesic patients. In that case, the impairment observed in patients with MTL damage could reflect intact implicit learning and the deficit in performance was due to the lack of a contribution from explicit memory. However, the hypothesis presented here is that these findings could also be due to the existence of priming effects based on implicit memory operating on these recently acquired declarative memories.

This description of memory system interactions somewhat blurs the dissociation between implicit and explicit memory, but follows from the broader idea that implicit learning phenomena are universal through cortex and even present in cortical representations of conscious memories. The possibility that the MTL plays a role during tasks that appear as implicit memory (i.e., without awareness) has been suggested to undercut the core conception of the standard model of memory systems in the human brain (Reder et al., 2009; Hannula & Greene, 2012). The approach to memory systems presented here is sufficiently flexible to account for these findings that otherwise do not fit neatly into the declarative/non-declarative taxonomy, without rejecting the general utility of this anatomical distinction.

Allowing for plasticity throughout the brain provides the possibility of statistical learning or priming of MTL-dependent (declarative) representations that produce effects that are still outside of awareness (of the statistics or source of priming) and implicit although the MTL memory system is necessary. The current framework for implicit learning presented here accommodates findings of priming of new associations, implicit recognition and priming-response learning without abandoning the useful heuristics of subjective experience and anatomical dependence for identifying contributions of implicit and explicit memory. However, evidence for these interactions is currently based on just a few paradigms and untangling overlapping contributions of multiple types of memory on behavior will be challenging and likely require strongly hypothesis-driven neuroimaging studies. Another well-studied example of a phenomenon that appears as implicit learning dependent on intact function of the MTL is the paradigm of contextual cuing.

## 9. Contextual cuing

In a contextual curing paradigm, participants are asked to search for a target hidden among a number of similar cues in a relatively standard search paradigm used to study visuospatial attention. Participants are not told that some of the displays are repeated and yet memory for the prior display is exhibited by a faster search time for the repeated arrays (Chun & Jiang, 1998). Unlike other implicit learning phenomena, damage to the MTL memory system leads to impairments in contextual cuing (Chun & Phelps, 1999; Manns & Squire, 2001) suggesting a more complex interaction between memory systems than in most implicit learning tasks.

The neural correlates of contextual cueing were examined in Greene, Gross, Elsinger, and Rao (2007) and found to include increased activity in the MTL for repeated arrays, even though participants were subsequently unable to consciously recognize the repeated stimulus arrays. The increased MTL activity is consistent with the findings from studies with patients with amnesia following MTL damage and the idea that the MTL is critical for this implicit memory phenomenon. In contrast, Westerberg, Miller, Reber, Cohen, and Paller (2011) manipulated the amount of explicit knowledge available to healthy participants during contextual cueing and found that activity in the MTL was increased for participants with high levels of explicit knowledge, but all participants showed reduced activity throughout ventral visual areas for repeated stimulus arrays. The reductions in activity were correlated with the magnitude of the cuing effect, suggesting a more traditional learning effect leading to increased efficiency in processing in the expression of the implicit learning in the contextual cuing paradigm.

The pattern of evoked activity observed in Westerberg et al. (2011) does not rule out the possibility that the MTL memory system is necessary to observe contextual cueing. The initial acquisition of a memory trace for the stimulus array may still depend on the MTL memory system but the subsequent fluent processing effect for re-presentation of the array occurs by priming this memory without conscious retrieval. This account is consistent with the idea that phenomena normally characterized as implicit learning might operate on MTL-based declarative memories. Even these MTL-dependent memories could pop to mind if primed and MTL retrieval processes themselves might come to be shaped by the statistics of experience with memory use. The shaping of memory use to match experience is a core idea behind the *rational analysis of memory* (Anderson & Schooler, 1991) in which it was shown that the statistics of experience predicted the availability of declarative memory. Of note, the accumulation of the memory use statistics is not thought itself to depend on conscious counting or calculation of the patterns of memory retrieval, but instead to reflect changes in activity levels (predicting speed and probability of retrieval) that are intrinsic to the retrieval process and represented outside of awareness.

By presenting implicit learning as a universal principle of plasticity throughout the brain, the framework here provides a way to account for phenomena like contextual cueing that are not easily incorporated into taxonomies defined solely by a key neural system materially supporting the process. However, we also avoid depending entirely on measuring subjective conscious experience since the effects of the underlying plasticity supporting implicit learning produce changes in neural activity that can be observed in functional neuroimaging studies. Even with neuroimaging, testing and characterizing the effects of implicit learning on explicit representations will be challenging due to the inability to rely on clearly interpretable evoked activity in the MTL that is normally a signal of explicit/declarative memory. The development of empirical protocols that show clear separation of memory types will be critical to identify consistent neural signatures of each memory type and support studies of how forms of memory may interact in tasks such as contextual cuing, implicit recognition (above) or complex skill learning.

## 10. Motor and sequence learning

An area of implicit learning in which the dissociation between improved performance and awareness is particularly clear is in motor learning. Practice improves motor performance in a rapid and easily observable way, but the basis of improvement generally cannot be verbally described. Studies of the neural basis of motor learning have produced abundant evidence for experience-based reshaping of activity within motor and motor planning cortical areas. Repeatedly executing a motor response sequence produces changes in activity in motor cortex and associated regions of both the basal ganglia and cerebellum (Ungerleider, Doyon, & Karni, 2002). These changes have inspired a model of motor learning based on two components (Doyon, 2008): a fast (immediate) and slow (consolidated) motor skill learning in which there are differential contributions of cortico-striatal and cortico-cerebellar circuits. Of note, a common finding in many of these neuroimaging studies is that practice leads to increased or more broadly distributed activity in the motor cortex and related structures. These changes have been interpreted as dynamic reorganization within motor control networks, but are notably different from the decreased activity observed following priming and category learning. The increased activity may reflect the emergence of regions supporting expert execution of the practiced skill or may potentially reflect the consequence of improved performance (e.g., faster movements that evoke more neural activity). In addition, most of the studies that have looked at motor reorganization have used paradigms where initial performance was supported by explicit knowledge of the sequence to be practiced. When performing a sequence following explicit instruction, the practice effects may reflect a mix of both explicit and implicit memory contributions.

The canonical task for selectively examining implicit motor skill learning is the Serial Reaction Time (SRT) task originally reported by Nissen and Bullemer (1987). Practice with the SRT task produces learning effects that are acquired at a normal rate by amnesic patients (with MTL damage) and are generally largely outside awareness in healthy participants. In the SRT task, participants make a series of motor responses to sequentially presented visual cues. The cue typically appears in one of four locations and the motor response is to press one of four corresponding response buttons (keyboard keys). After the correct response is made, the cue re-appears in another location after a brief delay (typically 250–500 ms) and participants continue to make a response to each re-appearance of the cue based on its location. Participants are not told that the cues follow an embedded repeating sequence and the sequential cue location essentially paces them through covertly practicing a sequence of motor responses. The effect of practicing is reflected in gradually decreasing reaction times (RTs) for each response. Knowledge of the specific embedded sequence is assessed by administering a series of cues that no longer follow the repeating sequence and measuring how much slower the RTs are. Patients with anterograde amnesia exhibit normal learning on this task (Nissen & Bullemer, 1987; Reber & Squire, 1994, 1998) in spite of not being able to subsequently recognize or identify the repeating sequence. Cognitively healthy participants also exhibit learning without awareness to a degree, but participants with an intact MTL memory system frequently acquire some explicit sequence knowledge of the embedded sequence during practice (Shanks & Johnstone, 1998).

The tendency to acquire explicit knowledge of the sequence has led to an extended debate on the degree to which performance improvements on the SRT task can be strongly tied to implicit learning for participants with an intact MTL memory system. From a memory systems perspective, the fact that learning is often not process pure (i.e., may be affected by both implicit and explicit memory) provides a challenge but not an insurmountable one. The first question is whether perceptual-motor sequence learning can occur in the absence of explicit knowledge. Evidence from learning by memory-impaired patients and the few studies that have managed to identify learning completely without awareness (Destrebecqz & Cleeremans, 2001; Sanchez, Gobel, & Reber, 2010) indicates that it can. Beyond this, the question is to identify the neural basis of implicit sequence learning and since there is a general tendency for concomitant explicit knowledge to be acquired, how these types of memory interact during skilled performance.

There have been a number of studies that have looked at neural activity evoked during SRT performance to examine the neural correlates of learning to perform the trained sequence better than untrained sequences (e.g., Grafton, Hazeltine, & Ivry, 1995; Rauch et al., 1997; Willingham, Salidis, & Gabrieli, 2002; Schendan, Searl, Melrose, & Stern, 2003; Seidler et al., 2005). The most consistent finding across these studies is an increase in activity in the basal ganglia during performance of the trained sequence as well as increases in cortical areas related to motor planning (Peigneux et al., 2000). These may reflect the signature of implicit learning in a motor sequencing domain and one that potentially parallels the development of visual expertise. Whereas implicit visual category learning via feedback is supported by posterior cortico-striatal loops between the posterior caudate and visual areas, perceptual-motor sequence learning may be supported by more anterior cortico-stiatal loops between the caudate and frontal cortical regions involved in motor function.

However, a challenge for identifying the neural signature of implicit learning in the motor domain is the fact that the expression of knowledge produces changes in task performance that may be difficult to separate from learning effects. For the SRT task, learning is exhibited by decreasing reaction times, but these faster reaction times themselves may be associated with eliciting different levels of motor activation. This raises the possibility that there are other brain regions that materially support sequence learning and the changes in motor activity reflect a consequence of this learning rather than the neural basis (Orban et al., 2010). Separating performance effects from learning effects is a challenge for many studies of implicit learning because of the potential for these effects to be within the same regions supporting basic task performance (e.g., sensory or motor cortex).

One way to attempt to better separate learning and performance effects is to use a task that does not depend on an RT measure to demonstrate knowledge of the implicitly learned repeating sequence. The Serial Interception Sequence Learning (SISL) task also guides participants through a covertly embedded repeating sequence of cues but requires a precisely timed response to a moving cue rather than a rapid response to cue appearance. This relatively new paradigm for examining implicit perceptual-motor sequence learning produces robust implicit sequence learning with low levels of conscious sequence knowledge even in healthy participants (Sanchez et al., 2010). A key difference between SISL and the SRT task is that the cues to the motor response appear on the screen moving vertically and participants attempt to make a motor response that is timed to intercept the cue as it crosses a target region. The presentation of cues is visually similar to a number of popular video games that use many simultaneously presented, rapidly moving cues and thus require sequential motor responses executed at a fast pace. The speed of the SISL task is adaptively adjusted for each participant to guarantee an average level of performance during training for which improvement or decline can be measured (e.g., ~75% correct). A repeating sequence of responses is covertly embedded in the same manner as the SRT task. Knowledge of this sequence is measured by contrasting performance during the repeated sequence and untrained sequences in a manner similar to the SRT task but using accuracy in responding as the dependent measure.

The experience of participants is very different in the two tasks. Because the SRT task is a wait-and-respond choice-RT task, participants spend the majority of the task time waiting for the next cue to appear. In the SISL task, cues are continually moving at a fairly rapid rate across the screen and this presentation appears to keep participants consistently engaged in task performance and seemingly with less time to attempt to identify or memorize the repeating sequence. In addition to producing robust implicit learning with low levels of explicit sequence knowledge, participants can learn sequences up to 80 items long in 2 h of training or extract the sequence from among high levels of irrelevant noise trials (Sanchez & Reber, 2012). Training appears to be fairly specific to practice with selective disruption of inter-response timing leading to virtually no expression of knowledge even when the same sequence of responses are required (Gobel, Sanchez, & Reber, 2011). Providing participants with explicit knowledge of the repeating sequence prior to training does not improve learning rate (Sanchez & Reber, 2013) indicating that performance is generally dependent on implicit learning with little explicit memory contribution.

Examining the neural correlates of implicit perceptual-motor sequence learning using the SISL task, reduced activity was found throughout cortical areas associated with motor control and task processing (Gobel, Parrish, & Reber, 2011). Increased activity was found in the basal ganglia, reinforcing the idea that cortico-striatal connections are critical for the cortical learning effects. The consistent importance of the basal ganglia across sequence learning tasks is further supported by the findings of impaired perceptual-motor sequence learning in patients with PD and resulting dysfunction of the basal ganglia (Siegert, Taylor, Weatherall, & Abernethy, 2006; Gobel et al., 2013). The difference in patterns of cortical activity (decreases versus increases for trained sequences) raises a question about whether the neural representation of implicit learning is reorganization to facilitate sequential performance or to represent new, trained motor plans. While the role of either (or both) of these mechanisms is not yet well understood, implicit learning in the motor domain appears to follow the same basic principles as other domains in that cortical processing is adaptively modified to improve performance following practice.

Another challenge in interpretation of evoked activity during sequence learning is the observation of increases in the MTL (Schendan et al., 2003) during sequence learning tasks. This could reflect a contribution of the MTL to sequence learning or may potentially reflect the concomitant development of explicit memory that often occurs in healthy participants (e.g., Sanchez et al., 2010). To assess whether this explicit memory plays an important role in improving task performance, Sanchez and Reber (2013) provided participants with full explicit knowledge of the repeating sequence prior to practice on the SISL task. No benefit was observed to sequence learning suggesting that the availability of explicit knowledge does not routinely contribute to implicit learning performance (note that in other tasks, like the SRT, explicit knowledge can change the strategy used for the task and lead to improved performance). Future research examining interactions among implicit and explicit memory for skill learning tasks will be needed to additionally clarify the roles of the neural systems that appear to support sequence execution (cortico-striatal circuits) and explicit task knowledge (MTL) and how they might contribute to complex skill learning processes.

The perceptual-motor sequence learning results described here are generally based on experimental paradigms that have used covertly embedded repeating sequences of cues. Another approach to studying sequence learning has been to use a complex set of rules to create sequential structure in motor responses (e.g., Cleeremans & McClelland, 1991). This alternate approach likely depends on the same implicit learning mechanisms within motor planning areas but was inspired by the first paradigm to be associated with the term implicit learning: artificial grammar learning (Reber, 1967).

## 11. Artificial grammar learning

The origin of the term implicit learning comes from an attempt to describe the subjective experience of participants who completed the artificial grammar learning (AGL) paradigm. In this paradigm, participants are shown strings of letters that are non-words but are constructed based on a finite state grammar. Participants are not informed of the underlying grammatical rules or method of constructing of the letter strings, but observe the set of strings during an unrelated task (e.g., copying from short-term memory). After exposure to the training set, participants are then told that the strings that had been previously seen were all constructed according to a hidden set of rules and they will now be expected to try to judge whether new strings follow those rules or not. Although participants are unable to describe the underlying rules, they are able to guess whether new strings follow the grammar's rules at a rate better than chance. The inability to describe the rules prior to successful discrimination of rule-following strings led to this phenomenon being described as the participants having implicitly learning the underlying rules (Reber, 1967, 1989).

Patients with anterograde amnesia due to damage to the MTL exhibit learning on the AGL paradigm that is similar to healthy older adults (Knowlton, Ramus, & Squire, 1992), indicating that this type of learning depends on nondeclarative memory. However, like the SRT task, further examination of learning in participants with an intact MTL memory system indicates that although verbalizeable knowledge of the underlying rule system is rare, there may be enough explicit memory of the study items to support grammaticality discrimination (e.g., Perruchet & Pacteau, 1990). The task is designed to capture the kinds of sequential symbolic processing thought to be crucial to the acquisition of language processing, but relatively little is known exactly about the content of learning in the AGL paradigm (Pothos, 2007). For example, it is unclear whether AGL reflects a process similar to those in category learning tasks that enable discrimination of rule-following strings from others, or if AGL is essentially a sequence learning task operating on symbols (letters) rather than motor responses.

A few neuroimaging studies have attempted to identify the neural correlates of AGL but have not identified a consistent candidate for the neural basis of this type of memory. Skosnik, Gitelman, Parrish, Mesulam, and Reber (2002) compared judgments of string grammaticality following AGL to judgments of recognition memory and reported differential activity in posterior parietal cortical areas. The increased activity for grammaticality was interpreted as reflecting the representation of sequential relationships among the letters and the regions exhibiting this effect have also been associated with language and general symbolic (math) computation. However, Lieberman et al. (2004) examined neural activity in AGL and reported key increases in the basal ganglia for grammatical items. While the basal ganglia have been seen to be involved in a number of implicit learning paradigms, the fact that patients with PD are able to perform AGL at a normal rate (Reber & Squire, 1999) suggests that the basal ganglia are not critical to this form of implicit learning. The differing results are difficult to integrate since it might be the case that the basal ganglia play an important role in healthy participants while patients with PD adopt a compensatory, explicit strategy to perform the task. Interpretation of the differences between studies will likely depend on a better characterization of exactly what information is extracted from the study items that supports the judgments made in an AGL task.

While the exact approach that healthy adults take to a complex learning task like AGL is unclear, a simplified version of the paradigm has been used in very young children to show the existence of a mechanism of statistical learning for language-like stimuli (Saffran, 2003). This type of learning is necessarily nonverbalizeable as it is observed in pre-language children. It is hypothesized that this phenomenon depends on similar implicit learning mechanisms to those that support AGL in the adult brain and therefore that this type of learning plays an important role in development of language in infancy. In this paradigm, infants are exposed to simple sequences that follow a statistical structure and subsequently exhibit preferential listening that indicates they have learned the underlying structure (Saffran, Aslin, & Newport, 1996). While the neural correlates of this process are not known, the phenomena indicates a role for implicit learning among relatively abstract stimuli and a role for mechanisms of implicit learning beyond sensory and motor cortical regions. This type of learning in infants is typically referred to as *statistical learning* although the statistics required are much simpler than would be needed to capture a typical finite state grammar in an AGL paradigm. Perruchet and Pacton (2006) explicitly compared statistical learning and artificial grammar learning paradigms and noted the similarity between approaches in spite of differences in terms used to describe the information learned (transitional probabilities versus sequential chunks). The mathematical approaches used to characterize learning in these two domains vary in assumptions about the types of processing carried out in the brain. Determining the operation of the underlying mechanism will likely depend on incorporating information about the computations carried out in the neural circuits supporting these kinds of memory.

## 12. Principles of implicit learning

Gradually learning across experience to extract statistical co-occurrences among environmental stimuli (or features) is a core idea across implicit learning tasks. It is hypothesized that this information is accumulated in regions associated with processing stimuli or producing responses, which leads to this implicitly acquired information being outside of conscious awareness. The model of implicit learning presented here is that pervasive and inherent plasticity throughout the human brain allows for this kind of gradual statistical abstraction within every cognitive processing domain. In every brain region, neural function is adaptively modified to improve future processing to reflect the regularly experienced demands of the environment.

This type of learning stands in contrast to the rapid learning of individual events that is the goal of the highly specialized and complex circuitry of the MTL memory system. The hippocampus and adjacent cortical areas support storage of specific individual episodes or events that can be retrieved consciously and in detail. McClelland, McNaughton, and O'Reilly (1995) pointed out that representing information in a distributed system (e.g., across a large population of neurons), rapid acquisition of new memory traces runs the risk of catastrophic interference such that new learning destroys previously acquired information. Rapid acquisition requires specialized circuitry that in the human brain is instantiated in the MTL memory system. This system likely has a much lower overall storage capacity as a consequence and explains the need for a gradual consolidation process by which information is stored durably into a separate long-term episodic memory (O'Reilly et al., 2011).

In contrast, distributed representation of information that is accumulated incrementally over a number of repetitions allows for extraction of underlying statistical structure and also leads to more efficient storage of large amounts of information. In a distributed system, the efficiency produced by this slow learning allows for generalization to novel, similar items in a way that would support categorization processes. This type of memory storage is relatively easily captured by local learning mechanisms that could be operating based on relatively simpler neurobiological mechanisms (compared to the MTL) within cortical processing networks, consistent with the idea that these mechanisms are available everywhere throughout the cortex and in many connections to subcortical regions. Local learning mechanisms making small, incremental changes in visual processing have also been shown to potentially account for repetition priming effects which, unlike most other implicit learning paradigms, are observable after a single experience (Stark & McClelland, 2000). Thus the same neural plasticity mechanism based on small changes in a distributed network may support both the rapidly observable effect of repetition priming and the gradual development of visual skill over many trials of training (e.g., Reber et al., 2005).

Across brain regions, implicit learning effects do not produce a single characteristic signature of evoked neural activity. Repetition suppression and fluent processing of trained stimuli are observed to occur in sensory and motor cortices and lead to reductions in evoked activity for trained stimuli. Increased activity is observed associated with learning that reflects organization of neural regions that represent new information that has been learned (e.g., by abstraction of environmental structure). Increased activity effects have also been observed in paradigms in which the basal ganglia play an important role in supporting learning. In visual category learning paradigms, the contribution of the basal ganglia may be related to learning via the feedback provided during training. In motor learning, experimenter-dependent feedback is often not provided, but since participants are likely aware of their relative success in performance, they may internally produce feedback signals. Alternately, the more direct role of the basal ganglia in supporting sequential behavior in motor planning may not require a feedback signal to support learning.

The role of the basal ganglia in several forms of implicit learning has occasionally caused it to be identified as a candidate structure for a coherent implicit memory system. The approach here explicitly rejects the idea of a specific and localizable implicit memory system that is solely responsible for the phenomena identified as memory without awareness. There are a number of implicit learning and memory phenomena that clearly do not depend on the basal ganglia (e.g., Reber & Squire, 1999). In addition, the basal ganglia also play an important role in several kinds of non-memory processing (e.g., reward processing, working memory) that indicate that it is not solely a memory system. Applying the term “implicit memory system” to this neural system is essentially a misnomer. The basal ganglia may influence several forms of implicit learning by its influence on cortical plasticity via cortico-striatal circuits, but some sensory and more abstract cortical learning processes do not depend on this system. The more comprehensive view here of implicit learning as a principle of plasticity that broadly includes a wide range of ways in which experience shapes cognitive processing to adapt to the statistics of the environment.

The breadth of potential changes following implicit learning pose an interpretation problem for diagnosing the role and mechanism by which this type of memory influences behavior using solely neuroimaging data. Because changes are not in one brain system (or even in a single direction), a specific neural signature of all types of implicit learning cannot be identified. Further, without the constraints from neuropsychological studies, interpretation of fMRI data can be complicated by the ability of healthy participants to remember the training context, irrelevant task details or if they become aware that they are improving on the task (i.e., the creation of any concomitant explicit memory not contributing to task performance). Remembering this extra contextual information depends on the MTL memory system and may result in observations of increased activity in that brain region even during an implicit learning task. For example, in Sanchez and Reber (2013) the availability of explicit memory did not lead to any direct benefit to the implicit learning process. In this context, increased MTL activity might reflect explicit memory that does not contribute to performance and is entirely independent of implicit learning.

Some neuroimaging studies with healthy participants have reported increased MTL activity during typical implicit learning (e.g. sequence learning in Schendan et al., 2003) or statistical learning paradigms (Turke-Browne, Scholl, Chun, & Johnson, 2009). It is unclear if these observations of MTL activity reflect this type of concomitant explicit memory or if they reflect a more interesting interaction such as statistical shaping of the use or valuation of explicit memories (e.g., Wimmer & Shohamy, 2012). Neuropsychological data about the effects of MTL damage can provide a useful constraint in this case. If memory-disordered patients exhibit normal learning after MTL damage, this is evidence for the MTL activity being related to memory processes that do not contribute directly to task performance. Data about explicit memory for key task information and its relationship to performance can be used as an extra constraint as well. Partial explicit memory is often observed in healthy participants following implicit learning but not consistently or correlated with overall learning (e.g., Sanchez et al., 2010). In neuroimaging, behavioral-activity correlational approaches may eventually be able to provide additional information to clarify the interpretation of complex patterns of brain activity data.

The potential ambiguity of many of the signals of implicit learning have therefore led some (e.g., Henke, 2010; Konkel & Cohen, 2009) to suggest a more direct focus on the characterization of the underlying learning processes (processing modes). Understanding the operating characteristics of implicit learning and how these differ from explicit memory is obviously critical to understanding human memory broadly. However, the challenges posed by the interpretation of implicit learning hallmarks should not lead us to overlook that measures such as conscious subjective experience and the role of the MTL are useful signals in most memory studies. Learning without awareness almost always indicates a basis in neural systems outside the MTL and although there are exceptions to this, it is a useful starting hypothesis. The fact that evoked activity in the MTL is difficult to interpret means drawing a reverse inference from fMRI data will be difficult (e.g., concluding that participants used implicit/explicit memory in a task based on absence/presence of MTL activity). However when task manipulations or behavioral measures support the identification of memory system use, these usefully constrain the interpretation of neuroimaging data (e.g., Reber et al., 2003; Nomura et al., 2007). In addition, the accumulation of data across studies will likely support stronger reverse inferences of this nature through Bayesian approaches that strengthen the connection between evoked activity and behavior across studies (Poldrack, 2006). As we come to better understand how different neural signatures emerge from the consequence of plasticity in all brain regions, we may be able to identify how potential specific neurobiological mechanisms that vary across the brain are related to the operating characteristics of implicit learning.

The lack of a distinct neural signature for the expression of implicit memory should also not be seen as an indication that the model of implicit learning presented here cannot be falsified. The idea of pervasive plasticity across the brain implies that there is not a single neural system that materially supports all implicit learning phenomena. It has been argued here that no such system has yet been identified but if it were, significant revision of the current theoretical approach would be needed. In addition, the idea of intrinsic plasticity throughout the brain is an important foundation to this approach. If future neuroscience research identifies the absence of significant long-term plasticity in high-level regions of the human cortex, the current framework would not provide additional predictive or interpretational value over theories based on a taxonomy of specific learning circuits. However, the current model provides an effective description of a broad range of the implicit learning phenomena that have been described. The framework proposed further allows for integrating results across paradigms to allow for studying implicit learning in the context of what plastic changes occur and how they interact with explicit memory and complex cognitive processing.

Being able to integrate approaches across behavior, neuropsychology and neuroimaging has depended on the development of unusual laboratory tasks that emphasize implicit learning and allow for experimental control over participants' strategies. This has popularized a handful of specific paradigms that in some cases have become synonymous with implicit learning phenomena. While these tasks are optimized for basic scientific study of memory systems, the process being studied is thought to play an important role in complex cognitive tasks, particularly cognitive skill acquisition. The characterization of implicit learning facilitates observation of contributions from this kind of learning in a variety of domains not typically thought of as implicit learning tasks. In these contexts, in addition to the contribution of implicit learning, there is a need to develop a theory of interactions among types of memory to understand how these neurally distinct processes can both influence behavior.

## 13. Implicit learning in complex cognition

Although laboratory studies of implicit learning use somewhat peculiar tasks (AGL, SRT, SISL) in an attempt to examine memory in a relatively process-pure context (i.e., implicit learning with relatively little explicit learning), the theory that changes occur everywhere in the brain means that implicit memory phenomena should be ubiquitous in daily life. However, the fact that these changes occur outside of awareness means that while implicit learning is going on continuously, we are generally unaware of the operation of these learning mechanisms. Instead, we can identify effects on behavior that reflect this kind of learning and see that implicit memory is an intrinsic part of our daily functioning.

The most obvious context in which to look for effects of implicit learning are tasks for which we learn or improve through repetitive practice. Physical and cognitive skills are routinely trained by practice and performance obviously improves with repetition. While there has been much theoretical debate over the past 40 years about the existence of learning outside of awareness, during this time, nobody has questioned the fact that when a child is taught a cognitive skill like long division, they are explicitly instructed in the procedure—and then given pages of worksheets to practice executing the procedure. If all learning were explicit, there would be no need to practice and yet it is undisputed that practice is needed to hone all forms of skill. While definitions of subject conscious experience are difficult to pin down precisely, our performance improves following practice and there is something intrinsic to this experience that we cannot report. Looking for the basis of improvement in the neural structures of the human brain, neuropsychological studies clearly show that this kind of learning is not supported by the same structures that support the experience of explicit memory (the MTL memory system). The core findings within the study of implicit learning are essentially showing that the mechanisms that support practice-based improvement also support extraction of environmental structure that can appear in tasks like artificial grammar learning, perceptual-motor sequence learning, probabilistic classification and category learning.

In complex real-world cognitive tasks, we should expect that overall improvement reflects a combination of types of memory. In the domain of music, this is elegantly described as the need for two entirely separate tasks required to prepare to perform in front of an audience (Chaffin, Logan, & Begosh, 2009). First, a piece is learned to be performed through repetitive practice that likely depends largely on implicit learning. Second, the musical structure of the piece is explicitly memorized by breaking it down hierarchically and studying the written music. Performers intuitively realize these to be separate, independent processes (the opening passage of the above citation laments the inadequacy of the single word memory to capture both processes). The former is based on improving accuracy and fluidity via implicit learning from repetition and the latter depends on explicit memory and the MTL memory system. From a memory systems perspective, we can propose hypotheses about the neural basis of the each type of memory, but are immediately faced with questions about the role of interactions between the systems that are relatively less well understood. The two types of memory may operate completely independently, but it is also possible that explicit knowledge guides practice to improve training and/or that practice to a fluid, habitual state enhances the memorization process.

Framing complex skill learning as dependent on both types of memory raises a critical question about the neurocognitive architecture that allows these types of memory to interact with each other. Interactions between implicit and explicit learning are very likely embedded in many other cognitive processes where learning occurs with practice. Reber and Kotovsky (1997) reported improving performance without awareness in a challenging puzzle problem-solving task for which the solution sequence was well-structured but difficult to deduce explicitly. Practice with the puzzle led to dramatic improvement in solution time in spite of participants' reports that they did not know how they were solving the puzzle. This type of automatic, implicit learning of sequential structure may contribute to other areas where problem solving is accomplished through a regular sequence of steps. Gross and Greene (2007) reported an effect of implicit learning on observations of analogical transfer in which participants extracted an abstract relational structure in a transitive patterning task and applied it to a novel stimulus set without reporting awareness of the analogy. Influences of implicit learning within complex problem solving indicate that these effects are likely to be an important component of highly skilled performance in complex tasks (e.g., underlying the intuitive knowledge of experts). One of the challenges of identifying the contribution of implicit learning to complex skill learning domains is that the lack of awareness of the implicit information by experts may generally lead to an inordinate focus on the explicitly learned knowledge and a relative lack of attention to the contribution from implicit learning.

Considering expertise as the result of interactions between both implicit and explicit learning processes should not be seen as counter to the core idea that these types of memory are distinct. Many areas of complex behavior rely on brain systems that are separate but operate in a cooperative fashion. For example, reading requires both visual and language processes and the interaction between these processes does not imply that vision and language do not depend on distinct types of processing within the brain. In complex skill learning, interacting systems for memorization of skill instruction and learning from the honing of performance through practice likewise do not imply these two processes are part of a single neurocognitive system. Understanding how neural and cognitive processing are shaped by experience separate from conscious memorization requires examination of the specific implicit learning processes that support this.

If repetition always produces improved cognitive processing through implicit learning processes, we should expect to find these effects in otherwise surprising contexts. A possible example of such an effect is the improvement in visuospatial ability that is observed after training in action-based video game play (Green & Bavalier, 2003). Core visuospatial abilities were not previously thought to be amenable to improvement by training, but after 10 h of video game practice, reliable improvements on novel visuospatial attention measures were observed. It is notable that the training experiment was inspired by the observation that measures of visual selective attention were higher in regular video game players who had apparently inadvertently been training their visuospatial attention abilities while playing. Prior to this study, however, nobody was aware that this kind of learning was going on, which is fairly strong support for this phenomenon to be based on implicit learning mechanisms.

A practical application of a memory systems approach that incorporates implicit learning during practice is in studies of effective rehabilitation following stroke. Boyd et al. (2007) examined implicit learning in patients attempting to recover motor function following damage. Rehabilitation is generally accomplished through extensive repetition and key questions about prognosis and success likely depend on intact implicit learning within the damaged motor system. The rehabilitation process is probably supported by the same improvement from practice mechanisms as motor skill learning in healthy participants, but the stroke-related damage to the physical performance system places significant constraints on how much improvement can be obtained.

Another area of particular recent interest in applied training-based improvement is in the recent reports of improving fluid intelligence through practice with a working memory (WM) task (e.g., Jaeggi, Buschkuehl, Jonides, & Shah, 2011). While WM is known to be a core cognitive function that contributes to a range of complex cognitive processes and fluid intelligence measures, it had been generally thought that WM capacity was a fixed constraint on cognition. However, a recent review by Morrison and Chein (2011), described a wide range of training studies with positive effects following extensive (8+ hours) practice on WM tasks. The most effective training methods appear to be those that depended on repetitive practice at a high level of difficulty (termed *core training* in their review). The role of repetitive practice and the unanticipated nature of the training effects both support the idea that implicit learning mechanisms also operate with WM neurocognitive networks to improve this cognitive function.

The approach of seeing the basis of implicit learning as pervasive plasticity throughout the human brain implies that effects like improvements following WM training or video game play should be observed more commonly as we realize we should be looking for them. Since this kind of learning is not based on an intention to learn, we can expect that experience is always subtly reshaping our perceptions, actions and thought processes. When our experience reflects consistent statistical structure, these implicit learning mechanisms adaptively modify processing to make it more fluid, more rapid and more accurate.

## 14. Conclusion

Because implicit learning is reflected in changes that are outside of awareness, it is impossible to subjectively estimate the relative magnitudes of our memory experience that depend on implicit or explicit memory. Our everyday experience of memory is largely retrieval of previously acquired facts and events, explicit memory that depends on the specialized circuitry of the MTL. Our awareness of this retrieval gives the impression that this is the bulk of our daily experience of memory. In contrast, implicit learning does not depend on a single circumscribed neural system but instead occurs in changes within processing systems across the brain. These ubiquitous changes result from plasticity within all the neural circuitry of the brain, not just the MTL memory system. While changes from individual experiences are likely to be relatively small, the breadth of the systems exhibiting this change suggest that a large fraction of the changes in neural systems that reflect experience are likely due to implicit memory processes.

Changes in speed and efficiency of processing are one particularly visible manifestation of the implicit learning process that emerges from experience, particularly repetition. Studies of implicit learning in perception, language, category learning and sequencing indicate that these changes also support extraction of the statistical structure of the environment beyond simple repetition. By extracting statistical relationships among stimulus features, this type of learning naturally extracts categorical structure (e.g., supporting object perception) and sequential structure (e.g., supporting parsing and structure in language). Through these kinds of processes, the inherent plasticity of neural processing supports elements of complex cognitive processes by implicit learning of the environment during experience.

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