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[Au9]

Glossary

dt0010

Adaptation Refers to the situation in which an exposure to a sensory input, such as seeing the color red, continues for a sufficiently long period of time so that the neuronal response is reduced when the same or a similar sensory input is experienced again a brief time later (usually immediately or within about 1 s). Many mechanisms have been proposed and vary with the particular circumstances of adaptation and may in some cases involve more complex implicit memory processes.

dt0015

Amnesia Refers to memory that is impaired selectively relative to other cognitive abilities, such as language, attention, and perception. The term is usually reserved for problems with conscious, explicit memory following damage to the medial temporal lobe system. Implicit memory is relatively spared in amnesia.

dt0020

Conscious Refers to the experience of being aware of oneself and the environment, and encompasses any perceptions, thoughts, and feelings that one is aware of at the moment

dt0025

Dissociation Dissociation in neuropsychology can be single or double or more. A single dissociation is demonstrated if a patient or group with a particular kind of brain dysfunction (e.g., to temporal cortex) is impaired on one task (e.g., an implicit memory test) but normal relative to a matched control group on another task (e.g., an explicit memory test). The best evidence comes from a double or higher dissociation. A double dissociation is demonstrated if a patient or group with a particular kind of brain dysfunction (e.g., to temporal cortex) is impaired on task A (e.g., an implicit memory test) but not another task B (e.g., an explicit memory test), whereas another patient or group with another kind of brain dysfunction (e.g., to frontal cortex) is impaired on task B but not task A, both relative to a matched normal control group.

dt0030

Lesion Lesion in the brain refers to damage to neuronal cells due to a variety of potential causes, such as stroke, tumor, or gunshot wounds.

Neocortex Newly evolved cerebral cortex of the central nervous system. It has six layers and four lobes (occipital, temporal, parietal, and frontal). Most, if not all, implicit memory is stored in the neocortex, particularly in areas beyond the primary sensorimotor areas.

dt0035

Neuropsychology A clinical specialization or field of scientific research focused on patients with brain dysfunction and characterizing the resulting cognitive problems.

dt0040

Occipital cortex Cortex in the occipital lobe is the most posterior region of neocortex and is responsible for visual perception. It includes the primary visual area (V1) in striate cortex and adjacent prestriate or extrastriate visual cortex lying anterior to V1. This lobe is retinotopically organized such that adjacent neurons respond to different but nonoverlapping parts of the visual field. Extrastriate visual areas contribute to implicit memory that involves perceptual representations.

dt0045

Temporal lobe Neocortex that is located ventrally and includes association areas for visual processing, primary and association areas for auditory processing, and multimodal association areas. Lateral parts of the temporal lobe support advanced visual and auditory perceptual processing, perceptual and conceptual knowledge and implicit memory. By contrast, the medial temporal lobe (hippocampus and parahippocampal cortical region) and related structures (e.g., connected thalamic nuclei, mammillary bodies, fornix, and retrosplenial cortex) has been implicated in explicit memory.

dt0050

Transcranial magnetic stimulation Refers to a noninvasive neuroscience technique that uses an electromagnetic coil to produce weak electrical activity in superficial regions of the cortex. This causes neural activity over these regions to be altered, typically disrupted so as to be impaired, enabling the causal role of these regions in cognition to be inferred. Logic of using the technique is the same as neuropsychology, enabling transient single or double dissociations to be produced in normal participants.

dt0055

p0010

Memory can influence behavior based on people's prior experience in the world, even without them being aware that this has happened. For example, people ride bicycles years after initially learning how, read a book faster and with greater comprehension the second time around, and make decisions about objects around them faster and more accurately as they gain more experience with them. In such cases, memory influences performance implicitly, without awareness. By contrast, people are consciously aware of explicit memory when they categorize objects or read words or when they recognize people, places, and objects as familiar or recollect details about their prior experience with them.

Early History

s0010 [Au4]

The notion of memory without awareness has been traced to thinkers as early as Descartes. This philosopher referred essentially to fear conditioning in which frightening childhood experiences can have a lifelong influence, even though one cannot remember the origin of the fear-inducing event. Leibniz also referred to insensible or unconscious perceptions that influence behavior without conscious memory of the source of such influences. However, among early thinkers, Maine de Biran offered the most detailed and the deepest analysis of memory for unconscious habits and their influence on

p0015

cognition and behavior. This philosopher has been credited with explaining that a habit can, with sufficient experience, eventually influence performance automatically and without being accompanied by awareness of using memory. He also distinguished between habits of motor actions and habits of emotional expression, and distinguished these two types of habits from conscious recollection (i.e., explicit memory). This is essentially an initial version of the now predominant, multiple systems theory of memory that distinguishes between systems for implicit memory and explicit memory. Herbart further proposed that ideas can lie below a threshold for awareness but still influence conscious cognition. Around this time, many philosophers started to develop further ideas about unconscious processing. For example, Hering criticized the large body of earlier scholarship for focusing exclusively on explicit memory and introduced the idea of organic or unconscious memory. Also around this time, psychologists, biologists, and medical scientists further articulated ideas about organic (implicit) memory and how it relates, or does not, to explicit memory. For example, by the 1890s, Freud described how his hysterical amnesia patients could not recall the traumatic events leading to the hysteria but still revealed memory for those events in other indirect ways, and Freud is well known for emphasizing the importance and power of unconscious memory on behavior. Notably, Ebbinghaus conducted the first true experiments on memory, but he focused exclusively on explaining explicit memory. Nonetheless, his primary testing method involved assessment of savings on relearning previously studied lists. Relearning did not require recollecting the preceding episode or lists but rather just relearning the list now presented again. This fits the definition of an implicit memory phenomenon. Indeed, Ebbinghaus acknowledged that his method of measuring savings on relearning assessed unconscious memory, as has been confirmed empirically more recently. Finally, it is notable that McDougall was the first psychologist to use the terms implicit and explicit memory.

s0015 Indirect Memory Tests

p0020 Implicit memory is memory that can be reactivated without a conscious strategy or intent to retrieve the memory and/or without conscious awareness that the memory has been reactivated. Consequently, changes in behavioral performance with more experience relative to less experience demonstrate implicit memory. Such tests of memory are indirect. People are not instructed to use their memory to do the task as they are on direct memory tests, such as categorization, recognition, or recall. Instead, on an indirect memory test, they do the task and perform differently depending upon their prior experience with aspects of the task, without awareness.

p0025 Indirect memory tests are the standard approach to assess implicit memory. On the other hand, direct tests are the standard approach to assess explicit memory. However, a thorny issue in memory research is that both direct and indirect memory tests can potentially reactivate both explicit memory with awareness and implicit memory without awareness to some extent. This remains a problem despite decades of research aimed at dissociating implicit and explicit memory. Nonetheless, several aspects of implicit memory have become clear.

Varieties of Priming

To reveal implicit memory on an indirect test, by definition, people are not asked about their memory. Thus a conscious report about memory cannot be used to measure implicit memory. Instead, a measure taken in response to an item that is old (i.e., repeated, studied) is compared to the response to a new item (i.e., un- or nonrepeated, un- or nonstudied item). New items are basically the control condition for the experimental memory condition(s). Priming is the difference in behavioral performance between an old item relative to a new item (Figure 1). For example, people press one of two keys to report whether an object is larger or smaller than a shoebox. Faster or more accurate key presses to old than new objects demonstrate priming. The priming difference is taken to reveal the magnitude of implicit memory.

Numerous studies have revealed some factors that consistently affect or do not affect priming. Priming is greater for meaningful than meaningless items (e.g., real words vs. nonsense letter strings). Priming can be specific to the sensory modality, becoming smaller when the modality changes from study to test. Priming can be perceptually specific, being smaller when stimuli at study and test are perceptually dissimilar than similar (e.g., resemblance of look or sound). While depth of processing (i.e., shallow perceptual vs. deep semantic) affects explicit memory (e.g., recognition), it has less or minimal effects on priming. Based on these findings, implicit memory is thus modality-specific, perceptually specific, and relatively insensitive to the depth of processing.

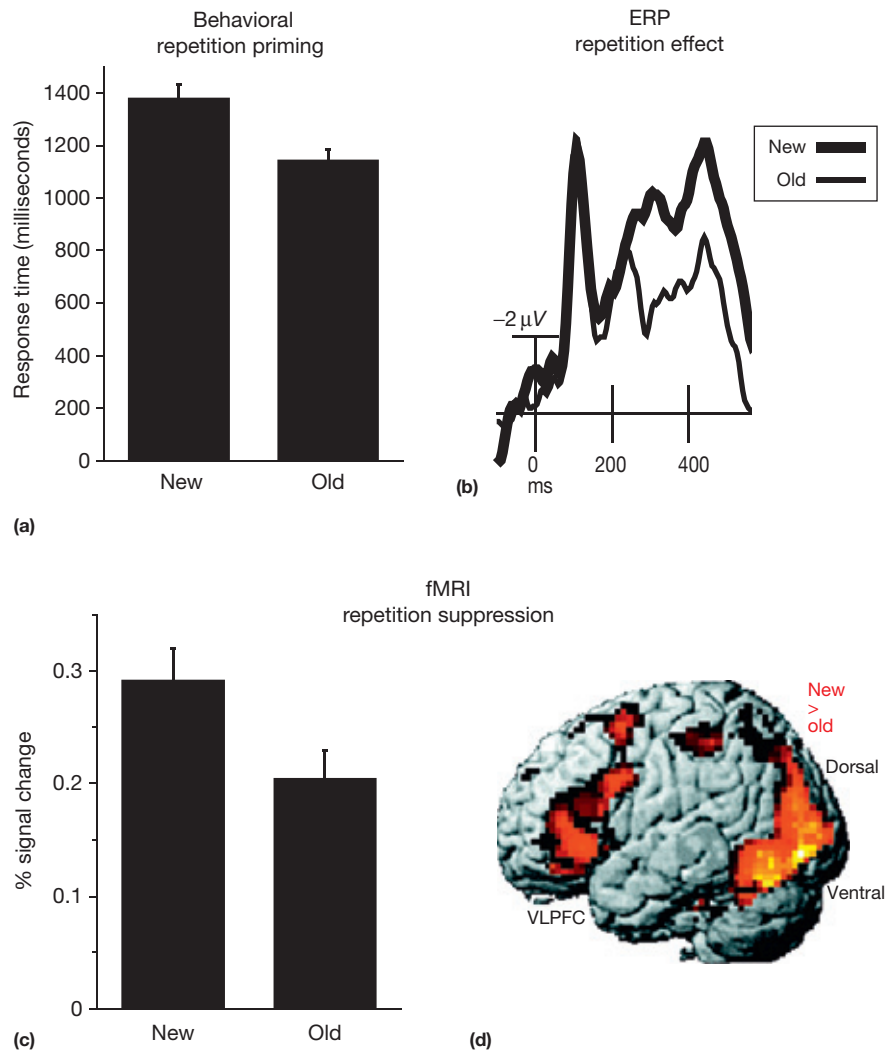
Short- and Long-Term

Implicit memory can last briefly (short-term implicit memory) or indefinitely (long-term implicit memory). Priming effects have been shown to last to some degree for 48 weeks or more, especially with meaningful pictures. In general, priming reflects long-term implicit memory when it is shown to last for 2 min or more or 4–9 or more other items are shown between the first and second presentation of the repeated item. Short-term implicit memory includes cases of immediate repetition in which an item is repeated with no other items in between first and second presentations, and items repeat with a very brief time interval of usually <2s and as little as no time between them. While long-term priming depends upon associative and long-term implicit memory processes, immediate repetition priming depends upon other memory mechanisms. Immediate repetition priming depends upon (1) working memory, (2) automatically sustained activation in knowledge networks, and/or, (3) for extremely brief presentations of items (e.g., <1 s) and extremely short delays (i.e., 200 ms or less), on nonassociative habituation (including sensory adaptation). Most research on implicit memory has focused on long-term priming. Short-term varieties have been the focus of studies of working memory, perception, and semantic memory. Thus most of the rest of this review focuses on long-term priming.

Processing

Varieties of priming vary not only in how long they last but also the processes that drive the effects. To appreciate the

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fo010 **Figure 1** Behavioral and neural effects related to implicit memory. Shown are data for a new object from a noncanonical view (e.g., top view of a bucket) and an old object repeated from the same noncanonical view as had been studied earlier in a separate learning session; note, behavioral and fMRI data from an fMRI version and ERP data from an ERP version of Schendan and Kutas' (2003) experiment on implicit memory during visual object categorization. (a) One measure of repetition priming is faster response times (RTs) for old relative to a new items. (b) Event-related brain potentials (ERPs) show that long-term repetition effects are observed only after about 200 ms. Shown is the repetition effect on the N3 complex to objects at a right frontal head site relative to the mean mastoids. The N3 is smaller (i.e., less negative) for old than new visual objects. (c) Relative to new items, repeated items show a reduced blood oxygenation level (BOLD) response, known as the repetition suppression effect. Percent signal change extracted from lateral occipital sulcus in ventral object processing area (see brightest yellow region in (d)). (d) fMRI activation (new greater than old objects) is shown on an individual canonical brain (Montreal Neurological Institute). Neural repetition suppression related to implicit memory is found in ventrolateral prefrontal cortex (VLPFC) and ventral and dorsal visual object processing areas of association cortex.

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different varieties of priming, a few words about processing and memory are needed. Transfer appropriate processing and encoding-specificity theories of memory emphasize the relation between information processing at study and processing during the memory test. For example, transfer appropriate processing theory says that memory depends upon the degree to which the processes recruited during the study (or learning) phase transfer appropriately to the memory test. Transfer will depend upon the degree to which the memory test recruits the same processes recruited during learning. The more similar the processes at study and test, the better memory will be.

In a similar vein, Roediger and colleagues have distinguished p0050 between data-driven and concept-driven tasks. Data-driven tasks during the memory test depend heavily on nonsemantic (i.e., perceptual, surface, or motor) processing. Consequently, the memory revealed on such tasks will be greatest if the study task also engaged the same nonsemantic information processing. On the other hand, concept-driven tasks during the memory test depend heavily on semantic processing (i.e., meaning, concepts, categories). Consequently, the memory revealed on such tasks will be greatest if the study task also engaged the same semantic information processing.

s0035 **Content**s0040 **Perceptual Implicit Memory**

p0055 Repetition priming refers to facilitated processing due to recent experience with the same stimulus. Repeating the exact same stimulus produces the most priming. Perceptual implicit memory changes perceptual processing. On a data- versus concept-driven account, perceptual repetition priming will be revealed best when data-driven tasks are used for the memory test. For example, on perceptual identification tasks, a word or object is presented very briefly (e.g., 50 ms). People try to read the word or name the object. Performance on such tasks is typically less accurate (e.g., <70% correct). Repeating the same word or object can increase this accuracy. The implicit memory driving the priming is perceptual because the priming effect is larger when the perceptual form of the item remains the same between the study and test phases than when the physical form changes. For example, priming is larger when a word is repeated in the same than a different font, or an object is repeated in the same view than a different one. Nonetheless, repetition priming typically does not drop to zero even when the perceptual form changes substantially as long as the core concept of the item remains the same between repetitions. For example, the word 'dog' in lowercase and uppercase ('DOG') still mean the same, and a dog seen from above or the side is still the same object. The priming effect remaining after a change in perceptual form from study to test is thought to reflect conceptual implicit memory. Thus, when exactly the same item is repeated, it is likely that both perceptual and conceptual implicit memory drive the repetition priming effect.

s0045 **Conceptual Implicit Memory**

p0060 By the data- versus concept-driven account, conceptual implicit memory will be revealed best when concept-driven tasks are used for the memory test. For example, when the perceptual form of the item changes between the study and test phases, any priming effect must depend upon aspects of the item that remain the same despite the perceptual changes, such as the meaning of the item. Conceptual implicit memory has been demonstrated when the modal form of the item changes from study to test. For example, repetition priming has been found when a picture of an object is studied and then its name is presented at test, and *vice versa*, though picture to word priming is often larger and more robust than the reverse.

s0050 **Semantic Implicit Memory**

p0065 Semantic priming can be considered a special case of conceptual priming in the sense that conceptual information or meaning drives the effect. However, both perceptual and conceptual implicit memory are revealed using repetition priming paradigms, and both can be long-lasting. By contrast, semantic priming paradigms all involve immediate repetition. No other items and only a brief time of typically 1 s or less intervene between the prime (i.e., study phase item) and the target (i.e., test phase version of the repeated item). Indeed, semantic priming effects do not typically last for more than a second or at most a few seconds.

p0070 On semantic priming tasks, the critical prime and target stimuli share no perceptual features, only some aspect of

meaning. For example, the priming word 'nurse' may be presented 500 ms before the target word 'doctor.' Subjects may read the priming word and then perform a lexical decision task on the target letter string. They decide whether the letter string is a real English word or not (e.g., a nonword like 'XPFQNV' or pseudo-word like 'BRILLIG'). Semantic priming is demonstrated when response times to target words are faster when they are related than unrelated to the prime words. Semantic priming effects depend upon the associative links among aspects of knowledge in a cortical neural network.

Brain Basis of Implicit Memory**Memory Systems**

Convergent evidence for dissociations between implicit and explicit memory and other varieties of memory led to the multiple systems theory of memory. By this account, different types of memory depend upon different brain systems. The implicit system supports implicit memory, and the explicit system supports explicit memory. The most important evidence for the multiple systems theory has come from dissociations between measures of implicit and explicit memory in patients with brain damage. However, convergent evidence from other methods (i.e., behavioral, neuroimaging, and brain potentials) is required to establish a memory system based on at least three criteria. (1) Double dissociations must establish that different brain systems are necessary for two different memory systems. For example, for implicit and explicit memory, damage to the implicit system impairs implicit but not explicit memory, whereas damage to the explicit system impairs explicit but not implicit memory. (2) Class-inclusion operations must be established, showing that the memory system operates on a diverse information (e.g., words, objects, faces, places, visual, auditory) during a particular class of tasks (e.g., categorization vs. recall). (3) A list of properties of the system must be specified that also describes how the system relates to other systems. All such evidence has been found to establish an implicit memory system in the neocortex outside of medial temporal lobe regions. Nonetheless, it is important to realize that single process accounts, including computational models, have been proposed that use a single memory system. Such single process accounts can explain findings of differences between different memory phenomena, such as priming and episodic recognition. This can be taken as evidence against the multiple systems theory. However, to date, support for these alternatives primarily constitutes evidence that they can, in principle, explain dissociations between memory phenomena and other results. Positive evidence for single process accounts has not yet been compellingly provided.

A possible exception could be single process accounts emerging from grounded (embodied) cognition theory. By this account, memory depends upon modality-specific systems for sensory processing (i.e., vision, hearing, touch, taste, smell) and motor action processing, as well as introspective states (e.g., emotion). In this view, memory, including implicit memory, also involves the cortical processes of simulation that recapitulate prior processing. During a simulation, prior information processing of the study item is activated again when a repeated item is processed later. Simulation takes place in

the divergence–convergence zones of the cortex beyond the primary sensorimotor areas. The critical difference between the theories is that the multiple systems theory proposes an amodal system apart from any sensorimotor areas, and supports conceptual knowledge and semantic memory for word, object, person, and place meanings, which underlies semantic and conceptual implicit memory. In contrast, the grounded cognition account says that sensorimotor processing areas underlie semantic memory, wholly or partially in addition to an amodal system. Thus the distinction between perceptual and conceptual implicit memory in the multiple systems account disappears in a grounded cognition account, which would instead have a single implicit memory system embodied in the sensorimotor systems. While some grounded cognition theories posit a single memory system for all types of memory (e.g., for both implicit and explicit varieties), other versions of grounded cognition also make no perceptual-conceptual distinction but are otherwise compatible with (or identical to) the multiple systems theories of memory.

s0065 Neuropsychology

s0070 *Implicit memory in amnesia*

p0085 The first clues about the brain basis of implicit memory came from cases of neurological patients with memory problems due to amnesia. Amnesic patients have medial temporal lobe damage and are impaired severely on explicit memory tests of recall and recognition. Korsakoff recorded the earliest anecdotal evidence of implicit memory in his amnesia patients. One patient was given an electric shock but failed to recollect this experience. Nonetheless, upon seeing the same device, he thought that the doctor might shock him. Likewise, Claparade pricked an amnesic with a pin. This patient later refused to shake the doctor's hand, despite having no recollection of the earlier unpleasant event.

p0090 Studies of patients with amnesia syndrome have provided perhaps the most important information about implicit memory. This is because these patients can be considered examples of people who have a selective impairment in explicit memory but spared implicit memory. As mentioned, an indirect memory test used to reveal implicit memory, in principle, also can be contaminated incidentally with episodic explicit memory. For example, when categorizing an object repeated from a prior study episode, a normal subject will do the task faster and more accurately with old than new objects, demonstrating repetition priming. However, they may also incidentally consciously recognize that they saw the object earlier in the experiment, demonstrating conscious episodic explicit memory for the prior study experience. In contrast, a patient with medial temporal lobe amnesia will be severely impaired on the latter conscious recognition process. Consequently, relative to normal people, in amnesia, any implicit memory measure is minimally or not contaminated with episodic explicit memory. Amnesic patients can thus provide potentially the purest behavioral measures of implicit memory. However, this advantage of amnesia research was not realized until studies of the famous amnesic patient HM who had an exceptionally severe amnesia following bilateral medial temporal lobe removal in 1953. Research with HM since the 1960s demonstrates remarkably intact abilities to improve performance on some tasks

with repeated experience, despite failing to recollect having experienced the materials before or recognize them as familiar. This was taken to demonstrate spared nonconscious memory, that is, implicit memory, in amnesia. Since then a large body of research has aimed at defining the memory preserved in amnesia, which is working memory, implicit learning, and implicit memory.

The large body of research with HM and other amnesics has demonstrated memory without conscious awareness for a wide variety of perceptual and conceptual repetition priming tasks and for semantic priming. Most of these studies used materials that were already known to the subjects, mostly real words and real objects. In contrast, evidence for spared implicit memory in amnesia is more mixed when novel materials are used that are not meaningful or include information with no preexisting representation, such as nonwords, novel visual patterns, or unrelated word pairs. Some studies show priming in amnesia, while others do not. The evidence suggests that implicit memory for novel information depends on the task and perhaps also the severity of the amnesia. p0095

While damage to the medial temporal lobe can produce amnesia for episodic explicit memory, it is important to note that the rest of the brain is intact, including the rest of the neocortex and subcortical structures. Consequently, spared implicit memory in amnesia indicates that implicit memory depends upon these spared structures. In particular, the implicit memory that supports priming depends upon the neocortex, particularly secondary and associative areas beyond primary sensorimotor regions. p0100

To avoid the circularity of defining any memory preserved in amnesia as implicit memory, it is important to obtain convergent evidence from other methods, of which evidence is substantial, though not without controversy. The vast literature on priming from studying normal subjects in cognitive psychology experiments using behavioral measures provides one set of evidence. Other evidence comes from other areas of neuroscience beyond neuropsychological work on amnesia. p0105

Impaired implicit memory with cortical lesions

s0075 The gold standard in neuropsychology is to obtain a double dissociation. Impaired explicit memory with spared implicit memory in amnesia constitutes a single dissociation. To demonstrate a double dissociation, patients need to be found who show spared explicit memory with impaired implicit memory, preferably in the same experiment. Indeed, this has been found. Patients with lateral occipital cortex damage or disconnection between right and left occipital cortex show spared recognition but impaired perceptual repetition priming. Patients with anterior temporal lobe lesions show spared perceptual implicit memory. Alzheimer's disease damages the medial temporal lobe plus higher association areas in the temporal lobe and other lobes. These patients have impaired explicit recognition and recall, as well as impaired conceptual repetition priming, but relatively spared perceptual repetition priming. Transcranial magnetic stimulation (TMS) disrupts neural processing transiently and has been used to show that disruption of processing in left ventrolateral prefrontal cortex (VLPFC) reduces both the cortical and behavioral effects of repetition priming during a categorization task. Consequently, VLPFC may be necessary to express implicit memory behaviorally in a priming paradigm. p0110

s0080 **Neurophysiology**s0085 **Neuronal repetition effects in nonhuman primates**

p0115 The best candidate for defining the neuronal basis of implicit memory is repetition suppression effects. However, most of this research has been done using short-term or immediate stimulus repetition. Further, most of the stimuli are pictures of objects, scenes, or faces, many of which would be unknown to nonhuman primates. In contrast, most human implicit memory studies use meaningful word stimuli or other known and meaningful stimuli. It thus remains unclear the extent to which nonhuman primate findings can explain human implicit memory at the neuronal level. Nonetheless, it is clear that neurons in the inferior temporal cortex along the ventral visual pathway are selective for object shape, and the activity of these neurons decreases with repetition. This neuronal repetition suppression occurs irrespective of whether the repeated stimulus is a passively viewed nontarget for the behavioral task or the target stimulus for the task. This suggests that repetition suppression is automatic, as would be expected for the neuronal mechanism of implicit memory. Short-term repetition suppression involves an input-fatigue mechanism in which the synaptic inputs to a neuron reduce their efficacy with repetition. However, several other mechanisms have been proposed to explain neuronal repetition suppression and implicit memory and may apply to other types of implicit memory (e.g., long-term). Further, evidence so far indicates that, like the human behavioral phenomenon, neuronal repetition suppression varies with delay between first and repeated presentations and duration of the stimuli. The effect also varies with the similarity between the test and study items, consistent with transfer appropriate processing and encoding-specificity accounts of memory. Other neuronal mechanisms may underlie other types of implicit memory, particularly the long-term varieties.

s0090 **Repetition suppression in human functional neuroimaging**

p0120 Functional brain imaging studies have revealed a similar observation by measuring changes in regional blood oxygenation or flow related to neural activity. Relative to the activation level in response to new items, repeated items show a reduced response, known as the repetition suppression effect (Figure 1). This effect is sometimes referred to as functional magnetic resonance adaptation (fMR-A) when the paradigm involves immediate repetition or very short delays or interstimulus intervals between first and second presentations. Notably fMR-A uses suppression to infer the representational characteristics of perceptual processing areas (e.g., representation of view, position, size), analogous to the visual cognition approach of using priming to infer how objects are represented (e.g., parts or multiple views of an object). However, human and animal evidence indicates that, as suggested based on behavioral evidence, the neural mechanism differs between different varieties of priming (e.g., fMR-A, immediate, and long-term). Mechanisms proposed for long-term implicit memory may not apply to short-term varieties, and conversely. This important consideration has, however, not yet been addressed systematically, leaving the neural mechanism unknown for the many neuroimaging studies using neural repetition suppression effects to characterize the representational properties of implicit memory.

Nonetheless, some recent work has started to do so, and p0125 some general principles about repetition suppression have emerged. Neural suppression occurs in secondary and associative cortex as opposed to primary sensorimotor cortex. For example, in the visual modality, early studies of priming-related suppression implicated only the ventral visual stream beyond primary visual cortex, like multiple systems accounts of memory implicated only the ventral visual stream in perceptual implicit memory. Recent work, however, shows that short- and long-term suppression occurs along both the ventral and dorsal visual streams. Evidence also indicates that suppression effects increase as processing proceeds from posterior to anterior posterior processing areas, consistent with the larger priming effects found behaviorally for conceptual priming (e.g., involving more anterior temporal areas) than for perceptual priming (e.g., involving more posterior occipitotemporal areas). Like behavioral priming measures of implicit memory, neural suppression can show perceptual specificity, especially in posterior perceptual processing areas. For example, object processing areas along the ventral stream show suppression that becomes smaller when repeated objects differ in viewpoint and lighting conditions and show relative invariance despite changes in size and spatial location; note, such a pattern is expected for a brain region that represents categorical knowledge about objects that can generalize across variations in size and where the object is observed. However, the full range of changes in perceptual properties has not yet been assessed for short- and long-term repetition (e.g., view changes up to 60° tested).

Overall, at a network level, the brain regions that show p0130 suppression effects are parts of the active task network implicated in selective attention and working memory, that also includes secondary perceptual processing areas, lateral prefrontal cortex, and intraparietal sulcus. This network is anticorrelated in its activity pattern with a default, resting state network implicated in episodic memory, mind wandering, and internally-directed attention. The default network includes medial prefrontal cortex, cingulate cortex, retrosplenial cortex, lateral posterior parietal cortex, and superior temporal gyrus. Consistent with anticorrelation of the active task and default networks, the default network regions show the opposite repetition effect. They show repetition enhancement, that is, greater activation for old than for new items. This is typically observed on episodic memory tests (e.g., recognition of an item as old and familiar).

Also like behavioral priming measures of implicit memory, p0135 neural suppression can show task-specificity. For example, when the task changes between the study phase and the memory test phase, suppression is reduced, especially in prefrontal regions and fusiform gyrus in the left hemisphere. This finding can be considered an example of violation of the transfer appropriate processing principle of memory, which predicts that processing differences between study and test will reduce memory. The task changes that reduce suppression can include inversions of the decision (e.g., Larger than a shoebox? vs. 'Smaller than a shoebox?'). While systematic neuroimaging studies have not yet been reported, behavioral studies suggest that even inversions of the response key mapping may reduce behavioral priming (e.g., yes and no mapped to 1 and 2 keys vs. 2 and 1 keys, respectively). However, whether decision or

motor-related aspects of the response are the locus of the stimulus–response mapping effect remains to be established. Nonetheless, this mapping clearly increases with repetition, as the reduction is substantial with multiple repetitions and less or none with a single repetition. Notably, most research on implicit memory and behavioral priming has involved a single repetition and so cannot depend substantially on stimulus–response learning. Consistent with this, studies with amnesia patients indicate that stimulus–response learning effects depend upon the medial temporal lobe system for episodic memory. Intriguingly, this suggests that stimulus–response mapping influences on repetition priming are more properly considered an episodic memory phenomenon in which episodic memory incidentally influences priming, instead of a characteristic of the implicit memory system. After all, indirect memory tests can recruit not only implicit but also explicit memory. This also suggests that stimulus–response learning cannot explain the remarkably spared priming effects established in amnesia patients. Nonetheless, studies of stimulus–response mapping and neural suppression have indicated that top-down processing from prefrontal cortex to other brain regions has a role in behavioral priming. For example, transiently disrupting processing in the VLPFC reduces stimulus–response learning effects, demonstrating a causal role.

Altogether, these human neuroscience findings have led to the suggestion of multiple different mechanisms for repetition suppression in priming paradigms. The first mechanism, referred to here as the tuning account, is the classic explanation. This account suggests that neural repetition suppression depends upon sharpening or tuning of neuronal receptive fields due to learning. The neural representation of the stimulus becomes more precisely tuned to its preferred stimulus (e.g., the shape of a particular dog from a specific view) with experience with that stimulus. Such effects show perceptual specificity such that memory decreases with changes in the perceptual form between the learned version of the stimulus (e.g., a different view of the dog or a different type of dog, say, poodle instead of collie) and the memory test version of it. Suppression due to neuronal tuning probably occurs in posterior perceptual processing areas implicated in perceptual representation or knowledge systems. Tuning-related suppression can also occur, to some extent, in more advanced stages of stimulus processing, such as in anterior temporal cortex for visual stimuli, implicated in conceptual knowledge about stimuli (e.g., meaning of a word or object). Indeed, grounded (embodied) theories of cognition would implicate both posterior and anterior stimulus processing areas because sensorimotor processing areas support not only perception and action but also meaning and memory. However, tuning-related suppression seems to have a limited relationship with priming of behavioral performance on tasks that require processing stimulus meaning, such as categorization.

Consequently, a second mechanism has been proposed more recently following new evidence that VLPFC has a causal role in behavioral priming that is response-specific. This account was motivated by the stimulus–response mapping findings that switching the task decision mapping from study to test reduces priming and repetition suppression. By this account, top-down inputs from prefrontal cortex onto other brain regions influence behavioral priming. Prefrontal cortex is implicated in cognitive control, attention, and working

memory. These control processes can become more automatic with increasing experience with an item. Consequently, the association between the stimulus and these control processes becomes stronger. This learning results in memory and behavioral priming that is response-specific.

Another explanation of behavioral priming uses a perceptual memory-based caching system to explain short-term priming with meaningless perceptual patterns, which does not show stimulus–response learning. By this computational account, perceptual processing results in perceptual representations. While meaningful stimuli engage processes related to categorizing and verbally labeling the stimulus, meaningless perceptual patterns do not; instead, they engage other perceptual processes based on the task requirements, such as the size of the object. A short-term perceptual memory process (i.e., the ‘cache’) briefly stores the binding of the percept and other task-specific perceptual information. In posterior cortex, this caching mechanism could presumably operate along with the tuning mechanism to explain implicit memory and priming, regardless of the task switch from study to test.

At the neuronal level, several mechanisms may also underlie repetition suppression. The input-fatigue mechanism (for adaptation with immediate repetition) and tuning and caching system mechanisms (for long-term perceptual repetition suppression) are three examples. However, other mechanisms are also possible and could also explain response-invariant suppression. Like the input-fatigue version, a firing rate-dependent fatigue mechanism (for adaptation) suggests that neuronal responses decrease with use (i.e., firing fatigues), but, in this case, repetition suppression is proportional to the firing rate in response to the first presentation. However, so far evidence has not favored this account. A facilitation model suggests that the time course of the neuronal response (i.e., onset latency and/or duration) decreases with repetition. While neuroimaging has provided some support, this can be assessed better using neurophysiological measures with temporal precision within the range of neuronal activity (milliseconds). In humans, electromagnetic brain potentials have supported facilitation models of long-term repetition, as category knowledge is activated about 50 ms earlier for repeated than for new objects.

Repetition effects on electromagnetic brain potentials in humans reveal the timing of long-term implicit memory

Event-related electrical potentials have defined the time course of memory processes in the neocortex. This evidence indicates that, for everyday cognition, long-term implicit memory starts relatively late in information processing, after the initial bottom-up activation through perceptual processing areas. Brain potentials show that long-term repetition effects are observed only after about 200 ms (Figure 1). The repetition effects are relatively long-lasting, until around 400 or 500 ms or so, indicating that implicit memory effects on information processing typically last for about 300 ms or longer. In particular, repetition typically affects mid-latency negativities between 200 and 500 ms that reflect activation of knowledge about words, objects, and faces. Negativity is typically reduced for repeated relative to new items. With meaningless stimuli, these effects are minimal or none. This is consistent with the idea that implicit memory reflects reactivation of perceptual and

conceptual knowledge representation systems. While priming can occur for nonsense stimuli, such effects are short-term and response-invariant, and explained using the caching mechanism. By contrast, long-term implicit memory of meaningful stimuli involves facilitation, tuning, and perhaps stimulus-response mapping mechanisms of neuronal suppression. The time course evidence indicates that all these mechanisms, under most circumstances, involve feedback from prefrontal to posterior perceptual and conceptual processing areas and/or feedback within the processing areas alone. By this time, electrical potentials recorded inside the skull at the cortical surface indicate that neurons in prefrontal cortex have started to become active. Brain potential evidence thus indicates that long-term implicit memory, which leads to neural repetition suppression and which is related to priming involves top-down feedback from prefrontal cortex to other brain regions.

p0165 Nonetheless, a handful of studies have shown repetition effects on earlier brain potentials not only for short-term but also long-term repetition. These effects are found on transient potentials related to the initial feedforward pass through perceptual processing areas, as well as automatic recurrent and feedback within these areas (but not yet from prefrontal cortex). The input-fatigue mechanism has been implicated in adaptation (immediate repetition) effects. The long-term effects are related to perceptual priming, regardless of meaning, and have been found with meaningful and meaningless stimuli. At last one such early repetition effect has been clearly linked to perceptual grouping processes implicated in gestalt perception of an object that is more than the sum of its parts. However, to observe such effects, the task may need to focus attention on perceptual details. For example, one study required subjects to determine if the nonsense visual pattern had a loop or not. Another study made perception highly challenging visually by presenting fragmented line drawings very briefly (for 0.02 s).

p0170 Notably, convergent evidence from cognitive psychology, neuropsychology, and neuroimaging suggests that implicit memory can influence explicit memory performance on recognition tests in which people decide whether an item is old and familiar from a prior study experience or is a new item. For example, electrical potentials during explicit memory (recognition) tests have revealed repetition effects between 200 and 400 ms. This is found when people can recognize items with some accuracy but report being unaware of retrieving memory. This has been taken as an implicit memory process that influences recognition performance but without awareness.

s0100 p0175 **Masked priming and short-term implicit memory**

In immediate repetition priming paradigms (e.g., semantic priming), when the study item is presented very briefly (e.g., for 50 ms) and masked, this prime stimulus is typically not reported by people. The prime is thus taken to have been processed only unconsciously. While it is as problematic to establish that the prime is unconscious as it is hard to establish that implicit memory is unconscious, clearly the prime is minimally available to conscious report under these masking conditions. In the standard paradigm, masking involves presenting a perceptually similar stimulus immediately before the prime (e.g., for 500 ms). This is the forward mask. The target item, which constitutes the memory test, is presented immediately

after the prime (e.g., for 500 ms) and also serves as a backward mask, though some studies use an additional backward masking stimulus similar to the forward mask. In studies of perception, such masking seems to minimize or eliminate influences of top-down feedback from the frontal lobe on posterior processing. Elimination of this feedback is thought to be the reason why the prime is processed largely or wholly outside of conscious awareness. Using the masked priming technique, early perceptually specific repetition effects have been found on electrical potentials as early as 100 ms after the appearance of the item. Overall, priming effects from these studies reveal contributions from bottom-up processing in posterior secondary and association cortex to feature orthographic, lexical, and conceptual levels of word processing and perceptual and conceptual levels of object processing. This variety of implicit memory, however, depends upon recent activation of the knowledge network by the prime that is ongoing when the target item appears shortly thereafter, as opposed to tuning or facilitation mechanisms. The fatigue mechanisms may also apply. Repetition suppression has been associated with masked priming in neuroimaging studies.

Antipriming

Priming studies use new items as the baseline condition to assess memory by comparing these responses to those for repeated (old) items. However, recent evidence suggests that a new item that has been intermixed with old items is not an entirely neutral baseline control. Instead, these new items reflect not merely processing of the novel item but also small antipriming effects on these new items as a by-product of the previous experience with the repeated items. Antipriming happens because objects are represented in perceptual systems in a distributed, overlapping fashion organized according to feature similarity. Further, individual neurons are tuned broadly to sets of features of objects, and a population code of sparse sets of neurons represents each object. Consequently, when an object is experienced, its representation becomes strengthened, consistent with tuning and facilitation mechanisms. However, the process of strengthening this representation also weakens the representations of other objects with which it shares features. For example, a dog has a head, body, and four legs. Experience with a dog strengthens its representation while also weakening the representation of other objects sharing one or more of its features (e.g., other animals with similar head, body, and/or leg features). Crucially, when an item with these overlapping features is later presented as a new item (mixed with repeated items) on a priming test, its neural activity is actually greater (than for repeated items) as part of a late process of connecting its relatively weaker representation back up. Electrical potentials indicate that this effect occurs after 1100 ms, which is over 200 ms after the behavioral response, and well after earlier perceptual and conceptual implicit memory and even after any incidental episodic recognition of the item. Instead, antipriming effects reflect a very late relearning effect, essentially encoding of new information into memory. However, in neuroimaging studies, due to the long time course of the blood response on which they depend (i.e., several seconds), neural repetition suppression effects likely reflect some combination of perceptual and conceptual implicit memory plus a small contribution of antipriming effects, at least in

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the left inferotemporal and left and right lateral occipital areas where antipriming effects appear.

s0110 Implicit Memory Can Result from Implicit Learning

s0115 Memory results from learning

p0185 Consequently, implicit learning (i.e., skill learning, procedural learning, motor learning, perceptual learning) can lead to implicit memory. This is not typically included as implicit memory proper, which instead focuses on priming phenomena. While memory following implicit learning could be explicit and revealed on recognition or recall tasks, it could also be implicit. Indeed, the typical method for demonstrating that learning has occurred in an implicit learning experiment is to test memory indirectly. Moreover, to demonstrate that learning is implicit, the gold standard practice is to demonstrate that the memory that results is implicit. To do so, both indirect tests and direct tests (i.e., recognition, recall) of memory are used. While the indirect tests do not measure priming per se, they do measure changes in performance for old relative to new information. The difference measured is not referred to as priming but, nonetheless, does fit the definition. The main exception is that implicit learning effects can be observed only after more than one experience with the repeated information. By contrast, repetition priming paradigms involve a single presentation of the to-be-repeated item at study (i.e., during learning). In fact, typically many experiences are required to observe implicit learning effects.

p0190 For example, one of the most widely-studied implicit learning tasks is the serial response time (SRT) task. In the spatial version, people see several locations light up one at a time (e.g., one of four boxes will light up on a computer screen). People press a key corresponding to the location on the screen that is lit. Locations light up either in a repeating sequence or a new order (e.g., random locations). Faster responses to repeated than new locations demonstrate implicit learning. This can be taken as a kind of location priming that demonstrates implicit memory for the repeating sequence of locations. If direct memory tests also indicate no conscious awareness of memory for the repeating sequence, then the implicit memory demonstrated on the task is taken to indicate that learning has occurred implicitly. Consistent with this, the large body of research with HM and other amnesics has also demonstrated memory without conscious awareness for perceptual, cognitive, and motor skills (e.g., mirror-reversed reading), rule learning, and SRT task learning. However, amnesic patients are impaired on implicit SRT task learning, if higher-order associations among multiple locations must be learned. Further, neuroimaging of normal subjects has demonstrated learning-related activation in the medial temporal lobe during implicit learning, despite no conscious awareness of having learned anything. This is observed during the early phase of implicit learning of higher-order associations when the most new information needs to be encoded. Evidence for medial temporal lobe involvement without awareness of memory has also been found for probabilistic classification learning and context learning. Thus the role of the medial temporal lobe is not in conscious (explicit) memory per se but rather has a role in some types of implicit learning and memory. Instead, the computational demands of the learning task determine whether medial temporal lobe is recruited (e.g., for higher-order

associations, sequence disambiguation, or contextual associations). In contrast, the basal ganglia have an established role in implicit learning. Neuroimaging demonstrates basal ganglia activation during implicit learning on a wide variety of tasks. Further, patients with Parkinson's disease have basal ganglia dysfunction and impaired implicit learning with spared episodic memory, whereas amnesic patients have impaired episodic memory and relatively spared implicit learning. This demonstrates a double dissociation between implicit learning and memory versus explicit memory.

See also: Amnesia (00021); Associative Learning (00036); Brain (00068); Consciousness (00105); Episodic Memory (00152); Event Related Potentials (00154); Memory (00229); Neuro and treatment/techniques (TMS, ECT) (00253); Neuro technologies (imaging, PET, SPECT, MRI, MEG) (00254); Perceptual Development (00270); Primate Cognition (00289); Semantic Memory (00315); Subliminal Perception (00350); Visual Perception (00371); Visual Representation (00372); Word Retrieval (00375); Working memory; Explicit memory; Sensory memory; Implicit learning; The psychology of reading.

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Relevant Websites

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Au8