Priming

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Introduction

Priming refers to a change in behavioral response to a stimulus, following prior exposure to the same, or a related, stimulus. Examples include faster reaction times to make a decision about the stimulus, a bias to produce that stimulus when generating responses, or the more accurate identification of a degraded version of the stimulus. From the memory perspective, the most exciting aspect to priming concerns evidence that it can occur in the absence of conscious memory for the prior exposure (an example of so-called 'implicit' or 'nondeclarative' memory). For instance, amnesic patients typically show intact levels of priming, despite their impairments in conscious ('explicit' or 'declarative') memory. Evidence like this led to the proposal that the brain regions supporting priming are different from the medial temporal lobe (MTL) regions believed to support declarative memory. Indeed, it is often assumed that priming is the by-product of prior processing of a stimulus, that is, arising from plasticity in multiple cortical regions whose primary role is perceptual/conceptual processing. As such, priming is likely to be one of the most basic expressions of memory, influencing how we perceive and interpret the world.

A Working Example

Priming can be measured using a range of different stimuli and tasks. To illustrate the breadth of neuroscientific data on priming, we initially focus on one specific paradigm – the word-stem completion paradigm – which has provided some of the most convincing evidence that priming involves memory systems, and associated brain regions, that differ from those involved in declarative memory. In the 'study' phase of this paradigm, participants perform an incidental task on a list of words (normally unaware that their memory for these words will be tested). At some time later, they are presented with three letters that form the start of words (word-stems) (see Figure 1(a)). Some of these stems can be completed with the words from the study phase, though in the 'indirect' version of this task, participants are not informed of any relationship between this test phase and the previous study phase. They are simply asked to complete the stem with the first word that comes to mind. Priming is indexed by the increased probability of completing stems with studied words, relative to the baseline probability of completing the stems when those words were not studied. Importantly, participants normally show this priming without reporting any conscious reference to the prior study phase.

Neuropsychological Evidence

When this task is given to amnesic patients, they typically show priming of equivalent magnitude to controls. However, when the instructions at test are changed, so that participants are asked to use the stems explicitly to recall studied words ('word-stem cued recall,' a 'direct' version of the task), amnesic patients typically perform worse than controls (Figure 1(b)). This dissociation is appealing because the stimuli are kept constant across the indirect and direct versions of the task; all that differs are the instructions. While amnesic patients are also known to have sparing of other forms of memory, such as motor skill-learning, the intriguing aspect of priming is that it can occur after a single stimulus presentation ('one-shot learning'), rather than requiring sustained training. Furthermore, a few patients with more posterior lesions (e.g., in occipital cortex) have shown the reverse pattern of impaired word-stem completion for visually studied words (indirect test), despite intact performance on a recognition memory test (direct test). This double dissociation between the two types of memory test is strong support for different memory systems underlying priming and declarative memory. Further support comes from reports that word-stem completion priming is less susceptible than is cued recall to the effects of healthy aging, and to some dementias like Alzheimer's disease.

Psychological Evidence

This dissociation of priming from declarative memory following brain damage is supported by functional dissociations between direct and indirect versions of the word-stem completion paradigm in healthy individuals. For example, performance on the direct version (word-stem cued-recall) is higher when the corresponding words are generated from semantic cues at study relative to when they are simply read, yet performance on the indirect version (word-stem completion) is higher when the words are read relative to being generated from cues. Similarly, presenting words auditorily rather than visually at study tends to impair performance on visual word-stem completion to a greater extent than on visual word-stem cued

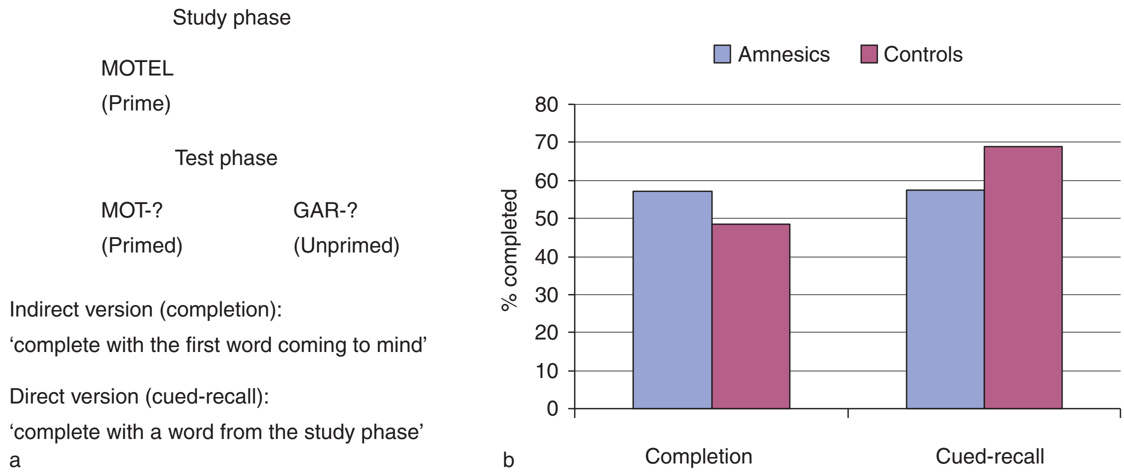

Figure 1 (a) Schematic of the word-stem completion paradigm. (b) Performance of amnesic patients and matched controls on indirect (completion) and direct (cued-recall) versions of the task. (b) Reprinted with permission from Graf P, Squire LR, and Mandler G (1984) The information that amnesic patients do not forget. *Journal of Experimental Psychology*: *Learning*, *Memory and Cognition* 10: 164–178, APA publishers.

recall, whereas use of a study task that engages semantic versus phonological processing of words tends to improve performance on word-stem cued recall to a greater extent than on word-stem completion. The reduced performance found on word-stem completion when words are generated or heard at study, rather than read, suggests that a component of priming in this task relates to the visual overlap between words and their stems, or more precisely, to overlap in the processes involved in visual word reading.

Nonetheless, though dissociations have been found between direct and indirect tests of memory, care must be taken when using performance on indirect tests as a pure measure of implicit memory: even though an indirect memory test does not refer participants to previous encounters with stimuli, participants may voluntarily, or involuntarily, recollect such encounters. For example, some participants may guess the relationship between the study and test phase of a word-stem completion task, and hence attempt to recall studied items in order to complete the stems. Moreover, even if a completion comes to mind involuntarily, participants may subsequently recognize that word as having come from the study phase. Though the latter eventuality may not affect behavioral measures of priming, it is important when measuring the neural correlates of priming, as discussed in the next two sections. As a consequence, considerable effort has been devoted to developing methods that minimize the contribution of explicit memory to priming.

Neuroimaging Evidence

Some of the first positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of priming used the word-stem completion paradigm. These studies consistently found reduced hemodynamic responses in extrastriate visual cortex for studied relative to unstudied word-stems (often in both direct and indirect versions of the task). This reduction is attributed to 'more efficient' or 'facilitated' visual processing of the stems corresponding to studied words, owing to the prior exposure to those words. Similar reductions have also been found in a number of regions including left inferior temporal and left inferior frontal cortices. Given that these regions are also generally activated by the task (e.g., vs. passive fixation), the reductions are consistent with facilitated processing within a language-related network that is engaged when reading words and completing word-stems, possibly including phonological, lexical, and semantic processes.

Some imaging studies have also reported hemodynamic increases in MTL cortices, even in indirect versions of the task. This illustrates the problem highlighted earlier that explicit memory may contaminate indirect tasks. In particular, even if this explicit memory is involuntary and does not affect the behavioral response, the poor temporal resolution of hemodynamic imaging techniques means that imaging data may include explicit memory processes arising subsequent to that response. More recent imaging experiments have therefore used variants of the word-stem completion paradigm that attempt to minimize contamination by explicit memory. For example, participants can be asked to complete stems with words from the study phase (i.e., word-stem cued recall), but if they cannot, they are asked to produce the first word coming to mind. Having produced a completion (through either approach), they then indicate whether they remember that word from the study phase. The critical trials used to isolate the neural correlates of priming are those stems completed with studied words but which participants indicated they did not remember. These trials are likely to provide a purer measure of implicit memory (despite occurring in the context of a direct memory task). When compared to a baseline condition (stems that did not correspond to studied words, but which were completed with a word that was correctly indicated as unstudied), event-related fMRI has replicated the reduced responses found in extrastriate, left inferior temporal, and left inferior frontal cortices (Figure 2(a)). Equivalent reductions in these regions were also found for 'remembered' trials (stems that were completed with a studied word and that word was indicated as studied), unlike in MTL cortex, where greater activity was found for remembered trials relative to primed trials (suggesting that explicit memory had been successfully minimized in primed trials). Furthermore, the reductions for primed and remembered versus baseline trials in these regions were also found when using an indirect version of the task akin to the standard word-stem completion task. Taken together, these results suggest that such hemodynamic reductions are not only implicit, but also automatic, consistent with a role for these regions in the priming observed in healthy individuals and in amnesic patients.

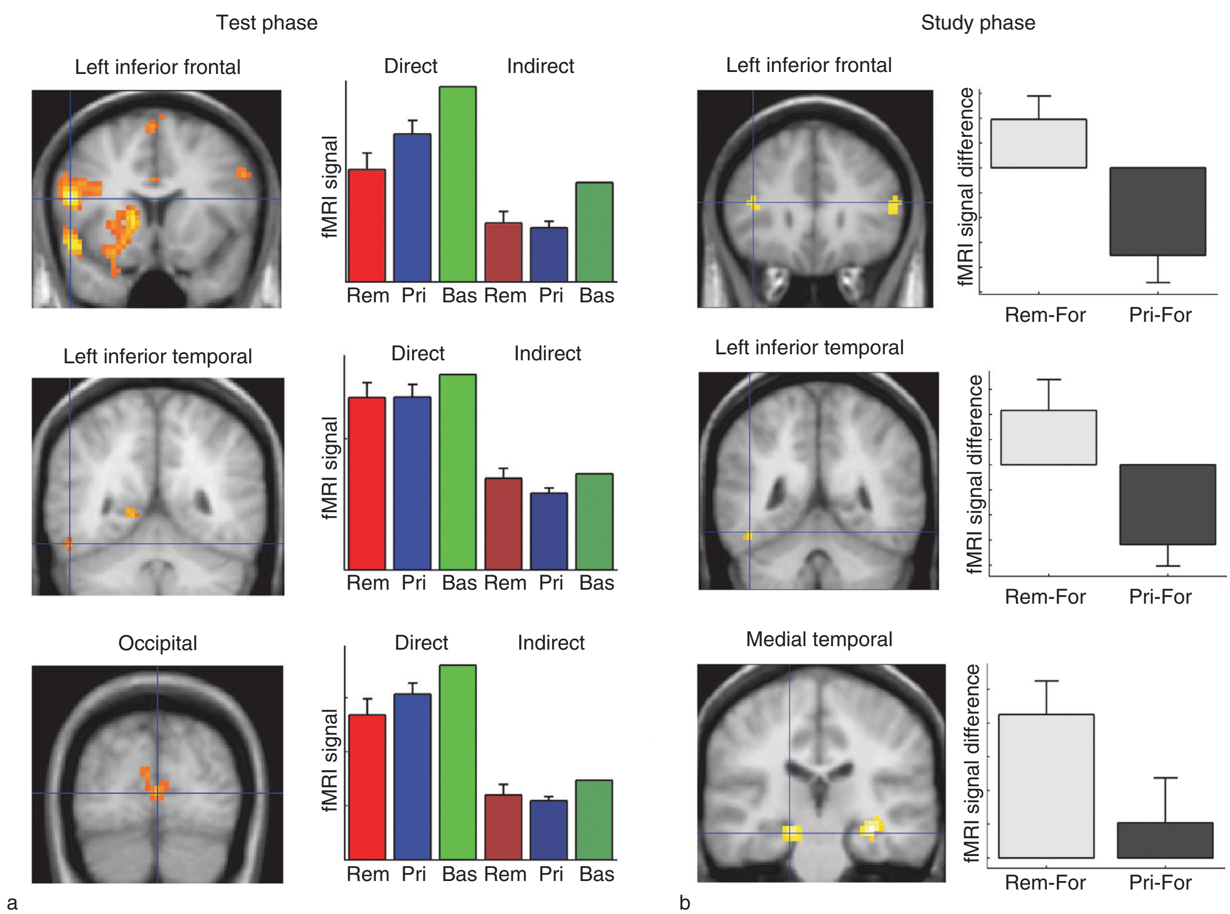

Figure 2 Event-related fMRI data from a word-stem completion paradigm. In the test phase (a), a number of regions including those shown in left inferior frontal, left inferior temporal and occipital cortices, exhibited reduced responses to primed stems (blues), and to remembered stems (reds), relative to baseline stems (greens), regardless of whether participants performed a direct (lighter colors) or indirect (darker colors) version of the paradigm. In the study phase (b), a number of regions including those shown in left inferior frontal and inferior temporal cortices showed reduced responses for subsequently primed relative to subsequently forgotten words (darker bar), whereas regions in medial temporal lobe showed increased responses for subsequently remembered (but not subsequently primed) relative to subsequently forgotten words (lighter bar). Rem, remembered; Pri, primed; Bas, baseline; For, forgotten (see text). (a) Adapted with permission from Schott BH, Henson RN, Richardson-Klavehn A, et al. (2005) Redefining implicit and explicit memory: The functional neuroanatomy of priming, remembering and control of retrieval. *Proceedings of the National Academy of Sciences of United States of America* 102: 1257–1262. (b) Adapted with permission from Schott B, Richardson-Klavehn A, Henson R, et al. (2006) Neuroanatomical dissociation of encoding processes related to priming and explicit memory. *Journal of Neuroscience* 26: 792–800. Copyright (2005) National Academy of Sciences, USA.

One can also use event-related imaging methods to examine differences at the time stimuli are encoded (i.e., during the study phase) as a function of the degree to which those stimuli show later priming (or the degree to which they show explicit memory). Using the same paradigm as above, for example, hemodynamic responses to the words at study differed for those words subsequently primed (completed with the studied word but not remembered) than those subsequently forgotten (completed with a different word). Such differences were found in a number of cortical regions, including the left inferior temporal and frontal regions that showed priming-related reductions at test. Again, the pattern in these regions differed from that in the MTL, which showed greater activity for words subsequently remembered versus words subsequently forgotten (Figure 2(b)). These findings suggest that priming is affected by how stimuli are encoded (on their initial presentation), possibly in addition to how that information is accessed at test. Yet further work has combined event-related fMRI with pharmacological interventions: for example, scopolamine and lorezapam, which are believed to modulate synaptic plasticity, have been shown to attenuate repetition suppression in the same inferior temporal and frontal regions during word-stem completion.

Electrophysiological Evidence

The time course of word-stem completion priming has also been investigating using electroencephalographic (EEG) and magnetoencephalographic (MEG) methods. For example, in a standard indirect completion task, event-related potentials (ERPs) to primed word-stems have been reported to diverge from those to baseline (unstudied) word-stems within 200 ms of the onset of the word-stem (Figure 3(a)). The same ERP effect was reported for words remembered during

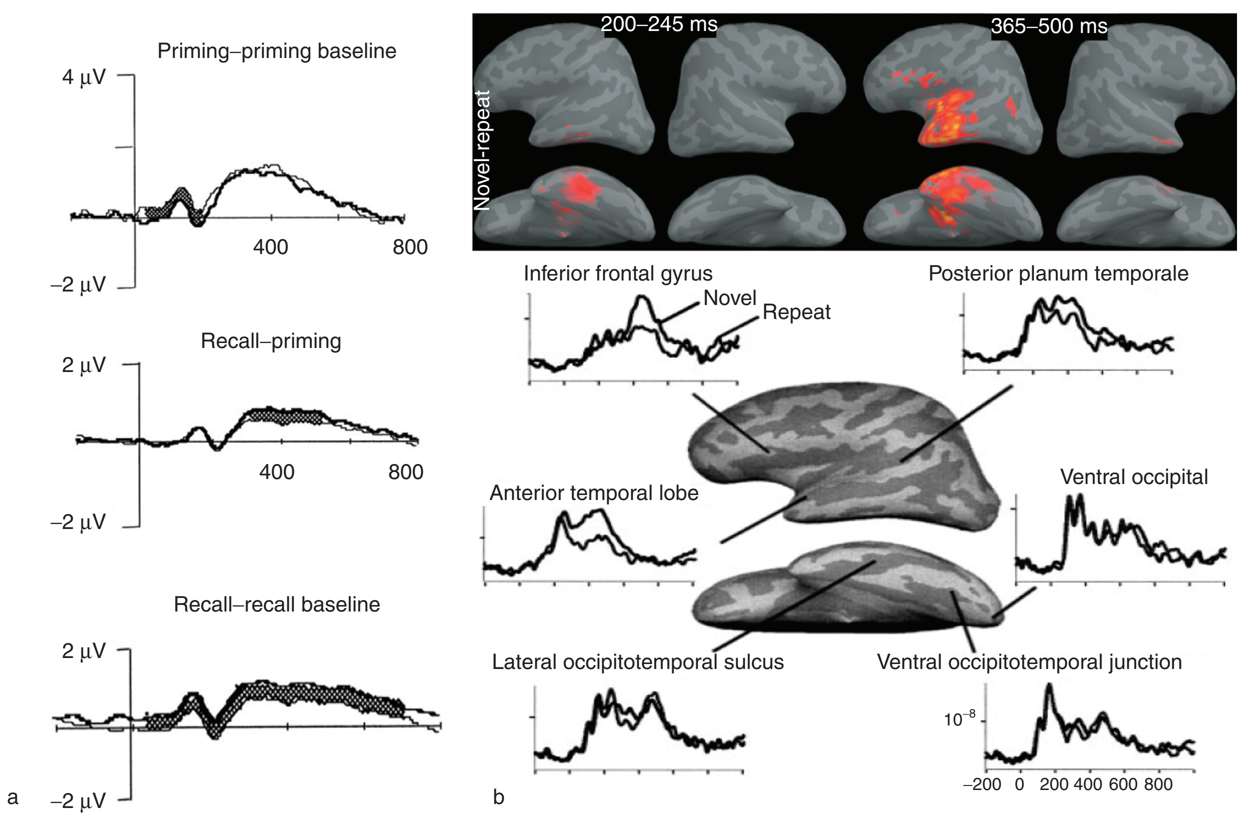

Figure 3 Electrophysiological data from a word-stem completion paradigm. In (a), the event-related potentials (ERPs) over right parietotemporal electrodes recorded by EEG diverge between primed and baseline stems (upper plot), and between recalled and baseline stems (lower plot), within 200 ms, whereas the ERPs to primed and recalled stems only differ from 300 ms onwards (topographies also differ). In the upper panel of (b), regions with reliable differential source-reconstructed event-related activity, inferred from MEG data, for repeated versus novel presentation of stems are shown for two time windows. In the lower panel, the reconstructed responses are shown for a number of regions of interest. (a) Data adapted with permission from Badgaiyan RD and Posner MI (1997) Time-course of cortical activations in implicit and explicit recall. *Journal of Neuroscience* 17: 4904–4913. (b) Data adapted with permission from Dhond RP, Buckner RL, Dale AL, Marinkovic K, and Halgren E (2001) Spatiotemporal maps of brain activity underlying word generation and their modification during repetition priming. *Journal of Neuroscience* 10: 3564–3571.

a direct cued-recall version of the task. However, when contrasting primed and remembered word-stems directly, differences only emerged after approximately 300 ms. These data suggest that priming occurs prior to explicit memory retrieval. Furthermore, and consistent with fMRI data described above, qualitative differences have been found in the study between the differential ERPs to words subsequently primed versus those subsequently remembered. More recently, related experiments (in which word-stems were repeatedly completed) have used the superior spatial resolution of MEG (combined with structural information from MRI) in an attempt to localize the evolution of repetition-related effects over the first few hundred milliseconds from stem onset. Interestingly, an initial repetition-related increase in electrical activity has been reported early in left inferior temporal cortex (lateral occipitotemporal sulcus), followed by a later decrease in both this region and left inferior frontal cortex (Figure 3(b)). Such spatiotemporal data suggest rapid interactions between brain regions, which would be invisible to hemodynamic techniques like fMRI. Indeed, such data afford greater opportunity to look at priming-related changes in the connectivity between different brain regions, for example, as a function of plasticity following initial processing of stimuli.

Summary

The above studies using the word-stem completion paradigm provide convergent evidence that priming reflects a form of memory dissociable from conscious memory, and can arise from a number of cortical regions outside the MTL. These regions are normally a subset of those engaged by the specific stimuli and task (in the above cases, a number of left inferior frontal, left inferior temporal, and occipital regions associated with word reading), suggesting that priming reflects a form of plasticity in these regions. The expression of priming is generally associated with reduced neural activity in these regions, possibly reflecting faster and/or more efficient processing (e.g., a 'greasing of the tracks'). This expression appears to occur very rapidly (around 200 ms) and automatically (regardless of precise task). Differences in neural activity have also been found during the initial processing of stimuli as a function of whether they are subsequently primed. This implicates important roles for factors such as attention and the type of processing in the nature of neural/synaptic changes assumed to underlie priming.

Similar conclusions have been reached using a number of other priming paradigms, though the specific network of cortical regions involved may differ. Indeed, the general finding of decreased hemodynamic responses to repeated stimuli (which has been called 'repetition suppression') has been observed repeatedly across a range of stimuli and indirect memory tasks. Interestingly, however, not all regions activated by initial presentations of stimuli show such decreases: early sensory regions, such as V1, for example, do not normally show repetition suppression. One possibility is that not all of the processing stages in a given task show stimulus-specific effects of prior processing (or alternatively, such effects of prior processing have lifetimes shorter than is typically tested). An interesting theoretical question is therefore which stages (and associated brain regions) show the largest effects of prior processing? Are they, for example, stages that involve greatest competition between alternative outputs/interpretations?

Other Common Measures of Priming

Another common measure of priming is the latency to identify (e.g., name) pictures of objects. This measure has shown priming effects that last up to a year. In a common neuropsychological version, in which degraded pictures are gradually clarified (the 'Gollin figures'), amnesic patients show strong priming (i.e., earlier identification for pictures identified previously). Researchers have also used such priming to investigate the representation of visual objects in the brain, by examining the extent to which priming-related effects (e.g., in different brain regions) generalize across different views of an object.

Another common type of priming is semantic priming, where the response to a probe word (e.g., HEAVEN) is speeded when preceded by a related prime word (e.g., HELL) relative to a nonrelated word (e.g., HILL). Such priming tends to be short-lived, often not surviving more than a second between the prime and probe. As with visual object priming, it has also been used as a tool, in this case to investigate the organization of semantic memory. Yet another type of priming that has been influential on a theoretical level is associative priming, where the priming of a probe stimulus is modulated by whether or not it has previously been paired with a context stimulus. According to theories that hypothesize a key role for MTL in forming associations, patients with MTL damage should not show such priming, even if such priming is shown to be implicit. At the moment, the data appear mixed.

There is also much interest in subliminal priming, in which the prime is presented so briefly (around 50 ms; often forward and backward masked) that participants show little to no awareness of the prime, and yet still show behavioral priming to a probe stimulus presented shortly afterwards (typically within a few hundred milliseconds). Indeed, this type of priming has been recommended for imaging studies of implicit processing, since it is easier to rule out contamination by explicit memory for the prime.

Theories of Priming

A broad distinction has been made between 'perceptual' and 'conceptual' priming. The main difference is that perceptual, but not conceptual, priming is affected by differences in the physical features of the prime and probe stimuli, whereas conceptual, but not perceptual, priming is affected by differences in the degree of semantic processing of the stimuli. This distinction is supported by dissociations in, for example, Alzheimer's patients, who reportedly show intact perceptual priming but impaired conceptual priming, presumably because the early sensory areas believed to be important for perceptual priming are less affected by the disease than anterior temporal regions believed to be important for conceptual priming. A related distinction assumes that priming is supported by specialized 'perceptual representation systems' that are distinct from the MTL memory system. In principle, this allows for dissociable forms of perceptual priming as a function of modality (e.g., visual vs. auditory).

Though useful heuristics, such broad distinctions do not seem sufficient for the varieties of priming that have been investigated. For example, the word-stem completion task discussed above is difficult to fit into the perceptual/conceptual dichotomy, since it is affected by variations in some physical properties, yet residual priming can still occur across modalities (even when voluntary explicit retrieval has been excluded). Furthermore, word-stem completion can be unaffected by the degree of semantic processing of primes (e.g., semantic vs. phonological), yet be reduced following very superficial (e.g., graphemic) processing of primes. These data are consistent with a contribution from a lexical component, in addition to perceptual components. Furthermore, other dimensions along which indirect tasks differ can also produce behavioral dissociations, such as the distinction between competitive and noncompetitive access to conceptual information, for example.

An alternative perspective is the 'component process' view of priming, according to which there are typically several processes involved in a given task that may be facilitated by prior processing. As with the related concept of 'transfer-appropriate processing,' the amount of priming will depend on the degree of overlap between the processes performed on the prime and those performed on the probe (Figures 4(a) and 4(b)). These processes may derive from interactions between brain regions that become configured according to the task demands. Therefore, "performance will depend on the interplay of components and the processes they mediate" (Moscovitch, 1994: 301). A behavioral measure like reaction time is likely to reflect the conglomeration of the times taken to perform each component process. Only by varying the stimuli and task can the key components in behavioral priming be isolated (Figures 4(b) and 4(c)). Alternatively, the concurrent acquisition of hemodynamic or electrophysiological data allows the opportunity to examine activity within the 'network' of brain regions (and the interactivity between those regions) that are configured for the current task.

Another important theoretical dimension is that between 'structural' and 'episodic' theories of priming. According to structural (or 'abstractionist') theories, priming reflects some modification, such as lowered thresholds of, or residual activity in preexisting representations. According to episodic (or 'instance') theories, any exposure to a stimulus can, in principle, leave some residual trace of its processing. Attempts to test these theories have used priming of novel stimuli (e.g., nonwords, or impossible objects) or examined the effects of context (e.g., novel associations) on priming. In general, this distinction is hard to evaluate in the absence of more detailed theories of the nature of representation in the brain (e.g., even nonwords can consist of familiar bigrams of letters). Nonetheless, one important class of episodic theories assumes that each stimulus and response within a task can become associated together, or bound into a single representation (or 'event record'). In such cases, repetition of the stimulus can directly cue retrieval of the associated response. Such stimulus–response associations have been shown to influence behavior, particularly in the case of subliminal (masked) priming, but also in the case of 'negative priming,' when the response to a probe stimulus is hindered if the same stimulus has previously been presented in the context of a different response (even if an implicit response). Such associations have also been shown to have dramatic effects on imaging data. Though stimulus–response associations can be minimized by ensuring that the response made to the probe is unrelated to the response made to the prime, it is clear that when present, such associations can have important consequences, possibly 'by-passing' several stages of processing that occurred on the prime (Figure 4(d)).

Future

One important future direction that provides strong evidence for the direct involvement of circumscribed

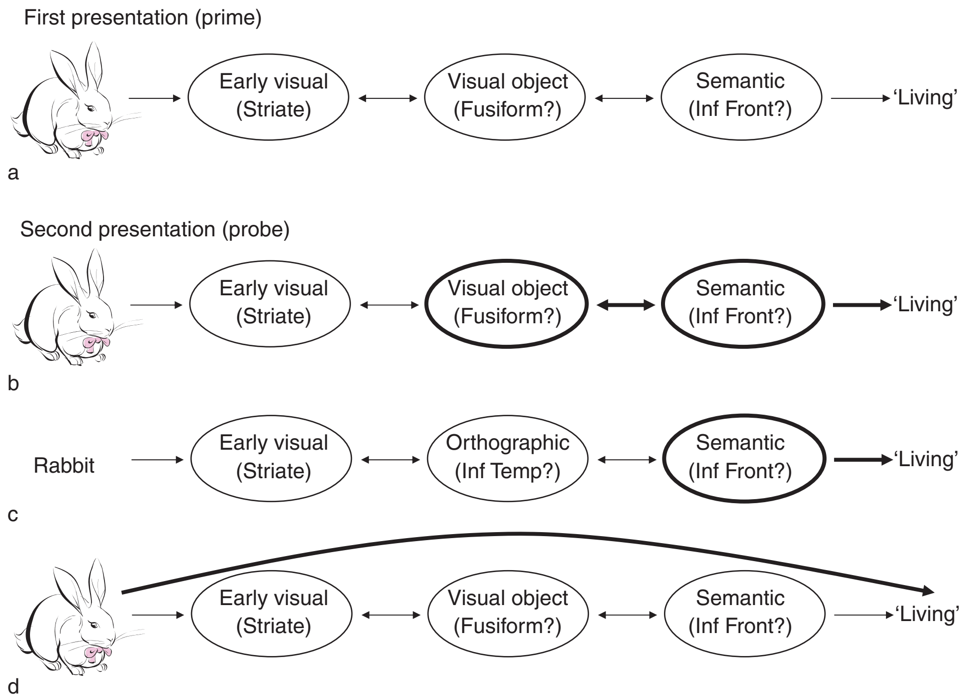

Figure 4 Schematic of the component process view of priming. (a) Initial presentation of an object in a semantic classification task (living vs. nonliving) involves interactions between a number of processing stages between the stimulus (left) and response (right). Putative brain regions associated with each stage are shown. (b) Repetition of the same object in the same task causes faster classification by virtue of facilitated processing in some (but not necessarily all) of the stages (facilitation indicated by darker lines). (c) A change in the stimulus involves re-processing in only one of the original stages (in this example), leading to reduced priming (and potential isolation of semantic component). (d) The formation of direct a stimulus–response association (event record) can also cause priming, even though it bypasses the initial processing stages. Inf, inferior; Front, frontal cortex; Temp, temporal.

brain regions in priming is the use of transcranial magnetic stimulation (TMS). In the only such study to date, either left inferior frontal cortex or a control site was stimulated approximately 300 ms after the initial presentation of a visual object. Frontal stimulation reduced the amount of priming for semantic classification of that object when it was repeated later (Figure 5(a)). Moreover, repetition suppression for that object, when later repeated, was abolished in left inferior frontal cortex, but not in occipital cortex (Figure 5(b)). This supports the existence of at least two components to priming in this task: for example, a visual component in occipital cortex and a verbal component in left inferior frontal cortex.

Another important future direction is the combination of multiple imaging modalities, such as the combination of spatial information in fMRI with the temporal information in MEG. Once the detailed time course of activity can be estimated in different brain regions, one can go further and explore changes in the covariance between these time courses, in order to infer directionality and possible causality. It will also be useful to acquire more fMRI and EEG/MEG data on amnesic patients, to confirm that priming-related changes in brain activity persist despite compromised activity in MTL.

From a theoretical perspective, more detailed models of the causes of priming are needed. According to the 'component process view' mentioned above, an important question is: What is the nature of processes that lead to facilitation when they are re-engaged, in a stimulus-specific manner, in relation to other processes that may not show such facilitation? And how does this component process view incorporate other evidence suggesting a role for direct stimulus–response associations, or episodic records? Some computational models have been used to fit behavioral priming; such models now need to be extended to the neural level, to make contact with the imaging and electrophysiological data described above. One important question for these models is: Is there a single neural mechanism underlying priming, or multiple mechanisms operating on different spatial and temporal scales (e.g., long-term potentiation/depression, or synaptic depression, or even firing-rate adaptation)?

A final important question is how priming and explicit memory, if truly dissociable, nonetheless interact in many circumstances. Some have suggested that the cause of priming (often described as increased 'fluency' of processing) can, under some conditions, be utilized by people in order to make an explicit memory judgment. In other words, people can

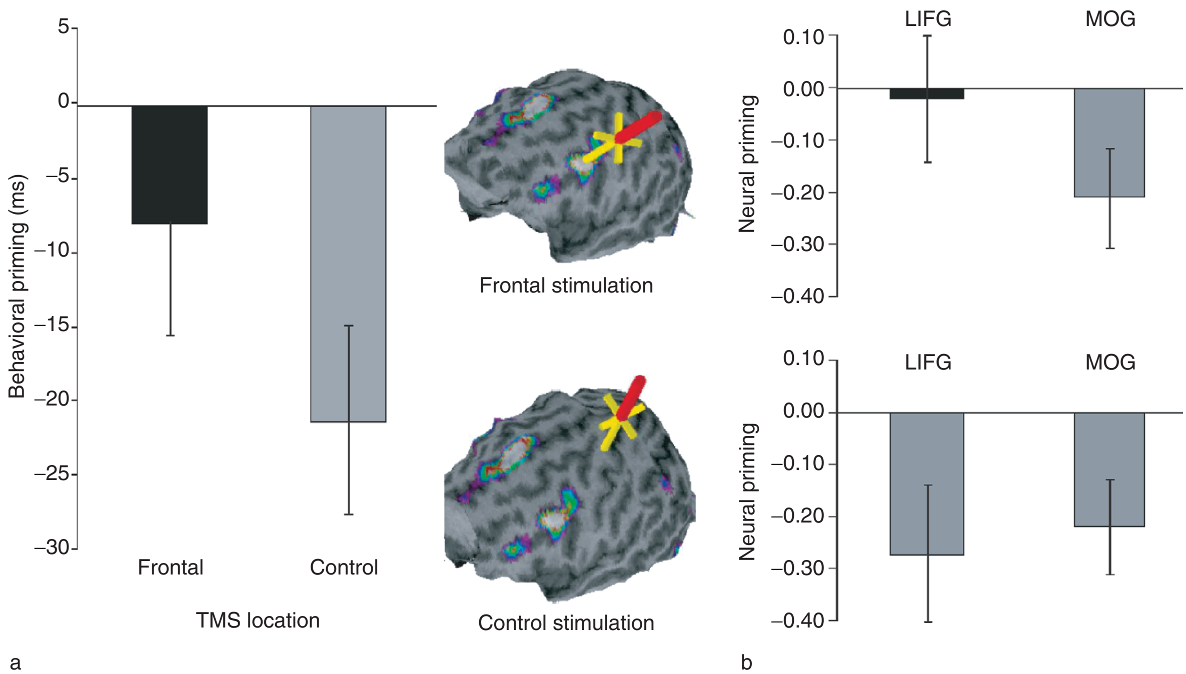

Figure 5 A transcranial magnetic stimulation (TMS) study of priming. (a) Using a semantic classification task like in **Figure 4**, TMS of left inferior frontal cortex (but not of a control region in left motor cortex) shortly after initial presentation of visual objects reduced subsequent behavioral priming. (b) TMS of the frontal region abolished fMRI repetition suppression in that region when the object was subsequently repeated but did not abolish repetition suppression in occipital cortex. LIFG, left inferior frontal gyrus; MOG, middle occipital gyrus. Adapted by permission of Macmillan Publishers Ltd: *Nature Neuroscience*. (Wig GS, Grafton ST, Demos, and Kelley WM (2005) Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience* 9: 1228–1233), copyright (2005).

attribute the feeling of faster/easier processing of a stimulus to a past encounter with that stimulus. A current controversy is whether amnesic patients can be encouraged or even taught to use such fluency cues to improve their memory judgments.

See also: Cognition: An Overview of Neuroimaging Techniques; Declarative Memory System: Anatomy; Electroencephalography (EEG); Memory Representation; Memory Disorders; Multiple Memory Systems.

Further Reading

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