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On the relation between conceptual priming, neural priming, and novelty assessment

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A consistently reported finding in functional neuroimaging studies which compare processing of new information to processing of old information is a reduction in blood flow, and hence neural activity, associated with the old condition. This deactivation has been labeled neural priming. Some investigators have hypothesized that neural priming is the physiological mechanism underlying conceptual priming—a facilitation in the semantic processing of repeated information. Others, however, have hypothesized that neural priming reflects novelty assessment—a mechanism which minimizes the probability that redundant information will be stored in long-term memory. In this paper, the conceptual priming and novelty assessment hypotheses are compared and contrasted in order to ask, and tentatively answer, the question: Are conceptual priming and novelty assessment cognitively and neurophysiologically distinct? Based on a review of the literature, it is suggested that whereas novelty assessment and conceptual priming are distinct cognitive entities, they cannot be presently separated neurophysiologically. That is, some novelty assessment deactivations may in fact reflect priming, and some priming deactivations may in fact reflect novelty assessment.

Key words: PET, fMRI, implicit memory, explicit memory, medial temporal, inferior prefrontal

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The main focus of research in cognitive psychology has been on the identification and characterization of mental processes that underlie behavior and cognition. Consideration of the brain in cognitive theorizing has been minimal until recently. Today, the situation is changing rapidly, thanks to the increasing availability of techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). These techniques provide on-line data about regional changes in brain activity that accompany mental activity. They have therefore created a great deal of excitement, and although far from perfect, and still rather primitive in many ways, they make possible the gathering of information about the regions of the brain that seem to be involved in different cognitive tasks and mental processes. They also help to adjudicate outstanding theoretical puzzles, as well as create new theoretical issues to pursue. In this article one such new issue will be discussed.

This issue has to do with the functional neuroimaging finding that when a stimulus object, such as a word, is presented repeatedly, and therefore presumably "processed" differently from its initial presentation, the neural activity in certain brain regions decreases. The prototypical situation is one in which the activity of the whole brain is measured, region by region, when a given stimulus is presented for the first time, and again when the same stimulus is presented for a second time. Comparison of the two activation patterns typically reveals regions where the neural activity is higher for "old" stimuli (those presented for the second time) than for the "new" stimuli (those presented for the first time), as well as regions in which the opposite occurs—greater activation for new than old stimuli (most brain regions, of course, show no change, implying either that those regions are not involved in the discrimination between new and old, or that the changes that do occur there are below the threshold of detection for the particular method used).

This article is concerned with the finding of decreased regional brain activity for old stimuli. Such decreases have been reported, in different studies, in a variety of brain regions. Two different interpretations have been proposed to account for the reduction of brain activity for repeated stimuli. One involves the concept of "conceptual priming", and the other the concept of "novelty assessment". This paper will discuss, compare, and contrast these two interpretations. The main purpose of this article is to ask, and tentatively answer the question, are conceptual priming and novelty assessment distinguishable from each other cognitively and neurophysiologically? Before proceeding, however, a quick look at the basic logic of functional neuroimaging that makes such a theoretical disagreement possible will be presented.

FUNCTIONAL NEUROIMAGING AND THE LOGIC OF SUBTRACTION

Both of the currently used main functional neuroimaging techniques—positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)—measure haemodynamic changes which are believed to arise from the synaptic activity of populations of neurons (Posner & Raichle, 1994). In PET, the process begins with the injection

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or inhalation of a radioactive tracer, typically oxygen 15 (O^{15}). This tracer is carried by the bloodstream to all parts of the body, including the brain. The unstable O^{15} emits photon particles which are recorded by detector crystals placed around the subject's head. The spatial resolution of PET is anywhere from 5 to 7 mm. Functional MRI, unlike PET, requires no radioactive tracer. Instead, it is used to monitor regional differences in the magnetic properties of hemoglobin in the blood. These properties differ for oxygenated and deoxygenated blood (Turner & Jezzard, 1994). The signal carried by differences in oxygenated and deoxygenated blood is referred to as BOLD for blood-oxygen-level-dependent changes (Rosen, Buckner & Dale, 1998). The spatial resolution of fMRI is anywhere from 3 to 5 mm. Brain regions that are differentially more involved in a particular cognitive process are more active than regions not or less involved, and therefore require and receive more capillary blood. The changes in regional cerebral blood flow (rCBF) are what is measured by PET and fMRI.

PET and fMRI generally provide similar results (Clark *et al.*, 1996; Dettmers *et al.*, 1996; Ojemann *et al.*, 1998), but fMRI has several advantages over PET. First, it is more accessible to researchers than PET is since the structural MRI scanner available at most hospitals can be readily modified for the measurement of functional changes of the brain. Second, because there is no radiation exposure to subjects, as there is with PET, subjects may be repeatedly scanned, permitting longitudinal studies to be carried out. Third, fMRI offers sharper spatial resolution than is achievable with PET. Finally, because useful images can be acquired more rapidly with fMRI than with PET (2–4 s versus 30–60 s), it is possible to measure the BOLD signal for individual events, such as individual items presented in a list, either for study or for test. This method is referred to as event-related fMRI (Buckner *et al.*, 1996; Dale & Buckner, 1997). It is perhaps the most exciting feature of fMRI, permitting more natural experimental designs to be used than is possible with PET. For an introduction to functional neuroimaging see Posner and Raichle (1994) or Roland (1993).

Different methods are used to relate the indirectly measured brain activity to cognition. The most widely used of these is the method of "subtraction". Brain activity is measured during two separate cognitive tasks that differ from one another with respect to specifically identifiable features, such as a cognitive "process", sensory modality, or type of information (Buckner & Tulving, 1995; Petersen, Fox, Posner, Mintun & Raichle, 1988, 1989; Roland & Friberg, 1985). Ideally the two comparison tasks differ by only a single feature alone, but in practice the ideal is seldom achieved. When blood flow recorded during one of the two tasks ("reference" or baseline task) is subtracted from blood flow during the other task ("target" or experimental task), the resulting pattern of brain activations is assumed to represent the functional neuroanatomy of the specified cognitive difference between the two tasks (Buckner & Tulving, 1995). This pattern consists of regions in which the activity is higher for the target task than the reference task, regions in which the activity is higher for the reference task than the target task, and regions (usually by far the most numerous) in which the activity levels between the two tasks do not differ. It is important to keep in mind that the observed activity differences may arise for one or both of two reasons: an activity increase in the target condition *or* an activity decrease in the reference condition. Adding a third condition for further comparison does not change the basic logic of the situation, although it may help to interpret the differences between the first two.

The subtraction method itself is logically neutral with respect to the designation of the two comparison tasks as target or reference. Such designations are always arbitrarily based on other grounds—tradition, the point of a particular study, the underlying theory, and the like. Given a particular designation, the regions in which the activity is higher for the target task are sometimes said to show "activations" while those in which the activity is higher for the reference task are said to show "deactivations". The logical status of both kinds of haemodynamic difference is the same: Both represent the net effect of all the features that distinguish the two cognitive tasks being compared.

Thus, with respect to the main issue of the present paper, it is important to note that the specific regional decreases in activation for old stimuli are physically identical with the increases of activation for new stimuli. This is why it is equally possible to think of them as expressing some kind of a reduction in neural activity associated with an "easier", already practiced, task (the "conceptual priming" account), or as some kind of an increase in neural activity associated with the occurrence of a biologically more relevant "unexpected" event (the "novelty assessment" account). These two interpretations of one and the same haemodynamic change are not simply expressions of preferences for emphasizing one or the other side of the same haemodynamic coin. They do reflect differences in the basic theory, and are worth attention for that reason.

COGNITIVE AND NEURAL PRIMING

"Priming" designates hypothetical processes that underlie the priming effect, the empirical finding that identification of objects is facilitated by the individual's previous encounter with the same or similar objects. Tests on which priming has been measured have been broadly classified into two categories: perceptual and conceptual (Toth, 2000).

On perceptual tests of priming, the retrieval cue bears a perceptual relation to the target (Schacter, 1987). A typical perceptual priming task is stem completion (Toth, 2000): Subjects study a list of words. Later, at test, they are given "stems" (initial three letters) of both studied and nonstudied words and instructed to say "the first word that comes to mind" (Graf & Mandler, 1984). Priming is said to have been demonstrated if the primed stems yield a higher proportion of targets than the nonprimed stems.

On conceptual tests of priming, the relation between the retrieval cues and target items has to do with meaning rather than physical form. For example, in the category exemplar generation task (Graf, Shimamura & Squire, 1985), subjects study a series of words (e.g., EAGLE) and later are required to generate instances of category names (e.g., BIRDS). Priming is demonstrated when subjects generate more previously studied instances than new instances.

Neural priming (Wagner, Koutstaal, Maril, Schacter & Buckner, 2000) refers to a decrease in neural activity which is observed when blood flow measured while subjects process new stimuli is compared to blood flow measured while subjects process the same stimuli again (old stimuli). A typical experiment involves measuring blood flow while subjects semantically encode a set of words and then scanning them again while they semantically encode the same set of words again (Demb *et al.*, 1995). Neural priming is demonstrated when blood flow in specific brain regions is lower in the repeated condition than in the initial condition.

The priming account of reductions in brain activity for repeated stimuli had its origin in the very first PET study of memory reported by Squire and colleagues (Buckner *et al.*, 1995; Squire, 1992). Measurement of blood flow in this study, in which the stem-completion task was used, showed a deactivation in a posterior (right extrastriate) cortical region: Blood flow was lower during the target task of *primed* stem completion than it was during the reference task of *nonprimed* stem completion. The authors suggested that this decrease in brain activation, or neural priming, represented the neural signature of priming effects observed at the behavioral level. The reasoning was that following prior exposure to a stimulus, subsequent processing of that stimulus would be more efficient thus requiring less neural activity (Buckner *et al.*, 1995; Squire, 1992). Tulving *et al.* (1994) also found several neocortical sites, including some in bilateral auditory areas in the temporal lobes, in which blood flow was reduced for previously heard sentences compared with new sentences, and suggested that some of these decreases reflected auditory priming.

Although the neural priming hypothesis was first linked to behavioral priming through a functional imaging study of perceptual priming (Squire *et al.*, 1992), the remainder of this paper will only focus on the relation between functional neuroimaging of conceptual priming and novelty assessment. This is because there is one important methodological difference between studies of perceptual priming on the one hand, and studies of conceptual priming and novelty assessment on the other. In studies of perceptual priming, the physical form of the stimulus is often changed from its initial to its repeated presentation, as is done on word stem and fragment completion tasks (initially the whole word is presented; subsequently only a stem or fragment of the word is presented). On the other hand, in studies of novelty assessment and conceptual priming, the physical format of the stimulus is preserved from its initial to its repeated presentation. Therefore, whereas studies of conceptual priming and novelty assessment are directly comparable, studies of perceptual priming and novelty assessment may not be.

Demb *et al.* (1995) were the first to attribute reductions in brain activity for repeated stimuli to processes related to conceptual priming. In their study, subjects were shown a series of words and were required to decide whether each word represented a concrete or abstract concept. After a short delay, the same set of words was repeated, and subjects were once again required to decide if the words were concrete or abstract. fMRI scans were recorded at both times from a small region of the brain in the prefrontal cortex. Behaviorally, subjects' reaction times for making concrete/abstract decisions were shorter for the repeated than the new stimuli. The fMRI scans revealed less blood flow in the left inferior prefrontal cortex (LIPFC) in the repeated (old) condition than in the new condition. The authors argued that this deactivation (neural priming) was a measure of semantic implicit memory and labeled it semantic repetition priming. The reasoning was that because the words had been primed, less neural activity was required to process them a second time.

Subsequent studies replicated Demb *et al.*'s (1995) findings linking LIPFC deactivations to conceptual priming and extended them to include other brain regions. First, Wagner and colleagues (1997) replicated Demb *et al.*'s (1995) findings on the concrete/abstract decision task and extended them to a different semantic encoding task, making living/non-living decisions, with both verbal and non-verbal stimuli. Subjects' reaction times for making semantic decisions were faster when the stimuli were old than when new. Associated with the faster responses were decreases in LIPFC activity (as with Demb *et al.*'s, 1995, study, scans were only taken from the frontal regions of the brain). Next, Buckner *et al.* (1998) examined changes in activity associated with the processing of old and new non-verbal stimuli. In this study, subjects were shown a series of pictures outside of the scanner. Later while being scanned, subjects either saw new pictures, old pictures, or a fixation cross, and had to determine whether the objects depicted in the picture could move on their own. Behaviorally, subjects' reaction times for making this decision were faster for repeated (old) than new items. Activity measured throughout the entire brain with fMRI was found to be lower for old pictures than new pictures in bilateral extrastriate cortex extending into inferior temporal cortex, left dorsal prefrontal cortex, and anterior cingulate. Buckner *et al.* (2000) next examined processing of old and new information on two different verbal tasks: verb generation and word stem completion. In the verb generation task (Petersen *et al.*, 1988), subjects were shown a series of nouns and were required to generate, as quickly as possible, corresponding verbs. For example, if subjects were shown the word "Ladder", a correct response would be to say "Climb". Following a short delay, subjects were shown the same set of words and once again required to generate verbs for each noun. Behaviorally, it was found that subjects' reaction times for generating verbs was faster to the repeated nouns than to the new nouns. In the word stem completion task, subjects were presented a series of auditory and visual words stems and were required to complete each with the first word that came to mind. Unlike typical cognitive studies of perceptual priming using the word stem completion task, there was no initial study phase. Following a short delay, the same set of word stems were repeated and once again subjects were required to say the first word that came to mind. As with the verb generation task, subjects reaction times for completing word stems was faster the second time around. Reductions in LIPFC, left frontal operculum, and left inferior temporal gyrus activity was revealed by fMRI in both tasks when the old condition was compared with the new conditions. In another fMRI study, Koutstaal and her colleagues (2000) showed subjects a series of pictures and asked them to determine whether the objects depicted in the pictures were larger or smaller than the size of a box they were shown as well. Later on, while being scanned, subjects were shown either the same pictures as before, different exemplars of the pictures shown earlier, or entirely new pictures. Their task was the same as before—to determine whether the objects in the pictures were larger than the box. Size discrimination response times were fastest for the identical old pictures, significantly slower for the new exemplars of old pictures, and slowest for new pictures. Brain activity in multiple frontal and bilateral late visual and posterior brain regions, including middle occipital, fusiform, fusiform/parahippocampal, precuneus, posterior cingulate, bilateral frontal operculum, bilateral posterior inferior frontal/precentral, left anterior inferior frontal, and superior frontal cortices was significantly lower in both old conditions compared with the new condition. Finally, Wagner and colleagues (2000) performed an fMRI study to examine within-task and cross-task processing of old and new words. In this study, subjects were first shown a set of words to encode either semantically (abstract/concrete decisions) or non-semantically (upper case/lower case decisions). Following this initial study phase, subjects were shown the same set of words again to encode semantically (abstract/concrete decisions). Thus in one condition, both stimuli and processes were repeated, whereas in the other condition only the stimuli were repeated. Behaviorally, subjects reaction times for making repeated semantic decisions were faster only when the old words had been initially studied semantically (within-task condition). Physiologically, the authors observed a deactivation in an anterior LIPFC site only when the initial and repeated tasks were the same (within-task condition; both semantic). However, a deactivation in a posterior LIPFC site was observed both when the initial and repeated tasks were the same (within-task condition; both semantic) and also when they differed (cross-task condition; non-semantic followed by semantic).

To briefly summarise, in this section a series of studies were reviewed which compared the processing of new information to the processing of old information. In each study, reductions in blood flow were associated with the processing of repeated information (neural priming). In most studies, deactivations were observed in multiple brain regions, although common to all studies was a deactivation in LIPFC. Associated with the reductions in blood flow was a concomitant decrease in the time needed to process the repeated (old) information. All of the studies reviewed in this section interpreted neural priming as the physiological mechanism underlying conceptual priming. The logic of this argument was that since repeated stimuli were primed as a result of their initial presentation, reprocessing the same information would be more efficient, thus requiring less time and neural activity.

NOVELTY/FAMILIARITY ASSESSMENT

The alternative view of repetition-related reductions in blood flow is that of novelty assessment (strictly speaking, since novelty and familiarity represent two sides of the same cognitive coin, one should speak of novelty-and-familiarity assessment. For convenience's sake, however, novelty/familiarity assessment will be abbreviated to novelty assessment). The origin of this idea goes much farther back into the history of psychology than does that of priming. It has been known for a long time that organisms react to new and unexpected stimuli differently than to otherwise identical but old and expected ones. The relevant research is usually classified under headings such as orienting response (Sokolov, 1963), habituation (Thompson & Spencer, 1966) and novelty detection (Knight, 1984). The common theme here is one related to memory broadly conceived: an organism's earlier encounters of stimulus objects and situations affect their subsequent encounters.

The novelty assessment account of regional brain deactivations in explicit-memory old/new comparisons was suggested by the findings of Tulving *et al.* (1994) in a study in which subjects studied a series of scenic "travel pictures" 24 hours prior to scanning. On the scan day, subjects were scanned while they were making recognition decisions about these old pictures and comparable but new pictures. Blood flow reductions were observed for old pictures relative to new ones in a number of brain regions. These included the hippocampal formation and parahippocampal gyrus in the right hemisphere, the medial dorsal thalamus, anterior cingulate, medial prefrontal, and orbitofrontal cortices. Tulving *et al.* (1994) suggested that some of these brain regions, where activity was greater during processing of novel pictures than processing of familiar pictures, were components of a neural novelty assessment system.

Tulving *et al.* (1996) also proposed that novelty assessment plays an important role in encoding information for long-term storage. They hypothesized that novelty assessment serves the organism by minimizing the probability that redundant information will be stored in long-term memory. The idea, dubbed "novelty-encoding hypothesis", is that the brain automatically screens all incoming and on-line information for its novelty/familiarity, and that the encoding of this information for long-term storage depends on the outcome of such screening: The probability of such storage is positively correlated with the novelty of the information. Simplifying greatly, the idea is that novel information is stored whereas familiar information is not.

Subsequent studies have replicated Tulving *et al.*'s (1994) findings during both verbal and non-verbal tasks and have extended them to include other brain regions as well. An early fMRI study which replicated Tulving *et al.*'s (1994) findings was conducted by Stern and her colleagues (1996). In this study, subjects were shown either new pictures or a single picture repeatedly under intentional encoding instructions. In all subjects tested, encoding of the repeated picture was associated with reductions in activity in the posterior portion of the hippocampus and adjacent parahippocampal gyrus bilaterally. Dolan and Fletcher (1997) first showed subjects a series of category-exemplar word pairs. Later, while being PET scanned, subjects were either shown the same pairs (old-old condition), new pairs (new-new condition), old categories paired with new exemplars (old-new condition), or new categories paired with old exemplars (new-old condition). The comparison between the old-old and new-new conditions revealed reductions in activity for old category-exemplar pairs in the left medial temporal lobe. Martin, Wiggs, and Weisberg (1997) measured blood flow, during different scans, while subjects viewed nonsense objects, silently named real objects, silently read pronounceable nonsense words, and silently read real words. Each of these four conditions were scanned twice—once when the task was performed for the first time and again when the same task was repeated; different stimuli were presented each time. It was observed that, on average, activity in the right hippocampus was lower during the second scan than the first. Next, Saykin and colleagues (1999) conducted an fMRI study to examine processing of new and old words. In this study, subjects first memorized a series of words. Later during scanning, subjects heard either new words or words that they had studied earlier. Comparison of the new and old conditions revealed lower hippocampal activity in the left hemisphere during the encoding of repeated words. Constable *et al.* (2000) examined processing of new and old scenes with event-related fMRI. In the task, subjects were shown intermixed lists of new and old (studied prior to the start of the functional scans) scenes and were asked to indicate whether they represented an indoor or outdoor scene. Blood flow in bilateral hippocampus was lower during the processing of old scenes compared to the processing of new scenes. Finally, Kirchhoff and her colleagues (2000) recently conducted an fMRI study which is directly relevant to the novelty-encoding hypothesis. To reiterate, this hypothesis states that the likelihood of successful encoding for long-term storage depends on the novelty of the information. In their study, subjects were scanned while viewing new and old words and pictures under incidental encoding instructions (indoor/outdoor decision). The comparison between processing new and old stimuli led to bilateral deactivations in inferior prefrontal cortex, posterior fusiform gyrus, parahippocampal/fusiform regions, and unilaterally in left anterior fusiform gyrus and left anterior prefrontal cortex during the incidental encoding of old pictures and words. Most importantly, the level of activity in these region predicted how well the pictures and words would later be remembered. The authors suggested that this finding indicates "... that the operations mediated by ventrolateral prefrontal and temporal regions, operations that appear to impact the efficacy of encoding, are engaged to a greater extent during novel events, perhaps yielding richer and more effective episodic traces for initial relative to repeated experiences". (p. 6179).

As in the section on priming, in this section a series of studies were reviewed which compared the processing of new information to the processing of old information. In each study, decreases in blood flow were associated with the processing of old information (hence increases in blood flow were associated with the processing of novel information). In most studies, deactivations were observed in multiple brain regions, although common to all studies was a deactivation in the MTL. All of the studies reviewed in this section interpreted familiarity-based reductions in activity (novelty-based increases in activity) in terms of novelty assessment.

DISCUSSION

In this paper a series of studies were reviewed in which the processing of old information was compared to the processing of new information. In every single study, a decrease in activity from the new condition to the old condition was observed, sometimes in multiple brain regions. Two different interpretations were offered for these findings. In one group of studies, deactivations in the old/new paradigm were hypothesized to underlie conceptual priming—because old information had been previously processed, subsequent processing would be more efficient and thus require less neural activity. In the second group, the main hypothesis was that deactivations in the old/new paradigm (activations in the new condition) reflected novelty assessment. Tulving *et al.* (1996) proposed that novelty assessment screens out redundant information in order to minimize the probability that it will be stored in long-term memory.

Separating conceptual priming from novelty assessment

The studies reviewed in this paper were classified depending on whether they adopted a conceptual priming or novelty assessment orientation. Despite differences in theoretical orientation, studies in the two groups were similar to each other with respect to their experimental designs and theoretical predictions. First, all studies compared processing of new information with processing of information that had been previously encountered. Second, both theoretical orientations predict that activity in the brain would be greater when the information is new compared to when it has been previously encountered. Given these similarities, it is important to ask whether the concepts of conceptual priming and novelty assessment represent distinct entities or whether they are just different labels to describe the same underlying cognitive process. Theoretical reasoning would seem to support the former position. Priming refers to a facilitation in perception and identification (Tulving & Schacter, 1990), whereas novelty assessment is concerned with long-term episodic encoding (Tulving *et al.*, 1996; Tulving, Markowitsch *et al.*, 1994). Priming predicts that something previously encountered will be processed more efficiently the second time around. Novelty assessment, on the other hand, predicts that the likelihood of successfully encoding of previously encountered things will be lower than novel things. Therefore, priming and novelty assessment, in a sense, are the opposite of each other: In relation to the first time something is encountered, priming facilitates its subsequent processing, whereas novelty assessment inhibits it.

Because the conceptual priming and novelty assessment hypotheses predict similar changes in blood flow (deactivations) and measure them on the same kind of tasks (old/new), it is important to ask whether some deactivations in novelty assessment studies could reflect conceptual priming and whether some deactivations in conceptual priming studies could reflect novelty assessment. There are two reasons for asking this question. First, since it was argued above that conceptual priming and novelty assessment represent different cognitive processes, it is important to be able to distinguish between them physiologically. Second, this question is also important because, typically, results from studies of novelty assessment and conceptual priming have been interpreted with respect to one orientation or the other but not both (for an exception see Tulving *et al.*, 1996). Logically, since priming predicts deactivations in the old condition (hence activations in the new condition) and novelty assessment predicts activations in the new condition (hence deactivations in the old condition), it must be possible for some conceptual priming deactivations to reflect novelty assessment and vice versa. Empirical evidence supports this position as well. With respect to the LIPFC, all priming studies reviewed in this paper have observed deactivations in this region associated with the primed (old) condition. However, Kirchhoff *et al.* (2000) observed that activity in this region was not only higher during processing of new information in comparison to processing of old information (adopting a novelty assessment orientation), but also that activity in this region predicted how well information would later be retained—evidence directly in support of the novelty encoding hypothesis (Tulving *et al.*, 1996; Tulving, Markowitsch *et al.*, 1994). Tulving *et al.* (1996) considered the alternative possibility, that some activations in novelty paradigms (regions higher during processing of novel information) could reflect priming. They acknowledged the possibility, however, rejected this interpretation for the MTL sites because of past neuropsychological findings indicating that amnesic patients with MTL lesions demonstrate intact priming (Gabrieli, 1998; Graf *et al.*, 1985; Squire, 1992; Warrington & Weiskrantz, 1970).

Because deactivations in studies of conceptual priming could represent novelty assessment and deactivations in studies of novelty assessment could represent conceptual priming, at present it is not possible to separate novelty assessment deactivations from priming deactivations in old/new experiments. What will be necessary in the future is the establishment of explicit criteria to distinguish priming deactivations from novelty assessment deactivations. These criteria may be based on experimental manipulations of the behavioral consequences of priming (decrease in RT) or novelty assessment (improvement in explicit memory; see Tulving & Kroll, 1995). For example, if an experimental variable can reduce or eliminate the decrease in RT associated with conceptual priming while leaving intact the memory-enhancing effects of novelty, then it could be argued that neural priming on this experimental paradigm is likely to only reflect novelty assessment. The converse could be used to associate neural priming with conceptual priming. There are many experimental variables which influence the magnitude of conceptual priming (for a review see Roediger & McDermott, 1993), however, the impact of these variables on the magnitude of the novelty assessment effect is unknown at present. When experimental variables are found that can independently affect novelty assessment or conceptual priming, it will then be possible to associate neural priming with one or the other theoretical perspective.

The relation between neural and behavioral priming

The objective in studies of priming is somewhat different from that in other functional imaging studies. In a typical functional neuroimaging experiment, the goal is to relate differences in brain activity between two conditions to the differences in the mental and cognitive processes that differentiate those two conditions. For example, in a typical study of novelty assessment, the goal is to identify brain regions which distinguish processing of new information from processing of old information by comparing blood flow measured during their respective conditions.

In studies of priming, the objective is instead to relate differences in blood flow between the primed and unprimed conditions to behavioral measures of priming. Thus it is not sufficient to examine blood flow differences between the primed and unprimed conditions alone, but a further step must be taken to relate these differences to the changes in behavior that occur between theses conditions (a decrease in reaction times). For example, in the Demb *et al.* (1995) study, differences in blood flow in the LIPFC between the unprimed and primed conditions were related to a concomitant decrease in response time. It is important to note that had the decrease in response time not been observed (or had it not been measured in the first place), it would not have been possible to claim that LIPFC deactivations underlie semantic repetition priming. Instead, the most logical interpretation would have perhaps been one of novelty assessment—activity in LIPFC increases when new words are processed in comparison to repeated words. Therefore, the simultaneous measurement of behavior (conceptual priming) with blood flow is necessary for the conceptual priming hypothesis, whereas this is not the case for the novelty assessment hypothesis.

Although necessary, the simultaneous measurement of neural and behavioral priming is not sufficient to support the hypothesis that neural priming underlies behavioral priming. This is because during old/new experiments, in addition to behavioral priming, other (unmeasured) changes in behavior may also occur. These may include an increase in the production of primed stimuli on implicit memory tasks such as word stem and word fragment completion, an increase in recall and recognition, and explicit awareness that the repeated stimuli have been previously encountered, to name a few. Many of these behavioral changes will occur in old/new experiments *regardless of whether they are explicitly measured.* Therefore, multiple changes in behavior will be associated with a single pattern of brain activity. In such a situation it is difficult to relate the changes in brain activity to a single behavioral dimension—any behavior or combination of behaviors (regardless of whether they are measured or not) may be related to the observed changes in brain activity. In fact, it is likely that the changes in brain activity reflect all of the behavioral dimensions which changed between the unprimed and primed experimental conditions to some extent. In this situation there are no logical grounds on which to relate the observed neural changes to only a single behavioral dimension as is done in studies on conceptual priming.

A solution to this problem may be to analyze the results from priming studies using a correlational rather than a subtraction approach. By correlating the differences in brain activity between the primed and unprimed conditions, voxel by voxel, with the behavioral measure of priming, it would be possible to identify brain regions in which neural priming is correlated with behavioral priming. Although this approach is still correlational, it is one step closer to establishing an association between changes in neural activity and changes in behavior.

Unsettled issues in novelty assessment and conceptual priming

In the preceding discussion, the association between neural priming and behavioral priming was questioned on the grounds that it would not be possible to establish, unambiguously, which behavioral changes were related to the observed brain activity changes. A further challenge to the link between neural priming and behavioral priming is the finding, by Wagner *et al.* (2000), that neural priming can be present in the absence of behavioral priming. In their study, behavioral priming was only observed when both the initial and repeated encoding tasks were the same (both semantic encoding; within-task condition). Behavioral priming was not observed in the cross-task condition (initial non-semantic encoding followed by semantic encoding). Yet, in posterior LIPFC, neural priming was observed in both the within-task condition, where behavioral priming was observed, as well as in the cross-task condition, where behavioral priming was not observed. This finding, demonstrating that neural priming can be observed in the absence of behavioral priming, raises doubts about the hypothesis that neural priming underlies behavioral priming.

A striking difference between studies on conceptual priming and those on novelty assessment is the location of the activity changes. The most consistent finding in conceptual priming studies has been an activity reduction in LIPFC, whereas the most consistent finding in studies on novelty assessment has been an activity reduction in the MTL (although Kirchhoff *et al.*, 2000, interpreted their LIPFC deactivations with respect to novelty assessment). This difference in deactivation foci may be one factor biasing the interpretation of the results towards either novelty assessment or conceptual priming. MTL deactivations have been interpreted with respect to novelty assessment and not conceptual priming because past neuropsychological studies have indicated that amnesic patients with MTL lesions demonstrate intact conceptual (and perceptual) priming (Gabrieli, 1998; Graf *et al.*, 1985; Squire, 1992; Warrington & Weiskrantz, 1970). On the other hand, the conceptual priming hypothesis is favored for LIPFC deactivations possibly because it has been theorized that conceptual priming may be mediated by the semantic memory system (Moscovitch, 1994; Tulving & Schacter, 1990) and that retrieval from semantic memory may rely on the LIPFC (Tulving, Kapur, Craik, Moscovitch & Houle, 1994).

It should be pointed out, however, that the novelty assessment hypothesis equally predicts deactivations within the MTL and the LIPFC for repeated (familiar) stimuli. In fact, Tulving *et al.* (Tulving *et al.*, 1996) hypothesized that the MTL and LIPFC together comprise a novelty-encoding network which functions to increase the likelihood that novel information is encoded into long-term memory and familiar information is not. They hypothesized that the novelty status of incoming and online information is first assessed by the MTL and if the information is determined to be novel, it is then passed on to the LIPFC for subsequent processing and encoding into long-term memory. Therefore, for novel information, it would be expected that both the MTL and LIPFC regions would be active, whereas, activity in these regions would be expected to be suppressed for familiar information, predictions in agreement with present findings. What is unclear at present, however, is why LIPFC and MTL deactivations have not been observed together in the same study (for an exception see Kirchhoff *et al.*, 2000). This is left as a puzzle to be resolved by future experiments.

CONCLUSION

In sum, a review of experiments comparing processing of new information to processing of old information was carried out. In all studies, a deactivation associated with processing repeated stimuli was observed, however, in one group of studies this was hypothesized to reflect conceptual priming whereas in the other group it was hypothesized to reflect novelty assessment. It was argued that conceptual priming and novelty assessment represent distinct entities theoretically, however, at present it is not possible to discriminate between their neural signatures. What needs to be established in the future is a criterion to identify changes in activity in old/new experiments as either reflecting novelty assessment or conceptual priming. Furthermore, the association between neural priming and behavioral priming was challenged on two fronts. First, it was argued that it is not possible to associate changes in brain activity in old/new experiments exclusively with behavioral priming because other aspects of behavior may change concurrently, and second, the finding that neural priming may occur in the absence of behavioral priming suggests that neural priming may not be the physiological mechanism underlying behavioral priming. This paper aimed to bring together two seemingly unrelated topics of functional neuroimaging research, novelty assessment and conceptual priming, in order to explore the relationships which exist between them cognitively and physiologically. It also demonstrates how modern functional neuroimaging can stimulate theoretically oriented research and discussion and thus is not simply a tool for "localization of function".

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