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IMPLICIT AND EXPLICIT MEMORY TESTS REACTIVATE COMMON MEMORY TRACES: SUPPORT FOR A UNITARY MEMORY SYSTEM

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ABSTRACT OF THE DISSERTATION IMPLICIT AND EXPLICIT MEMORY TESTS REACTIVATE COMMON MEMORY TRACES: SUPPORT FOR A UNITARY MEMORY SYSTEM

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The structure of human memory is heatedly debated. While some researchers claim that there are two or more memory systems (Graf & Schacter, 1985; Mitchell & Brown, 1988; Tulving, 1985), others believe that memory is unitary (Bentin et al., 1992; Roediger, 1990). Behavioral and neuroimaging research presented in this dissertation examines a unitary model of human memory using implicit and explicit memory tests for object locations. Specifically, the behavioral experiments tested a) if implicit memory could occur without explicit memory, b) if implicit memory correlated with explicit memory and c) if both tests were equally affected by the strength of memory traces. It appeared that implicit memory for object locations was greater for explicitly recalled, compared to not recalled, items. Implicit memory was correlated with explicit recall. Stronger memory traces were associated with higher recall and higher implicit memory for object locations. The fMRI experiment tested a) if increases in neural activity were related to enhancement of implicit memory and b) re-engagement of encoding-related brain regions during implicit memory test for locations. Consistent with the findings reported in the earlier studies of explicit memory, improvement of implicit memory for

locations was associated with increased neural activity in task-specific and attentional networks. In addition, implicit spatial memory depended on the magnitude of reactivation in the encoding-related brain regions. These findings indicated that implicit and explicit memory may rely on similar facilitatory mechanisms. Taken together, behavioral and neuroimaging evidence supported a unitary model of human memory and suggested that both, implicit and explicit, spatial memory tests access common memory representations. It was proposed that reactivation of memory traces is a key factor for performance on implicit and explicit memory tests. Implicit and explicit tests may differ in their ability to reactivate memory representations. This difference may account for dissociation between performance on implicit and explicit memory tests observed in the previous studies.

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LIST OF ABBREVIATIONS

Brodmann Area
Blood-Oxygen-Level Dependent
Frontal Eye Field
Fusiform Gyrus
Inferior Frontal Gyrus
Inferior Parietal Lobule
Inferior Temporal Gyrus
Middle Frontal Gyrus
Middle Occipital Gyrus
Supplementary Eye Field
Superior Frontal Gyrus
Superior Parietal Lobule
Transfer Appropriate Processing

CHAPTER 1

Background: Memory systems

Conscious recollection of previous experiences is known as explicit memory. Explicit memory is examined with free recall, cued recall, and recognition tasks. Another form of memory is implicit. Implicit memory occurs without awareness. It is indicated through facilitation of task performance or priming (Graf & Schacter, 1985; Henson, 2003; Rouder, Ratcliff & McKoon, 2000; Schacter & Buckner, 1998; Tulving & Schacter, 1990). A typical priming experiment includes two phases: a study phase, where subjects are shown stimuli, and a test phase, where implicit memory for the stimuli is tested. For example, during the study phase a list of words is presented. Then, during the test phase, memory can be tested indirectly by having subjects complete stems of either studied words or non-studied words (Graf & Mandler, 1984). Priming is indicated when the stems of studied words are completed with studied, but not with new, words.

Many behavioral, neuroimaging and lesion studies have demonstrated dissociation between performance on explicit and implicit memory tests. This dissociation is often used as evidence for multiple memory systems (e.g., Mitchell & Brown, 1988; Schacter & Buckner, 1998; Tulving & Schacter, 1990). However, some researchers have argued that dissociation can also be consistent with a unitary memory system (e.g., Berry, Shank & Henson, 2008; McKoon & Ratcliff, 1986; Roediger, 1990).

A model of memory in which multiple memory systems are posited presumes that implicit and explicit memory tasks recruit distinct memory systems and subsystems (e.g., Schacter & Tulving, 1994). For example, such form of implicit memory as perceptual priming relies on perceptual and association neocortex. In contrast, episodic memory, which is a form of explicit memory, relies on medial temporal lobe (MTL) and prefrontal cortex.

Schacter & Tulving (1994) defined criteria to identify different memory systems. One of these criteria is selectivity of each system for a specific information domain. For example, amnesiac patients with damage in Medial Temporal Lobe (MTL) show impaired performance on explicit memory tasks (e.g., recall and recognition), but normal priming in word-stem completion (Graf, Squire & Mandler, 1984; Warrington & Weiskrantz, 1970), word-fragment-completion (Vaidya, Gabrieli, Keane & Monti, 1995) and picture naming tasks (Cave & Squire, 1992; Verfaellie, Gabrieli, Vaidya, Croce & Reminger, 1996). On the other hand, patients with damage of basal ganglia (such as in Parkinson's disease or in Huntington's disease), show impaired implicit memory on motor skill learning tasks, but normal performance on explicit memory tests (Ferraro, Balota & Connor, 1993; Willingham & Koroshetz, 1993).

Another criterion for identification of distinct memory systems is the covering evidence of dissociation provided by different studies. Dissociation of implicit and explicit memory has often been shown in non-clinical populations. For example, implicit memory seems to be less flexible than explicit memory (Cohen, Poldrack & Eichenbaum, 1997; Diens & Berry, 1997; Schacter, Dobbins & Schnyer, 2004), decays less rapidly (e.g., Mitchell & Brown, 1988), is not affected by levels of processing manipulations (e.g., Roediger & McDermott, 1993; Tulving & Schacter, 1990), is not subject to interference (Tulving & Schacter, 1990), and is impaired by a change in stimulus format between study and test (Biederman & Cooper, 1991; Roediger & Blaxton, 1987; Wiggs & Martin, 1994). Moreover, priming can occur even in the absence of explicit memory for studied stimuli (Gabrieli, 1998; Richardson-Klavehn & Gardiner, 1996).

Neuroimaging studies have provided evidence for multiple memory systems by

showing different patterns of brain activation associated with explicit and implicit memory (Schott, Richardson-Klavehn, Henson et al., 2005; Schott, Richardson-Klavehn, Henson et al., 2006). Thus, explicit retrieval often corresponded with increased activation in visual, medial temporal, anterior cingulate and prefrontal cortices (e.g., Buckner, Raichle, Miezin, & Petersen, 1996; Cabeza & Nyberg, 1997). Behavioral priming often corresponded with decreased activation in the fusiform and middle occipital cortices, the left inferior frontal gyrus, cerebellum and some other regions (Buckner, Goodman, Burock, Rotte, Koutstaal et al., 1998; Henson, 2003; Schacter & Buckner, 1998; Wig, Grafton, Demos & Kelly, 2005).

A real life situation may require the involvement of both implicit and explicit memory. Consequently, a single stimulus episode may create memory traces in both implicit and explicit memory systems. Thus, according to the multiple memory systems view, multiple memory traces are created during encoding. A memory trace is a representation of learned experience which contains information about the properties of the stimulus (Hintzman, 1986). Neurally, a memory trace may be a unique network of neurons processing different properties of the stimulus. For example, shape, color, spatial location, semantic meaning of a stimulus may be processed by distinct but interacting groups of neurons. In addition, each memory trace may contain information about the time when it was created (Nadel, Samsonovich, Ryan & Moscovitch, 2000). Implicit and explicit memory traces are independent (Jacoby, Toth, Yonelinas & Debner, 1994). Memory traces in the implicit memory system may be accessed with implicit memory tests. Memory traces in the explicit memory system may be accessed with explicit memory tests.

Despite the evidence of dissociation between implicit and explicit memory

systems, some theorists questioned a multi-system nature of human memory. For example, some researchers suggested that there is a lack of strong evidence for implicit memory in normal subjects. Consequently, there is no need to separate implicit memory into a distinct memory system (Butler & Berry, 2001). It was also suggested that a unitary model of memory is more simple and parsimonious than a multi-system model. For a unitary memory system view, it is unlikely that one stimulus event creates multiple memory traces. A more parsimonious explanation would be that a stimulus event creates a single memory representation. In support of this view, some neuroimaging studies demonstrated that priming and recognition depended on common memory representations (Turk-Brown, Yi & Chun, 2006). In the Turk-Brown et al.'s fMRI study, subjects classified briefly presented indoors/outdoors pictures. Evidence for priming was indicated when the repeated trial was classified faster than the first trial. After the classification task, subjects performed an unexpected recognition test. It was found that behavioral and neural priming were significantly greater for remembered than for not remembered items. Using the evidence from behavioral and ERP studies, Bentin, Moscovitch & Heth (1992) proposed that "performance on both implicit and explicit tests of memory is influenced by a common trace that may be tapped at different levels of awareness as determined by the demand characteristics of the task and the retrieval operation they induce" (p. 1281).

To demonstrate that human memory indeed may be unitary, the proponents of a unitary memory system have to explain the dissociation between implicit and explicit memory tests in normal and amnesiac participants. In non-clinical population, the differences between performance on implicit and explicit memory tests may be explained with the differences in the types of processing underling these tests (Ratcliff & McKoon,

1988). Prior processing of the stimuli makes later processing of those stimuli more fluent. Performance on implicit and explicit memory tests may respond to different thresholds of fluency and familiarity (Jacoby & Dallas, 1981; Mandler, 1980). Also observed differences between explicit and implicit performance may reflect a compatibility between the cognitive processes used during study and test (Roediger, 1990). The similarity of cognitive processing used during study and test, or transfer-appropriate processing (TAP) may be the primary determinant of memory performance (Roediger, 1990). Consequently, the "dissociations between tests reflect the operation of different processes" (p. 1048), but not different memory systems. For example, Weldon and Roediger (1987) found that memory for pictures and words depended on whether the processes at study transferred to test, but did not depend on whether the test was implicit or explicit. Also in Blaxton's (1989) study subjects performed either conceptually driven tasks (e.g., free recall) or data driven tasks (e.g., fragment completion). The conceptually driven tasks were performed more successfully when subjects formed mental images of item at study. The data driven tasks were performed more successfully when the physical features of study and test items matched in terms of modality and typography. Blaxton concluded that the overlap between cognitive processing at study and test explains dissociation between memory tasks better than multiple memory systems.

In support of a unitary model, some studies found that explicit and implicit memory have similar properties. Thus, it was found that both implicit and explicit memory rely on perceptual similarity between study items and test items (Snodgrass & Hirshman, 1994), that implicit memory is not immune to interference (Lustig & Hasher, 2001), that deep encoding produces more priming than shallow encoding (Brown & Mitchell, 1994; Challis & Brodbeck, 1992), and that under certain experimental conditions implicit memory may become as flexible or even more flexible than explicit memory (Willingham, 1997).

The strongest argument for multiple systems model is the impairment of amnesiac patients on explicit, but not implicit, memory tests (Cave & Squire, 1992; Graf et al., 1984; Knowlton & Squire, 1994; Vaidya et al., 1995; Verfaellie et al., 1996; Warrington & Weiskrantz, 1970). Some researchers think that this phenomenon cannot be explained with a unitary memory model (e.g., Poldrack & Foerde, 2008). This argument is weakened by the findings that amnesiac patients are often impaired not only on explicit memory tests but also on implicit memory tests (Jernigan & Ostergaard, 1993; Ostergaard, 1999). Based on the results of two experiments where amnesiac patients showed lower level of priming than normal controls, Ostergaard (1999) concluded that word priming is impaired in amnesia. Simulation studies also showed that a unitary memory model could account for differences in performance on implicit and explicit memory tests in amnesic patients. For example, impaired performance on explicit memory tests and spared performance on implicit memory tests in amnesiacs was predicted by a single-system connectionist model of learning (Kinder & Shanks, 2003).

Simulation studies also showed that dissociation between implicit and explicit memory in non-clinical population is consistent with a unitary system view (Kinder & Shanks, 2001, 2003; Shanks, Wilkinson, & Channon, 2003; Berry, Shanks & Henson, 2008). For example, Berry, Shanks & Henson (2008) applied a single system computational model to investigate relationships between priming, recognition and fluency in a continuous identification paradigm. The model was conceptually similar to signal detection models of recognition. The main assumption was that "a single familiarity signal drives priming and recognition tasks but is scaled differently and is subjected to different sources of noise for each task" (p. 98). The simulation results indicated that the single system computational model was able to account for dissociation between implicit and explicit memory.

Simulation studies have indicated that human memory may be unitary despite dissociation of performance on implicit and explicit memory tests. However, these studies were criticized for modelling memory deficit outside the memory system (e.g., response system or perceptual system) (Poldrack & Foerde, 2008). According to Poldrack & Foerde, the usage of other systems to explain memory deficit undermines parsimony of a unitary system model. Considering this critique, a unitary view of human memory needs to be strengthened by studies showing similarity between implicit and explicit memory. For example, the dependence between performance on implicit and explicit memory tests may reflect similarity. The evidence that enhancement of performance on implicit memory relies on the same behavioral and neural mechanisms as explicit memory may provide additional support for a unitary memory system view.

In four behavioral and neuroimaging experiments presented here, the hypothesis of a unitary memory system was tested using object locations as stimuli. The choice of spatial domain was grounded by several factors. Firstly, it seems that in the spatial domain, implicit and explicit memory are related. For example, it is known that while explicit memory is hippocampus dependent, implicit memory does not depend on hippocampus (e.g., Vaidya et al., 1995). However, it seems that in the spatial domain, the hippocampus may be involved in both explicit and implicit spatial memory tasks. The role of hippocampus for explicit spatial memory is well established (e.g., Burgess, Maguire & O'Keefe, 2002). Recently, the involvement of the hippocampus into implicit spatial memory tasks was also reported. Thus, Chun & Phelps (1999) tested implicit memory for spatial context in patients with damage in hippocampus and adjacent brain structures. They found that patients had preserved skill learning, but impaired learning of spatial context.

Secondly, if transfer appropriate processing is a key factor determining memory performance, then many existing studies have not adequately controlled for differences between study and test. For example, word priming experiments often manipulate depth of processing at encoding by having subjects rate word pleasantness in deep encoding or count syllables in shallow encoding. The test involves the completion of word stems. Although rating words for pleasantness, and stem completion, tasks both require semantic processing, syllable counting does not. Thus, in the terms of the TAP framework (Morris, Bransford, & Franks, 1977), shallow processing during study did not transfer appropriately to test.

Word stimuli may be a particularly poor choice for studies interested in comparing explicit and implicit memory because words consist of a hierarchy of features such as syllables, letters and t-junctions. To assure a comparable transfer appropriate processing, non-hierarchically structured stimuli should be used. Information about spatial locations may be suitable. For example, if a word can be easily broken down into smaller features, it is difficult to imagine how a location of a single object could be broken down into smaller parts. For this reason, it seems that processing object locations at study and at test will produce a good study-to-test transfer of processes.

Thirdly, unlike processing of word stems and word fragments which does not occur very often in daily life, people process spatial information on a regular basis. This makes spatial tasks more ecologically valid compared to word stem or word fragment completion tasks. Finally, spatial information is special. For example, processing of word stems and word fragments may heavily depend on person's verbal skills (Mitchell & Brown, 1988). Processing of spatial locations occurs automatically (Andrade & Meudell, 1993; Ellis, 1990; Hasher & Zack, 1979). Consequently, spatial tasks may introduce less noise compared to lexical tasks.

1.1 Experiment 1: Implicit and explicit memory for object locations *Introduction*

Whether human memory is treated as a unitary system or multiple systems depends on the results of explicit and implicit memory tests. Because behavioral, neuroimaging, and lesion studies provided substantial support for both views, the question about the number of memory systems is still heatedly debated.

Experiment 1 was conducted to reveal dissociation between implicit and explicit spatial memory. Three criteria for assessment of dissociation between implicit and explicit memory systems were chosen: differences in priming for recalled and forgotten spatial stimuli, correlation between performance on explicit and implicit spatial memory tests, and changes in implicit and explicit spatial memory as a function of the strength of initial memory trace.

Based on findings that priming does not correlate with explicit memory (Mitchell & Brown, 1988; Stark & McClelland, 2000), the proponents of multiple memory systems claimed independence of explicit and implicit memory. In contrast, the proponents of a unitary system proposed that priming and explicit memory tap a common memory representation (e.g., Bentin et al., 1992; Jacoby, 1983). Consequently, priming for recalled stimuli may be higher than for not recalled.

The findings that explicit (Craik & Lockhart, 1972; Craik & Tulving, 1975; Lockhart & Craik, 1990), but not implicit (Roediger & McDermott, 1993; Shimamura, 1986; Tulving & Schacter, 1990), memory is susceptible to the strength of initial memory traces were often interpreted as evidence for multiple systems model. Consequently, the evidence for a unitary model will be provided if the strength of memory traces equally affects both types of memory.

In Experiment 1, a two-phase experimental design was used (Figure 1). The first phase was a study phase. During the study phase, subjects learned object and spatial information about black and white drawings located on a 4 x 4 visible matrix. Subjects' learning was either incidental or intentional. Supposedly, learning intentionality affects the strength of initial memory traces. The strength of memory traces may depend on the firing rates in neurons processing stimulus properties and the strength of connections between groups of neurons comprising the memory trace. Intentional learning requires more effort and more cognitive processing compared to incidental learning. This may be related to higher firing rates of neurons involved into encoding. Consequently, intentional learning may be associated with stronger memory traces than incidental learning.

The second phase was a test phase. During the test phase, subjects' implicit and explicit memory were examined. Implicit memory for object locations was tested with a Search task. Subjects did not know that their memory is tested. Explicit memory was tested with a Free Recall task administered before and after implicit memory test. The Free Recall task required subjects to recollect objects and locations presented in the Object Detection task. Although implicit memory seems not to be affected by explicit memory tests administered earlier (Mitchell & Brown, 1988), cued recall and recognition tasks were not appropriate for Experiment 1. The main reason was that both tasks introduced subjects to "correct" and "incorrect" perceptual information. "Incorrect" perceptual information could create its own memory trace and interfere with performance on implicit memory test.

1.1.1 Method

Participants

Participants were twenty seven undergraduates (54% female, mean age = 20.0, SD = 1.9) from Rutgers University participating for course credit. Participants were randomly assigned either to the incidental learning condition (n = 14) or to the intentional learning condition (n = 13). All subjects were treated in accordance with Rutgers University IRB guidelines.

Design and Procedure

Study phase

During the study phase, subjects performed two tasks. The first one was a Dot Detection task (Figure 2). For the Dot Detection task, all subjects were instructed to look at the computer screen and to press a response button as quickly as possible every time when any object appears on the screen. The objects were small (0.5 x 0.5 in) white squares (dots) that were presented one at a time in a random location on a black background of the 4 x 4 invisible matrix for a total of 48 trials. All squares were identical. The frequency of stimulus presentation was the same for all spatial locations. Such uniformity of the stimuli was needed to persuade subjects that the only goal of this task was to measure response time. The Dot Detection task established a baseline response time (RT) for each subject.

The second task was an Object Detection task (Figure 3). This task primed subjects with object locations. To manipulate the strength of initial memory traces,

subjects were randomly assigned either to the incidental learning condition (weak memory traces) or to the intentional learning condition (strong memory traces). Incidental learning is truly incidental only when subjects do not expect any memory test (Mandler, Seegmiller & Day, 1977; Naveh-Benjamin, 1987).

Following the Mandler et al.'s logic, subjects in the incidental learning condition were told that they were participating in the "Speed of Detection" experiment. Subjects received instructions to press the response button as quickly as possible when any object appears on the computer screen. Subjects in the intentional learning condition received instructions to respond as quickly as possible when any object appears on the screen and also to memorize objects and object locations for the future memory test.

The objects were 16 black and white line drawings. A pilot study showed that all objects were easily recognizable. Objects were presented on a white background in one of 16 locations 4 x 4 matrix. Eight of the 16 objects appeared in constant location for a total of two to eight times and were called constant objects. For example, a picture of a frying pan appeared four times in the top-left corner. Eight other objects (variable objects) appeared in two to eight different locations that were not associated with the constant objects. Variable objects were introduced in order to decrease the probability that subjects in the incidental learning condition would figure out the real goal of the Object Detection task. Variable objects appeared one time in each location. For example, a picture of a lobster appeared in four different locations. Overall, subjects viewed the pan and the lobster four times each, but while the picture of the pan was associated with one location, the picture of the lobster was associated with four locations.

Previous studies showed that repeated presentation of objects in constant locations leads to priming (Maljkovic & Nakayama; 1994, 1996; Musen, 1996). For example, in the Musen's study subjects had to name spatial locations of objects that were repeatedly presented in constant locations. Musen found that naming RT decreased across repetition trials. With reference to Experiment 1, these findings predict the larger magnitude of priming for constant object than for variable objects. Consequently, further in the manuscript, constant objects will be referred as primed objects and variable objects will be referred as foils.

Each trial in the Dot Detection and the Object Detection tasks started with an empty grid presented for either 500, 1000 or 1500 ms. The interval was randomly chosen by a computer. After that, a dot (in the Dot Detection task) or an object (in the Object Detection task) appeared in one of 16 locations. In previous studies, a peak of priming was observed when subjects viewed a stimulus for 250 ms. Priming significantly decreased when subjects viewed a stimulus for 40 ms or 1900 ms (Zago, Fenske, Aminoff & Bar, 2005). Based on these findings, subjects' response time was limited to 1000 ms. It was expected that subjects in the incidental learning condition would detect dots and objects equally fast. Subjects in the intentional learning condition would detect dots faster than objects due to additional processing load required for stimuli memorization (e.g., Sternberg, 1998).

<u>Test phase</u>

The test phase began right after completion of the study phase. It consisted of the Free Recall task administered before the Search task (explicit memory test), the Search task (implicit memory test) and the Free Recall task administered after the Search task (explicit memory test).

The Free Recall task required subjects to recollect objects and their locations. The answers had to be written down in a 4 x 4 empty matrix. Specifically, names of objects

had to be placed in locations as they appeared during the Object Detection task. For subjects in the incidental learning condition, the Free Recall task was completely unexpected. For subjects in the intentional learning condition, the Free Recall task was expected. Subjects performed the Free Recall task until they could no longer remember any information. It took about 15 minutes on average. Subjects' recall accuracy for objects and locations was computed. Hits were calculated as a percent of objects placed in the correct location(s). False alarms (FA) were calculated as a percent of objects placed in the incorrect location(s). Corrected hits were calculated as a difference between Hits and FAs. Object recall accuracy was calculated as a percent of primed objects and foils that subjects recalled (without considering the correctness of object's location).

Right after the Free Recall task, subjects performed an implicit memory task. In the previous studies, implicit memory for spatial context was studied using a search task (Chun & Jiang, 2003; Chun & Phelps, 1999). This idea was adopted for the current study. The search task was used to measure implicit memory for locations. It required subjects to find a target object on the 4 x 4 matrix filled with 12 different objects. Priming was indicated when subjects found primed objects faster than foils and new objects.

Each trial of the Search task (Figure 4) started with the presentation of a target object in the center of the computer screen for 2000 ms. The target presentation was followed by an empty matrix presented for 1000 ms (ISI). After empty matrix, subjects saw a search display consisting of the 12 objects located along the outer border of the matrix. Subjects viewed the search screen until they found and clicked on the correct object with the mouse cursor. After subjects had chosen the correct object, the empty matrix was presented again for 1000 ms (ITI). All subjects were instructed to find a target object and click on it as quickly as possible. The Search task began with six practice trials where participants searched for a number. During the first part of the Search task (96 trials), subjects had to search for a target objects that previously appeared during the Object Detection task (old objects). All search displays consisted of six primed objects and six foils. Differences in the search displays were achieved through variation in the foil's positions. Although primed objects and foils occupied the same locations as in the Object Detection task, subjects were not informed about this relationship.

Each primed objects always appeared in the constant location and served as a target on the six different trials. Each foil appeared in the variable locations and served as a target on a total of 4 to 12 different trials. Repeated presentation of the stimuli could lead to learning of spatial information and decrease in search time. However, this effect may be more pronounced for primed stimuli compared to foils.

In the second part of the Search task (48 trials), all old objects were placed in new locations. In addition, 12 new objects were introduced. During the second part of the Search task, the search display consisted of six primed objects in new locations, four foils in new locations and two new objects in random locations. In the second part of the Search task, each object served as a target on a total of 2 trials.

Overall, there were primed trials (primed objects placed in primed locations), foil trials (foils placed in primed locations), unprimed trials (primed objects placed in new locations), unprimed foil trials (foils placed in new locations), and new trials (new objects placed in random locations). Priming was measured as a difference in the search RT on primed trials and on the other types of trials. For example, if subjects are primed with object locations during the Object Detection task, they will find primed objects in primed locations faster than primed objects in new locations or new objects. Right after the Search task, subjects performed an unexpected Free Recall task. The procedure was identical to the Free Recall task preceded the Search task. It was expected that repeated presentation of stimuli during the Search task would enhance explicit recall after the Search task.

In order to explore a structure of human memory system, the effects of learning condition on explicit and implicit memory were tested.

Predictions:

If intentional learning subjects, compared to incidental learning subjects, recall more information explicitly and also demonstrate more priming, it will support a unitary memory system. If subjects in the intentional learning condition, compared to subjects in the incidental learning condition, show superior explicit memory, but comparable priming effect, it will support multiple memory systems.

In the Search task, the first and the last repetitions were critical trials because they could be directly associated with free recall before and after the Search task. Consequently, in order to explore the relationship between explicit and implicit memory, the data were analysed in the following way:

1) Recall success on the Free Recall task *preceded* the Search task was coded for recalled and forgotten items. Search RT on the *first* repetition trial was collapsed across two levels of recall (recalled vs. forgotten) and compared using a GLM repeated measures analysis with recall success as a repeated factor and learning condition as a between-subject's factor.

2) Recall success on the Free Recall task *followed* the Search task was coded for recalled and forgotten items. Search RT on the *last* repetition trial was collapsed across two levels of recall (recalled vs. forgotten) and compared using a GLM repeated

measures analysis with recall success as a repeated factor and learning condition as a between-subject's factor.

Predictions:

If search RT for recalled stimuli is significantly lower than search RT for not recalled stimuli, it will support a unitary memory system. If search RT is not different for recalled and not recalled stimuli, it will provide support for multiple memory systems.

One piece of evidence supporting independence of two memory systems is the lack of correlation between performances on implicit and explicit memory tests (Kinder & Shanks, 2003). In order to examine correlation between explicit and implicit memory for locations, data were analysed in the following way. Recall success on the Free Recall task was rated on a scale of 0 to 3. The scale reflected subjects' recall score. The rating was assigned to each item in the Search task. Thus, "0" was assigned if subjects forgot the object. "1" was assigned if subjects recalled the object, but placed it in the incorrect location. "2" was assigned if subjects recalled the object and placed it in both correct and incorrect locations. "3" was assigned if subjects recalled the object and placed it in the correct location(s) only. A correlation analysis was conducted on search RT for the *first* repetition trial and recall score *before* the Search task. Also the correlation analysis was conducted on search RT for the *last* repetition trial and recall score *after* the Search task.

Predictions:

If recall score and search RT are correlated, it will support a unitary memory system view. If recall score and search RT are not correlated, human memory relies on multiple memory systems.

1.1.2 Results

Study phase

Subjects' RT during the Dot Detection task and the Object Detection task (Figure 5) was a subject of a paired t-test. In the incidental learning group of subjects, there was no significant difference in Dot Detection RT and Object Detection RT, t(13) = 0.96, p=0.36. In the intentional encoding group of subjects, the Dot Detection task was performed significantly faster than the Object Detection task, t(12) = -4.32, p=0.001. *Test phase*

Search task

In order to discourage subjects from selecting objects other that targets, the same search display was presented until participants found the correct object. Because participants could not proceed to the next trial unless they clicked on the correct object, the accuracy on the Search task was forced to be 100%. However, sometimes, subjects used more than one attempt to find a correct object. The trials where the correct object were not found with the first attempt were excluded from the further analysis. Overall, subjects found 94% of trials (SD = 3%) with the first attempt.

To rule out the effect of individual objects on subject's performance, an item analysis was conducted using the Univariate Analysis of Variance with object as a random factor. The item analysis demonstrated that there was no group x object interaction. The *p*-values for all types of trials and repetitions were larger than 0.05 (the range was 0.094 - 0.99). These findings suggest that the effect of objects was similar in all groups of subjects and could be disregarded in the further analysis.

Subjects' RT was analyzed using a GLM procedure. The subject's responses of 3 *SD* above the group mean were removed. Removed outliers totaled less than three percent of the data. The Greenhouse-Geisser adjustment was applied when needed. Search RT for primed objects was analyzed with a GLM repeated measures with repetition as a repeated

factor and learning condition as a between-subject's factor. The GLM analysis revealed a significant learning condition x repetition interaction, F(3.36, 84.0) = 2.96, p = 0.032, a main effect of repetition, F(3.36, 84.0) = 28.54, p < 0.001, and a main effect of learning condition, F(1, 25) = 6.86, p = 0.015 (Figure 6). Overall, subjects in the intentional learning condition had lower search RT than subjects in the incidental learning condition. The between-subject's effect diminished as a function of repetition. Search RT for the foils was also analyzed with a GLM repeated measures with repetition as a repeated factor and learning condition as a between-subject's factor. There was a significant learning condition x repetition interaction, F(11, 275) = 2.2, p = 0.014, significant effect of repetition trial, F(11, 275) = 4.19, p < 0.001, but no main effect of learning condition, F(1, 25) = 0.4, p = 0.84 (Figure 6). Overall, subjects performed first trials slower than the last trials. This effect was more pronounced in the incidental learning group of subjects.

The mean response time for the first and for the last repetitions of primed stimuli and foils is presented in Table 1. A t-test showed that during the first repetition, intentional learning subjects found primed objects faster compared to incidental learning subjects, t(25) = -3.55, p = 0.002. The effect of encoding condition on the first repetition of foils was marginally significant, t(25) = 1.96, p = 0.06.

There was no between-subject's difference in RT for the last repetition of primed objects, t(25) = 1.46, p = 0.16, and for the last repetition of foils, t(25) = -1.01, p = 0.32. In both groups of subjects, search RT for the first repetition of primed objects correlated with search RT for the last repetition of primed objects, r = 0.28, p = 0.013 for incidental learning group, and r = 0.28, p = 0.02 for intentional learning group.

The first repetitions of primed trials were compared to the first repetitions of foil, unprimed and new trials. Foils were compared to unprimed foils and new trials. The *p*-

values are presented in Table 2. In the incidental learning group of subjects, search RT for primed stimuli was significantly faster than search RT for foils, but was not different from new trials and unprimed trials. The fact that foil trials were significantly slower than new trials implies that performance on foil trials may be inhibited. In the intentional learning group of subjects, search RT on primed stimuli was significantly faster than search RT on foils, on new trials and on unprimed trials. Search RT for the foils did not differ from search RT for the new stimuli.

Free Recall task

Tables 3 and 4 present hits, false alarms, corrected hits, object recall and recall confidence data for primed objects and foils. A t-test revealed that *before* the Search task, subjects in the intentional learning condition recalled more primed objects than subjects in the incidental learning condition, t(25) = 4.62, p < 0.001. However, *after* the Search task, no between-subject's differences were observed, t(25) = 1.6, p = 0.12. Incidental learning subjects and intentional learning subjects also did not differ in recall of foils *before* and *after* the Search task as well as in recall of new objects, all *p*-values > 0.4.

When the Free Recall task was administered *before* the Search task, subjects in the intentional learning condition recalled more spatial information compared to subjects in the incidental learning condition. This pattern of results held for the primed objects, t(25) = 5.23, p < 0.001 for hits and t(25) = 5.15, p < 0.001 for corrected hits, and for the foil objects, t(25) = 3.3, p = 0.003 for hits, and t(25) = 3.4, p = 0.002 for corrected hits. When the Free Recall task was administered *after* the Search task, there were no differences between groups whether the object was primed, foil or new, all p-values > 0.5.

Overall, subjects significantly improved their explicit memory for the stimuli

during the Search task. Thus, in the incidental group of subjects, recall of primed objects and locations was significantly larger *after* the Search task compared to recall *before* the Search task, t(13) = -8.3, p < 0.001 for objects and t(13) = -8.5, p < 0.001 for locations. In the intentional learning group of subjects, recall of primed objects was also significantly larger *after* the Search task, t(12) = -5.7, p < 0.001, and recall of locations was marginally larger *after* the Search task compared to recall *before* the Search task, t(12) = -2.1, p = 0.057.

Subjects in the incidental learning condition also significantly improved their explicit memory for the foils and their locations, t(13) = -3.8, p = 0.002 for objects and t(13) = -2.56, p = 0.024 for locations. In contrast, subjects in the intentional learning condition improved only memory for the foil objects, t(12) = -5.57, p < 0.001, but not for the foils' locations, t(12) = 0.4, p = 0.7.

The relationship between recall success and search RT

All responses in the Free Recall task were divided into two groups: recalled objects (without considering correctness of object locations) and forgotten objects. A GLM repeated measures analysis with recall success (recalled items vs. forgotten items) as a repeated measure and learning condition as a between-subject factor was conducted on search RT. Search RT on the *first* repetition trial was examined as a function of recall success in the Free Recall task *preceded* the Search task. Search RT on the *last* repetition trial was examined as a function of recall success in the Free Recall task *preceded* the Search task. Search RT on the *last* repetition trial was examined as a function of recall success in the Free Recall task *followed* the Search task. Because after completion of the Search task, some subjects were able to recall all objects, the missing RTs for not-recalled stimuli were replaced with the group averages. It did not change group means but provided more degrees of freedom.

A GLM analysis showed that search RT for primed objects on the *first* repetition

trial depended on the recall success in the Free Recall task administered *before* the Search task (Figure 7). There was a main effect of learning condition, F(1, 25) = 5.36, p = 0.029, and a main effect of recall success, F(1, 25) = 13.9, p = 0.001. Subjects in the intentional learning condition found primed objects faster than subjects in the incidental learning condition. Subjects found recalled objects faster than forgotten objects. There was no learning condition x recall success interaction (Figure 7), F(1, 25) = 1.57, p = 0.22, meaning that the effect of recall success on search RT was independent of the learning condition. Post-hoc t-test revealed that in both groups of subjects, recalled primed objects were found significantly faster than forgotten primed objects, t(13) = -3.0, p = 0.01 for incidental learning group of subjects, and t(12) = -2.37, p = 0.035 for intentional learning group of subjects.

As for the foils, there was only the marginal effect of the learning condition, F(1, 25) = 3.26, p = 0.08, no main effect of recall success, F(1, 25) = 1.48, p = 0.23 and no learning condition x recall success interaction, F(1, 25) = 0.85, p = 0.37. In both groups of subjects, there was no difference in search time for recalled and forgotten foils, t(13) = -0.2, p = 0.84 for incidental learning group of subjects, and t(12) = -1.57, p = 0.14 for intentional learning group of subjects.

A GLM analysis showed that the recall success in the Free Recall task administered *after* the Search task depended on search RT for primed objects on the *last* repetition trial. Subjects found recalled objects faster than forgotten objects, F(1, 25) =5.35, p = 0.029. However, there was no main effect of learning condition, F(1, 25) =0.39, p = 0.54, and no learning condition x recall success interaction (Figure 7), F(1, 25) == 0.13, p = 0.72. As for the foils, there was no main effect of learning condition, F(1, 25) == 0.7, p = 0.4, no main effect of recall success, F(1, 25) = 0.9, p = 0.35 and no learning condition x recall success interaction, p > 0.9.

To find out if there was a significant priming effect for recalled and forgotten objects, subjects' search RT for recalled and not recalled primed objects was compared to search RT for new objects using a one-sample t-test. Mean search RT for new stimuli was 1014 ms (SD = 219 ms) in the incidental learning group of subjects and was 1066.68 ms (SD = 208 ms) in the intentional learning group of subjects. If search RT for primed stimuli is faster than search RT for new stimuli, then there is a significant priming effect. On the *first* repetition trial of the Search task, subjects in the incidental learning condition showed no difference in search RT for not recalled primed objects and search RT for new objects, t(13) = 0.39, p = 0.7, indicating a lack of priming effect. However, search RT for recalled primed objects was significantly faster than search RT for new objects, t(10) = -2.8, p = 0.018. In the intentional learning group of subjects, t(12) = -7.7, p < 0.001. The t-test showed that on the *last* repetition trial of the Search task, there was the priming effect for forgotten and recalled primed objects in both groups of subjects, all p -values < 0.004.

<u>The correlation of recall scores before the Search task and search RT on the first</u> <u>stimulus repetition</u>

There was a significant correlation between recall scores and search RT for primed objects, r = -0.33, p = 0.003 for subjects in the incidental learning condition, and r = -0.44, p < 0.001 for subjects in the intentional learning condition. Overall, these results mean that faster RT in the Search task was associated with better recall of object locations in the Free Recall task. There was no relationship between recall scores and search RT for the foils , r = -0.09, p = 0.38 for subjects in the incidental learning condition.

The correlation of recall scores after the Search task and search RT on the last stimulus repetition

There was a significant correlation between recall scores and search RT for the primed objects, r = -0.23, p = 0.04 for subjects in the incidental learning condition, and r = -0.24, p = 0.04 for subjects in the intentional learning condition. Overall, these results mean that faster RT in the Search task was associated with better recall of object locations in the Free Recall task. There was no relationship between recall score and search RT for the foils in incidental learning subjects, r = -0.15, p = 0.12, and in intentional learning subjects, r = -0.09, p = 0.39.

1.1.3 Discussion

Experiment 1 was conducted in order to collect empirical evidence for dissociation of implicit and explicit memory systems. Predictions were based on the correspondence between performance on implicit and explicit memory tests and on the effects of the initial memory trace strength on both types of memory. The strength of memory traces was manipulated during the study phase. This process was validated by the results of the Dot Detection and the Object Detection tasks. The results suggest that participants in the intentional learning condition exerted greater effort to encode stimulus information than participants in the incidental learning condition. Consequently, intentional learning subjects acquired stronger memory traces.

Explicit memory for objects and locations was tested using the Free Recall task. Explicit recall was examined at points preceding and following the implicit memory task. In the explicit test preceding the implicit memory test, subjects in the intentional learning condition (who supposedly had stronger initial memory traces) recalled more objects and locations compared to subjects in the incidental learning condition (who supposedly had
weaker initial memory traces). These findings are consistent with the predictions and earlier work (e.g., Lockhart & Craik, 1990). In the explicit test following the implicit memory test, there was no difference in recall performance between subjects with strong and weak memory traces. Overall, both groups of subjects significantly improved their explicit memory for the stimuli during the implicit memory task.

Implicit memory for spatial locations was tested using the Search task. The priming effect was calculated based on within-subject comparisons. Weak memory traces did not produce a significant priming effect because subjects exhibited no difference in search RT between the first primed, the first new and the first unprimed trials. In contrast, strong memory traces did produce a significant priming effect because search RT for the first primed trial was significantly faster than search RT for the first new and the first primed trials.

Consistent with previous findings (Musen, 1996), the stimulus repetition during the Search task resulted in implicit learning of primed locations. The learning effect was indicated by the decrease in search RT across several repetitions. By the end of the Search task, the effect of memory trace strength on priming had disappeared. Converging evidence from the explicit and implicit memory tests in Experiment 1 clearly indicated a parallel acquisition of explicit and implicit memory during the Search task. The similar effect was observed previously in motor sequence learning experiments (Willingham & Goedert-Eschmann, 1999).

Three pieces of empirical evidence, as emerged in Experiment 1, supported a unitary memory system. The first piece of evidence, in effect, is the finding that initial memory trace strength had equal effect upon implicit and explicit memory. If implicit memory and explicit memory belonged to the two distinct systems, then the strength of initial memory traces would influence these two systems differently (Graf & Mandler, 1984; for review, see Roediger & McDermott, 1993).

Specifically, explicit memory would exhibit greater sensitivity to trace strength than would implicit memory (e.g., Tulving & Schacter, 1990). In Experiment 1, weak memory traces were associated with low recall performance and absence of priming. In contrast, strong memory traces were associated with high recall and high priming effect (Figures 8 and 9).

Repeated presentation of primed objects in constant locations during the Search task not only enhanced subjects' search RT (implicit memory), but also improved subjects' recall of objects and locations (explicit memory). These findings imply that the strength characteristic of initial memory traces had a similar influence on implicit and on explicit memory tests.

The second piece of evidence for a unitary memory system is based on analysis of priming effect for recalled and for not recalled items. According to Richardson-Klavehn & Gardiner (1996), priming can occur even without the presence of explicit memory for the given stimuli. Consequently, if implicit and explicit memory tests tap different memory systems, priming effects for recalled and for not recalled stimuli should not differ. Experiment 1 clearly demonstrated that the magnitude of priming was greater for recalled than for not recalled stimuli. These findings were consistent across intentional and incidental learning conditions and were observed at the beginning of the Search task as well as at the end of the Search task.

This evidence, however, may be not very conclusive due to problems with definition of stochastic dependence of implicit and explicit memory tests based on implicit performance for recalled and forgotten items (Poldrack, 1996). According to Poldrack, to determine stochastic dependence of tests one needs a large number of subjects and items (or subject items) to have a sufficient power to determine the dependence effect. In this study, the number of subject items was small (27 *6 = 162). This opens the possibility that performance on the Search task may be independent from performance on the Free Recall task. However, the evidence of correlation between recall scores and search RT may provides additional support for dependence of implicit and explicit measures of memory.

The third piece of evidence for a unitary memory system came from a correlation analysis of search RT and subjects' recall confidence for locations. In Experiment 1, search RT and recall confidence correlated. The faster response time corresponded to more confident recall. These findings were replicated in incidental and intentional learning conditions and across different time points of the implicit memory task. According to Jacoby (1983), correlation between priming and explicit retrieval may suggest that they have to be considered within common framework.

In summary, Experiment 1 supported a unitary system view of spatial memory. However, two limitations of this experiment may influence the results interpretation. The first limitation of Experiment 1 concerns the assumption that subjects are unaware of the relationship between study and test stimuli if they are not informed about it. Priming tasks usually do not relate subjects to any specific learning experiences. However, toward the middle of the testing session, participants may spontaneously become aware of the study-test relationship (Bowers & Schacter, 1990; Mace, 2003a). Such spontaneous study-test awareness may improve priming (Mace, 2003b; Richardson-Klavehn & Gardiner, 1995). If subjects in Experiment 1 were aware of the study-test relationship, they could have used an explicit retrieval strategy to facilitate performance during the course of the Search task. Experiment 2 will address this issue by manipulating subjects' study-test awareness. Subjects in Experiment 1 will be compared to study-test aware and study-test unaware subjects in Experiment 2. The results of this comparison may provide information about subjects' awareness in Experiment 1.

The second limitation of Experiment 1 concerns the differences in the amount of perceptual information provided by the free recall and the Search tasks. While the Search task provided subjects with object representations, the Free Recall task did not involve any perceptual information and mostly relied on subjects' ability to visualize learned stimuli. Although perceived stimuli and mental images could be represented and processed similarly (Borst & Kosslyn, 2008), a lack of perceptual information may complicate recall, especially for subjects who did not exert any substantial effort in the encoding of stimuli. Consequently, it may be not completely appropriate to compare implicit and explicit tests possessing distinct perceptual properties.

This issue will be addressed in Experiment 3. In Experiment 3, subjects' explicit memory for locations and objects will be tested with a Cued Recall task. A pattern of results obtained in the Cued Recall task will be compared to the pattern of results obtained in the Free Recall task of Experiment 1. If these patterns appear similar, then the presence of perception-related differences between the implicit and explicit memory tests in Experiment 1 could be disregarded.

1.2 Experiment 2: Implicit memory in study-test aware and study-test unaware subjects

Introduction

The enhancement effect of study-test awareness upon priming is modulated by the

strength of initial memory traces. In previous studies, study-test awareness facilitated priming when subjects had strong, but not weak, initial memory traces (Mace, 2003b; Richardson-Klavehn, Lee, Joubran, Bjork, 1994). For example, in Mace's study, subjects learned words either in the shallow encoding condition (weak memory traces) or in the deep encoding condition (strong memory traces). During the test, subjects completed word stems, some of which belonged to the studied words. Mace found that study-test awareness enhanced priming in deep, but not in shallow, encoding.

These findings were interpreted in terms of priming "contamination". It was suggested that study-test awareness enhances priming by "contaminating" it with explicit memory (Butler & Berry, 2001; Kinoshita, 2001; Mace, 2003a,b; Richardson & Klavehn et al., 1994; Richardson-Klavehn & Gardiner, 1995; Richardson-Klavehn, Gardiner & Java, 1996; Schacter, Bowers, Booker, 1989). Indeed, deep encoding usually results in better explicit retrieval than shallow encoding (Craik & Lockhart, 1972; Craik & Tulving, 1975; Lockhart & Craik, 1990). Consequently, subjects in the deep encoding condition have more resources to enhance priming compared to subjects in the shallow encoding condition.

In Experiment 1 of this study, intentional learning produced greater explicit recall compared to incidental encoding. If during the Search task, participants became studytest aware, intentional encoding subjects would have more resources for priming facilitation than incidental encoding subjects (Mace, 2003b). The limitation of Experiment 1 was that subjects' study-test awareness was not measured. Meanwhile, there are at least two reasons why subjects' study-test awareness during the Search task may be important. The first reason is that study-test awareness could magnify the priming effect in intentional learning subjects, while keeping the priming effect constant in incidental learning subjects. It is possible that intentional and incidental learning produced comparable amount of priming. However, priming was facilitated with awareness in the former case and was not facilitated in the latter case. The second reason arises from a concern for a purity of testing strategies used in Experiment 1. If during the Search task, participants were study-test aware and used explicit retrieval strategies, then the Free Recall task and the Search task could be just two variations of an explicit memory task. In this case, correlation between explicit and implicit measures of memory, as well as the reliance of both types of memory on the memory trace strength, would describe the processing similarity between two explicit memory tasks. In this case, the results of Experiment 1 could not be interpreted as evidence for a unitary memory system. In contrast, if in Experiment 1 subjects were unaware of the study-test relationship and did not use explicit retrieval strategies in the Search task, then the Free Recall task and the Search task used distinct approaches to examine subjects' memory.

Experiment 2 was conducted in order to explore the effects of study-test awareness on priming. The performance of study-test aware subjects and study-test unaware subjects could be then compared to performance of subjects in Experiment 1. If subjects in Experiment 1 performed the Search task similarly to study-test aware subjects, it may indicate that they were study-test aware. If subjects in Experiment 1 performed the Search task similarly to study-test unaware subjects, it may indicate that they were studytest unaware.

Traditionally, participants' study-test awareness is measured using self-report questionnaires. However, collection of self-reports was not appropriate for the current study. Indeed, if subjects would need to report their study-test awareness after every item, they would become aware of study-test relationship in the very beginning of the Search

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task. If subjects would need to report their study-test awareness after the Search task, they could confuse study-test awareness with the knowledge acquired during the task.

To manipulate study-test awareness, one group of subjects was given explicit instructions informing them about study-test relationship. Another group of subjects was told that they are going to perform a reaction time task. These participants were given no information about study-test relationship. In addition, there was a control group of subjects that was not pre-exposed to the stimuli and provided a performance baseline for the Search task.

Experiment 2 resembled Experiment 1 except that in Experiment 2 no explicit memory tests were conducted. In Experiment 2, a two-phase experimental design was used (Figure 10). During the study phase, subjects learned object and spatial information about the black and white drawings located on a 4 x 4 visible matrix. Learning was either incidental or intentional. The test phase examined subjects' implicit memory for the drawings' locations using the Search task. Subjects performed the Search task either being aware of relationship between stimuli in the study and the test phases, or being unaware of the study-test relationship. A 2 x 2 factorial design was used. Learning condition (incidental learning vs. intentional learning) and study-test awareness (aware vs. unaware) were between-subject's factors.

1.2.1 Method

Participants

Participants were eighty six undergraduates (70% female, mean age = 20.6, SD = 4.1) from Rutgers University participating for course credit. Participants were randomly assigned to one of four experimental conditions or to a control condition. In Experiment 2, participants were in the incidental learning/study-test unaware condition (n = 20), in

the incidental learning/study-test aware condition (n = 17), in the intentional learning/study-test unaware condition (n = 20), in the intentional learning/study-test aware condition (n = 15) and in the control condition (n = 14). All subjects were treated in accordance with Rutgers University IRB guidelines.

Design and Procedure

Study phase

The study phase was exactly the same as in Experiment 1. Subjects performed two tasks. The first task was the Dot Detection task that established a baseline response time (RT) for each subject. The second task was the Object Detection task. During this task subjects learned objects and their locations either incidentally or intentionally. Supposedly, while incidental learning created weak memory traces, intentional learning created strong memory traces.

Test phase

Subjects in experimental conditions started the test phase right after they completed the Object Detection task. Subjects in the control condition did not perform the Object Detection task. They started the test phase right after they completed the Dot Detection task. Because control subjects were not pre-exposed to the objects and their locations before the Search task, they provided a baseline for search RT.

The test phase examined subjects implicit memory for object locations. Implicit memory was tested using the Search task, the same as in Experiment 1. During this task, subjects sometimes had to search for a target objects that previously appeared during the Object Detection task (old objects). Sometimes, subjects had to search for a target object that either did not appear at all in the Object Detection task, or appeared in the different location. Experimental subjects were randomly assigned either to the study-test unaware condition or to the study-test aware condition. Subjects in the study-test unaware condition did not know about the relationship between stimuli in the Object Detection task and stimuli in the Search task. They were asked to perform a reaction time task and were instructed to find a target object and click on it with the mouse cursor as quickly as possible. The subjects in the study-test aware condition were also instructed to find a target object and to select it with the mouse click as quickly as possible. However, they were informed about relationship between stimuli in the Object Detection task and stimuli in the Search task. Subjects in the study-test aware condition received the following instructions: "During the test session, you will have to search for objects. All objects will be the same and will be located in the same spatial locations as in the Object Detection task". Subjects in the study-test aware condition were intentionally misinformed that "all objects will be the same as in the Object Detection task". If subjects knew that only some of the objects appeared previously, they would start guessing if the object appeared before or not. The processing of guesses would introduce extra noise. Knowledge that "all objects appeared before" reduced noise and made subjects exert equal efforts for processing of previously viewed as well as new objects.

Two measures of priming were taken. The within-subject's priming was indicated when search RT on primed trials was faster than search RT on foil, unprimed and new trials. The between-subject's priming was indicated when experimental subjects found primed stimuli faster than control subjects. Overall, larger differences in RT were associated with the larger priming effect. Based on previous research, it was expected that search RT on primed trials will be faster for primed compared to all other trials and that experimental subjects will be faster than control subjects. Predictions:

• If awareness affects priming, then study-test aware subjects will exhibit larger priming compared to study-test unaware subjects.

• If the effect of study test awareness depends on the strength of initial memory traces, priming will be enhanced only in the intentional learning condition.

• If subjects in Experiment 1 were study-test aware, their performance will resemble performance of study-test aware subjects. If subjects in Experiment 1 were study-test unaware, their performance will resemble performance of study-test unaware subjects.

Incidental learning subjects and intentional learning subjects were separately compared on search RTs in Experiment 1, Experiment 2 in the study-test aware condition and Experiment 2 in the study-test unaware condition. If subjects in Experiment 1 were study-test aware, their performance would resemble performance of study-test aware subjects. If subjects in Experiment 1 were study-test unaware, their performance would resemble performance of study-test unaware subjects.

In addition, all groups of subjects in the experiments 1 and 2 were subjected to a hierarchical agglomerative cluster analysis using a centroid clustering method and the proximity measure of squared Euclidean distances on unstandardized data. The cluster analysis was conducted on all types of search trials, treating repetitions as separate trials. Because the data consisted of three large classes of trials (primed, foils and new), we have chosen a three-cluster solution.

Presumably, trials that belong to the same cluster are similar to some extent. For example, if primed stimuli are in the same cluster with foils, unprimed and new stimuli, it may indicate the similarity in processing of all these trials. If primed stimuli belong to a different cluster than foils, unprimed and new stimuli, it may indicate the processing dissimilarities between primed trials and other types of trials.

A cluster content was compared between groups of subjects participated in the experiments 1 and 2. The main assumption was that groups of subjects with similar cluster content are more similar to each other than groups of subjects with distinct cluster content. For instance, if subjects in Experiment 1 have a cluster content similar to study-test unaware subjects in Experiment 2, then subjects in Experiment 2 may be study-test unaware.

To validate that the groups with the similar cluster content belong together, but differ from other groups of subjects, we conducted a Linear Discriminant Analysis (LDA). The generalization performance of the Linear Discriminant (LD) model was cross-validated using a leave-one-out strategy.

1.2.2 Results

Study phase

To examine how encoding manipulations worked, subjects' performance on the Dot Detection task and the Object Detection task (Figure 11) was compared. For each encoding group, a paired t-test on dot detection RT and object detection RT was conducted.

Consistent with Experiment 1, there was no significant difference between dot detection RT and object detection RT, t(26) = -1.4, p = 0.17, in the incidental learning group of subjects. In the intentional learning group of subjects, dot detection RT was significantly lower than object detection RT, t(24) = -5.76, p < 0.001.

Test phase

As in the Experiment 1, subjects' accuracy was forced to be 100%. Participants found 96% of correct objects (SD = 21%) with the first attempt. The responses that took more than one attempt were excluded from the data analysis.

To rule out the effect of individual object on subject's performance, an item analysis was conducted using the Univariate Analysis of Variance with object as a random factor. There was no group x object interaction, *p*-values for all five types of trials were larger than 0.1 (the range was 0.13 - 0.68). These findings suggest that individual objects had a similar effect in all groups of subjects. Consequently, the effect of object was disregarded in the further analysis.

Subjects' RT was analyzed using a GLM procedure. The subject's responses of 3 *SD* above the group mean were removed. Removed outliers totaled less than three percent of the data. The Greenhouse-Geisser adjustment was applied when needed. The GLM with the trial type and repetition as repeated measure factors and group as a between-subject's factor showed a significant trial x group interaction, F(41.92, 838.4) = 3.2, p<0.001; main effect of trial type, F(10.48, 838.4) = 80.45, p<0.001, and main effect of group, F(4, 80) = 2.79, p = 0.032 (Figure 12).

The visual analysis of Figure 12 indicated that the largest between-group differences were observed when subjects searched for primed objects located in primed locations. Indeed, when the primed trials were removed from the analyses, no between-group differences were observed, F(4, 80) = 1.79, p = 0.14. The analysis of foil trials across 12 repetitions showed that the search RT was not affected by the subject's experimental condition, F(4, 80) = 1.6, p = 0.17. In contrast, when only primed trials were analyzed, between group differences were highly significant, F(4, 81) = 8.39, p < 0.001.

Duncan's post-hoc test demonstrated that control subjects and incidental learning studytest unaware subjects spent more time to find primed stimuli than incidental learning study-test aware, intentional learning study-test unaware and intentional learning studytest aware subjects.

The visual analysis of Figure 12 also revealed that there was a learning effect as a function of a stimulus repetition. The effect was more pronounced for primed trials compared to other types of trials. The GLM with repetition as a repeated factor showed that primed stimuli RT became faster toward the sixth repetition, F(3.64, 294.71) = 72.6, p < 0.001. A repetition x group interaction was also significant, F(14.56, 294.71) = 3.42, p < 0.001. It suggests that the largest between-group difference were observed during the first and the second repetitions. By the sixth repetition between-subjects' differences disappeared.

Although the above analyses revealed the effect of the subject's experimental condition on search RT, it is worth noting that this effect may be smoothed when analyzed across six repetitions. The most pronounced and the most "clean" effect of experimental condition on search RT was observed during the first repetition trial.

A two factor ANOVA (learning condition x study-test awareness) was conducted on the first repetition of primed stimuli and foils. Means and standard deviations are presented in Table 5. For primed stimuli, there was a significant main effect of learning condition, F(1, 68) = 27.36, p < 0.001, and significant main effect of study-test awareness, F(1, 68) = 15.75, p < 0.001, with faster search in the intentional learning condition and in the study-test aware condition. There was no learning condition x studytest awareness interaction (Figure 13.A), F(1, 68) = 0.35, p = 0.56.

The same pattern of results was found for foil stimuli. There was a significant

main effect of learning condition, F(1, 68) = 15.97, p < 0.001, and significant main effect of study-test awareness, F(1, 68) = 4.97, p < 0.029, with faster search in the intentional learning condition and in the study-test aware condition. There was no learning condition x study-test awareness interaction (Figure 13.B), F(1, 68) = 0.99, p = 0.32.

Post-hoc tests revealed significant differences within each encoding group as a function of awareness. Incidental learning study-test aware subjects were significantly faster than incidental learning study-test unaware subjects, t(35) = 2.12, p = 0.04 for primed stimuli and t(35) = 2.1, p = 0.04 for foils. Intentional learning study-test aware subjects were significantly faster than intentional learning study-test unaware subjects on primed trials, t(33) = 3.89, p < 0.001, but not on foil trials, t(33) = 0.96, p = 0.34.

When the control group was included into the analysis, the ANOVA conducted on RTs in primed trials showed a significant between-subject's effect of experimental condition, F(4, 81) = 13.14, p < 0.001. Duncan's post-hoc test revealed three subsets of subjects. Control subjects and incidental learning study-test unaware subjects made up the slowest subset. Incidental learning study-test aware subjects and intentional learning study-test unaware subjects in the previous subset, but significantly slower than intentional learning study-test aware subjects. The ANOVA conducted on search RT for foils showed a significant effect of experimental condition on RT, F(4, 81) = 6.2, p < 0.001. As indicated by Duncan's post-hoc test, subjects in the incidental learning study-test unaware condition took more time to find foils compared to subjects in other groups.

To reveal a within-subject's priming effect, the first repetition of primed stimuli was compared to the first repetition of foils, unprimed and new stimuli. The first repetition of foils was compared to the first repetition of unprimed foils and new stimuli. The predictions were that subjects in the experimental groups would find primed objects in primed locations faster than other types of trials. A paired *t*-test was conducted. Only first repetitions were analyzed. Subjects in the incidental learning study-test aware condition, subjects in the intentional learning study-test unaware condition and subjects in the intentional learning study-test aware condition had similar patterns of results (Table 6). Subjects in these groups found primed objects in primed locations faster than foils in primed locations, faster than primed objects in new locations and faster than new objects. Search RT for foils in primed locations was not significantly different from search RT for foils in new locations and for new stimuli. These results indicated a facilitated performance on primed trials compared to other trials.

There was no priming effect in incidental learning study-test unaware subjects (Table 6). Although they found primed stimuli faster than foils, search RT for unprimed and new stimuli did not differ from search RT on primed stimuli. Surprisingly, this group of subjects spent more time to find foils in primed locations compared to foils in new locations and new objects. These results might indicate inhibition of performance on foil trials.

In the control group of subjects, search RT was not different for primed stimuli, foils and unprimed stimuli. Search RT for foils was the same as for unprimed foils. However, search RT for new objects was faster than for primed stimuli and foils. Because new stimuli were presented at the end of the Search task, these results may indicate a task adaptation.

Comparison of Experiment 1 and Experiment 2

Subjects within the same learning condition were compared using two criteria: search RT on primed trials and relationship between primed trials and other types of

trials. Specifically, subjects in the intentional learning condition in Experiment 1, subjects in the intentional learning/study-test aware condition in Experiment 2 and subjects in the intentional learning/study-test unaware condition in Experiment 2 were compared. It was found that search RT for primed stimuli differed in these three groups of subjects, F(2,45)=8.4, p=0.001. Duncan's post-hoc test revealed that intentional learning subjects in Experiment 1 and intentional learning study-test aware subjects in Experiment 2 found primed objects significantly faster than intentional learning study-test unaware subjects in Experiment 2. These data suggests that in Experiment 1, intentional learning subjects may be study-test aware.

Subjects in the incidental learning condition in Experiment 1, subjects in the incidental learning/study-test aware condition in Experiment 2 and subjects in the incidental learning/study-test unaware condition in Experiment 2 were also compared. The ANOVA revealed that between-subject's differences that were only marginally significant, F(2, 48)=2.7, p=0.074. The relationship between performance on primed, unprimed and new trials in three groups of subjects was compared. According to the tables 2 and 6, incidental learning subjects in Experiment 1 as well as incidental learning/study-test unaware subjects in Experiment 2 showed no differences between primed, unprimed and new trials. This pattern was different from that demonstrated by incidental learning/study-test aware subjects. These findings suggest that incidental learning subjects in Experiment 1 may be study-test unaware.

The cluster analysis performed on all trials of the Search task was conducted in all groups of subjects participated in the experiments 1 and 2. We found that in some groups of subjects, the content of clusters was similar (Figure 14). For example, the content of all three clusters in the incidental learning/study-test aware condition and in the intentional

learning/study-test unaware condition was identical. The first cluster included the first repetition of primed trial, the second cluster included second through sixth repetitions of primed trials, the third cluster included all other trials.

The content of clusters in the intentional learning group in Experiment 1 was very much similar to that in the intentional learning/study-test aware group in Experiment 2. The first cluster included first through sixth repetitions of primed trials. The second cluster included almost all repetitions of foil trials and all repetitions of unprimed, unprimed foil and new trials. The third cluster was different and included the eleventh repetition of foil trial in the former group and the twelfth repetition of foil trial in the latter group. These results may imply similarity between intentional learning subjects in Experiment 1 and intentional learning study-test aware subjects in Experiment 2.

The content of clusters for incidental learning subjects in Experiment 1 was similar to the content of clusters for incidental learning/study-test unaware subjects in Experiment 2. The first cluster included the first repetition of primed trial, almost all foil trials and all unprimed, unprimed foil and new trials. The second cluster included second through sixth repetitions of primed trials. The third cluster included the ninth repetition of foil trial in the former group and the twelfth repetition of foil trial in the latter group.

The cluster structure in the control group of subjects was dissimilar to the cluster structure in all other groups. The first cluster included first through forth repetitions of primed trials, almost all foil trials, and all unprimed, unprimed foil and new trials. The second cluster included fifth and sixth repetitions of primed trials. The third cluster included the eleventh repetition of foil trial.

Based on the cluster content, we suggested that all subjects in Experiment 1 and Experiment 2 formed four groups. The group 1 consists of control subjects. The group 2

consists of incidental learning subjects in Experiment 1 and incidental learning/study-test unaware subjects in Experiment 2. The group 3 consists of incidental learning/study-test aware subjects and intentional learning/study-test unaware subjects in Experiment 2. The group 4 consists of intentional learning subjects in Experiment 1 and intentional learning/ study-test aware subjects in Experiment 2.

To validate the distinction between these four groups, we conducted LDA. Subjects' group membership was a dependent variable. Independent variables were 24 different types/repetitions of trials (i.g., six repetitions of primed trials, twelve repetitions of foil trials, two repetitions of unprimed trials, two repetitions of unprimed foil trials and two repetitions of new trials). LDA classified subjects with 71.4\% of accuracy. According to Wilk's test, the LD model was highly significant, p<0.001. To estimate the LD model's generalization, we cross-validated the model's performance using a leaveone-out strategy (Table 7).

A chance performance of the LD model for four classes is 25%. Cross-validation showed a good generalization performance for groups 2, 3 and 4. According to a binomial test, classification of these groups was significantly above chance, p<0.05. Classification of the group 1 was , however, at chance, p>0.1. Moreover, according to Table 7, the group 1 was misclassified as the group 2. These results suggest that control subjects may be very much similar to incidental learning subjects in Experiment 1 and to incidental learning/study-test unaware subjects in Experiment 2. Consequently, it is possible that all subjects in our study represented not four, but three, distinct groups.

To test this hypothesis, we conducted LDA on three groups of subjects (Table 8). The group 1 consisted of control subjects in Experiment 2, incidental learning subjects in Experiment 1 and incidental learning/study-test unaware subjects in Experiment 2. The group 2 consisted of incidental learning/study-test aware subjects and intentional learning/study-test unaware subjects in Experiment 2. The group 3 consisted of intentional learning subjects in Experiment 1 and intentional learning/study-test aware subjects in Experiment 2.

LDA on these three groups classified subjects with 82% of accuracy. According to Wilk's test, LDA model was highly significant, p>0.001. To estimate the model's generalization, we cross-validated the performance of LD model using a leave-one-out strategy (Table 8).

A chance performance of LDA for three classes was 33.3%. The cross-validation showed a good generalization performance which was significantly above the chance, p<0.05, according to a binomial test. These results suggest that in Experiment 2, the incidental learning subjects were study-test unaware. Furthermore, their performance was very much similar to performance of control subjects that were not even pre-exposed to the stimuli. It also appears that intentional learning subjects in Experiment 1 were very much similar to intentional learning/study-test aware subjects in Experiment 2, but different from intentional learning/study-test unaware subjects in Experiment 2.

1.2.3.Discussion

Experiment 2 tested the effect of study-test awareness on priming in incidental and intentional learning subjects. The strength of memory traces was manipulated during the study phase. The results of the Dot Detection task and the Object Detection task suggested that subjects in the intentional learning condition acquired stronger memory traces compared to subjects in the incidental learning condition.

Implicit memory for spatial locations was examined during the test phase with the Search task. Priming was calculated based on the within-subject's and the betweensubject's comparisons. Priming effect was revealed in intentional learning/study-test aware, intentional learning/study-test unaware and incidental learning/study-test aware subjects. These subjects performed primed trials significantly faster than other types of trials. No priming effect was observed in incidental learning/study-test unaware subjects and control subjects because their search RT was similar for primed, unprimed and new stimuli. Despite the fact that subjects in the incidental learning/study-test unaware condition acquired the same amount of information as subjects in the incidental learning/study-test aware condition, they were not able to access this information during the Search task.

Based on the previous research, it was predicted that the strength of initial memory traces would affect priming. Indeed, subjects with strong initial memory traces demonstrated a larger priming effect than subjects with weak memory traces. These results are consistent with previous findings (Brown & Mitchell, 1994; Challis and Brodbeck, 1992; Richardson-Klavehn et al., 1994; Richardson-Klavehn & Gardiner, 1998) and support the idea that attention paid during encoding influences implicit memory (Hawley & Johnston, 1991).

Consistent with the predictions, study-test awareness affected subjects' performance on the Search task. Study-test aware subjects found primed stimuli faster compared to study-test unaware subjects. Moreover, study-test awareness enhanced priming irrespective to the strength of initial memory traces. These results are inconsistent with previous findings. In earlier work, study-test awareness enhanced priming only when initial memory traces were strong, but not weak (Bowers & Schacter, 1990; Mace, 2003b; Mulligan, Guyer & Beland, 1999; Richardson-Klavehn et al., 1994). Consequently, a "contamination" account for priming facilitation was proposed (e.g., Richardson-Klavehn et al., 1996; Schacter et al., 1989). This account suggests that awareness results into the usage of explicit knowledge for performance on implicit memory task. Indeed, subjects with strong initial memory traces, could recollect a good amount of learned information. In contrast, subjects with weak initial memory traces did not remember much of studied information and, consequently, could not use explicit "contamination" to improve priming.

If "contamination" was a reason for priming facilitation, how would participants use it in the Search task? To find a target object in the Search task, subjects had to make several steps. The first step was to memorize the target object. The second step was to maintain the image of the target during the inter stimulus interval. The third step was to look at the search matrix and choose an object identical to the target object. The forth step was to click on the chosen object with the mouse cursor. If subjects used explicit retrieval strategy in the Search task, then they had to recollect where the target appeared in the Object Detection task. Then, in order to predict the target's location, subjects would have to place the mouse cursor into the predicted location. After the search screen appeared, subjects would need to look at the object in the predicted location and decide if the target object and the object in the predicted location match. If they match, subjects would have to simply click on the object without conducting further search.

This strategy could reduce RT because the process of search will be shortened by removing the actual search process from the chain of the trial events. In contrast, if subjects predicted location incorrectly and the target object and the object in the predicted location mismatched, subjects would need to start search all over again. This would cause RT to increase because subjects spent time to match objects and then, they spent extra time to search for the object. Thus, it seems that explicit contamination can improve priming only when subjects are able to recollect most of spatial information.

Experiment 1 showed that incidental learning subjects were able to recollect less than 20% of spatial information. This means that in more than 80% of cases, these subjects would predict the target appearance in the incorrect location. From this point of view, usage of explicit retrieval strategy would make search in the study-test aware subjects even slower than search in the study-test unaware group of subjects. In contrast, it appeared that study-test aware subjects were significantly faster than study-test unaware subjects. This evidence suggests that incidental learning subjects did not use explicit retrieval strategy to facilitate priming.

Observed in the earlier studies interaction between study-test awareness and the strength of initial memory traces may have an explanation other than explicit "contamination". Thus, most of the previous studies used word stimuli. As it was noted earlier, word stimuli consist of hierarchy of such features as letters, t-junctions and so on. While strong memory traces were obtained during processing of whole words, weak memory traces were obtained during processing of word features. During test, the whole word processing was required. Consequently, the better transfer between study and test processes was in the strong memory traces condition compared to the weak memory traces condition.

In contrast to the previous studies, this study used locations as the stimuli. In this experiment, spatial locations did not contain a hierarchy of features and were processed holistically. Presumably, the strength of memory traces in experiments 1 and 2 varied independently of the processing specificity. As the result, the enhancement of priming effect with study-test awareness was observed independently of the strength of initial memory traces and, consequently, independently of subjects' explicit memory for the

stimuli.

While Experiment 1 provided strong evidence for a unitary model of spatial memory, this findings could be challenged if subjects were study-test aware during the Search task. The concern for a purity of test strategies in Experiment 1 was addressed through comparison of the Search task performance in study-test aware and study-test unaware subjects in Experiment 2 with subjects in Experiment 1. The results of the cluster analysis, LDA and the comparison of priming effects indicated that in Experiment 1, at least incidental learning subjects were study-test relationship, they did not employ the explicit retrieval strategies to perform on the implicit memory task. Consequently, the correlation between measures of implicit and explicit memory in Experiment~1 could be due to the similarity between tested memory representations.

1.3 Experiment 3: Cued recall of spatial locations in incidental and intentional learning subjects

Introduction

It is known that explicit recall is higher for strong, compared to weak, memory traces (e.g., Lockhart & Craik, 1990). Consistent with this view, in Experiment 1, intentional learning subjects recalled more objects and more locations than incidental learning subjects. The results of Experiment 1 were, however, inconsistent with view of spatial processing as automatic (Andrade & Meudell, 1993; Ellis, 1990; Hasher & Zack, 1979). The proponents of this view posit that spatial memory "is usually as accurate when subjects expect to be tested for this as when they do not" (Hasher & Zacks, 1979, p. 375). In other words, according to the automaticity framework, explicit recall of spatial information in the incidental learning condition should not differ from explicit recall of

spatial information in the intentional learning condition.

One possible explanation for the between-subject's effect in Experiment 1 is the lack of perceptual information in the Free Recall task. For example, incidental learning might be more vulnerable to the absence of perceptual information compared to intentional learning. The vulnerability to the specific testing conditions could disguise real memory for locations. To rule out the above possibility, it was important to test explicit memory for spatial information using cued recall. In a cued recall task, subjects are given a perceptual cue about the items that should be recalled. For example, subjects may be shown an object and asked to recall where this object appeared in the previous task. If intentional learning subjects recall more spatial information than incidental learning subjects, then the lack of perceptual information did not affect subjects' free recall. If there is no recall differences in the incidental and intentional learning conditions, then the lack of perceptual information altered subjects' ability to retrieve spatial information. The latter findings may suggest that the results of Experiment 1 need to be reconsidered. Specifically, it will be questioned if the memory strength manipulation used during encoding actually worked. Consequently, it will question the source of variance between subjects in the implicit memory test.

In Experiment 3, the study phase was the same as in the experiments 1 and 2. Subjects performed the Dot Detection task followed by the Object Detection tasks. The test phase examined subjects' recall for spatial location using a Cued Recall task. During this task, participants were shown a target object. The task was to retrieve locations where that object appeared during the Object Detection task.

1.3.1 Materials and Methods

Participants

Participants were thirty seven undergraduates (56.8% of female, mean age = 19.9, SD = 2.6) from Rutgers University participating for course credit. Participants were randomly assigned either to the incidental learning condition or to the intentional learning condition. All subjects were treated in accordance with Rutgers University IRB guidelines.

Design and Procedure

Study phase

As in the previous experiments, subjects performed the Dot Detection task and the Object Detection task. The latter was performed either under incidental learning instructions or under intentional learning instructions. The procedure was the same as described in Experiment 1 of this study.

Test phase

A Cued Recall task was designed to be perceptually similar to the Search task in the experiments 1 and 2 (Figure 15). The Cued Recall task, as well as the Search task, started with presentation of a target object in the center of the computer screen for 2000 ms. A target was one of 28 objects. Sixteen objects appeared previously during the Object Detection task and 12 objects were new. The target presentation was followed by an empty screen presented for 1000 ms (ISI). After that, subjects saw an empty 4 x 4 matrix.

Subjects made their choices by clicking on the locations with the mouse cursor. The checked location changed the color from white to gray. After subjects made choice(s), they clicked on the "NEXT" button to proceed to the next trial. If subjects thought that the target object was new, they clicked on "NEXT" without making any prior choices. After subjects clicked on "NEXT", the empty matrix was presented for 1000 ms (ITI).

Successful performance on the Cued Recall task required subjects to answer three questions. Firstly, subjects had to decide if a target object was old or new. If subjects believed that the target object was old (presented previously in the experiment), they had to check at least one location for this object before clicking on "NEXT". If the subject believed that the target object was new, they had to click on "NEXT" without making any prior choices. The number of hits was a portion of old objects correctly identified as old. The number of false alarms was a portion of new objects erroneously identified as old. Based on the number of hits and false alarms, the d-prime scores were calculated.

Secondly, if the object was old, subjects had to decide if during the Object Detection task the object appeared in a single location (primed stimulus) or in multiple locations (foil). If subjects checked one location, it suggested that the target is a primed stimulus. If subjects checked more than one location, it suggested that the target is a foil. In the analysis of primed/foil recognition, the information about correctness of checked locations was not taken into consideration. This analysis considered only correctness of reported objects and disregarded correctness of reported spatial locations.

Thirdly, subjects had to recall where the target object was located. Recall accuracy (ACC) for spatial locations was calculated on two levels of subjects' confidence. A high level of confidence was when subjects have chosen only correct location(s). A low level of confidence was when subjects have chosen both correct and incorrect locations. Each primed object had only one correct location. Foils had between two and eight correct locations with the mean of five locations. The accuracy for foil locations was calculated as a raw number of correctly recalled foil's locations over five.

1.3.2 Results

Study phase

For each learning condition, a paired t-test on dot detection RT and object detection RT was conducted. The results of the study phase replicated results of experiments 1 and 2 (Figure 16). There was no significant difference between dot detection RT (M = 289.83, SD = 56.6) and object detection RT (M = 290.71, SD = 50.47), t(18) = -0.06, p = 0.95, in incidental learning subjects. In intentional learning subjects, dot detection RT (M = 256.0, SD = 14.7) was significantly faster than object detection RT (M = 377.00, SD = 93.1), t(16) = -5.23, p < 0.001.

Test phase

Object recognition

Subjects in the intentional learning condition recognized old objects better than subjects in the incidental learning condition. They had more Hits, t(35) = 4.86, p < 0.001, less FA, t(35) = -2.48, p=0.018, and larger d-prime scores, t(35) = 5.58, p < 0.001. Means and standard deviations for hits, false alarms and d-primes are reported in Table 9.

The d-prime scores showed that subjects in the intentional learning condition recognized both primed objects, t(35) = 3.6, p = 0.001, and foils, t(35) = 4.17, p < 0.001, better than subjects in the incidental learning condition. Subjects in the intentional encoding group recognized primed stimuli and foils equally good: d-primes did not differ, t(17) = -1.57, p = 0.131. Subjects in the incidental encoding group recognized foils better than primed stimuli: d-primes differ significantly, t(18) = 2.7, p = 0.014.

Recall of locations

Item analysis performed using a Univariate analysis of variance with object as a

random factor revealed no group x object interaction, p > 0.8 for primed objects and p > 0.35 for foils.

Intentional learning subjects, compared to incidental learning subjects, recalled significantly more locations of primed objects with high level of confidence, t(35) = 3.7, p = 0.001, and with low level of confidence, t(35) = 4.9, p < 0.001 (Table 10). Also subjects in the intentional learning condition, compared to subjects in the incidental learning condition, recalled significantly more locations of foils with high level of confidence, t(35) = 3.9, p < 0.001, and with low level of confidence, t(35) = 4.7, p < 0.001.

Subjects' RT on the first correct choice they made was analyzed. The results are presented in Table 11. A t-test revealed no difference in RT between incidental learning subjects and intentional learning subjects, p-values > 0.2.

Because the strength of initial memory trace could depend on the number of stimulus repetitions during encoding, a frequency of repetitions could also influence cued recall. Correlation analysis of the frequency of stimulus repetition during the Object Detection task with recall accuracy for locations was performed. Correlations are presented in Table 13. Subjects in both learning conditions recalled more spatial locations for stimuli presented more frequently during the Object Detection task. Stronger relationship between recall and the number of repetitions was found for foils compared to primed stimuli.

1.3.3. Discussion

Experiment 3 was conducted in order to tests how the strength of initial memory traces affects cued recall. The results did not support the idea that spatial locations are processed automatically. Intentional learning subjects, compared to incidental learning

subjects, better recognized old objects, better discriminated primed objects from foils and had higher recall accuracy for locations. These results are consistent with the findings of Experiment 1 and suggest that the lack of perceptual information was not a critical factor for free recall in Experiment 1.

As it was mentioned above, the Cued Recall task and the Search task shared perceptual properties. However, the experimental procedure was different in these two tasks. While the Search task did not require participants to reconstruct any previous experiences, the Cued Recall task required them to recollect object locations. Perceptual similarity along with procedural differences makes comparison of implicit and explicit memory tasks especially appealing. Such comparison may indicate if the memory trace strength affects implicit and explicit memory in different degree (as predicted by the multiple memory systems view). To investigate how incidental and intentional learning influence performance on implicit and explicit memory tests, incidental and intentional learning subjects were compared across three different memory tasks. These tasks were the Search task without study-test awareness (implicit memory task in Experiment 2), the Search task with study-test awareness (implicit memory task in Experiment 2) and the Cued Recall task (explicit memory task in Experiment 3). The multiple memory systems view predicts that the strength of initial memory traces will affect the Cued Recall task more than the Search task. The unitary memory system view predicts that the strength of initial memory traces will equally affect implicit and explicit memory tests.

Because the measure of implicit memory was subjects' RT and the measure of explicit memory was subjects' recall accuracy, it was not possible to compare the tests directly. Therefore, the *z*-scores for each task were calculated (Figure 17). To calculate the *z*-scores, the means and standard deviations of each task (implicit memory with

awareness, implicit memory without awareness and explicit memory) were used. The *z*-scores of RT were reversed in order to get the larger *z*-scores for the faster performance.

The *z*-scores within each learning condition were analysed using a Univariate Analysis of Variance. There were no differences in the *z*-scores within each learning condition (p > 0.9) (Figure 17). This clearly indicates that the difference between intentional and incidental learning subjects is independent of the test used. These findings may support the idea that implicit and explicit memory tests access common memory representation.

The differences in the cognitive mechanisms of implicit and explicit memory tests are not very well understood. Some researchers believe that these tests use different routes or strategies to access a common memory trace (Bentin et al., 1992; McKoon & Ratcliff, 1986; Whittlesea & Price, 2001; Witherspoon & Moscovitch, 1989). With regard to the experiments 2 and 3 of this study, it suggests that the strategies used in the Cued Recall task should be different from strategies used in the Search task. If the differences between the search strategies in the study-test unaware condition and the cued recall strategies are obvious, the differences between the search strategies in the studytest aware condition and the cued recall strategies are not that evident. For example, it is possible that study-test aware subjects used explicit recall strategies to perform on the Search task.

To examine the differences between the strategies used in the Search task by the study-test aware subjects and the strategies used in the Cued Recall task, subjects' RT in the Cued Recall task in Experiment 3 and subjects' search RT in Experiment 2 were compared. If RT in the Cued Recall task could predict search RT in study-test aware subjects, then study-test aware subjects could use explicit retrieval strategy. Using

subject's RT for the high confidence responses in the Cued Recall task, the average search time for subjects using recall strategy was calculated. In the Cued Recall task, RT in incidental learning subjects' was 792.38 ms. RT in intentional learning subjects was 703.1 ms. Thus, if subjects correctly retrieved all objects their RT time on the Search task could be 792.38 ms in the incidental learning condition and 703.1 ms in the intentional learning condition. However, incidental learning subjects recalled only 15% of primed stimuli (or 6 x 0.15 objects). Intentional learning subjects recalled 42% of primed stimuli (or 6 x 0.42 objects). Consequently, the predicted RT has to account for not recalled stimuli. For example, the objects that were not recalled could be found with the average search RT observed in control subjects (1130 ms). Thus, for incidental learning subjects, the predicted search RT was 792.38 x (6 x0.15) + 1130 x (6 x (1-0.15))/6 = 1079.4 ms. For intentional learning subjects, the predicted search RT was $703.15 \times (6 \times 0.42) + 1130 \times (6 \times (1-0.42))/6 = 950.72 \text{ ms.}$ The predicted values were compared with the real search RT using a one-sample t-test. It was found that predicted RTs were significantly greater that the real RTs in the Search task, t(16) = -2.17, p =0.045 for incidental learning subjects and t(14) = -9.8, p < 0.001 for intentional learning subjects.

The results show that RT in the Cued Recall task failed to predict subjects' RT in the Search task. These findings indicate that study-test aware subjects do not use explicit retrieval strategies to perform implicit memory test. The strategy used in the Search task allows for significantly faster access to learned information than the Cued Recall task. These findings are in accord with the previous research demonstrated that implicit and explicit memory tests use different strategies to access a common memory representation (Bentin et al., 1992; McKoon & Ratcliff, 1986; Witherspoon & Moscovitch, 1989; Whittlesea & Price, 2001).

Experiments 1, 2 and 3 examined spatial memory and indicated that implicit and explicit tests engaged different strategies, but tested memory representations that had very similar properties. The high degree of similarity between implicit and explicit memory representations suggested that implicit and explicit memory tasks tested a single memory representation. These findings lead to the conclusion that spatial memory is unitary.

Earlier studies conducted on lexical and pictorial information rarely obtained such a strong evidence for similarity between implicit and explicit memory systems. One possibility is that memory for different types of information may have different structure. For example, spatial memory may be unitary, but lexical memory may rely on multiple memory systems. Another possibility is that in the stimulus domains other than spatial, it was difficult to control for the transfer appropriate processing. Consequently, if the control over the transfer appropriate processing would be achieved, the results of this study could be replicated in other experimental settings.

CHAPTER 2

2.1 The fMRI study of implicit memory for object locations in study-test aware and study-test unaware subjects

Introduction

The dissociation of neural activity associated with explicit and implicit memory tests is often interpreted as evidence for multiple memory systems (e.g., Schacter & Buckner, 1998; Schott et al., 2005, 2006). Explicit retrieval is thought to be related to the increases in neural activity (e.g., Buckner, Raichle, Miezin, & Petersen, 1996; Cabeza & Nyberg, 1997). For example, explicit retrieval of locations increased neural activity in right middle occipital gyrus, supramarginal gyrus, and superior temporal sulcus (Kohler, Moscovitch, Winocur, Houle & McIntosh, 1998). Bilateral lingual and fusiform gyri were activated during explicit retrieval of object identity (Kohler et al., 1998). While successful explicit recollection was associated with BOLD increase in hippocampus, intentional retrieval efforts increased BOLD signal in anterior prefrontal cortex (Schacter, Alpert, Savage, Rauch, & Albert, 1996; Schacter & Buckner, 1998).

Priming is often related to the decreases in neural activity (Buckner et al., 1998; Henson, 2003; Schacter & Buckner, 1998; Wig et al., 2005; Grill-Spector, Henson & Martin, 2006). For example, in the word stem completion tasks, primed stimuli, compared to unprimed, induced less neural activity in bilateral occipitotemporal cortex, left superior temporal regions, precuneus and right angular gyrus (Badgaiyan, Schacter & Alpert, 1999; Buckner, Koutstaal, Schacter & Rosen, 2000). In the lexical and semantic priming experiments, the neural reductions were observed in the anterior prefrontal cortex (Demb, Desmond, Wagner, et al., 1995; Thiel, Haupt, Habedank et al., 2005; Wagner, Desmond, Demb, et al., 1997). The reduced neural activity for primed compared to novel objects was found in frontal, middle occipital and posterior cingulate cortices along with fusiform gyrus and precuneus (Koutstaal, Wagner, Rotte, Maril, Buckner & Schacter, 2001). Studies of face perception revealed that repeated presentation of faces decreased neural responses in the fusiform gyrus (Henson, Shallice & Dolan, 2000; Henson, Shallice, Gorno-Tempini & Dolan, 2002).

There is no agreement on why the reduction of neural activity occurs (Grill-Spector et al., 2006). Most often the reduction is interpreted as facilitation of perceptual processing (e.g., Schacter & Buckner, 1998). The facilitation of perceptual processing may, or may not, signal differences between implicit and explicit memory systems. For example, it was shown that the reduction of neural activity heavily depends on stimulus repetition, but only weakly depends on RT in priming tasks (Sayres & Grill-Spector, 2006). At the same time, neural reductions occurred not only during priming tasks, but also during stimulus recognition (Sayres & Grill-Spector, 2006) and working memory tasks (Tomasi, Ernst, Caparelli & Chang, 2006). This suggests that priming and recognition tasks may depend on common memory representations (Turk-Brown, et al., 2006).

Because the direct comparison of neural responses during implicit and explicit memory tests did not yield consistent results, the present study uses an alternative approach. Arguably, the differences in neural underpinnings of implicit and explicit memory may reflect the differences in the performance strategies but not the differences in memory representations. To investigate if implicit and explicit memory tests tap different memory representations, the neural mechanisms underlying the enhancement of implicit retrieval were examined and compared to the neural mechanism underlying the enhancement of explicit retrieval. The term "implicit retrieval" is used to make a parallel with explicit retrieval. This term was used previously in memory literature (Anooshian & Seibert, 1996; Carlesimo et al., 1995; De Goede & Postma, 2008; McKoon & Ratcliff, 1996) to refer to the successful performance on implicit memory tests.

If explicit and implicit memory tests tap a common memory representation, than successful implicit retrieval may rely on the same neural mechanisms as successful explicit retrieval. In the realm of explicit memory, the dynamics of neural activity between successful and unsuccessful retrieval performance was extensively studied (e.g., Kensinger, Clarke, Corkin, 2003; Skinner & Fernandes, 2007). These studies yielded quite consistent results that remembered items elicited greater neural activity compared to familiar, new or forgotten items. For example, remembered items, compared to familiar items, raised neural activity in superior parietal and inferior parietal cortices (Henson, Rugg, Shalice et al., 1999), as well as in dorsolateral prefrontal cortex, the MTL and the fusiform gyrus (Eldrige, Knowlton, Furmanski et al., 2000). Keeping in mind these findings, the current event-related fMRI study examined neural dynamics within the domain of implicit memory. If this fMRI study demonstrates that successful, compared to unsuccessful, implicit retrieval also increases neural activity it may provide evidence for similarity between implicit and explicit memory systems. In contrast, if successful, compared to unsuccessful, implicit retrieval decreases neural activity, it may provide evidence for dissociation of implicit and explicit memory systems.

The experimental design was the same as that used in Experiment 2. In the study phase, subjects performed the Object Detection task. During this task, subjects incidentally learned object and spatial information. In the test phase, subjects performed the Search task. The Search task was used to test subjects' implicit memory for locations. According to the previous studies (Haxby, Grady, Horwitz, Ungerleider et al., 1991; Ungerleider & Mishkin, 1982), encoding of object-related information is associated with ventral pathway, whereas encoding of spatial information is associated with the dorsal pathway. Association between two is implemented by hippocampus and parahippocampal gyrus (e.g., Düzel, Habib, Rotte et al., 2003; Nyberg, McIntosh, Houle et al., 1996). The tasks used in the present experiment involved processing of spatial and object information. Consequently, it was expected that neural activity will change in parietal cortex responsible for spatial processing (e.g., Corbetta & Shulman, 2002; Sala, Rama & Courtney, 2003); in inferior temporal cortex (specifically, FFG) responsible for objects processing (Köhler, Moscovitch, Winocur, Houle & McIntosh, 1998) as well as in MTL (hippocampal/parahippocampal cortices) that contributes to spatial processing and binding of information into associations (Smith & Milner, 1989; Ploner, Gaymard, Rivaud-Pechoux, Baulac et al., 2000; Düzel et al., 2003; Nyberg et al., 1996; Sommer, Rose, Glascher, Wolbers & Büchel, 2005).

To manipulate the performance success on the implicit memory task, subjects were given either study-test aware or study-test unaware instructions. In Experiment 2 of this study, given similar encoding, study-test aware subjects exhibit the higher level of priming compared to study-test unaware subjects. Contrasting of neural responses of study-test aware and study-test unaware subjects could reveal differences between successful and unsuccessful implicit retrieval.

In Experiment 2, study-test aware subjects were faster than study-test unaware subjects on primed, but not on new, trials. Consequently, it is logical to expect that neural activity will depend on awareness also only in primed, but not in new, trials. The studytest aware instructions did not emphasize the differences between trials. In opposite, despite the fact that 33% of the test stimuli either were new or were placed in new
locations, instructions emphasized that ALL stimuli appeared previously during the Object Detection task. In Experiment 3 of this study, even though subjects were informed that they would view old and new stimuli, they were not always able to separate old objects from new. So, it seems possible that when subjects are told that all stimuli are old, they will treat new stimuli as old and will apply the same strategy to perform on old and new trials. The strategical similarities in processing of old and new trials may result in the similar patterns of neural activity. To reveal the strategy-related commonalities, studytest aware and study-test unaware subjects were contrasted on primed trials, foils and new trials. The activation maps of these contrasts were subjected to a conjunction analysis. The general effect of awareness may be shown in the brain regions demonstrating between-subject's differences on all types of trials. The priming specific effects may be shown in the brain regions demonstrating between-subject's differences on primed, but not new or foil, trials.

The contrast between study-test aware and study-test unaware subjects is the summation of neural activity across several seconds of the search trial. Each search trial, however, consisted of four two second events (TR = 2 sec). The first event of the search trial is the presentation of a target object. The target object is presented in the center of the screen and therefore, does not possess distinct spatial properties. The second event corresponds to the inter-stimulus interval and the beginning of search. The third event corresponds to subjects' responses. The forth event is the inter-trial interval. It is possible that differences in neural activity of study-test aware and study-test unaware subjects may be observed only during subjects' response. It is also possible that study-test awareness influences subjects' neural activity across all events of the trial. For example, when the target object is presented it does not possess distinct perceptual properties. However,

study-test aware subjects know that during the Object Detection task objects were presented in spatial locations. They also know that the target object will be soon presented within the spatial context and will occupy a distinct location on the 4 x 4 matrix.

Although according to the experiments 1 and 3 of this study, most of the time subjects are not able to recall these locations, the expectation that the object will appear in some location may increase neural activity in brain regions processing spatial information. In fact, it may happen even before the object appears in spatial context. Such effects were often observed in the studies on visual search (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Kastner & Underlaider, 2001; Luks, Sun, Dale, Miller & Simpson, 2008; Ress, Backus & Heeger, 2000). In these studies, subjects either expected or not that the stimulus appear in the cued location. The expectation of the stimuli increased activity in IPS, SPL, IPL and FEF, SEF, MFG, and extrastriate cortex before the stimulus actually appeared (Kastner et al., 1999). According to the biased competition model of selective attention (Desimone & Duncan, 1995; Duncan, 1998), multiple stimuli compete for neural representations. Selected attention to spatial locations biases the competition in favor of the stimulus presented in that location and pre-activates visual cortex (Kastner et al., 1999). The behavioral changes correspond to increases in neural activity in extrastriate, parietal and frontal cortices (Kastner & Underlaider, 2001). The biasing signal in the visual cortex may be generated by the frontal eye fields, the supplementary eye fields and superior parietal cortex that also increased neural activity during expectation period (Kastner et al., 1999). The biasing effect of attention was also observed in the working memory studies (Rose, Schmid, Winzen, Sommer & Buchel, 2005; Lepsien & Nobre, 2006). For example, when subjects prepared to see a face, they

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pre-activated the fusiform gyrus. When subjects prepared to see a scene, they preactivated the parahippocampal gyrus (Lepsien & Nobre, 2006). In the Rose et al.'s study, the modulatory effect of attention on lateral occipital cortex was related to recognition success during the explicit memory task.

It seems that successful implicit retrieval also may be related to pre-activation of task-specific brain regions. However, this question was not studied before. With regard to the current study, study-test awareness may increase subjects' attention to the stimuli. Especially, to the spatial properties of the stimuli. Attention to the spatial properties of the stimuli may modulate brain activity in brain regions responsible for spatial processing. Among these regions may be superior and inferior parietal cortex, precuneus, middle occipital and supramarginal gyri (Büchel, Coull & Friston, 1999; Courtney, Ungerleider, Keil & Haxby, 1996; Kohler et al., 1998). According to the visual search and working memory studies, activation of these regions may occur even before the spatial properties of the objects are actually presented.

If successful performance on implicit memory task is related to the attention modulated increases in neural activity, it may suggest certain degree of similarity between implicit and explicit memory. If during priming task, attention does not affect neural activity, it may suggest separability of implicit and explicit memory.

Another evidence that seems characterizes successful explicit retrieval is reactivation of encoding-related brain activity during explicit memory test. Reactivation was defined as re-engagement of encoding-related brain regions during retrieval (Kahn, Davachi & Wagner, 2004). Behavioral studies supported the idea of reactivation by showing that memory performance may be determined by similarity between encoding and test processes (e.g., Morris et al., 1977). Recent neuroimaging studies revealed similarity of neural activity during encoding and neural activity during retrieval (Johnson & Rugg, 2007; Habib, McIntosh & Tulving, 2000; Kahn et al., 2004; Nyberg, Petersson, Nilsson, et al., 2001; Persson & Nyberg, 2000; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler, Petersen & Buckner, 2000; Woodruff, Johnson, Uncapher, & Rugg, 2005).

Because explicit memory is often associated with increased neural activity, it was expected that explicit retrieval is also associated with increased activity in the encodingspecific regions. Indeed, Persson & Nyberg (2000) examined similarities between encoding and explicit retrieval of spatial locations and found reactivation in bilateral inferior parietal cortex. Participants in the Kahn et al.'s (2004) study encoded words either by imagining them in spatial context, or by reading the words backwards. During the test, items that were imagined within spatial context elicited reactivation in right posterior parahippocampal brain region. Vaidya et al. (2002) had subjects encode pictures and words. At test, participants were shown words. Some of these words were encoded as words and some of them were encoded as pictures. Vaidya et al. found reinstatement of activity in left fusiform gyrus for words encoded as picture vs. words encoded as words. In the Nyberg et al., (2000) study, subjects had to memorize either a single visual stimulus (a word) or a complex visual-auditory stimulus (a word and a sound). During retrieval, subjects had to decide if a target word was presented alone, was paired with the sound, or was not presented at all. Nyberg et al. found that if during encoding the word was associated with the sound, then, during retrieval the auditory cortex activated even in the absence of auditory stimulation. Taken together, these findings suggest that brain regions increased activity during encoding may be reactivated during explicit retrieval.

Unfortunately, the phenomenon of reactivation was studied mostly during explicit

retrieval. Meanwhile, priming also may depend on reactivation processes. Because priming is often associated with decreased neural activity, it is possible that the brain regions deactivated during encoding will be also deactivated during implicit retrieval. This hypothesis was supported by the Schott et al.'s (2006) findings of priming-related deactivation in left fusiform gyrus (BA37) and bilateral inferior frontal gyrus at study and also at test. Thus, it appears that while explicit memory is characterized by reactivation of encoding-related brain activity, priming may be characterized by re-deactivation of encoding-related brain activity.

It is known that visual perception and visual memory often rely on common neural correlates (Slotnick, 2004) which may be related to perceptual and procedural similarities between study and test. Consequently, when interpreting the results of reactivation studies, it is important to factor out the reactivation and re-deactivation that occurred due to perceptual or processing similarity between study and test. The reactivation and re-deactivation related to memory processes themselves, may provide important information about neural plasticity in memory tests. For example, if successful implicit retrieval is associated with reactivation of encoding-related brain activity, it will resemble findings in the explicit memory domain and may provide support for a unitary memory system. If successful implicit retrieval is associated with re-deactivation of encoding-related brain activity, it will differ from findings in the explicit memory domain and may provide support for multiple memory systems.

Reactivation was examined using a conjunction analysis. The brain activation maps representing learning of spatial information were overlaid with the activation maps representing implicit memory for locations. Learning-related neural activity was characterized by changes in the BOLD signal during the last repetition of primed stimuli during the Object Detection task. Implicit memory for locations was characterized by changes in the BOLD signal during the first repetitions of primed stimuli, foils and new stimuli in the Search task. The between-subject's differences were examined by contrasting neural activity in study-test aware and study-test unaware subjects. To disentangle perceptual processes from memory processes during the test session, the control group of subjects was included to the study. Control subjects did not participate in the study phase of the fMRI experiment and were not pre-exposed to the stimuli. Consequently, any conjunction between encoding-related activity and test-related activity in control subjects was due to perceptual similarities between the Object Detection and the Search tasks. In contrast, those brain regions that overlaid in the experimental, but not in the control, groups of subjects may indicate priming-related reactivation processes.

2.1.1 Materials and Methods

Participants

Participants were twenty five undergraduates (64% of female, mean age = 19.8, SD = 2.5) from Rutgers University participating for course credit. Participants were either in the control group or in the experimental groups. All subjects in the experimental groups learned spatial information incidentally. During the test, subjects were randomly assigned either to the study-test aware condition (n=9) or to the study-test unaware condition (n=8). Control subjects (n = 8) were not pre-exposed to the stimuli. They provided a baseline performance.

Design and Procedure

The stimuli and procedure were similar to those used in Experiment 2, but were adjusted to the event-related functional magnetic-resonance imaging (fMRI) study. All subjects started the scanning session with two blocks of Dot Detection task that provided a baseline response time. Blocks consisted of 20 trials each and were separated by the sixteen seconds of rest. Right after the Dot Detection task, subjects in the experimental groups performed two blocks of Object Detection task (Figure 18). Blocks were separated by the sixteen seconds of rest. Blocks consisted of 40 trials each. There were 50% of primed trials and 50% of foils. Trials were presented in the random order. Each trial was analyzed as an event.

The experimental designs of the Dot Detection and the Object Detection tasks were identical. Each trial lasted for 4000 ms. The trial started with the presentation of empty matrix for either 400 or 800 ms followed by an object presentation. Subjects had to press a mouse key as quickly as possible to indicate the presence of object within 1000 ms after the object appeared. Right after the subjects' response, the empty matrix was presented again for a period of time needed to complete the 4000 ms time slot (ITI).

Unlike Experiment 2, the fMRI study employed only incidental learning of spatial information. Incidental leaning was less beneficial for explicit recall than intentional learning in the experiments 1 and 3. Consequently, the probability that subjects use explicit retrieval strategy in the Search task was lower for participants in the incidental learning condition.

Right after the Object Detection task, subjects performed eighteen blocks of the Search task (Figure 19). Blocks were separated by the sixteen seconds of rest. Blocks consisted of eight trials each. The first twelve blocks were comprised of primed stimuli (37.5%) and foils (62.5%). The last six blocks were comprised of unprimed stimuli (25%), unprimed foils (50%) and new stimuli (25%). Trials were presented in the random order. Each trial was analyzed as an event. Each trial in the block lasted for eight seconds. The trial started with the presentation of a target object in the center of the computer screen for 2000 ms followed by the presentation of an empty matrix for 1000 ms. After the empty matrix, a search screen appeared. Subjects were instructed to find the target object on the search screen and click on it with the mouse cursor as quickly as possible. The search screen was presented until subjects found a correct object but no longer than for 4000 ms. After subjects responded, the empty matrix was presented again for time needed to complete 8000 ms time slot (ITI).

The Search task was used to examine subjects' implicit memory for object locations. As in Experiment 2 of this study, subjects' study-test awareness was manipulated. Study-test unaware subjects did not know about the relationship between stimuli in the Object Detection task and in the Search task. Subjects in the study-test aware condition, were explicitly informed about the study-test relationship. Also instructions encouraged subjects to imagine where the target could be located. Control subjects were not pre-expose to the stimuli. Consequently, they were also study-test unaware.

Image acquisition

The fMRI experiment was conducted using a Siemens 3 T Allegra head-only MR system. In the beginning of the experiment, a high resolution structural image (TR¹ = 2000 ms, TE²= 4.38 ms, slice thickness = 1mm, FOV³ = 220, number of slices = 176, resolution = 0.8594 x 0.8594 x 1) was acquired using MPRAGE (a magnetization-prepared rapid acquisition in gradient echo) sequence. Functional data (BOLD signal) were collected using a gradient echo, echo-planar sequence (TR =2000 ms, TE = 30 ms,

¹ TR = the time between scanning successive fMRI volumes

² TE = Echo Time (the time between the 90 degree pulse and the maximum in the echo in a spin-echo sequence) (Hornak, 1996)

³ FOV = Field of View (the distance across an image) (Hornak, 1996) retrieved from <u>http://www.cis.rit.edu/htbooks/mri/gloss.htm</u> on 10/02/2008

slice thickness = 4 mm, FOV = 220, number of slices 32, resolution = 3.4375 x 3.4375 x 4.0). A total of 207 volumes were collected during the Object Detection task. A total of 800 volumes were collected during the Search task for control and study-test unaware subjects. A total of 830 volumes were collected during the Search task for study-test aware subjects. The Search task was longer in the study-test aware, compared to study-test unaware, condition due to the longer set of instructions preceding the task. *Data analysis*

The images were processed and analyzed with FSL 4.0 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) software. On each raw BOLD, nonlinear noise reduction (SUSAN (Smallest Univalue Segment Assimilating Nucleus)); motion correction (MCFLIRT (Jenkinson, Bannister, Brady, & Smith , 2002)); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 9mm; multiplicative mean intensity normalization of the volume at each time point and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=25.0s) were applied. A hemodynamic response function (HRF) was modeled using a Gamma function. The registration to high resolution structural (MPRAGE) and standard MNI (the Montreal Neurological Institute) space images was carried out using FLIRT (Jenkinson & Smith, 2001; Jenkinson et al., 2002).

The FEAT (FMRI Expert Analysis Tool) was used for the first- and higher-level analyses. The higher-level analysis was carried out using a fixed effects model⁴. Z-statistics images were thresholded with GRF-theory-based maximum height thresholding with a voxel corrected significance threshold of P<0.05 (Worsley, 2001). Subjects' neural

⁴ In the fixed effects model the random effects variance was forced to zero in FLAME

responses during the Object Detection and the Search tasks were analyzed using a General Linear Model. Functional localization was determined using the Harvard-Oxford cortical and sub-cortical structural atlases.

Study phase

To identify neural activity preceding the Search task, the last repetition of primed stimuli during the Object Detection task was analyzed. The learning effect during the Object Detection task was measured as the difference between the first repetition and the last repetition of primed stimuli. Because study-test aware and study-test unaware subjects were in the same learning condition, the data was combined across groups.

Test phase

In the Search task, the first repetitions of primed stimuli, foils and new stimuli were of interest. A first-level analysis computed the BOLD signal on these trials for each subjects. The group means were computed using a higher-level analysis. The higher-level analysis also examined differences in neural activity between study-test aware and studytest unaware subjects on primed, foil and new trials.

Conjunction analysis

A conjunction analysis was conducted using inclusive masking. Firstly, each activation map has been binarized. Then, the binarized maps of interest were summed and thresholded so that the final mask included only regions where all maps of interest overlaid.

To reveal the general effects of awareness on priming, the activation maps representing the Aware - Unaware contrasts on primed, foils and new trials were overlaid. The final mask that included all three contrasts represented the general effects of awareness. This network of regions was defined as the awareness-related. The network of brain regions sensitive to study-test awareness on primed trials only was defined as the priming-specific.

To reveal reactivation of encoding-related brain regions during the Search task, the conjunction analysis of encoding-related neural activity and test-related neural activity was conducted. The study-test aware, study-test unaware and control subjects were analyzed. The brain regions where the encoding-related activity overlaid with the test-related activity in all three groups of subjects was characterized as the perceptiondependent. The perception-dependent reactivation could appear because pf perceptual and processing similarity between study and test. The conjunction of encoding-related brain regions with regions sensitive to study-test awareness was conducted to reveal the priming-related neural reactivation.

Linear Discriminant Analysis (LDA)

To assess the magnitude of reactivation in every subject, we calculated the difference between the percent of BOLD signal change during the first repetition of primed stimuli in the Search tasks and during the last repetition of primed stimuli in the Object Detection task in every brain region that was reactivated. The reactivation was indicated if the differences between test-related and encoding-related brain activity were positive or around zero. The percent of BOLD signal change was calculated using the Featquery tool (the FSL tool calculating a time series statistics)

We hypothesized that if successful implicit retrieval is associated with reactivation of encoding-related brain regions, then study-test aware and study-test unaware subjects may be classified based on the magnitude of reactivation. To classify study-test aware from study-test unaware subjects we used a Linear Discriminant Analysis (LDA). LDA was conducted using R(http://www.r-project.org/). We tested several LD models. The independent variables in the first model included behavioral (search RT) and neuroimaging (the magnitude of reactivation) data. Other models were tested using only neuroimaging data. The reason behind testing of several LD models was to investigate whether subjects could be classified based on reactivation data only. *Time series analysis*

To understand the neural dynamics within primed trials, the time series were analyzed. The time series were extracted from the regions showing between-subject's differences as a function of awareness using the Featquery tool⁵. The neural dynamics was analyzed across four time points of the trial. The first point corresponded to the target presentation, the second point corresponded to the inter-stimulus interval and beginning of search, the third time point corresponded to subjects' behavioral response and the forth time point corresponded to the inter-trial interval.

To model HRF, a gamma function with mean lag of 6 seconds was used. The pick of activity for each event of the trial was expected to be in 6 seconds (3 TRs) after onset of this event. Consequently, a percent of signal change for the first time point (between 0 and 2 sec) was measured between sixth and eighth seconds after the trial onset. A percent of signal change for the second time point (between 2 and 4th sec) was measured between eighth and tenth seconds after the trial onset. A percent of signal change for the third time point (between 4 and 6th sec) was measured between tenth and twelfth seconds after the trial onset. A percent of signal change for the forth time point (between 6 and 8th sec) was measured between twelfth and fourteenth seconds after the trial onset.

2.1.2 Results

Behavioral Results

⁵ Featquery is the FSL tool calculating a timeseries statistics

Behavioral data of the fMRI experiment replicated findings of previous experiments in this study. As in the experiments 1, 2 and 3, during the study phase, subjects detected dots and objects equally fast, t(16) = -2.066, p < 0.05). During the test phase, subjects found 95% of target objects with the first attempt (*SD* = 0.03). Responses that took more than one attempt were excluded from the further analysis of behavioral and neuroimaging data. The effect of individual object on the Search task performance was examined using a Univariate Analysis of Variance with group as a between-subject's factor and object as a random factor. There was a significant main effect of group, *F*(2, 136.1) =25.9, *p* < 0.001, a significant main effect of object, *F*(25, 50.2) = 15.9, *p* < 0.001, but no group x object interaction, *p* > 0.4. These findings suggest that although individual objects influenced subjects' performance, this effect was similar in all groups of subjects.

Subjects' RT was analyzed using a GLM procedure. The subject's responses of 2.5 *SD* above the group mean were removed. Removed outliers totaled less than three percent of the data. The Greenhouse-Geisser adjustment was applied when needed. The GLM with trial type and repetition as repeated measure factors and group as a between-subject's factor showed a significant main effect of trial type, F(23, 483) = 13.15, p<0.001, but no main effect of group, F(2,21) = 1.7, p = 0.2 and no trial x group interaction, F(46, 483) = 0.76, p = 0.88 (Figure 20).

The most pronounced effect of experimental condition on search RT was observed on the first repetition of primed stimuli (Figure 20). A one-way ANOVA supported this observation, F(2, 22) = 3.96, p = 0.034 (Figure 21). Duncan 's post-hoc test showed that while control and study-test unaware subjects did not differ from each other, they were significantly slower than study-test aware subjects.

As in the previous experiments of this study, to measure the priming effect, search

RT on the first repetition of primed trials was compared to search RT on the first repetition of foil, unprimed and new trials using a paired t-test. The means and standard deviations are presented in Table 13. There was no priming effect in the control group of subjects because search RT on primed trials did not differ from search RT on foil trials, t(7) = 1.61, p = 0.15, from search RT on unprimed trials, t(7) = -0.2, p = 0.85, and from search RT on new trials, t(7) = -0.65, p = 0.54. No priming effect was also observed in the study-test unaware group of subjects because search RT on primed trials, t(7) = 0.12, p = 0.9, from search RT on unprimed trials, t(7) = 1.06, p = 0.3, and were slower than search RT on new trials, t(7) = 2.44, p = 0.045.

In contrast, study-test aware subjects demonstrated a significant priming effect. Search RT on primed trials was greater than search RT on foil trials. This effect, however, did not reach statistical significance, t(8) = -1.3, p = 0.23. Search RT on primed stimuli was significantly faster than search RT on unprimed trials, t(8) = -2.17, p = 0.031(one-tailed), and on new trials, t(8) = -4.1, p = 0.004 (two-tailed).

Imaging Results

Study phase

Relative to the baseline, the last repetition of primed objects in the Object Detection task increased neural activity in bilateral occipital pole, superior devision of left lateral occipital cortex (LOC), left superior parietal lobule (SPL), left postcentral gyrus, left frontal pole, left superior frontal gyrus and right middle frontal gyrus (MFG) extended to the precentral gyrus. The decrease in neural activity was observed in bilateral cuneus, bilateral postcentral/precunual region, right central/parietal opercular and insular cortices, right posterior cingulate cortex and inferior devision of right LOC (Figure 22, Table 14). Compared to the first repetition, the last repetition of primed stimuli reduced neural activity in bilateral occipital pole, left cuneus and right superior parietal lobule (SPL). Increased neural responses were observed in right supramarginal gyrus, right SPL, right middle frontal gyrus (MFG) and left putamen (Figure 22, Table 14).

Test phase

The first repetition of primed stimuli

During the first repetition of primed stimuli, control subjects activated bilateral precentral gyrus, right superior frontal gyrus, left supplementary motor cortex and left occipital pole increased neural activity compared to the baseline. The decreases of neural activity were observed in right precuneus extended to right posterior cingulate gyrus and left cerebellum (Table 16).

In the study-test unaware group of subjects, primed stimuli activated right supplementary motor cortex and right superior frontal gyrus, left precentral gyrus, left paracingulate, left frontal pole, left insula and left putamen. The decreases were observed in right precuneus, right paracingulate cortex extending to medial frontal cortex, right LOC, right supramarginal gyrus, left angular gyrus and left frontal pole (Table 17). In the study-test aware group of subjects, first repetition of primed stimuli activated bilateral middle frontal gyrus, bilateral thalamus, left occipital pole, left insular and frontal orbital cortices and left frontal pole. The deactivation was observed in right paracingulate and medial frontal cortices and left cerebellum (Table 18). Contrary to the predictions, not changes in hippocampal activity during encoding or testing was found. *The contrast between study-test aware and study-test unaware subjects*

The comparison of neural responses to primed trials (Table 19) revealed that study-test aware, compared to study-test unaware, subjects (Aware(Primed – Rest) >

Unaware(Primed – Rest)) stronger activated bilateral MFG (BA6) that approximately corresponded to the frontal eye fields (FEF), bilateral LOC/SPL (BA7), bilateral occipital pole (BA18), the medial dorsal nucleus of right thalamus, right precuneus (BA31) and left precentral gyrus (BA4). Study-test unaware, compared to study-test aware, subjects (Unaware(Primed – Rest) > Aware(Primed – Rest)) stronger activated the anterior part of the left inferior frontal gyrus (IFG, BA46) and the temporo-occipital and anterior parts of the right middle temporal gyrus (MTG, BA21) (Figure 23).

The comparison of neural responses to new trials (Table 20) revealed that studytest aware, compared to study-test unaware, subjects ($Aware_{(New-Rest)} > Unaware_{(New-Rest)}$) stronger activated bilateral LOC, bilateral temporooccipital fusiform cortex, bilateral precenral gyrus, right occipital pole, left superior frontal gyrus and left precuneus. Studytest unaware, compared to study-test aware, subjects (Unaware_{(New-Rest)} > Aware_{(New-Rest)}) stronger activated bilateral cerebellum and right precentral gyrus.

The comparison of neural responses to foil trials (Table 21) revealed that studytest aware, compared to study-test unaware, subjects (Aware_(Foil-Rest) > Unaware_(Foil-Rest)) stronger activated superior devision of bilateral LOC anteriorly, bilateral occipital pole, inferior devision of right LOC and left cerebellum. Study-test unaware, compared to study-test aware, subjects (Unaware_(Foil-Rest) > Aware_(Foil-Rest)) stronger activated bilateral MTG, bilateral precuneus, superior devision of right LOC posteriorly, right MFG, left frontal pole, left posterior cingulate cortex and left superior temporal gyrus.

The conjunction of neural responses on primed, foil and new trials

To examine the general effect of awareness on the Search task performance, the awareness-related changes during primed, foil and new trials were subjected to a conjunction analysis. It was revealed that study-test aware subjects, compared to studytest unaware subjects, had greater neural activity in bilateral LOC (BA7), right occipital pole (BA18) and left precentral gyrus (BA4) on all three types of trials (Figure 23).

The neural responses in bilateral frontal eye fields (BA6) were greater in aware versus unaware subjects on primed and new trials, but not on foil trials. Awarenessrelated changes in left inferior frontal gyrus, right middle temporal gyrus, right precuneus and right thalamus were unique for primed trials (Figure 23).

<u>Time series analyses of Aware – Unaware contrast</u>

To examine if study-test awareness induced early neural responses, the dynamics of BOLD signal in awareness-related regions was investigated (Figure 24 and Figure 25). Please note, that on the figures 24 and 25, events are called "2s", "4s", "6s" and "8s". However, neural activity corresponded to each event is taken six seconds (3 TR) later after the onset of each event.

The network of brain regions that was unique for primed trials (priming-specific network) consisted of left inferior frontal gyrus, right cuneus, right thalamus and right MTG. Figure 23 illustrates neural dynamics in this network during the first repetition of primed stimuli. The priming-specific decreases in the left inferior frontal gyrus were significant during all time points of the trial [2 sec: t(15) = -5.85, p < 0.001; 4 sec: t(15) = -4.1, p = 0.001; 8 sec: t(15) = -3.89, p = 0.001].

The priming-specific decreases in the right middle temporal gyrus were significant only between 2nd and 4th seconds of the trial [2 sec: t(15) = -1.82, p = 0.09; 4 sec: t(15) = -2.11, p = 0.05; 6 sec: t(15) = -0.763, p = 0.457; 8 sec: t(15) = -2.05, p = 0.06]. The priming-specific increases in the right precuneus were significant across first three time points [2 sec: t(15) = 2.8, p = 0.014; 4 sec: t(15) = 3.28, p = 0.005; 6 sec: t(15) = 2.79, p = 0.014; 8 sec: t(15) = .54, p = 0.6]. The priming-specific increases in the right thalamus were significant only between 2^{nd} and 4^{th} seconds of the trial [2 sec: t(15) = 1.518, p=0.15; 4 sec: t(15) = 3.069, p = 0.008; 6 sec: t(15) = 1.753, p=0.1; 8 sec: p>0.9].

The network of brain regions where awareness increased activation on all types of trials (strategy-related network) comprised of bilateral frontal eye fields, left precentral gyrus, superior devision of bilateral LOC and right occipital pole. Figure 25 illustrates neural dynamics in this network during the first repetition of primed stimuli.

While left frontal eye fields showed only marginally significant increase in activity in aware subjects compared to unaware subjects between 2^{nd} and 4^{th} seconds of the trials [4 sec: t(15) = 1.72, p = 0.1], right frontal eye fields showed significant awareness-related increase between 2^{nd} and 6^{th} seconds of the trial [4 sec: t(15) = 2.62, p = 0.02; 6 sec: t(15) = 5.23, p < 0.001; 2 sec and 8 sec: p > 0.3].

Left precentral gyrus was more active in aware subjects compared to unaware subjects during the first 4 seconds and the last 2 seconds [2 sec: t(15) = 3.64, p = 0.002; 4 sec: t(15) = 2.533, p = 0.023; 6 sec: t(15) = 1.561, p = 0.139; 8 sec: t(15) = 2.376, p = 0.031]. Right occipital pole was more active in aware subjects compared to unaware subjects during all time points of a trial [2 sec: t(15) = 1.896, p = 0.08; 4 sec: t(15) = 1.88, p = 0.08; 6 sec: t(15) = 2.52, p = 0.023; 8 sec: t(15) = 1.72, p = 0.1]. Left LOC/SPL (BA7) was significantly more active in aware subjects compared to unaware subjects during the first four seconds of the trial [2 sec: t(15) = 3.23, p = 0.006; 4 sec: t(15) = 3.77, p = 0.002; 6 sec and 8 sec: p > 0.1].

Right LOC/SPL (BA7) was marginally more active in aware subjects compared to unaware subjects during the first four seconds of the trial [2 sec: t(15) = 1.82, p = 0.09; 4 sec: t(15) = 2.04, p = 0.06; 6 sec and 8 sec: p > 0.2].

To ensure that pre-activation is not a general phenomenon characterizing study-

test awareness, the time series were extracted from right and left hippocampus. Primed trials were analyzed (Figure 26). A *t*-test revealed no difference in hippocampal activity between groups of subjects. All *p*-values were larger than 0.3.

Conjunction of encoding-related and test-related neural activity

The neural responses to the last repetition of primed stimuli during encoding were overlaid with the neural responses to the first repetition of primed stimuli during testing. This conjunction analysis had two stages. Firstly, the conjunction analysis was applied to the study-test aware, the study-test unaware and the control groups of subjects. Secondly, these three resulting masks were overlaid to reveal commonalities between groups of subjects. It was found that right central/parietal operculum and insular cortices, right posterior cingulate gyrus and bilateral precuneus deactivated during the last repetition of primed stimuli in the Object Detection task and also deactivated during the first repetition of primed stimuli in the Search task (Figure 27). Commonalities between control, studytest unaware and study-test aware subjects suggest that right central/parietal operculum cortex, right posterior cingulate gyrus and bilateral precuneus were deactivated as the result of perceptual similarity between study and test stimuli, but not priming.

Encoding-related neural activity was conjuncted with awareness-related neural activity. It was found that superior devision of left LOC and bilateral occipital pole activated during the last repetition of primed stimuli in the Object Detection task and also responded stronger in study-test aware, compared to study-test unaware, subjects during the Search task (Figure 28).

Right precuneus deactivated during the last repetition of primed trial in the Object Detection task. It also decreased its activity as a function of study-test awareness (Figure 29). The learning effect was indicated as the change in neural responses to the last repetition of primed stimuli compared to the first repetition of primed stimuli in the Object Detection task. The regions showing the learning effect were also sensitive to processing of primed stimuli during the Search task. Thus, right middle occipital gurus showed learning related decrease during the Object Detection task. However, during the Search task, the same region showed larger activity in the study-test aware condition compared to the study-test unaware condition (Figure 30). Although, this particular area increased its activation in both groups of subjects, the increase was larger in the studytest aware group.

Remarkable, that neither of conjunction masks between encoding-related and awareness-related regions overlapped with the regions that showed sensitivity to perceptual similarity between encoding and testing tasks.

Linear Discriminant Analysis

LDA for study-test aware and study-test unaware subjects was conducted. The independent variables were the magnitude of reactivation in in left LOC/SPL, left OP (MOG), right OP (MOG) and right precuneus and search RT. The magnitude of reactivation was calculated for each subject as a difference between the percent of BOLD signal change during the Search task and during the Object Detection task.

The linear discriminant function strongly correlated with search RT, r = -0.71, reactivation in left LOC/SPL, r = 0.66, and left middle occipital gyrus, r = 0.46. Weaker correlations were observed between LD function and right middle occipital gyrus, r = 0.24 and right precuneus, r = 0.16.

A Multivariate Analysis of Variance (MANOVA) was conducted. A Wilk's test was used to test if a discriminant model as a whole is significant. Wilk's test for the full model (all five variable were included) was significant, p = 0.048. LDA performed on all five variables was able to correctly classify 88% of subjects. Generalization was tested using leave-one-out cross-validation and yielded 76.5% (Figure 31.A).

In order to reveal the role of each variable for LDA performance, one variable at a time was removed from the analysis and LDA was conducted on four variables left. When left LOC/SPL was removed from the analysis, *p*-value increased and became only marginally significant, p = 0.057. When left occipital pole was removed from the analysis, *p*-value was virtually the same as for the full model, p = 0.049. When right occipital pole was removed, *p*-value decreased, p = 0.02. When right precuneus was removed, *p*-value decreased, p = 0.02. When search RT was removed from the model, *p*-value in Wilk's test increased and became not significant, p = 0.14. The latter results suggest the important role of behavioral correlates for discrimination between successful and unsuccessful performers on implicit memory test.

The findings that discriminant model became more significant when right precuneus or right middle occipital gyrus were removed from the model (along with low correlations between these variables and the discriminant function) suggest that these two brain regions may be not very important for successful performance on the Search task. The next step was to test discriminant model when both right OP and right precuneus were excluded from the LD model. According to Wilk's test, LDA model for left LOC/SPL, left OP and search RT was highly significant, p = 0.007.

Cross-validation for reduced subset of variables improved compared to crossvalidation for the whole subset (Figure 31.B). The improvement in classification was seen for study-test aware, but not for the study-test unaware group of subjects. Two study-test unaware subjects were classified as study-test aware in both full and reduced subsets of variables. However, posterior probabilities for one of the subjects improved for the reduced subset of variables. This subject was classified as study-test aware with 92.5% of probability if all variables were used. However, if reduced subset was used, the subject was classified as study-test aware with 64.8 % of probability.

Another question concerned the possibility to classify subjects based on the magnitude of reactivation only. For this purpose, the classification was attempted using different combinations of brain regions. The classification was at chance when all brain regions were used in the model (Figure 31.C). However, when the model included only left LOC/SPL, left MOG and right precuneus, subjects were correctly classified with generalization accuracy 65% (Figure 31.D). LDA on all other combinations of brain regions failed to classify study-test unaware and study-test unaware subjects.

2.1.3 Discussion

Dissociation of implicit and explicit memory was investigated using the fMRI technique. In this study, subjects incidentally learned objects and object locations during the Object Detection task. The comparison of RT in the Dot Detection and the Object Detection tasks revealed no differences. Learning during the Object Detection task was associated with increase of neural activity in left putamen. Such increase may be related to generation of expectancy during the task (Rossell, Bullmore, Williams & David, 2001) or motor learning (Doyon, Song, Karni et al., 2003; Duff, Xiong, Wang, Cunnington, Fox & Egan, 2007). Being a part of striatum, putamen could be activated as a result of implicit learning (Reiss, Campbell, Leslie et al., 2005). Taken together these findings validate the incidental nature of learning during the Object Detection task.

During the test phase, subjects' implicit memory for object locations was tested using the Search task. Consistent with the findings of Experiment 2, implicit memory for spatial locations was greater in study-test aware, compared to study-test unaware, subjects. While search RT in study-test unaware and control subject did not differ, studytest aware subjects were faster than both unaware and control subjects. In addition, studytest aware, but not study-test unaware or control, subjects found primed stimuli significantly faster than unprimed and new stimuli.

The neural correlates of implicit retrieval for spatial locations were found in the extended network of regions in frontal, parietal, occipital and temporal lobes. Further analysis of primed, foil and new trials revealed that study-test aware, compared to unaware, subjects had larger neural activity in bilateral FEF, bilateral LOC/SPL, left precentral gyrus and right occipital pole during primed, foil and new trials. As it was suggested earlier, this effect may be related to the general effect of awareness on subjects' performance. Specifically, it may be related to increase in attention to the stimuli in study-test aware subjects. Consistent with this idea are findings that the same network of regions was revealed in the studies of visual attention (Kastner et al., 1999) and planning (Fincham, Carter, van Veen, Stenger, & Anderson, 2002).

The enhancement of priming was also related to the priming-specific changes of neural activity that were observed only when subjects searched for primed stimuli. The priming-specific network of brain regions showed reduction of neural activity in the left IFG (BA46) and right MTG (BA21) and increases of neural activity in the right precuneus, right thalamus and left occipital pole.

Previous research has demonstrated that the left IFG can be a basis for conceptual priming (Wig et al., 2005). In many studies, the BOLD decreases in the left IFG was found for primed compared to new stimuli in the lexical and semantic priming tasks (Demb et al., 1995; Schott et al., 2006; Wagner, Koutstaal, Maril, Schacter & Buckner,

2000). Thus, it is possible that although the Search task requires spatial processing, it may also involve some semantic processing of target objects. This semantic processing could be more efficient in study-test aware, compared to study-test unaware, subjects.

However, in study-test aware subjects, the neural activity in left IFG was not only decreased compared to study-test unaware subjects, it was also deactivated compared to the baseline (rest). The previous studies suggested that the task-dependent deactivation may be explained by "a shift of resources away from ongoing, but inessential, processes to an increasingly demanding cognitive task" (Habeck, Rakitin, Moeller et al., 2005, p.208) and by reallocation of processing resources (McKiernan, Kaufman, Kucera-Thompson & Binder, 2003). Also deactivation may result from redistribution of cerebral blood flow to the areas that are active (Shmuel, Yacoub, Pfeuffer, et al., 2001). In addition, deactivation may be a result of "gating" input to areas that are not involved in task performance (Gusnard & Raichle, 2001) and may reflected inhibition of neural activity in order to prevent unwanted spread of activation in a network important for the task performance (Frith, Friston, Liddle & Frackowiak, 1991). Considering that the Search task did not require semantic processing but required spatial processing, deactivation of IFG in this experiment could suggest reallocation of processing resources to the spatial processing areas.

The neural increase in precuneus and left occipital pole (MOG) may be associated with spatial processing (Kohler et al., 1998). Also it may reflect pursuit and saccade eye motion (Berman, Colby, Genovese, et al., 1999) that subjects made during search for the objects. The increases of thalamic activity may be necessary for transformation of neural priming to its behavioral counterpart (Walla, Lehrner, Nasel et al., 2003). It was reported that thalamic lesions interfered with motor skill learning (Exner, Weniger & Irle, 2001) and led to disconnection between processing streams of neural priming and behavioral response (Walla et al., 2003). These findings suggest that enhancement of priming depends on activation of the task-specific and attentional networks along with transformation of neural priming into its behavioral correlates.

Explicit memory studies consistently demonstrated that remembered, compared to familiar or forgotten, items induce larger neural activity (Eldrige et al., 2000; Henson et al., 1999). This study demonstrated that the larger priming effect was also related to the increases of neural activity. Taken together, these findings indicate that enhancement of priming, as well as enhancement of explicit recall, is associated mostly with increases of neural activity. Similarity in the mechanisms providing improvement of implicit and explicit retrieval may suggest that memory traces tested during implicit and explicit tests have similar properties. Arguably, such similarity may indicate that information is encoded by a single memory system, but not by distinct memory systems and subsystems.

The hippocampus is necessary for remembering of object locations (Burgess et al., 2002). Specifically, hippocampus is important for implicit memory of spatial context (Chun & Phelps, 1999). It was expected that processing of object locations during the Object Detection task and the Search task would involve hippocampus. Contrary to the expectations, there were no changes in hippocampal activity during encoding or testing. One explanation for these results is that in the current study the task-related neural activity was contrasted to the resting baseline. The hippocampus may be active during resting. Another explanation for the lack of hippocampal activity may be directly related to the tasks used in this study. All tasks had very low memory load. To encode locations, subjects did not exert any efforts. Also, subjects were not required to navigate, or create spatial maps of object positions, or think about spatial relationships between objects. Previous studies have shown that spatial tasks with low memory load do not require involvement of hippocampus. For example, memory for object locations in virtual environment was tested in patients with hippocampal damage (Shrager, Bayley, Bontempi, Hopkins & Squire, 2007). The patients performed normally when memory load was low (they had to memorize one or two locations). However, the patients' performance declined when memory load was increased up to five locations.

Another evidence that may provide support for a unitary memory system is the dynamics of neural activity in primed trials. Studies on visual search and visual working memory (Kastner et al., 1999; Lepsien & Nobre, 2006) demonstrated that attention to the specific location influences neural activity. It was suggested that if the same modulation will be observed in the implicit memory tasks, then the attentional modulation mechanisms described above may be common for explicit and implicit memory tasks. In this fMRI study, the time series were extracted from the brain regions that showed sensitivity to study-test awareness.

As it was noted earlier, study-test awareness was related to the higher level of attention to the stimuli. The specific question that was addressed in this experiment concerned the activation of spatial processing brain regions during target presentation. During the Object Detection task, target objects were associated with particular spatial locations. However, in the beginning of the Search task, targets was presented centrally and were not related to any distinct spatial information. The subject's expectation that the target will appear later during the trial in some location could induce neural activity in the spatial processing regions. The time series analysis revealed that study-test aware subjects, who exhibited greater priming, activated left precuneus and left LOC/SPL during processing of the target objects. The left LOC/SPL region was the part of the strategy-related network that changed its activity irrespective to the trial type. Consequently, pre-activation of this region may reflect the attentional operations themselves (Kastner & Underleider, 2001). On the other side, left precuneus was a part of priming-specific network. Because the role of precuneus in processing of spatial information is well defined (Mellet, Tzourio, Crivello, et al., 1996; Ogiso, Kobayashi & Sugishita, 2000; Cavanna & Trimble, 2006), pre-activation of precuneus may be related to the enhancement of implicit memory for spatial locations in study-test aware subjects. Thus, it appears that attention to the stimuli modulates behavioral performance and its neural correlates not only in working memory tasks but also in implicit memory tasks. These findings suggest similarity between implicit and explicit memory systems.

The main criticism of priming studies is the lack of control over explicit recall and explicit retrieval strategies during priming tasks. According to earlier work, successful explicit recollection is associated with the BOLD increase in hippocampus. Intentional retrieval efforts are associated with BOLD increases in anterior prefrontal cortex (Schacter et al., 1996; Schacter & Buckner, 1998). Consequently, if study-test aware subjects used either explicit recall or explicit retrieval strategies in the Search task, hippocampus and/or anterior prefrontal cortex would be activated. However, no hippocampal activity was observed either in study-test aware or in study-test unaware subjects. Also the neural activity in anterior prefrontal cortex was below the baseline in study-test aware subjects. Taken together these findings indicate that in order to improve priming, study-test aware subjects did not engage explicit retrieval strategies but used other mechanisms to control for performance.

One such mechanism may be related to reactivation of previously acquired

memory traces. Many behavioral studies showed that retrieval strongly relates to compatibility between encoding and retrieval processes (Morris et al., 1977; Weldon & Roediger, 1987). It was suggested that such dependence of retrieval from encoding is related to reinstatement or reactivation of encoding-related neural activity during retrieval (e.g., Norman & O'Reilly, 2003). Recent neuroimaging studies of explicit memory supported theoretical suggestions and behavioral data. The findings were consistent across many studies: Brain regions activated during encoding were reactivated during retrieval (Johnson & Rugg, 2007; Persson & Nyberg, 2000; Kahn et al., 2004; Woodruff et al., 2005; Vaidya et al., 2002; Nyberg et al., 2000, 2001; Wheeler et al., 2000). The only study that reported reactivation during implicit memory test actually found redeactivation (deactivation was observed during encoding and also during test) (Schott et al., 2006). From that study, it was not clear if re-deactivation is a phenomenon related to perceptual similarities between study and test stimuli, or it was a phenomenon relate to priming itself. If re-deactivation is related to the magnitude of priming, it suggests that implicit memory is orthogonal to explicit memory. If priming is actually related to reactivation, it suggests similarity between implicit and explicit memory systems.

In the fMRI experiment of this study, the effects of perceptual similarity and the priming effect were disentangled. The effect of perceptual similarity was observed in right parietal operculum cortex, right posterior cingulate cortex and bilateral precuneus. All these areas were deactivated during encoding and were also deactivated during search for primed stimuli. Posterior cingulate cortex is important for memory and visuospatial processing (Vogt, Vogt & Laureys, 2005). Parietal operculum cortex is involved in processing of coherent, but not random, visual motion (Antal, Baudewig, Paulus & Dechent, 2008). It was reported that increase in visual attention decreases activity in

precuneus (Tomasi et al., 2006). Thus, the similarities between study and test may be related to some sort of visual attention that subjects have to sustain to detect the stimuli and respond as quickly as they detected them.

The priming-specific reactivation was observed in left LOC/SPL, bilateral occipital pole (MOG), right precuneus and right cuneus. All these regions were reactivated during the Search task. Because these regions are involved in processing of object and spatial information, reactivation of these regions may indicate that incidentally encoded associations between objects and locations were revived during the Search task. Remarkably, the reactivation occurred in both study-test aware and study-test unaware subjects. During search for primed stimuli, study-test unaware subjects exhibited the same level of BOLD signal change in the reactivated brain regions as it was during encoding. Study-test aware subjects increased activity in reactivated regions above the encoding level. This means that in order to improve performance on priming task, subjects not only need to reactivate encoding-related patterns of neural activity, but they also need to exceed this level. Arguably, the increases above the encoding level occur because reactivation related to the spatial processing is not stimulus specific. The initial memory traces were weak. So, subjects were not able to reactivate neurons engaged in processing of the specific spatial location associated with the object. Most probably, the reactivation occurred in neurons engaged in processing of any spatial information during encoding.

If reactivation is a key factor for successful performance, then study-test aware subjects and study-test unaware subjects may be classified based on the magnitude of reactivation. To test this possibility LDA was conducted. The results of LDA indicated that subjects indeed could be classified as aware or unaware based on reactivation in left LOC/SPL, bilateral OP (MOG)and right precuneus and search RT. The performance of the LD model was improved when reactivation in precuneus and right MOG was removed from the model. Importantly, the LDA was able to classify aware and unaware subjects based only on reactivation in left LOC/SPL, left MOG and right precuneus. The results of LDA suggest that reactivation indeed is the important factor for implicit retrieval success.

The present fMRI study of neural reactivation differed from previous studies in several aspects. First, it addressed reactivation of encoding-specific regions during implicit memory test. Second, this experiment allowed to disentangle reactivation related to perceptual similarities between study and test stimuli from reactivation related to priming. Third, in this study, subjects performed encoding and implicit retrieval within one scanning session. Both tasks were analyzed in order to reveal reactivation. In contrast, some of the previous studies inferred reactivation from the content-related difference during retrieval. For example, Wheeler et al. (2006) had subjects to encode the word-sound and word-picture associations outside the scanner. The testing session took place next day in the scanner. The reactivation was inferred from how preparatory cues and their validity influenced inferior temporal and parieto-occipital cortices. Forth, this study manipulated the magnitude of priming and allowed to discriminate between successful and unsuccessful test performance. While the previous studies addressed reactivation qualitatively, in terms of involvement of certain brain regions into the task, they did not address the quantitative differences. This fMRI study demonstrated that successful performance on implicit memory test requires that reactivated regions increased neural activity above the level of neural activity during encoding.

As it was consistently shown in studies of explicit memory, successful explicit

retrieval requires reactivation of encoding-related brain regions. The fMRI study presented here clearly indicated that successful implicit retrieval also requires reactivation of encoding-related brain regions. This neuroimaging evidence suggests similarities between implicit and explicit memory.

In summary, the current fMRI study is the first to systematically investigate the questions of neural dynamics and neural reactivation during successful and unsuccessful performance on priming task. The result were compared to the previously reported findings in the realm of explicit memory. It was found that successful performance on implicit memory test as well as successful performance on explicit memory test requires the increases in neural activity, depends on attentional modulation of neural response and induce reactivation of encoding-related brain activity during testing. Such similarity in the mechanisms of successful performance contradicts the notion of orthogonality between implicit and explicit memory systems. It provides support for a unitary memory system at least in the domain of spatial information.

GENERAL DISCUSSION

The dissociation between performance on implicit and explicit memory tests was taken as an evidence for multiple memory systems. The main tenet of the multiple memory systems view is that two (or more) memory systems differ functionally and neurobiologically (Schacter & Tulving, 1994; Tulving & Schacter, 1990). The proponents of this view suggested that during encoding, every memory systems creates its own memory trace (Graf & Schacter, 1985; Mitchell & Brown, 1988; Tulving, 1985). During retrieval, different types of tests (implicit and explicit) access different memory traces. In contrast, the proponents of a unitary memory system suggested that during stimulus encoding only one memory trace is created. Dissociation between implicit and explicit memory tests may be determined by compatibility between processes at study and at test but not by access to different memory traces (Bentin et al., 1992; Roediger, 1990; Witherspoon & Moscovitch, 1989). While the compatibility between study and test appears to be a key factor for memory studies (Morris et al., 1977), studies of implicit memory often disregarded this factor.

The four experiments of this study investigated the question of separability of implicit and explicit memory systems while controlling for transfer appropriate processing between study and test. Using spatial locations as the stimuli, it was shown that implicit that implicit spatial memory for recalled stimuli was significantly higher than for not recalled stimuli. In addition, contrary to the predictions of the multiple memory systems view, the strength of memory traces acquired during encoding equally affected subjects' performance on both implicit and explicit spatial memory tests. The neuroimaging experiment revealed that in accord with the explicit memory fMRI studies, the enhancement of implicit memory corresponded to the increases of neural activity in the task-specific and attentional networks. It was also shown that successful implicit retrieval corresponded to the higher degree of attentional modulation in the spatial processing regions. Finally, implicit memory depended on reactivation of encodingrelated brain regions. These findings were consistent with the earlier findings in the domain of explicit memory. Taken together, these results provided support for a unitary memory system by substantiating the idea of common memory representation for implicit and explicit memory tests (Bentin et al., 1992).

Performance on both implicit and explicit spatial memory tests may depend on subjects' ability to reactivate memory traces acquired during encoding. A model of memory trace reactivation may provide an explanation for how implicit and explicit tests work within a unitary memory system. It also my offer the explanation for how awareness influences implicit memory.

A model of memory trace reactivation

During encoding, participants acquire information about a stimulus event. During acquisition, a memory trace of this event is created (Bentin et al., 1992). The memory trace contains information about stimulus properties and also about time when the trace was created. In the literature, the time of the trace creation is sometimes referred as a "time-stamp" (Nadel, Samsonovich, Ryan & Moscovitch, 2000). Most probable, a "time-stamp" information is not absolute (e.g., "it happened at 10.30 am"), but relative to the other events (e.g., "it happened after that ...", or "it happened at the same time with ..."). The strength of memory traces may depend on firing rates in neurons processing stimulus properties during encoding. Also it may depend on the strength of connections between groups of neurons processing stimulus properties. Thus, a memory trace may be represented as the combination of weights assigned to each stimulus property and connections between these properties (Figure 32).

The retrieval success, either in implicit or in explicit memory tests, may depend on whether the memory traces acquired during encoding are reactivated. It seems that the probability of reactivation may be affected by several factors. One factor is the similarity between the memory trace created during retrieval (the secondary memory trace) and memory traces created during encoding (initial memory traces). Another factor is the strength of initial memory traces. The third factor is the size of the search space.

Humans are able to detect similarity between two events even if they are not aware of this similarity (Lewicki, 1986). If no similarity between the secondary and the initial memory traces is detected, the secondary memory trace is treated as new. If the secondary memory trace and at least one of the initial memory traces seems similar, people's behavior becomes biased toward the feature(s) of the stimuli that appear similar (Lewicki, 1986). Earlier work indicated that the initial memory traces may be reactivated as a function of its similarity with the secondary memory trace. Thus, the initial trace with high similarity to the secondary trace may be activated stronger than the initial memory trace with low similarity (Hintzman, 1986). There are several types of similarity. One of them is the perceptual similarity. For example, in the Snodgrass & Hirshman (1994) study, subjects viewed fragmented picture. Then, subject's memory was tested with explicit and implicit memory tests. Subjects performed both types of tests better when the fragmentation levels of the study and test pictures was similar. Another type of similarity is the processing similarity (or transfer appropriate processing) between study and test. The effect of processing similarity was previously shown in both explicit (e.g., Morris et al., 1977) and implicit (e.g., Weldon & Roediger, 1987) memory tests.

The strength of initial memory traces may be important for reactivation processes because the stronger traces have the larger weights in the network. The larger weight makes the memory trace stand out in the huge search space containing millions of memory traces. Consequently, it is possible, that the similarity between initial and secondary memory traces will be first searched among traces with larger weights, and only then, among traces with lower weights. Consistent with this idea, many previous studies demonstrated that strong memory traces are retrieved better than weak memory traces. For example, both explicit (e.g., Craik & Tulving, E., 1975; Hyde & Jenkins, 1973) and implicit memory tests (Brown & Mitchell, 1994; Challis & Brodbeck, 1992) benefited from deep encoding compared to shallow encoding. Also subjects better recalled information acquired intentionally compared to information acquired incidentally (Thompson & Paivio, 1994). In accord with the previous findings, the experiments 1, 2 and 3 of this study also showed that strong memory traces were associated with greater success in explicit and implicit retrieval of spatial information.

Finally, reactivation of initial memory traces may depend on the size of the search space. Thus, it is more difficult to find two similar traces if the search space consists of thousands of memory traces, compared to the search space that consists of only several memory traces. It seems that at least two factors can limit the search space. One of them is the "time-stamp" information that relates to time when the initial memory trace was created. When subjects know when the tested information was acquired, the neurons processing stimuli during that time period may increase its firing rates above the baseline (Figure 33).

Another factor that may limit the search space is information about the specific stimulus properties that are tested. When subjects know on what stimulus properties they have to focus, the neurons processing this particular property may increase its firing rates above the baseline (Figures 34).

Implicit and explicit memory tests seem differ in their ability to limit the search space. In the explicit memory tests, instructions direct subject's attention to the time when the initial memory trace was acquired (e.g., "What object did you see *two items ago*?", or "Have you seen these words in the *previous task*?"). In explicit memory tests, subjects are usually informed about stimulus properties that they need to reconstruct. In implicit memory tests, subjects perform indirect memory tasks such as word stem completion, perceptual identification or visual search. Usually, subjects are not informed about time when they encoded information. They are also not informed about the stimulus properties tested during the task. Thus, during implicit memory tests, the search space is larger

compared to that during explicit memory tests.

It is known that priming is very specific to perceptual, semantic and processing properties of encoded information (Schacter et al., 2004). The large size of the search space in implicit memory tests may be the reason for this specificity. If the secondary memory trace does not exactly replicate the initial memory trace, the probability to find similarity between two traces in the large search space is very low. Thus, the probability of initial memory traces reactivation is higher during explicit memory test than during implicit memory test.

It is important to note that reactivation may include not only properties that the secondary and the initial memory traces share, but also "information that the probe itself does not contain" (Hintzman, 1986, p. 412). It seems that implicit and explicit tests differ in their ability to reactivate information that the secondary and the initial memory trace do no share. Because explicit tests require subjects to reconstruct the encoded event, subjects may actively search for required information and sometimes even try to fit different properties of the stimuli to recreate the initial memory trace. Implicit tests are more "passive". Subjects do not try to reinstate the initial memory trace. Consequently, the non-shared properties may be reactivated only if neural activation will spread in the network from the shared to non-shared property of the trace.

For example, in the present study, subjects learned objects and object locations during encoding. During implicit memory test, subjects were presented with target objects that shared object, but not spatial, properties of learned stimuli. To successfully perform on the Search task, subjects had to reactivate spatial properties of target objects. The model of memory trace reactivation could explain this process in the following way. When the target object is presented, the memory trace of this event is created. The
similarities between this new memory trace and traces created earlier are searched. When the search space is large, like in the study-test unaware condition, the similarities between the secondary and the initial memory traces are not detected. Consequently, the initial memory trace is not reactivated. The secondary memory trace is treated as new. Subjects demonstrate no priming effect in the search task. When subjects are informed that target objects are the same as learned objects, study-test awareness limits the search space to the traces created during encoding. When the search space is limited by the study-test awareness, the similarities between the secondary and the initial memory traces are easier to detect. If similarities are detected, the initial memory trace may be reactivated. It means that not only information about the object, but also information about object's location, may be reinstated. Figure 35 illustrates the process of reactivation in the Search task.

To summarize, the reactivation framework suggests that memory performance depends on detection and processing of similarity between secondary and initial memory traces. When similarity is detected, the initial memory traces may be reactivated.

The probability of reactivation depends on the strength of the initial memory traces, on similarity between initial and secondary memory traces and on the size of the search space. Explicit and implicit memory tests may differ in their ability to reactivate initial memory traces. The probability of reactivation may be higher during explicit memory tests compared to implicit memory tests because explicit memory tests efficiently narrow the scope of search.

Although the model of memory trace reactivation explains dissociation between implicit and explicit memory tests, it may present only a partial account of human memory. First of all, the support for the model was obtain during the studies of spatial memory. Consequently, at the time it is not possible to generalize findings to other types of information (such as emotions, preferences or lexical material).

Secondly, in the presented here experiments, a memory load was very low. It is unclear how reactivation processes behave when memory load increases. The future studies should look at how memory load, complexity of initial memory traces as well as the degree of similarity between initial and secondary memory traces may affect reactivation in implicit and explicit memory tests.

Lastly, the future studies should examine if the reactivation model can account for dissociation of implicit and explicit memory in patients with amnesia. The dissociation of implicit and explicit memory in amnesiacs is the strongest argument for multiple memory systems. Some researchers believe that a unitary memory system cannot account for the data showing spared conceptual and perceptual priming in amnesiac patients (Poldrack & Foerde, 2008). If it turns out that the reactivation model accounts for data from amnesiac studies, it will strengthen a unitary system view.

Conclusion

Converging behavioral and neuroimaging evidence indicated a high degree of similarity between representations of implicit and explicit spatial memory. The success in implicit retrieval of spatial information highly correlated with the success in explicit retrieval of spatial information. The strength of memory traces acquired during encoding equally affected both types of tests. The neural dynamics and reactivation of encodingrelated brain regions during the successful implicit retrieval of spatial information resembled those observed during the successful explicit retrieval. Such similarities suggest that both implicit and explicit memory tests may depend on the same form of neural plasticity. The reactivation of encoding-related brain regions during retrieval may be a key factor for successful implicit and explicit retrieval. Dissociation between performance on implicit and explicit memory tests may be explained by different ability of implicit and explicit tests to reactivate initial memory traces. Performance on both tests may be improved when the scope of search is narrowed. Overall, the results of this study provided support for unitary spatial memory.

REFERENCES

- Andrade, J., & Meudell, P. (1993). Short report: is spatial information encoded automatically in memory? *Quarterly Journal of Experimental Psychology*, 46(2), 365-375.
- Anooshian, L. J., & Seibert, P. S. (1996). Diversity within spatial cognition: Memory processes underlying place recognition. *Applied Cognitive Psychology*, 10(4), 281-299.
- Antal, A., Baudewig, J., Paulus, W., & Dechent, P. (2008). The posterior cingulate cortex and planum temporale/parietal operculum are activated by coherent visual motion. *Visual Neuroscience*, *25*(*1*), 17-26.
- Badgaiyan, R. D., Schacter, D. L., Alpert, N. M. (1999) Auditory priming within and across modalities: evidence from positron emission tomography. *Journal of Cognitive Neuroscience*, 11, 337-348.
- Beckmann, C., Jenkinson, M., & Smith, S. (2003). General multi-level linear modeling for group analysis in FMRI. *NeuroImage*, *20*, 1052-1063.
- Bentin, S., Moscovitch, M., & Heth, I. (1992). Memory with and without awareness: performance and electrophysiological evidence of savings. *Journal of Experimental Psychology: Learning, Memory and Cognition, 18*, 1270-1283.
- Berman, R. A., Colby, C. L., Genovese, C. R., Voyvodic, J. T., Luna, B., Thulborn, K. R., & Sweeney, J. A. (1999). Cortical networks subserving pursuit and saccadic eye movements in humans: a fMRI study. *Human Brain Mapping*, *8*, 209-225.
- Berry, C. J.; Shanks, D. R. & Henson, R. N. A. (2008). A single-system account of the relationship between priming, recognition, and fluency. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 34, 97-111.
- Biederman, I. & Cooper, E. E. (1991). Priming contour-deleted images: evidence for intermediate representations in visual object recognition. *Cognitive Psychology*, 23, 393-419.
- Borst, G., & Kosslyn, S. M. (2008). Visual mental imagery and visual perception: structural equivalence revealed by scanning processes. *Memory and Cognition*, *36*, 849-862.
- Bowers, J. S., & Schacter, D. L. (1990). Implicit memory and test awareness. *Journal of Experimental Psychology: Learning, Memory and Cognition, 16(3),* 404-416.
- Brown, A. S., & Mitchell, D. B. (1994). A revaluation of semantic versus nonsemantic processing in implicit memory. *Memory and Cognition*, *22*, 33–541.

Büchel, C., Coull, J.T., Friston, K.J. (1999). The predictive value of changes in effective

connectivity for human learning. Science, 283, 538-541.

- Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., & Dale, A. M. (1998). Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron*, 20(2), 285-96.
- Buckner, R. L., Koutstaal, W., Schacter, D. L. & Rosen, B. R. (2000). Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain*, *123*, 620-640.
- Buckner, R. L., Raichle, M. E., Miezin, F. M. & Petersen, S. E. (1996). Functional anatomic studies of memory retrieval for auditory words and visual pictures. *Journal of Neuroscience*, *16*, 6219–6235.
- Burgess N., Maguire, E. A., & O'Keefe J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*, 625–641.
- Butler, L. & Berry, D. (2001). Implicit memory: intention and awareness revisited. *Trends in Cognitive Science*, **5**, 192-197.
- Cabeza, R., & Nyberg, L. (1997). Imaging Cognition: An Empirical review of PET studies with normal subjects. *Journal of Cognitive Neuroscience*, *9*, *1-26*.
- Carlesimo, G. A., Fadda, L., Marfia, G. A., & Caltagirone, C. (1995). Explicit memory and repetition priming in dementia: evidence for a common basic mechanism underlying conscious and unconscious retrieval deficits. *Journal of Clinical and Experimental Neuropsychology*, *17*, 44–57.
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*, *129*, 564-583.
- Cave, C. B., Squire, L.R. (1992). Intact and long-lasting repetition priming in amnesia. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 18,* 509–520.
- Challis, B.H., & Brodbeck, D.R. (1992). Level of processing affects priming in word fragment completion, *Journal of Experimental Psychology: Learning Memory and Cognition*, *18*, 595–607.
- Chun, M. M. & Jiang, Y. (2003). Implicit, long-term spatial contextual memory. *Journal* of *Experimental Psychology: Learning, Memory and Cognition, 29(2), 224-234.*
- Chun, M. M. & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nature Neuroscience*, *2*, 844-847.

Cohen, N. J..Poldrack, R. A., & Eichenbaum, H. (1997). Memory for items and memory

for relations in the procedural/declarative memory framework. *Memory*, *5*, 131-178.

- Corbetta, M., & Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(*3*), 201-215.
- Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex, *Cerebral Cortex*, 6, 39–49.
- Craik, F. I. M., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior*, 11, 671-684.
- Craik, F. I. M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, 104, 268-294.
- De Goede, M., & Postma, A. (2008). Gender differences in memory for objects and their locations: A study on automatic versus controlled encoding and retrieval contexts. *Brain and Cognition*, *66*(*3*), 232-242.
- Demb, J., Desmond, J., Wagner, A., Vaidya, C., Glover, G. H., & Gabrieli, J. D. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: A functional MRI study of task difficulty and process specificity. *Journal of Neuroscience*, 15(9), 5870-5878.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*,193-222.
- Dienes, Z., & Berry, D. (1997). Implicit learning: Below the subjective threshold. *Psychonomic Bulletin and Review*, *4*, 3-23.
- Doyon, J., Song, A. W., Karni, A., Lalonde, F., Adams, M. M., & Ungerleider, L.,G. (2002). Experience-dependent changes in cerebellar contributions to motor sequence learning. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 1017–1022.
- Duff, E., Xiong, J., Wang, B., Cunnington, R., Fox, P., & Egan, G. (2007). Complex spatio-temporal dynamics of fMRI BOLD: A study of motor learning. *Neuroimage*, *34*(1), 156-168.
- Duncan, J. (1998). Converging levels of analysis in the cognitive neuroscience of visual attention. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 353, 1307-1317
- Düzel, E., Habib, R., Rotte, M., Guderian, S., Tulving, E., & Heinze, H.J. (2003). Human hippocampal and parahippocampal activity during visual associative recognition

memory for spatial and non-spatial stimulus configurations. *Journal of Neuroscience*, 23, 9439 -9444.

- Eldridge, L. L., Knowlton, B. J., Furmanski, C., S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neuroscience*, *3*(*11*), 1149-1152.
- Ellis, N. R. (1990). Is memory for spatial location automatically encoded? *Memory and Cognition*, *18*(6), 584-592.
- Exner, C., Weniger, G., & Irle, E. (2001). Implicit and explicit memory after focal thalamic lesions. *Neurology*, *57*, 2054-2063.
- Ferraro, F., Balota, D. A., & Connor, L. T. (1993). Implicit memory and the formation of new associations in nondemented Parkinson's disease individuals and individuals with senile dementia of the Alzheimer type: a serial reaction time investigation. *Brain and Cognition*, 21, 163–180.
- Fincham, J. M., Carter, C. S., van Veen, V., Stenger, V. A., & Anderson, J. R. (2002). Neural mechanisms of planning: a computational analysis using event-related fMRI. Proceedings of the National Academy of Sciences of the United States of America, 99, 3346-3351.
- Frith, C. D., Friston, K. J., Liddle, P. F., & Frackowiak, R. S. (1991). A PET study of word finding. *Neuropsychologia*, *29*,1137-1148.
- Gabrieli, J. D. (1998). Cognitive neuroscience of human memory. *Annual Review of Psychology*, 49, 87-115.
- Gazzaniga, M.S., Ivry, R.B., & Mangun, G.R. (2002). *Cognitive Neuroscience: the Biology of the Mind*, 2nd edition. W W Norton & Company: New York.
- Graf, P. & Schacter, D. L. (1985). Implicit and Explicit Memory for New Associations in Normal and Amnesic Subjects. *Journal of Experimental Psychology: Learning*, *Memory*, & Cognition, 11(3), 501-518.
- Graf, P., & Mandler, G. (1984). Activation makes words more accessible, but not necessarily more retrievable. *Journal of Verbal Learning and Verbal Behavior*, 23, 553-568.
- Graf, P., Squire, L. R., & Mandler, G. (1984). The information that amnesic patients do not forget. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10, 164–178.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*, 14-23.

- Gusnard, D.A., & Raichle, M. E. (2001). Searching for a baseline: functional imaging and the resting human brain. *Nature Reviews Neuroscience*, *2*, 685-694.
- Habeck, C., Rakitin, B.C., Moeller, J., Scarmeas, N., Zarahn, E., Brown, T., et al. (2005).
 An event-related fMRI study of the neural networks underlying the encoding, maintenance, and retrieval phase in a delayed-match-to-sample task. *Cognitive Brain Research*, 23, 207-220.
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, *108*(3), 356-388.
- Hawley, K. J. & Johnston, W. A. (1991). Long-term perceptual memory for briefly exposed words as a function of awareness and attention. *Journal of Experimental Psychology: Human Perception Performance*, *17*, 807-815.
- Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., et al. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Science*, 88, 1621-1652.
- Henson, R. N. A. (2003). Neuroimaging studies of priming. Progress *in Neurobiology*, *70*, 53-81.
- Henson, R. N. A., Rugg, M. D., Shalice, T., Josephs, O., & Dolan, R. J. (1999).
 Recollection and familiarity in recognition memory: An eventrelated functional magnetic resonance imaging study. *Journal of Neuroscience*, *19*, 3962–3972.
- Henson, R. N. A., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*, 1269–1272.
- Hintzman, D. L. (1986). "Schema abstraction" in a multiple-trace memory model. *Psychological Review*, *93(4)*, 411-428.
- Hornak, J. P. (1996). The Basics of MRI. Retrieved on October 2, 2008, from Web site: <u>http://www.cis.rit.edu/htbooks/mri/gloss.htm</u>
- Jacoby, L. L. (1983). Perceptual enhancement: persistent effects of an experience. Journal of Experimental Psychology: Learning, Memory and Cognition, 9, 21-38.
- Jacoby, L. L. & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General*, *110*, 306-334.
- Jacoby, L. L., Toth, J. P., Yonelinas, A. P., & Debner, J. A. (1994). The relationship between conscious and unconscious influences: Independence or redundancy? *Journal of Experimental Psychology: General*, *123(2)*, 216-219.

- Jenkinson, M., & Smith S. (2001). A Global Optimisation Method for Robust Affine Registration of Brain Images. *Medical Image Analysis*, *5*, 143-156.
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimisation for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*, 825-841.
- Jernigan, T. L. & Ostergaard, A. L. (1993). Word priming and recognition memory are both affected by mesial temporal lobe damage. *Neuropsychology*, *7*, 14–26.
- Johnson, J. D., & Rugg, M. D. (2007). Recollection and the Reinstatement of Encoding-Related Cortical Activity. *Cerebral Cortex*, *17(11)*, 2507-2515.
- Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. *Journal of Neuroscience*, 28, 4172–4180.
- Kastner, S., & Ungerleider, L. G. (2002). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*, 1263-1276.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22, 751-761.
- Kensinger, E. A., Clarke, R., J., & Corkin, S. (2003). What Neural Correlates Underlie Successful Encoding and Retrieval? A Functional Magnetic Resonance Imaging Study Using a Divided Attention Paradigm. *Journal of Neuroscience*, 23(6), 2407-2415.
- Kinder, A. & Shanks, D. R. (2003). Neuropsychological dissociations between priming and recognition: A single-system connectionist account. *Psychological Review*, *110*, 728-744.
- Kinder, A., & Shanks, D.R. (2001). Amnesia and the declarative/nondeclarative distinction: A recurrent network model of classification, recognition, and repetition priming. *Journal of Cognitive Neuroscience*, 13, 648–669.
- Kinoshita, S. (2001). The role of involuntary aware memory in the implicit stem and fragment completion tasks: a selective review. *Psychonomic Bulletin and Review*, *8*(1), 58-69.
- Knowlton, B. J., & Squire, L. R. (1994). The information acquired during artificial grammar learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 20*, 79-91.
- Köhler, S., Moscovitch, M., Winocur, G., Houle, S., & McIntosh, A.R. (1998). Networks of domain-specific and general regions involved in episodic memory for spatial

location and object identity. *Neuropsychologia*, 36(2), 129-42.

- Koutstaal, W.; Wagner, A. D.; Rotte, M.; Maril, A.; Buckner, R. L. & Schacter, D. L. (2001). Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, 39, 184-199.
- Lepsien, J. & Nobre, A. C. (2007). Attentional Modulation of Object Representations in Working Memory. *Cerebral Cortex*, *17*(9), 2072-2083.
- Lewicki, P. (1986). Processing information about covariations that cannot be articulated. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 12,* 135-146.
- Lockhart, R. S., & Craik, F. I. M. (1990). Levels of processing: A retrospective commentary on a framework for memory research. *Canadian Journal of Psychology*, *44*, 87-112.
- Luks, T. L., Sun, F. T., Dale, C. L., Miller, W. L., & Simpson, G. V. (2008). Transient and sustained brain activity during anticipatory visuospatial attention. *Neuroreport*, *19*(*2*), 155-159.
- Lustig, C. & Hasher, L. (2001). Implicit memory is not immune to interference. *Psychological Bulletin*, *127*(5), 629-650.
- Mace, J. H. (2003a). Involuntary aware memory enhances priming on a conceptual implicit memory task. *American Journal of Psychology*, *116*, 281-290.
- Mace, J. H. (2003b). Study-test awareness can enhance priming on an implicit memory task: evidence from a word completion task. *American Journal of Psychology*, *116(2)*, 257-279.
- Maljkovic, V. & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory* & *Cognition*, *22(6)*, 657-672.
- Maljkovic, V. & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, *58*(*7*), 977-991.
- Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, *87*, 252–271.
- Mandler, J. M., Seegmiller, D., & Day, J. (1977). On the coding of spatial information. *Memory & Cognition*, *5*, 10-16.
- McKiernan, K. A., Kaufman, J. N., Kucera-Thompson, J., & Binder, J. R. (2003). A parametric manipulation of factors affecting task-induced deactivation in functional neuroimaging. *Journal of Cognitive Neuroscience*, *15*, 394-408.

- McKone, E. & Dennis, C. (2000). Short-term implicit memory: visual, auditory, and cross-modality priming. *Psychonomic Bulletin Review*, *7*, 341-346.
- McKoon, G., & Ratcliff, R. (1996). Separating implicit from explicit retrieval processes in perceptual identification. *Consciousness and Cognition: An International Journal*, *5*(4), 500-511.
- Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., & Mazoyer B. Functional anatomy of spatial mental imagery generated from verbal instructions. *Journal of Neuroscience*, *16(20)*, 6504-6512.
- Mitchell, D. B., & Brown, A. S. (1988). Persistent repetition priming in picture naming and its dissociation from recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 14(2), 213-222.*
- Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning & Verbal Behavior*, *16*(5), 519-533.
- Mulligan, N. W., Guyer, P. S., & Beland, A. (1999). The effects of levels-of-processing and organization on conceptual implicit memory in the category examplar production test. *Memory & Cognition*, *27*(*4*), 633-647.
- Musen, G. (1996). Effects of task demands on implicit memory for object-location associations. *Canadian Journal of Experimental Psychology*, *50*, 104-111.
- Nadel, L., Samsonovich, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory: computational, neuroimaging, and neuropsychological results. *Hippocampus*, *10*(*4*), 352-368.
- Naveh-Benjamin, M. (1987). Coding of spatial location information: an automatic process? *Journal of Experimental Psychology: Learning, Memory and Cognition, 13*, 595-605.
- Norman, K.A. & O'Reilly, R.C. (2003). Modeling Hippocampal and Neocortical Contributions to Recognition Memory: A Complementary Learning Systems Approach. *Psychological Review*, *110*, 611-646.
- Nyberg, L., Habib, R., McIntosh, A.R., & Tulving E. (2000). Reactivation of encodingrelated brain activity during memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(20), 11120-11124.
- Nyberg, L., McIntosh, A. R., Houle, S. Nilsson, L. G., & Tulving, E. (1996). Activation of medial temporal structures during episodic memory retrieval. *Nature*, *380*(6576), 715-717.

Nyberg, L., Petersson, K. M., Nilsson, L. G., Sandblom, J., Aberg, C., & Ingvar, M.

(2001). Reactivation of motor brain areas during explicit memory for actions. *Neuroimage*, *14*, 521–528.

- Ogiso, T., Kobayashi, K., & Sugishita, M. (2000). The precuneus in motor imagery: a magnetoencephalographic study. *Neuroreport*, *11(6)*, 1345-1349.
- Ostergaard, A. L. (1999). Priming deficits in amnesia: now you see them, now you don't. *Journal of the International Neuropsychological Society*, 5, 175-190.
- Persson, J., & Nyberg, L. (2000). Conjunction analyses of cortical activations common to encoding and retrieval. *Microscopy Research and Technique*, *51*, 39–44.
- Ploner, C. J., Gaymard, B. M., Rivaud-Pechoux, S., Baulac, M., Clemenceau, S., Samson, S. et al. (2000). Lesions affecting the parahippocampal cortex yield spatial memory deficits in humans. *Cerebral Cortex*, *10(12)*, 1211-1216.
- Poldrack, R. A. (1996). On testing for stochastic dissociations. *Psychonomic Bulletin & Review*, *3*, 434-448.
- Poldrack, R. A. & Foerde, K. (2008). Category learning and the memory systems debate. *Neuroscience & Biobehavioral Reviews*, 2, 197-205.
- Ratcliff, R. & McKoon, G. (1988). A retrieval theory of priming in memory. *Psychological Review*, *95*, 385-408.
- Ratcliff, R. & McKoon, G. (2000). Modeling the effects of repetition and word frequency in perceptual identification. *Psychonomic Bulletin and Review*, *7*, 713-717.
- Reiss, J. P., Campbell, D. W., Leslie, W. D., Paulus, M. P., Stroman, P. W., Polimeni, J. O., et al (2005). The role of the striatum in implicit learning: a functional magnetic resonance imaging study. *Neuroreport*, *16*,1291-1295.
- Ress, D., Backus, B. T., & Heeger, D. J. (2003). Activity in primary visual cortex predicts performance in a visual detection task. *Nature Neuroscience*, *3*, 940-945.
- Richardson-Klavehn, A. & Gardiner, J. M. (1995). Retrieval volition and memorial awareness in stem completion: an empirical analysis. *Psychological Research*, 57, 166-178.
- Richardson-Klavehn, A. & Gardiner, J. M. (1998). Depth-of-processing effects on priming in stem completion: tests of the voluntary-contamination, conceptualprocessing, and lexical-processing hypotheses. *Journal of Experimental Psychology: Learning, Memory and Cognition, 24*, 593-609.
- Richardson-Klavehn, A., & Gardiner, J. M. (1996). Cross-modality priming in stem completion reflects conscious memory, but not voluntary memory. *Psychonomic Bulletin and Review*, *3*, 238–244.

- Richardson-Klavehn, A., Gardiner, J. M., & Java, R. I. (1996). Memory: Task dissociations, process dissociations, and dissociations of consciousness. In G. Underwood (Eds.), *Implicit cognition* (pp. 85–158). Oxford University Press.
- Richardson-Klavehn, A., Lee, M. G., Joubran, R. & Bjork, R. A. (1994). Intention and awareness in perceptual identification priming. *Memory and Cognition*, 22(3), 293-312.
- Roediger, H. L. (1990). Implicit memory. Retention without remembering. *American Psychologist*, 45, 1043-1056.
- Roediger, H. L. & McDermott, K. B. (1993). Implicit memory in normal human subjects. In H. Spinnler & F. Boller (Eds.), *Handbook of Neuropsychology* (pp. 63-131). Amsterdam: Elsevier.
- Roediger, H. L., Blaxton, T. A. (1987). Effects of varying modality, surface features, and retention interval on priming in word-fragment completion. *Memory and Cognition*, 15(5), 379-388.
- Rose, M., Schmid, C., Winzen, A., Sommer, T., & Buchel, C. (2005). The functional and temporal characteristics of top-down modulation in visual selection. *Cerebral Cortex*, 15(9), 1290-1298.
- Rossell, S. L., Bullmore, E. T., Williams, S. C., & David, A. S. (2001). Brain activation during automatic and controlled processing of semantic relations: A priming experiment using lexical-decision. *Neuropsychologia*, *39*, 1167–1176.
- Rouder, J. N., Ratcliff, R. & McKoon, G. (2000). A neural network model of implicit memory for object recognition. *Psychological Science*, *11*, 13-19.
- Sala, J. B., Rama, P., & Courtney, S. M. (2003). Functional topography of a distributed neural system for spatial and nonspatial information maintenance in working memory. *Neuropsychologia*, 41(3), 341-56.
- Sayres, R., & Grill-Spector, K. (2006). Object-selective cortex exhibits Performance-Independent Repetition Suppression. *Journal of Neurophysiology*, *95(2)*, 995-1007.
- Schacter, D. L., & Buckner, R. L. (1998). On the relations among priming, conscious recollection, and intentional retrieval: evidence from neuroimaging research. *Neurobiology of Learning and Memory*, *70*(1-2), 284-303.
- Schacter, D. L., & Tulving, E. (Eds.). (1994). *Memory systems* 1994. Cambridge, MA: MIT Press.
- Schacter, D. L., Bowers, J., & Booker, J. (1989). Intention, awareness, and implicit memory: The retrieval intentionality criterion. In S. Lewandovsky, J. C. Dunn, &

K. Kirsner (Eds.), *Implicit memory: Theoretical issues* (pp. 47–66). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

- Schacter, D. L., Dobbins, I. G., & Schnyer, D. M. (2004). Specificity of priming: a cognitive neuroscience perspective. *Nature Reviews Neuroscience*, *5*, 853-862.
- Schacter, D.L., Alpert, N.M., Savage, C.R., Rauch, S.L., & Albert, M.S. (1996). Conscious recollection and the human hippocampal formation: Evidence from positron emission tomography. *Proceedings of the National Academy of Sciences*, 93, 321-325.
- Schott, B. H., Henson, R. N., Richardson-Klavehn, A.; Becker, C.; Thoma, V.; Heinze, H. & Düzel, E. (2005). Redefining implicit and explicit memory: the functional neuroanatomy of priming, remembering, and control of retrieval. *Proceedings of the National Academy of Sciences*, *102*, 1257-1262.
- Schott, B.H., Richardson-Klavehn, A., Henson, R.N., Becker, C., Heinze, H.J., & Duzel, E. (2006). Neuroanatomical dissociation of encoding processes related to priming and explicit memory. *Journal of Neuroscience*, *26*(3), 792-800.
- Shanks, D.R., Wilkinson, L., & Channon, S. (2003). Relationship between priming and recognition in deterministic and probabilistic sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29, 248–261.*
- Shmuel, A., Yacoub E., Pfeuffer, J., Van de Moortele, P. F., Adriany, G., Hu, X., et al. (2002). Sustained negative BOLD, blood flow and oxygen consumption response and its coupling to the positive response in the human brain. *Neuron*, 36,1195-1210.
- Shrager, Y., Bayley, P. J., Bontempi, B., Hopkins, R. O., & Squire, L. R. (2007). Spatial memory and the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, 104(8), 2961-2966.
- Skinner, E. I., & Fernandes, M. A. (2007). Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia*, 45(10), 2163-2179.
- Slotnick, S. D. (2004). Visual Memory and Visual Perception Recruit Common Neural Substrates. *Behavioral and Cognitive Neuroscience Reviews*, *3*, 207-221.
- Smith, M.L., & Milner, B. (1989). Right hippocampal impairment in the recall of spatial location: encoding deficit or rapid forgetting? *Neuropsychologia*, *27*(1), 71–81.
- Smith, S. (2002). Fast Robust Automated Brain Extraction. *Human Brain Mapping*, *17*, 143-155.

Snodgrass, J. G. & Hirshman, E. (1994). Dissociations among implicit and explicit

memory tasks: the role of stimulus similarity. *Journal of Experimental Psychology: Learning, Memory and Cognition, 20,* 150-160

- Sommer, T., Rose, M., Glascher, J., Wolbers, T., & Buchel C. (2005). Dissociable contributions within the medial temporal lobe to encoding of object-location associations. *Learning & Memory*, *12*(*3*), 343-351.
- Stark, C. E. L., & McClelland, J. L. (2000). Repetition priming of words, pseudowords, and nonwords. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 26, 945-972.
- Sternberg, S. (1998). Inferring mental operations from reaction-time data: How we compare objects. In D. Scarborough & S. Sternberg (Eds), *Methods, models, and conceptual issues: An invitation to cognitive science* (pp. 365-454). Cambridge, MA, US: The MIT Press.
- Thiel A., Haupt, W. F., Habedank, B., Winhuisen, L., Herholz, K., Kessler, J., Markowitsch, H. J., & Heiss, W. D. (2005). Neuroimaging-guided rTMS of the left inferior frontal gyrus interferes with repetition priming. *Neuroimage*, 25, 815-823.
- Tomasi, D., Ernst, T., Caparelli, E. C, Chang, L. (2006). Common deactivation patterns during working memory and visual attention tasks: An intra-subject fMRI study at 4 Tesla. *Human Brain Mapping*, *27*, 2006.
- Tulving, E. (1985). How many memory systems are there? *The American psychologist*, *40*, 385-398.
- Tulving, E. & Schacter, D. L. (1990). Priming and human memory systems. *Science*, 247(4940), 301-306.
- Turk-Browne, N. B., Yi, D. & Chun, M. M. (2006). Linking implicit and explicit memory: common encoding factors and shared representations. *Neuron*, 49, 917-927.
- Ungerleider, L. G. & Mishkin, M. (1982). Two cortical visual systems. In D.J. Ingle, M. A. Goodale & R. J. W. Mansfield (Eds). *Analysis of Visual Behavior* (pp. 549-586). Cambridge, MA: MIT Press.
- Vaidya, C. J., Zhao, M., Desmond, J. E., & Gabrieli, J. D. (2002). Evidence for cortical encoding specificity in episodic memory: memory-induced re-activation of picture processing areas. *Neuropsychologia*, *40*(*12*), 2136-2143.
- Vaidya, C.J., Gabrieli, J.D.E., Keane, M. M., and Monti, L.A. (1995). Perceptual and conceptual memory processes in global amnesia. *Neuropsychology*, *9*, 580-591.

Verfaellie, M., Gabrieli, J.D.E., Vaidya, C.J., Croce, P., and Reminger, S.L. (1996).

Implicit memory for pictures in amnesia: Role of etiology and priming task. *Neuropsychology*, *10*, 517-528.

- Vogt, B. A., Vogt, L., & Laureys, S. (2006). Cytology and functionally correlated circuits of human posterior cingulate areas. *Neuroimage*, *29*(*2*), 452-466.
- Wagner, A. D., Desmond, J. E., Demb, J. B., Glover, G. H., &. Gabrieli, J. D. E. (1997). Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. *Journal of Cognitive Neuroscience*, 9, 714–726.
- Wagner, A. D., Koutstaal, W., Maril, A., Schacter, D. L., & Buckner, R. L. (2000). Task-specific repetition priming in left inferior prefrontal cortex. *Cerebral Cortex*, 10, 1176-1184.
- Walla, P., Lehrner, J. P., Nasel, C., Baumgartner, C., Deecke, L., & Lang, W. (2003). Preserved memory traces within diencephalic amnesia. *Journal of Neural Transmission*, 110, 537-54.
- Warrington, E. K. & Weiskrantz, L. (1970). Amnesic syndrome: Consolidation or retrieval? *Nature*, *228*, 628-630.
- Weldon, M. S. & Roediger, H. L. (1987). Altering retrieval demands reverses the picture superiority effect. *Memory and Cognition*, *15*, 269-280.
- Wheeler, M. E., Shulman, G. L., Buckner, R. L., Miezin, F. M., Velanova, K., Petersen, S. E. (2006). Evidence for separate perceptual reactivation and search processes during remembering. *Cerebral Cortex*, *16*, 949–959.
- Wheeler, M., Petersen, S., & Buckner, R. (2000). Memory's echo: vivid remembering reactivates sensory-specific cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(20), 1125-1129.
- Whittlesea, B. W. A., & Price, J. R. (2001). Implicit/explicit memory versus analytic/nonanalytic processing: Rethinking the mere exposure effect. *Memory* and Cognition, 29(2), 234-246.
- Wig, G. S., Grafton, S. T., Demos, K. E., & Kelley, W. M. (2005). Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience*, *8*, 1228-1233.
- Wiggs, C. L. & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinions in Neurobiology*, *8*, 227-233.
- Willingham, D. B. (1997). Implicit and explicit memory do not differ in flexibility: Comment on Dienes & Berry, 1997. *Psychonomic Bulletin and Review*, 4, 587-591

Willingham, D. B., & Goedert-Eschmann, K. (1999). The relation between implicit and

explicit learning: Evidence for parallel development. *Psychological Science*, *10*(6), 531-534.

- Willingham, D. B., & Koroshetz, W. J. (1993). Evidence for dissociable motor skills in Huntington's disease patients. *Psychobiology*, *21*(3), 173-182.
- Witherspoon, D., & Moscovitch, M. (1989). Stochastic independence between two implicit memory tasks. *Journal of Experimental Psychology: Learning, Memory,* & Cognition, 15(1), 22-30.
- Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Contentspecificity of the neural correlates of recollection. *Neuropsychologia*, 43, 1022– 1032.
- Worsley, K. J. (2001). Statistical analysis of activation images. In P. Jezzard, P.M. Matthews and S.M. Smith (Eds.), *Functional MRI: An Introduction to Methods* (pp. 251-270). OUP.
- Zago, L., Fenske, M. J., Aminoff, E., & Bar, M. (2005). The rise and fall of priming: how visual exposure shapes cortical representations of objects. *Cerebral Cortex*, *15(11)*, 1655-1665.

APPENDIX A: TABLES

Table 1

Mean search RT for primed objects and foils on the first repetition trial and on the last repetition trial

		Primed	objects		Foils				
Group	First repetition		Last rep	Last repetition		First repetition		Last repetition	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Incidental learning	922.08*	250.07	476.69	168.77	1148.31	246.82	955.09	128.44	
Intentional learning	613.07	197.26	393.69	119.55	1001.82	110.68	1017.42	187.59	

Note. * a significant between-group's difference.

	Pairs of trials						
Group	Primed vs. Foils	Primed vs. Unprimed	Primed vs. New	Foils vs. Unprimed foils	Foils vs. New		
Incidental learning, explication	0.004*	0.38	0.141	0.947	0.048**		
Intentional learning, explication	< 0.001 *	< 0.001 *	< 0.001 *	0.033*	0.345		

Experiment 1: p-values for the paired t-test on different types of trials

Note. * The trial mentioned first in the comparison pair is faster than the trial mention second in the comparison pair. ** the trial mentioned first in the comparison pair is slower than the trial mention second in the comparison pair. Bold font means that the differences are significant.

Group	Hits (%	6)	False a (%)	alarms	Correc hits (Hits-F	eted FA)	Object (%)	recall	Recall confide (%)	ence
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Free recall before the Search Task									
Incidental learning	0.17	0.13	0.01	0.01	0.16	0.13	0.21	0.18	0.48	0.39
Intentional learning	0.56	0.25	0.02	0.02	0.55	0.25	0.59	0.24	1.55	0.76
			F	ree reca	all after	the Sea	arch Tas	sk		
Incidental learning	0.69	0.24	0.02	0.02	0.67	0.24	0.73	0.22	1.96	0.66
Intentional learning	0.74	0.28	0.03	0.04	0.71	0.29	0.85	0.16	2.14	0.68

Subjects' performance on the free recall task administered before the Search Task (right after the Object Detection task) and after the Search Task: Primed stimuli

Group	Hits (%	%)	False a (%)	alarms	Correc hits (Hits-I	cted FA)	Object (%)	t recall	Recall confid (%)	ence
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
		Free recall before the Search Task					ask			
Incidental learning	0.08	0.05	0.03	0.02	0.04	0.05	0.41	0.11	0.83	0.35
Intentional learning	0.17	0.09	0.04	0.02	0.13	0.08	0.45	0.14	0.97	0.33
			I	Free rec	all after	the Sea	arch Ta	sk		
Incidental learning	0.14	0.08	0.04	0.02	0.1	0.07	0.65	0.2	1.47	0.5
Intentional learning	0.16	0.08	0.04	0.04	0.12	0.09	0.64	0.16	1.53	0.42

Subjects' performance on the free recall task administered before the Search Task (right after the Object Detection task) and after the Search Task: Foils

		Primed stimuli		Foil	S
Group	Ν	Mean	SD	Mean	SD
Control group	14	1068.6	226.1	1039.05	134.4
Incidental learning, study-test unaware	20	1086.68	262.18	1226.35	158.14
Incidental learning, study-test aware	17	882.55	323.6	1092.53	223.69
Intentional learning, study-test unaware	20	806.31	232.44	1019.17	152.38
Intentional learning, study-test aware	15	520.96	167.72	967.9	160.8

Search RT for the primed stimuli and for the foils on the first repetition trial

	Pairs of trials						
Group	Primed vs. Foils	Primed vs. Unprimed	Primed vs. New	Foils vs. Unprimed foils	Foils vs. New		
Control group	0.53	0.32	0.03**	0.125	0.02**		
Incidental learning, study-test unaware	0.008*	0.33	0.44	0.003**	< 0.001**		
Incidental learning, study-test aware	0.007*	0.006*	0.01 [*]	0.79	0.49		
Intentional learning, study-test unaware	0.002*	< 0.001 *	0.003*	0.22	0.70		
Intentional learning, study-test aware	< 0.001 *	< 0.001 *	< 0.001 *	0.86	0.116		

Experiment 2: p-values for the paired t-test on different types of trials

Note. * The trial mentioned first in the comparison pair is faster than the trial mention second in the comparison pair. ** the trial mentioned first in the comparison pair is slower than the trial mention second in the comparison pair. **Bold** font means that the differences are significant.

Cross-validation of LDA (%): four groups

			Predicted group					
		1	2	3	4			
Original	1	21.43	57.14	7.14	14.29	100		
	2	11.76	44.12	35.29	8.82	100		
group	3	0	21.62	59.46	18.92	100		
	4	0	7.14	32.14	60.71	100		

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Table 8Cross-validation of LDA (%): three groups

		Pre		Total%	
		1	2	3	
-	1	70.83	20.83	8.33	100
Original	2	24.32	54.05	21.62	100
group	3	7.14	32.14	60.71	100

Group	Hits		False Aları	ms	d-prime			
	Mean	SD	Mean	SD	Mean	SD		
			Old stimuli	recognition				
Incidental learning	0.79*	0.14	0.20*	0.20	2.10*	0.87		
Intentional learning	0.96	0.05	0.06	0.12	3.75	0.93		
	Primed stimuli recognition (subjects placed an object in the single location either correct or incorrect)							
Incidental learning	0.43	0.18	0.22*	0.16	0.68*	0.48		
Intentional learning	0.58	0.29	0.11	0.13	1.81	1.26		
	Foils reco	gnition (subj e	ects placed a either correct	an object in a t or incorrect	more than or :)	ne location		
Incidental learning	0.49*	0.22	0.17	0.12	1.00*	0.44		
Intentional learning	0.75	0.25	0.16	0.12	2.15	1.04		

Recognition of the old stimuli, primed stimuli and foils during the cued recall test (accuracy of chosen locations is not taken into consideration)

Note. * significant differences between the incidental learning group of subjects and the intentional learning group of subjects.

	Pı	rimed stir	nuli		Foils			
Group	High confidence responses		Low confidence responses		High confidence responses		Low confidence responses	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Incidental learning	0.15*	0.14	0.31*	0.21	0.14*	0.07	0.16*	0.06
Intentional learning	0.45	0.32	0.72	0.30	0.25	0.11	0.28	0.10

Mean ACC of cued recall of spatial locations for primed objects and foils as a function of *learning condition*.

Note. * significant differences between the incidental learning group of subjects and the intentional learning group of subjects.

Table 11*RT* for high confidence recall of object locations

Group	Primed	stimuli	Foils		
-	MEAN	SD	MEAN	SD	
Incidental learning	792.38	239.32	815.49	281.60	
Intentional learning	703.15	144.94	789.71	186.60	

Correlation between frequency of stimuli presentation during the Object Detection task and accuracy of recall for locations during the cued recall task

Group	Ν	Primed objects	Foils						
Incidental learning	144	0.17*	0.47**						
Intentional learning	152	0.16^	0.54**						
<i>Note</i> . ^ p < 0.1, * p < 0.05, ** p < 0.001									

Group		Primed	l	Foils]	New		
	Mean	SD	Mean	SD	Mean	SD		
Control	1405.19	303.93	1241.06	157.94	1480.56	401.04		
Study-test unaware	1403.75	335.09	1313.69	343.00	1160.88	142.70		
Study-test aware	1133.22	220.97	1218.22	185.68	1286.50	203.4		

Subjects' RT on the first search trial for the primed stimuli, foils and new stimuli

Brian regions showing chang	ges in neural activity for t	he last repetition trial of primed
stimuli compared to the rest l	baseline in the Object Det	tection task

	Brain region	Voxels	х	у	Z	Z-max	Р			
	Last repetition > Rest									
Right	MFG/ precentral	257	38	-1	55	4.82	0.016			
Left	SFG	129	-22	22	58	4.73	0.027			
Left	Frontal pole	401	-34	63	7	5.35	0.010			
Left	Postcentral gyrus/ SPL	303	-46	-38	57	4.97	0.014			
Left	LOC/ SPL	1645	-25	-64	56	6.01	< 0.001			
Left	Occipital pole	24360	-7	-92	-5	10.4	< 0.001			
		Last rep	etitior	ı < Re	st					
Right	Postcentral gyrus/ precuneus	2085	17	-44	53	5.16	<0.001			
Right	Posterior cingulate cortex	984	9	-22	46	5.26	0.00216			
Right	Central and parietal opercular cortices (extending to insula)	3950	41	-12	19	5.66	<0.001			
Right	Cuneus (bilateral)	38382	14	-76	26	9.26	< 0.001			
Right	Occipital pole/ LOC, inferior devision	323	36	-94	-7	5.35	0.0129			
Left	Postcenral gyrus	635	-16	-38	52	5.01	0.00514			
Left	Precuneus	98	-5	-54	52	4.54	0.0313			

Bria	in regions	showing	changes	in neural	activity	for the	last re	epetition t	rial c	compare	d to
the f	first repeti	tion trial	in the Ol	oject Dete	ection tas	sk					

	Brain Area	Voxels	Х	У	Z	Z-max	Р			
First repetition > Last repetition										
Right	superior devision of LOC	126	25	-92	26	4.70	0.028			
Left	Cuneus, Occipital pole	3632	-4	-88	29	6.06	< 0.001			
	Last repe	tition > F	'irst re	epetiti	on					
Right	anterior devision of supramarginal gyrus	2032	42	-34	37	5.32	<0.001			
Right	SPL	1148	24	-45	63	5.86	0.001			
Left	Putamen	96	-21	2	10	4.51	0.032			

	Brain Region	Voxels	х	у	Z	Z-max	Р				
Control _(Primed>Rest)											
Right	SFG	109	14	3	73	4.89	0.029				
Right	Precentral/MFG	4292	30	-6	53	8.44	< 0.001				
Right	Precentral/IFG	65	59	16	29	4.66	0.037				
Left	Precentral gyrus	23938	-32	-9	56	13.90	< 0.001				
Left	Precentral gyrus	1082	-55	4	30	5.97	0.002				
Left	Suplementary motor cortex	3663	-3	5	50	6.98	< 0.001				
Left	Occipital pole	141018	-12	-101	5	15.10	< 0.001				
Left	Thalamus	598	-13	-21	6	5.87	0.006				
Control _{(Primed<rest)< sub=""></rest)<>}											
Right	Precuneus/posterior cingulate	419477	9	-53	33	12.00	<0.001				
Left	Cerebellum	605	-16	-47	-45	5.35	0.006				

BOLD signal change in the control group of subjects: primed stimuli

	Brain Region	Voxels	Х	У	Z	Z-max	Р				
Study-test unaware _(Primed>Rest)											
Right	SFG	6789	27	-1	62	7.86	< 0.001				
Right	Suplementary motor cortex	59	9	6	65	4.65	0.040				
Left	Frontal pole	149	-24	62	-11	5.23	0.025				
Left	Precentral gyrus	18361	-40	-10	60	10.10	< 0.001				
Left	Paracingulate gyrus	2680	-1	12	48	7.51	< 0.001				
Left	Insular cortex/Orbitofrontal cortex	65	-33	24	-2	4.63	0.039				
Left	Lingual gyrus	13185 5	-4	-87	-6	16.40	<0.001				
Left	Putamen	62	-24	1	-1	4.50	0.039				
	Study-te	est unawa	re _{(Prin}	ned <re< td=""><td>st)</td><td></td><td></td></re<>	st)						
Right	Paracingulate gyrus/ medial frontal cortex	39047	14	41	-9	8.66	<0.001				
Right	Planum temporale/STG	39336	62	-32	16	7.52	< 0.001				
Right	Precuneus	12864 4	10	-54	26	10.90	<0.001				
Right	supramarginal gyrus, anterior devision	68	66	-29	38	4.51	0.038				
Right	LOC, superior devision	743	51	-69	35	5.35	0.004				
Left	frontal pole/IFG	428	-36	40	13	5.27	0.009				
Left	Angular gyrus	469	-40	-55	32	5.44	0.008				

BOLD signal change in in study-test unaware subjects : primed stimuli

	Brain Region	Voxels	X	у	Z	Z-max	Р				
	Study-test aware _(Primed>Rest)										
Right	MFG/precentral	919	46	11	31	5.36	0.002				
Right	Thalamus	147	10	-14	10	4.75	0.025				
Left	MFG/precentral	51399	-31	-5	58	13.20	< 0.001				
Left	Insular/frontal orbital cortex	154	-33	23	0	5.06	0.025				
Left	Frontal pole	340	-35	54	24	6.09	0.012				
Left	Occipitall pole	17186 9	-15	-98	11	19.80	<0.001				
Left	Left Thalamus	1242	-11	-17	6	6.40	0.001				
Study-test unaware (Primed <rest)< td=""></rest)<>											
Right	Paracingulate/ frontal medial cortex	42459 8	7	48	-7	11.10	<0.001				
Left	Cerebellum	352	-17	-71	-41	4.94	0.011				

BOLD signal change in in study-test aware subjects : primed stimuli

Study-test aware vs. study-test unaware subjects: the first repetition of **primed** stimuli

	Brain Region	Voxels	х	у	Z	Z-max	Р			
Study-test unaware _(Primed>Rest) > Study-test aware _(Primed>Rest)										
Right	Middle temporal gyrus, temporooccipital part,	94	67	-46	10	4.86	0.033			
Right	Middle temporal gyrus, anterior part	83	57	2	-32	4.55	0.035			
Left	IFG	493	-49	41	2	5.09	0.007			
Study-test aware _(Primed>Rest) > Study-test unaware _(Primed>Rest)										
Right	MFG	877	33	0	43	5.95	0.003			
Right	Superior devision of lateral occipital complex, SPL	1862	19	-64	65	6.51	<0.001			
Right	Precuneus	162	8	-71	34	4.55	0.024			
Right	Occipital pole, MOG	1298	25	-96	21	8.31	< 0.001			
Right	Thalamus (dorso- medial nucleus)	132	13	-18	10	4.72	0.027			
Left	MFG	410	-33	0	42	5.54	0.009			
Left	Precentral gyrus	168	-34	-20	54	4.85	0.023			
Left	Superior devision of lateral occipital complex/ SPL	3159	-20	-62	65	8.72	<0.001			
Left	Occipital pole, MOG	122	-20	-101	14	6.36	0.029			
	Brain Region	Voxels	х	у	Z	Z-max	Р			
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Study-test unaware _(New>Rest) > Study-test aware _(New>Rest)										
Right	Precentral gyrus	1907	41	-10	33	6.52	< 0.001			
Right	Precentral gyrus	277	24	-20	63	5.07	0.015			
Right	Supperior devision of lateral occipital cortex	2521	38	-63	38	6.32	<0.001			
Right	Pallidum	257	25	-7	-4	5.05	0.016			
Right	Cerebellum	218	11	-39	-16	5.10	0.018			
Left	Occipital pole	130	-17	-100	1	5.68	0.026			
Left	Cerebellum	3017	-10	-87	-32	6.02	< 0.001			
Left	Cerebellum	2418	-48	-69	-38	6.90	< 0.001			
Left	Cerebellum	466	-5	-65	-16	5.30	0.010			
Left	Cerebellum	236	-20	-70	-30	4.82	0.017			
Left	Cerebellum	208	-1	-67	-42	4.98	0.019			
Study-test aware _(New>Rest) > Study-test unaware _(New>Rest)										
Right	Precentral gyrus	566	29	-2	43	5.92	0.010			
Right	Superior devision of lateral occipital complex, SPL	4087	18	-61	55	6.62	<0.001			
Right	Temporal occipital fusiform cortex,	3546	22	-60	-14	6.77	<0.001			
Right	Right occipital pole	1871	24	-96	21	7.61	< 0.001			
Left	Superior frontal gyrus	967	-7	13	66	6.14	0.002			
Left	Inferior frontal gyrus,	1407	-49	8	22	6.55	< 0.001			
Left	Precentral	9516	-36	-20	54	7.93	< 0.001			
Left	Frontal orbital cortex	772	-24	34	-8	5.45	0.004			
Left	Superior devision of lateral occipital complex, SPL	3545	-20	-58	59	8.87	<0.001			
Left	Temporal Occipital fusiform cortex	699	-37	-56	-9	5.53	0.004			
Left	Temporal pole, STG	143	-34	15	-38	5.16	0.025			
Left	Cuneus	879	-10	-86	23	5.08	0.003			

Table 20 *Study-test aware vs. study-test unaware subjects: the first repetition of* **new** *stimuli*

Note. All coordinates are in MNI template space (MNI = Montreal Neurological Institute)

Table 21

	Brain Region	Voxels	х	у	Z	Z-max	Р
Study-test unaware _(Variable>Rest) > Study-test aware _(Variable>Rest)							
Right	MFG	748	46	10	-39	5.46	< 0.001
Right	Precentral gyrus	1252	44	-9	34	6.27	< 0.001
Right	LOC superior devision	654	36	-70	44	5.72	0.001
Right	LOC, superior devision	268	12	-75	49	5.33	0.011
Right	MTG, temporooccipital part	147	68	-45	2	5.07	0.027
Right	Lingual gyrus	571	12	-74	-1	5.64	0.002
Left	Precentral gyrus	1217	-47	-3	40	7.67	< 0.001
Left	Frontal pole	1617	-41	47	4	6.27	< 0.001
Left	Posterior cingulate	489	-10	-41	32	5.27	0.003
Left	MTG, temporooccipital part	194	-48	-53	7	5.00	0.019
Left	STG, anterior devision	168	-55	-7	-8	4.78	0.023
Left	SPL/angular gyrus	95	-36	-54	45	4.63	0.043
Left	Precuneus	222	-7	-75	41	5.26	0.015

Study-test aware vs. study-test unaware subjects: the first repetition of foils

Study-test aware_(Variable>Rest) > Study-test unaware_(Variable>Rest)

Right	LOC, superior devision	4897	23	-66	64	6.83	< 0.001
Right	LOC, inferior devision	485	49	-79	-10	5.41	0.003
Right	LOC, inferior devision	168	53	-74	8	5.05	0.023
Right	Occipital pole	2740	27	-96	18	8.66	< 0.001
Left	Precentral gyrus	1970	-36	-19	54	7.59	< 0.001
Left	LOC, superior devision	3091	-20	-58	63	8.83	< 0.001
Left	Occipital pole	301	-25	-97	22	6.27	0.009
Left	Cerebellum	1810	-33	-57	-23	5.50	< 0.001

Note. All coordinates are in MNI template space (MNI = Montreal Neurological Institute)



Figure 1. The summary of the experimental design: Experiment 1.



Figure 2. The design of the Dot Detection task.



Figure 3. The design of the Object Detection task.



Figure 4. The design of the Search task.



Figure 5. Mean RT in the Dot Detection and the Object Detection tasks as a function of learning condition: Experiment 1.



Figure 6. Subjects' performance on the Search task: Experiment 1.

In the word-number labels of the trials, the word part describes trial type, the number part describes repetition. For example, the label "Primed 1" means the first repetition of primed objects. Vertical lines separate different types of trials. Overall, there were five types of trials. Among them are primed objects placed in primed locations (Primed), foils placed in primed locations (Foil), primed objects placed in new locations (Unprimed), foils placed in new locations (Unprimed foil) and new objects (New).



A. Primed stimuli: Before the Search task

B. Primed stimuli: After the Search task



- **C.** Foils: Before the Search task
- **D**. Foils: After the Search task

Figure 7. Search RT for primed objects as a function of recall success in the Free Recall task in the incidental and intentional learning subjects: Experiment 1



Figure 8. Performance on implicit and explicit memory tasks: Primed stimuli. **A.** - RT on the first repetition and the last repetition during the Search task; **B.**- recall of object during the Free Recall tasks administered before the Search task and after the Search task; **C.** - recall of locations during the Free Recall tasks administered before the Search task and after the Search task.



Figure 9. Performance on implicit and explicit memory tasks: Foil stimuli. **A.** - RT on the first repetition and the last repetition during the Search task; **B.**- recall of objects during the Free Recall tasks administered before the Search task and after the Search task; **C.** - recall of locations during the Free Recall tasks administered before the Search task and after the Search task and after the Search task.



Figure 10. The summary of the experimental design: Experiment 2.



Figure 11. Mean RT in the Dot Detection and the Object Detection tasks as a function of learning condition: Experiment 2.



Figure 12. Subjects' performance on the Search task: Experiment 2. In the word-number labels of the trials, the word part describes trial type, the number part describes repetition. For example, the label "Primed 1" means the first repetition of primed objects. Vertical lines separate different types of trials. Overall, there were five types of trials. Among them are primed objects placed in primed locations (Primed), foils placed in primed locations (Foil), primed objects placed in new locations (Unprimed), foils placed in new locations (Unprimed foil) and new objects (New).



A. Primed stimuli

B. Foils

Figure 13. Search RT as a function of learning condition and study-test awareness: Experiment 2.

First presentation of (**A**) primed objects in primed locations and (**B**) foils in primed locations.



Figure 14. Cluster analysis of trial types and repetitions in the Search task. **P** stands for primed stimuli; **F** – for foils; **U** – for unprimed stimuli, **UF** – for unprimed foils; **N** – for new stimuli. The letter means type of the trial. Number means repetition. For example, P1 means the first repetition of primed stimulus.



Figure 15. The design of the Cued Recall task: Experiment 3.



Figure 16. Mean RT in the Dot Detection and the Object Detection tasks as a function of learning condition: Experiment 3.



Figure 17. The z-scores in implicit (Experiment 2) and explicit (Experiment 3) memory tests.

A) Trial design





Figure 18. The summary of the experimental design for the Object Detection task: the fMRI experiment.

A) The structure of a single trial. B) The experimental design. The Dot Detection task had a similar structure and design.

A) Trial design



Figure 19. The summary of the experimental design for the Search task: the fMRI experiment.

A) the structure of a single trial; B) the experimental design.



Figure 20. Subjects' performance on the Search task: The fMRI experiment. In the word-number labels of the trials, the word part describes trial type, the number part describes repetition. For example, the label "Primed 1" means the first repetition of primed objects. Vertical lines separate different types of trials. Overall, there were five types of trials. Among them are primed objects placed in primed locations (Primed), foils placed in primed locations (Foil), primed objects placed in new locations (Unprimed), foils placed in new locations (Unprimed foil) and new objects (New).



Figure 21. Primed stimuli search RT in study-test unaware, study-test aware and control groups of subjects: The fMRI experiment.



Figure 22. Neural responses during the Object Detection task Red color - the brain regions where the last repetition of primed stimuli > Rest; Blue color – the last repetition of primed stimuli < Rest; Pink color– First repetition > Last repetition; Green – Last repetition > First repetition. 1) left frontal pole, 2) left putamen, 3) right parietal operculum cortex; 4) posterior cungulate gyrus, 5) ight angular/supramarginal gyrus, 6) right SPL, 7) left lingual gyrus, 8) bilateral calcarine/precuneal cortex, 9) left LOC, 10) bilateral cuneus, 11) bilateral lingual gyrus/occipital FF cortex.



Figure 23. The fMRI contrasts between study-test aware and study-test unaware subjects Red color – study-test aware subjects > study-test unaware subjects; Blue color - study-test aware subjects < study-test unaware subjects. Small images show conjunction between aware > unaware contrast for primed stimuli, foils and new stimuli. Green color – conjunction between primed stimuli and new stimuli in aware > unaware contrast. Yellow color – conjunction between primed stimuli, new stimuli and foil stimuli in aware > unaware contrast.



Figure 24. The differences in the BOLD signal between study-test aware and study-test unaware subjects in the priming-specific network of regions.



Figure 25. The differences in the BOLD signal between study-test aware and study-test unaware subjects in the awareness-related network of regions.



Figure 26. The differences in the BOLD signal between study-test aware and study-test unaware subjects in right and left hippocampus for primed trials.



Figure 27. The decreased neural activity during the last repetition of primed stimuli in the Object Detection task and during the first repetition of primed stimuli in the Search task: The results of conjunction analysis.

1. Right posterior cingulate cortex; 2. central and parietal parts of right operculum cortex;

3. bilateral precuneus.







B. Bilateral occipital pole (middle occipital gyrus)

Figure 28. The brain regions activated during the last repetition of primed stimuli in the Object Detection task and also activated more in aware, compared to unaware, subjects in the Search task: The results of conjunction analysis.

OD – the Object Detection task, ST – the Search task.



Figure 29. Right precuneus deactivated in the unaware compared to aware subjects and also it was deactivated during the last repetition of primed stimuli during the Object Detection task: The results of conjunction analysis.



Figure 30. The learning-related decreases during the Object Detection task and awareness-related changes during the Search task in right cuneus: The results of conjunction analysis.



Figure 31. LDA: the results of cross-validation.

A. Full model (reactivation and search RT). **B.** The model included subjects search RT and reactivation in left LOC/SPL and left MOG. **C.** The model included reactivation in all four brain regions. **D.** The model included reactivation in left LOC/SPL, left MOG and right precuneus.



Figure 32. Memory traces acquired during encoding represented as connections between neuronal groups processing different stimulus features.



Figure 33. Neurons processing information during the specified time period increase firing rates.



Figure 34. Neurons processing spatial properties of the stimuli increase firing rates.




Presentation of target object reactivates spatial properties in the encoded stimuli. A. The target object is presented. Covariance between memory trace of the target object and the initial memory trace is detected. B. The change in one of the nodes of the network changes weights assigned to each connection. C. The spatial property of the object are reactivated.

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PUBLICATIONS

- <u>Manelis, A.</u>, Hanson, C., & Hanson, S. J. (*submitted*). Are there multiple systems in spatial memory?
- <u>Manelis, A.</u>, Hanson, C., & Hanson, S. J. (*in preparation*). Implicit memory for spatial locations depends on reactivation of encoding-related brain regions.
- <u>Manelis, A.</u>, Hanson, C., & Hanson, S. J. (*in preparation*). The new facet of the loci method: Variable spatial context improves incidental learning of objects.

PRESENTATIONS

Manelis A., Hanson C., Hanson S. J. (2008). *Object recall as a function of spatial context and subject's intention to learn*. OPAM 2008.

<u>Manelis, A.</u>, Hanson, S. J., Hanson, C. (2006). Cross-modality and within-modality processing of lexical and pictorial components in complex visual stimuli. Talk at the New Jersey Psychological Association meeting.