

NEUROPSYCHOLOGICAL DISSOCIATION BETWEEN RECOGNITION FAMILIARITY AND PERCEPTUAL PRIMING IN VISUAL LONG-TERM MEMORY

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ABSTRACT

The present study examined whether the same brain region mediates visual-perceptual repetition priming and a familiarity component of visual recognition memory. In two experiments, familiarity-based recognition was measured in an individual (M.S.) with impaired visual repetition priming due to a lesion of right occipital cortex. In both experiments, M.S. demonstrated intact recognition familiarity despite his visual nondeclarative memory impairment. These results converge with other behavioral results to indicate that recognition familiarity does not depend on the same memory system that mediates perceptual priming.

Key words: long-term memory, visual recognition, occipital cortex

INTRODUCTION

Research on human memory demonstrates that there are multiple forms of long-term memory, each supported by distinct processes and neuroanatomic substrates (Cohen and Squire, 1980; Gabrieli, 1998; Graf and Schacter, 1985; Squire, 1992; Tulving and Schacter, 1990). One form of long-term memory is explicit or declarative memory. Declarative memory mediates the learning and remembrance of new events and facts (Cohen and Squire, 1980; Gabrieli, Cohen and Corkin, 1988; Graf and Schacter, 1985; Squire, 1992), and is often assessed using direct tests of memory that make reference to the original learning experience and that require conscious recollection of an aspect of the experience. Declarative memory supports *recognition*, the ability to determine whether a test stimulus was previously encountered in a particular spatial and temporal learning context. Other forms of long-term memory have been collectively referred to as implicit or nondeclarative memory (Graf and Schacter, 1985; Squire, 1992). Nondeclarative memory consists of experience-induced changes in many distinct systems, including perceptual systems that play a significant role in the identification of words and objects (Schacter and Tulving, 1994; Squire, 1992). These forms of memory are often assessed using tests that do not make direct reference to the study experience and do not require conscious recollection of the experience. Rather, memory is measured indirectly as a change in test-phase

performance attributable to study-phase experience. One form of nondeclarative memory is *repetition priming*, a facilitation or bias in performance with a stimulus due to prior processing of the same or a related stimulus. Priming is perceptual when it reflects prior processing of stimulus form; priming is conceptual when it reflects prior processing of stimulus meaning (Roediger and McDermott, 1993).

Neuropsychological and neuroimaging studies indicate that declarative and perceptual nondeclarative memory depend on anatomically distinct neural substrates. Declarative memory is subserved by a medial temporal and diencephalic neural network that includes the hippocampal formation, adjacent parahippocampal and perirhinal cortices, and the medial thalamus and mammillothalamic tract (Squire, 1992). Insult to these structures results in a global amnesia characterized by a specific impairment of declarative memory with sparing of nondeclarative memory (e.g., Cohen and Squire, 1980; Gabrieli, Keane, Stanger et al., 1994; Schacter, 1992; Squire 1992). For example, global amnesia is associated with impaired recognition but spared perceptual and conceptual priming (e.g., Cermak, Verfaellie and Chase, 1995; Graf, Squire and Mandler, 1984; Vaidya, Gabrieli, Keane et al., 1995; Warrington and Weiskrantz, 1970). Neuroimaging studies provide convergent evidence demonstrating activation in medial temporal structures during recognition and cued recall (e.g., Gabrieli, Brewer, Desmond et al., 1997; Schacter, Alpert, Savage et al., 1996; Squire, Ojemann, Miezin et al., 1992).

Perceptual nondeclarative memory, in contrast, is subserved by modality-specific sensory cortices, with insult to these regions resulting in a selective impairment of modality-specific nondeclarative memory. For example, lesions of right visual cortex result in spared visual recognition memory but impaired visual repetition priming (Fleischman, Gabrieli, Reminger et al., 1995; Fleischman, Vaidya, Lange et al., 1997; Gabrieli, Fleischman, Keane et al., 1995; Keane, Gabrieli, Mapstone et al., 1995; Vaidya, Gabrieli, Verfaellie et al., 1997). This dissociation suggests that a nondeclarative memory system in right occipital cortex may be involved in memory for visual form-specific information that is necessary for visual repetition priming but not for visual recognition memory. Neuroimaging studies have revealed decreased activation in right extrastriate visual cortex during visual repetition priming (e.g., Buckner, Petersen, Ojemann et al., 1995; Schacter et al., 1996; Squire et al., 1992).

Behavioral studies complement these neuroanatomic studies, revealing functional dissociations between recognition and perceptual priming (for reviews see, Richardson-Klavehn and Bjork, 1988; Roediger and McDermott, 1993). Recognition accuracy is enhanced by conceptual encoding and is often unaffected by changes in perceptual form. In contrast, perceptual priming is greatest when study and test perceptual forms match and is unaffected by manipulations of conceptual encoding (e.g., Jacoby, 1983; Jacoby and Dallas, 1981; Winnick and Daniel, 1970). These and related results indicate that the declarative memory that subserves recognition is functionally distinct from the nondeclarative memory that subserves perceptual priming.

Although it is generally agreed that declarative and perceptual nondeclarative memory reflect functionally and anatomically separable memory systems, it is

less clear whether declarative and nondeclarative memory jointly contribute to certain kinds of mnemonic judgments. One class of memory models, dual-process models of recognition, raise the possibility that both declarative and nondeclarative memory mediate recognition judgments. Specifically, dual-process theories of memory posit that recognition judgments are based on two processes, *recollection* and *familiarity* (e.g., Atkinson and Juola, 1974; Gardiner, 1988; Jacoby, 1983, 1991; Jacoby and Dallas, 1981; Mandler, 1980, 1991). Recollection is thought to derive from declarative memory processes and involves the conscious remembrance of a prior experience. Familiarity, in contrast, is posited to be an attribution process that reflects memory without conscious remembrance (e.g., Jacoby and Dallas, 1981). Familiarity is thought to be a subjective sensation that derives from the more fluent *perceptual* processing of a stimulus due to prior stimulus perception (e.g., Jacoby and Dallas, 1981; Mandler, 1980; Yonelinas, Regehr and Jacoby, 1995). Within the context of recognition, this sense of familiarity is attributed to having previously encountered the stimulus. For example, Jacoby and Dallas (1981) suggest that "due to prior exposure, an item appears to jump out from the page. Because of this fluent processing, the item seems familiar and is judged to be old" (p. 333).

Importantly for the present purposes, the same perceptual nondeclarative (implicit) memory that supports perceptual priming has been posited to support familiarity-based recognition judgments (e.g., Cermak and Verfaellie, 1992; Cermak, Verfaellie, Sweeney et al., 1992; Dorfman, Kihlstrom, Cork et al., 1995; Gardiner, 1988; Jacoby and Dallas, 1981; Johnston, Hawley and Elliot, 1991; Mandler, 1991). For example, Dorfman et al. (1995) propose "that the process or system underlying implicit memory can support some degree of recognition...recognition can be mediated by the same activation-based process that underlies priming" (p. 247). Gardiner (1988) proposes that "recognition memory may entail two processes, one of which may also give rise to priming effects in implicit memory tests" (p. 312; but see Richardson-Klavehn, Gardiner and Java, 1996). Similarly, while noting that familiarity may reflect both prior perceptual and conceptual processing, Toth (1996) argues that the parallels between familiarity and repetition priming "strongly suggest that similar mnemonic processes underlie familiarity and implicit memory" (p. 135). Thus, according to this perspective a common perceptual nondeclarative memory system is thought to subserve both perceptual priming and recognition familiarity.

Some support for the assertion that recognition familiarity derives from a perceptual fluency process comes from behavioral studies where fluency of test-item processing was directly manipulated. Manipulations designed to enhance test-item perceptual fluency serve to increase participants' willingness to embrace the test item as having been previously studied, regardless of whether or not the item had actually been encountered (e.g., Forster, 1985; Jacoby and Whitehouse, 1989; Johnston, Dark and Jacoby, 1985; Johnston et al., 1991; Kelley, Jacoby and Hollingshead, 1989). To the extent that such effects derive from enhanced test-item perception, then these results suggest that recognition memory is partially mediated by a familiarity process that is perceptual in nature. It is important to note, however, that these results do not inform us as to

whether this process depends on the same long-term nondeclarative memory that supports perceptual priming.

Other behavioral evidence is inconsistent with the suggestion that the same nondeclarative memory supports recognition familiarity and perceptual priming. First, recognition familiarity is also modulated by manipulations of test-item conceptual processing (Whittlesea, 1993), manipulations that presumably would have no effect on perceptual priming (Roediger and McDermott, 1993). Second, in contrast to perceptual priming, increasing the extent of conceptual processing at the time of stimulus encoding increases recognition familiarity (Jacoby, 1991; Jacoby and Kelley, 1991; Toth, 1996; Wagner and Gabrieli, 1998; Wagner, Gabrieli and Verfaellie, 1997). Finally double dissociations between recognition familiarity and perceptual priming have been reported: when the extent of conceptual encoding and the similarity between study and test perceptual forms are inversely manipulated, recognition familiarity increases with conceptual encoding whereas perceptual priming increases with study-test perceptual similarity (Wagner et al., 1997). Collectively, these findings indicate that perceptual priming and recognition familiarity do not depend on entirely overlapping processes.

Functional dissociations, however, do not rule out the possibility that recognition familiarity and perceptual priming depend on the same nondeclarative memory. It remains possible that, while perceptual priming depends on perceptual nondeclarative memory, recognition familiarity may depend on multiple forms of memory including perceptual nondeclarative memory. For example, Toth (1996) suggests that recognition familiarity may reflect both conceptual and perceptual nondeclarative memory. Thus, although not entirely reflecting perceptual nondeclarative memory, recognition familiarity may still depend on this form of memory. Alternatively, the perceptual nondeclarative memory that supports perceptual priming may make little to no contribution to recognition memory. Rather, recognition familiarity may depend on conceptual nondeclarative memory (Wagner et al., 1997) or may be entirely dependent on declarative memory processes (e.g., Knowlton and Squire, 1995; Squire and Knowlton, 1994; Wagner and Gabrieli, 1998). Importantly, these two hypotheses make opposite assertions about the contributions of perceptual nondeclarative memory to recognition performance. The former posits that the same perceptual nondeclarative memory that supports perceptual priming also supports recognition familiarity, whereas the latter posits that perceptual nondeclarative memory does not mediate recognition familiarity.

One test of these two hypotheses would be to examine the status of recognition familiarity when the perceptual nondeclarative memory system that supports perceptual priming is impaired. Here, we sought to test these hypotheses by using the inclusion/exclusion procedure (Jacoby, 1991) to examine the status of recollection-based and familiarity-based recognition in a patient (M.S.) who is known to have an impairment of visual nondeclarative memory. Specifically, M.S., who has a large lesion of the right occipital lobe, fails to demonstrate visual repetition priming, but nevertheless demonstrates normal recognition memory (Fleischman et al., 1995, 1997; Gabrieli et al., 1995; Vaidya et al., 1997). M.S.'s visual repetition priming deficits include the failure to demonstrate:

(a) visual word-identification priming (Fleischman et al., 1995; Gabrieli et al., 1995), (b) modality-specific priming in visual word-stem completion (Gabrieli et al., 1995), and (c) font-specific priming in word-stem completion (Vaidya et al., 1997). We reasoned that, to the extent that the nondeclarative memory that yields perceptual priming is the same as that which supports recognition familiarity, then M.S. should demonstrate preserved recollection but impaired familiarity in recognition. Alternatively, to the extent that recognition and perceptual priming are not dependent on the same nondeclarative memory, then M.S. should demonstrate intact recollection and familiarity in recognition.

In two experiments, the inclusion/exclusion procedure was used to index the contributions of recollection and familiarity to recognition judgments by M.S. and control participants. This procedure, developed by Jacoby and colleagues, is an analytic technique that is posited to decompose memory performance into the separate contributions of recollection and familiarity (Jacoby, 1991; for a discussion see, Curran and Hintzman, 1995, 1997; Jacoby, Begg and Toth, 1997; Jacoby, Yonelinas and Jennings, 1998; Yonelinas and Jacoby, 1996a). The procedure depends on two conditions that make explicit reference to the study episode: *inclusion*, where recollection and familiarity work in concert to support memory, and *exclusion*, where recollection and familiarity work in opposition. In the inclusion condition, participants are instructed to provide positive recognition responses (i.e., respond "old") to items from both a critical set and a second set. Under these instructions, positive recognition judgments to items from the critical set can be based on familiarity alone [$F(1-R)$], recollection alone [$R(1-F)$], or both familiarity and recollection [RF]. Hence, $P(\text{"old"} | \text{Inclusion}) = R + F(1-R)$. In the exclusion condition, participants are instructed to provide positive recognition judgments only to items from the second set; items from the critical set are to be treated as unstudied items in this condition. For the critical items, these instructions serve to pit recollection and familiarity in opposition: Recollection leads to a "new" judgment, whereas familiarity leads to an "old" judgment, such that $P(\text{"old"} | \text{Exclusion}) = F(1-R)$. With these two conditions and a few assumptions (e.g., that recollection and familiarity are independent processes, and that recollection reflects a discrete process and familiarity reflects a signal-detection process) the inclusion/exclusion procedure allows for estimation of the contributions of recollection and familiarity that is unbiased by between condition and between group differences in response criterion (for details see, Yonelinas et al., 1995).

EXPERIMENT 1

In Experiment 1, the inclusion/exclusion procedure was used in conjunction with a read/anagram encoding manipulation (Verfaellie and Treadwell, 1993). In the first phase of the experiment, participants solved anagrams (e.g., *DTSNA* for *STAND*) and real words. Next, participants studied a second list of words presented auditorily. Finally, yes-no recognition was performed under either inclusion or exclusion instructions, where the read and anagram-solved words formed the critical set. Previous studies have revealed greater recollection-based

recognition following anagram solution than following word reading, possibly due to the additional conceptual processing required for anagram solution (Jacoby, 1991; Jennings and Jacoby, 1993; Verfaellie and Treadwell, 1993). In contrast to perceptual priming, which is greater for read than for anagram-solved words (e.g., Allen and Jacoby, 1990; Schwartz, 1989), recognition familiarity is either unaffected by read/anagram manipulations (Jennings and Jacoby, 1993) or greater following anagram solution (Jacoby, 1991; Verfaellie and Treadwell, 1993). To the extent that recognition familiarity is dependent on the same nondeclarative memory that yields perceptual priming, then M.S.'s recognition familiarity should be impaired relative to controls and familiarity should be greater for read than for anagram-solved items.

Materials and Methods

Participants

The participants were M.S. and six male controls (mean age, 28 years; mean education, 15.8 years). M.S. is a 32 year-old, right-handed male with 16 years of education (29 years old at time of testing). M.S. had most of his right occipital lobe removed for the treatment of pharmacologically intractable epilepsy at the age of 14 (Figure 1). The excision included all of Brodmann areas 17 and 18 and a portion of area 19, and resulted in a macula-splitting, left homonymous hemianopsia. Since the operation, M.S. has been seizure free and no longer takes medication. Apart from the hemianopsia, he appears to be neuropsychologically intact, with a Full-Scale IQ of 110 on the Wechsler Adult Intelligence Scale-Revised (WAIS-R) and a Wechsler Memory Scale-Revised (WMS-R) General Memory score of 119 (Attention/Concentration index of 92 and Delayed Recall index of 118; Fleischman et al., 1995).

Tests

Stimuli were presented on a Macintosh IIfx computer, and consisted of 160 five-letter nouns with word frequencies ranging from 40-to-470 occurrences per million (Kucera and Francis, 1967). The words were divided into two unique sets, one for the inclusion condition and another for the exclusion condition. The assignment of sets to conditions was counterbalanced across participants. For each condition, a visual study list, an auditory study list, and a recognition test list were created. Each visual study list consisted of 24 words, 12 designated to be read aloud and 12 designated to be presented in an anagram format. Anagrams were created by fixing the second and fourth letter of each word in their correct positions; these letters were underlined. The remaining three letters were randomly reversed (e.g., UQHSE for HOUSE). This approach ensured that the target word was the only possible solution for the anagram. The visual study list consisted of a pseudo-random order of the 24 stimuli, with the constraint that no more than 3 anagram or 3 read trials occurred consecutively. Next, 32 words were selected for the auditory study list. Finally, the remaining 24 stimuli served as foils for the recognition test. In the recognition test, the 80 stimuli (visually studied, auditorily studied, and foils) were pseudo-randomly ordered, with the constraint that no more than 3 items of the same kind could appear consecutively. All assignments of words to conditions were random.

Procedure

Prior to beginning the experiment, participants were given practice at the anagram task. Participants were presented five anagrams, one at a time. They were told that the second and fourth letter of each anagram were in their correct positions, and that they should rearrange the remaining three letters to form a word. Following practice, the experiment was initiated.

The experiment had two study-test conditions, exclusion and inclusion. For each, there were three components: visual study of read and anagram-solved words, auditory study of words, and yes-no recognition. Participants began with the exclusion condition. First, words and anagrams were visually presented one at a time in the center of a computer screen. Participants read each word aloud and attempted to solve each anagram, stating the solution aloud. Following word reading or correct anagram solution, the experimenter depressed a

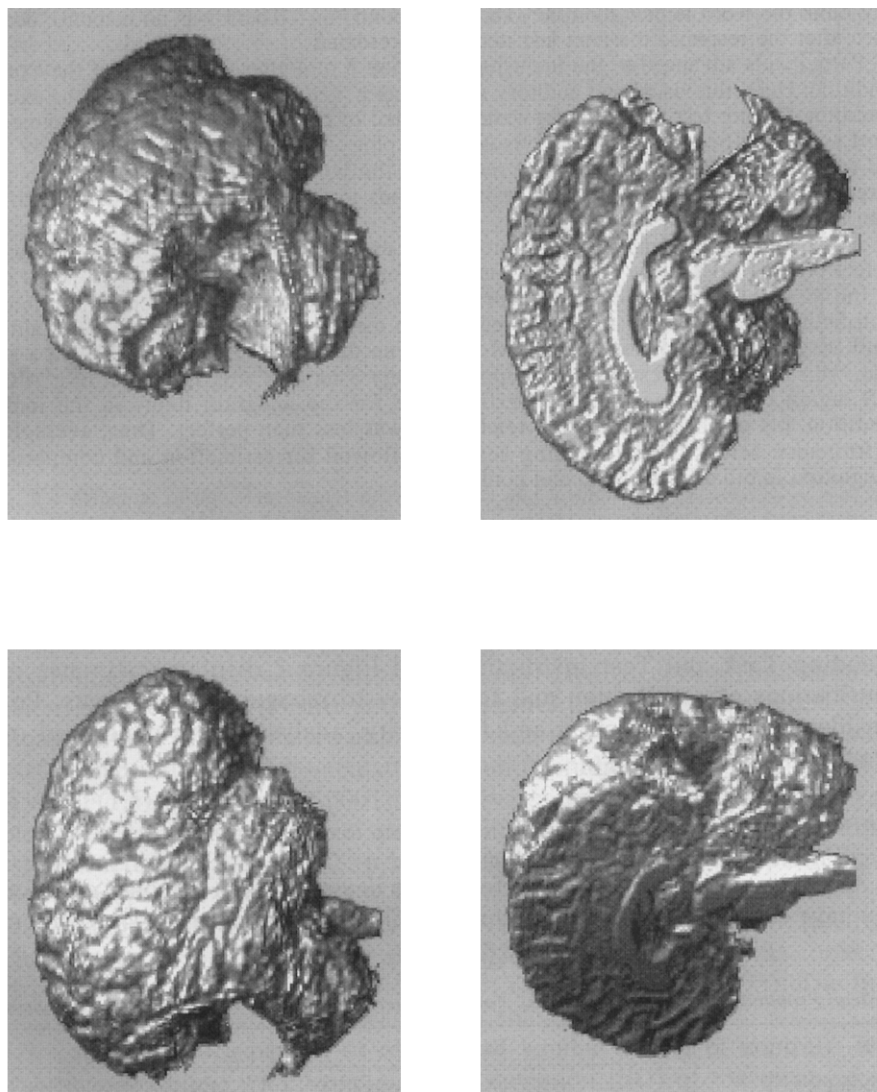


Fig. 1 – Three-dimensional MRI renderings of M.S.'s right hemisphere, illustrating the extent of his right occipital lobe resection. M.S.'s left hemisphere is entirely intact.

computer key to end the trial; the next trial was initiated 2 sec later. If a participant failed to solve an anagram, he was encouraged to try again until a maximum of 30 sec had elapsed; at this point the solution was provided. Following visual study, an auditory study list was presented via a tape recorder at a rate of one word every 3 sec. Participants repeated the words aloud and attempted to remember them for a later memory test. Finally, yes-no recognition was performed under exclusion instructions. Test words were presented one at a time in the center of the computer screen for 1 sec. For each test word, participants were instructed to determine if they encountered the word during the auditory study list; if so, then they were to respond "yes". They were further instructed that if they remembered the word as having been a read or anagram-solved item from the first, visual study list or if they think the word is new then they should respond "no". There was no response deadline; 1 sec after the response the next test item was presented.

Participants advanced to the inclusion condition 5 min after completion of the exclusion condition. Here, the visual and auditory study phases were identical to those in the exclusion condition. During test, participants were instructed to respond "yes" if they recognized the word as having been in either the visual study phase or the second auditory study phase, and to respond "no" if they did not recognize the word as having been in either phase. Care was taken to emphasize that the instructions for this recognition test were different from those in the exclusion condition.

All control participants were run through the entire experiment once. M.S. demonstrated perfect performance in the inclusion condition for both the read and anagram items during an initial testing. This perfect performance would have precluded estimation of the contributions of familiarity to M.S.'s recognition memory, as it would have constrained the familiarity estimate. For this reason, M.S. was run through the entire experiment a second time, with this second test occurring approximately 3 months after the initial test. Although M.S. again demonstrated perfect performance for the anagram items in the inclusion condition, his performance for the read items was less than perfect. Thus, averaging his performance across the two testing sessions allowed for estimation and comparison of recognition familiarity for M.S. and controls.

Results and Discussion

All analyses were conditionalized on successful anagram solution during study. Table I displays the probabilities of responding "yes" to test words across Encoding Task and Test Instruction, and Figure 2 displays estimates of the contributions of recollection and familiarity to recognition judgments. Prior to consideration of recollection and familiarity, analyses were conducted on the recognition data.

Heard and New Items

Analyses of base rates were performed to detect shifts in response criterion that may have occurred due to Test Instruction (Graf and Komatsu, 1994; Roediger and

TABLE I
Mean Probability of Responding "Yes" Following Read and Anagram Encoding in Experiment 1

Encoding	Inclusion		Exclusion	
	M.S.	Controls (SD)	M.S.	Controls (SD)
Read	.83	.72 (.25)	.42	.35 (.11)
Anagram	1.00	.88 (.09)	.13	.13 (.09)
Heard	.65	.68 (.19)	.59	.62 (.13)
New	.31	.27 (.17)	.35	.19 (.19)

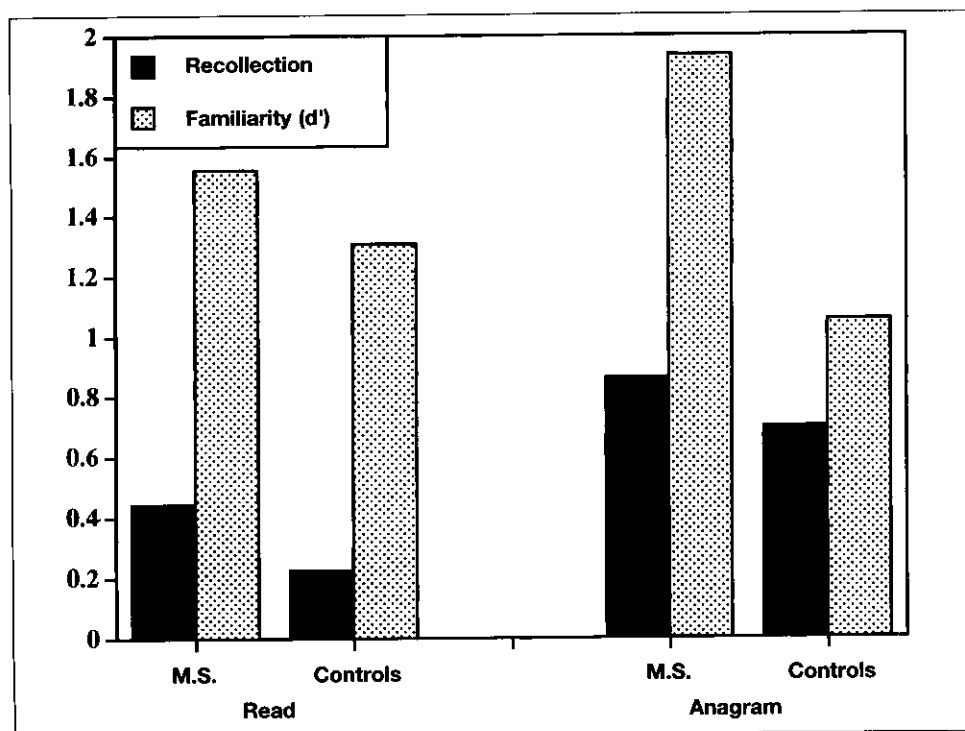


Fig. 2 – Estimates of the contributions of recollection and familiarity to recognition of read and anagram-solved items in M.S. and control participants.

McDermott, 1994; Yonelinas et al., 1995; Yonelinas and Jacoby, 1996b). A two-factor repeated measures analysis of variance (ANOVA) was performed on the data from control participants, with factors of Test Instruction (Inclusion vs. Exclusion) and Item Type (Heard vs. New). Control participants responded "yes" significantly more often to heard items (.65) than to new items (.23), indicating successful discrimination between studied and unstudied items (main effect of Item Type, $F(1,5) = 119.26$, $p < .0001$). There was a trend towards increased "yes" responses under inclusion (.47) than under exclusion (.40) instructions (main effect of Test Instruction, $F(1,5) = 3.78$, $p > .10$). This trend suggests that participants may have adopted a more lenient criterion for responding "yes" based on familiarity in the inclusion condition (Jacoby, Toth and Yonelinas, 1993; Roediger and McDermott, 1994; Yonelinas et al., 1995). This criterion shift was corrected for during computation of process estimates (Yonelinas et al., 1995). The Item Type \times Test Instruction interaction was not reliable ($F < 1.0$).

M.S. demonstrated a pattern of responding similar to that of controls, with his performance falling within one standard deviation (SD) of the mean of the controls (Table I). M.S. responded "yes" more often to heard (.62) than to new (.33) items, indicating successful discrimination between studied and unstudied items. M.S. demonstrated a similar pattern of responding under inclusion (.48) and exclusion (.47) instructions.

Visually Studied Items

A two-factor repeated measures ANOVA was performed on the probabilities of responding "yes" to words from the visual study phase, with factors of Test Instruction and Encoding Task (Read vs. Anagram). The probability of responding "yes" was higher under inclusion (.80) than under exclusion (.24) instructions, indicating that control participants were able to follow the instructions (main effect of Test Instruction, $F(1,5) = 53.04$, $p < .001$). The probability of responding "yes" was similar following read (.53) and anagram (.51) encoding (main effect of Encoding Task, $F < 1.0$). The interaction was significant ($F(1,5) = 12.40$, $p < .05$). Planned comparisons revealed that control participants were more likely to exclude anagram-solved relative to read items ($F(1,5) = 8.07$, $p < .05$), and were marginally more likely to include anagram-solved relative to read items ($F(1,5) = 4.58$, $p = .09$).

M.S. demonstrated a pattern of responding similar to that of controls, with his performance falling within one SD of the mean of the control participants on all measures except inclusion of anagram-solved items where his performance was superior that of control participants (although his performance remained within the range of that of controls). M.S. responded "yes" more often under inclusion (.92) than under exclusion (.28) instructions, indicating that he was able to follow the instructions. The probability of responding "yes" was similar following read (.63) and anagram (.57) encoding. Finally, M.S. was more likely to include and to exclude items following anagram encoding.

Recollection and Familiarity

Estimates of the contributions of recollection and familiarity across Encoding Task were derived for the control participants and for M.S. (Figure 2). Because analyses of base rate performance indicated that control participants may have adopted a more lenient response criterion in the inclusion relative to the exclusion condition, unbiased estimates of recollection and familiarity were computed using a dual-process signal-detection method that incorporates between condition and between group differences in response criterion (Yonelinas et al., 1995). Separate one-factor ANOVAs were performed to examine the effects of Encoding Task on recollection and familiarity in control participants. These analyses revealed that recollection was greater after anagram than after read encoding ($F(1,5) = 13.21$, $p < .05$; see also, Jacoby, 1991; Jennings and Jacoby, 1993; Verfaellie and Treadwell, 1993). Familiarity, however, was similar for both encoding conditions ($F < 1.0$). Thus, in contrast to perceptual priming, recognition familiarity was unaffected by the read/anagram manipulation (Jennings and Jacoby, 1993; but see Jacoby, 1991; Verfaellie and Treadwell, 1993).

Importantly, M.S.'s process estimates fell within one SD of the mean of control participants on both measures of familiarity, with recognition familiarity being modestly greater following anagram solution. It is important to note, however, that M.S.'s perfect performance for anagram-solved items under inclusion instructions constrains the estimate of familiarity in this condition.

Thus, it is difficult to draw conclusions about the relative contributions of familiarity following word reading and anagram solution or about the status of familiarity in M.S. from the anagram condition. Nevertheless, process estimates from the read condition clearly reveal that M.S. demonstrates intact recognition familiarity. M.S.'s recollection was within one SD of the mean of controls in the read condition and above one SD (but still within the range) in the anagram condition. As with control participants, anagram solution relative to word reading produced markedly greater recollection in M.S..

EXPERIMENT 2

Experiment 1 demonstrated that M.S.'s recognition familiarity was intact. However, M.S. was at ceiling for anagram-solved items, limiting the inferences that can be drawn from this condition. In Experiment 2, we further examined the status of recognition familiarity in M.S. by investigating the effects of varying conceptual encoding via a levels-of-processing manipulation (Craik and Lockhart, 1972) on recollection and familiarity. Initially, participants made semantic or perceptual judgments for visually presented words. Then they studied a list of words presented auditorily. Finally, they performed yes-no recognition under inclusion or exclusion instructions. Previous studies indicate that both recollection and familiarity are greater following semantic than following perceptual encoding (Toth, 1996; Wagner and Gabrieli, 1998). In contrast, perceptual priming is unaffected by levels-of-processing manipulations (e.g., Jacoby and Dallas, 1981). To the extent that recognition familiarity is dependent on the same nondeclarative memory that yields perceptual priming, then M.S.'s recognition familiarity should be impaired relative to controls and familiarity should be unaffected by the encoding manipulation.

Materials and Methods

Participants

The participants were M.S. (31 years old at time of testing) and 6 male controls (mean age, 29.8 years; mean education, 17.0 years).

Tests

Stimuli consisted of 180 concrete nouns with word-lengths ranging from 3-to-10 letters and word frequencies ranging from 0-to-148 occurrences per million (Kucera and Francis, 1967). Words represented human-made entities (e.g., FORK) or natural entities (e.g., snail), and were printed in uppercase (e.g., LETTUCE) or lowercase letters (e.g., barrel). There were 45 words of each type: human-made/uppercase, human-made/lowercase, natural/uppercase, and natural/lowercase. The words were divided into six 30-item blocks, with the constraint that each block consisted of an equal number of human-made and natural entities and an equal number of uppercase and lowercase words.

Two unique sets of materials were created, one for inclusion and another for exclusion. Each set consisted of a visual study list created from one block, an auditory study list created from another block, and a test list consisting of studied items plus distractor items from a third block. For visual study, half of the words were assigned to a semantic encoding condition and half to a perceptual encoding condition. For both the visual and auditory

study lists, words were pseudo-randomized with the constraints that there were no more than three consecutive human-made or natural words and uppercase or lowercase words. In addition, for visual study there were no more than three consecutive semantic or perceptual encoding trials. Each test list was pseudo-randomized with the constraints that there were no more than three consecutive human-made or natural words and uppercase or lowercase words. In addition, for visual study there were no more than three consecutive semantic or perceptual encoding trials. Each test list was pseudo-randomized such that there were no more than three consecutive targets or foils.

Procedure

The procedure was similar to that in Experiment 1. There were two study-test conditions – exclusion and inclusion – each with three components: visual study, auditory study, and yes-no recognition. Participants began with the exclusion condition. First, participants studied visually presented words by answering a semantic or a perceptual question about each. Prior to each word, a levels-of-processing question (“Human-made?” or “UPPERCASE?”) appeared in the center of the screen for 1 sec. A word was then presented in the center of the screen for 1 sec, and participants answered the question for that word by pressing either a “yes” key or a “no” key on the keyboard. The computer advanced to the next question-word event after 500 msec. After visual study, the auditory list was presented at a rate of one word every 2 sec; participants were instructed to remember the words for a later test. Finally, yes-no recognition was performed under exclusion instructions. Test words were presented one at a time in the center of the computer screen for 1 sec. As in Experiment 1, participants were instructed to determine whether they remember encountering the test word in the auditory study list, and, if so, to respond “yes”. Participants were instructed to respond “no” to words from the initial visual study list and to new words. There was no response deadline; 1 sec after the response the next test item was presented.

Participants advanced to the inclusion condition 5 min after completion of the exclusion condition. The study phases were identical to those in the exclusion condition. During test, participants were instructed to respond “yes” to words from the visual and auditory study phases, and to respond “no” if they did not recognize the word as having been in either phase. Care was taken to emphasize that the instructions for this recognition test were different from those in the exclusion condition.

Results and Discussion

Table II displays the probabilities of responding “yes” to test words across Level of Processing and Test Instruction, and Figure 3 displays the process estimates.

TABLE II
Mean Probability of Responding “Yes” Following Semantic and Perceptual Encoding in Experiment 2

Encoding	Inclusion		Exclusion	
	M.S.	Controls (SD)	M.S.	Controls (SD)
Semantic	.93	.76 (.20)	.20	.31 (.25)
Perceptual	.80	.54 (.33)	.27	.28 (.20)
Heard	.80	.83 (.08)	.60	.80 (.13)
New	.40	.27 (.17)	.10	.17 (.17)

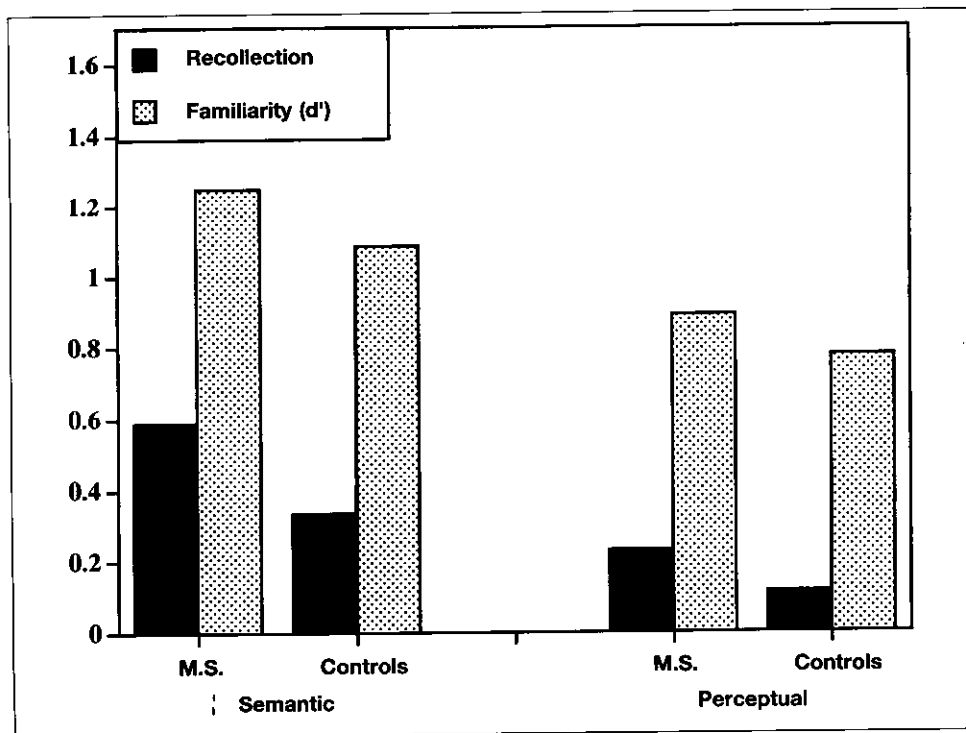


Fig. 3 – Estimates of the contributions of recollection and familiarity to recognition of items following semantic or perceptual encoding in M.S. and control participants.

Heard and New Items

To detect shifts in response criterion that may have occurred due to Test Instruction, a two-factor repeated measures ANOVA was performed on the data from control participants, with factors of Test Instruction and Item Type. Control participants responded “yes” significantly more often to heard items (.81) than to new items (.22), indicating successful discrimination between studied and unstudied items (main effect of Item Type, $F(1,5) = 125.43$, $p < .0001$). The probability of responding “yes” was similar under inclusion (.55) and exclusion (.49) instructions (main effect of Test Instruction, $F < 1.0$), and the interaction was not reliable ($F(1,5) = 1.04$, $p > .35$).

M.S. demonstrated a pattern of responding similar to that of controls, with his performance falling within one SD of the mean of the control participants on all measures except for heard items under exclusion instructions (where his performance was below one SD, but still within the range of control participants; Table II). M.S. responded “yes” more often to heard (.70) than to new (.25) items, indicating successful discrimination between studied and unstudied items. However, M.S. responded “yes” more often under inclusion (.60) than under exclusion (.35) instructions suggesting that he may have adopted a more lenient criterion for responding in the inclusion than in the exclusion condition.

Visually Studied Items

A two-factor repeated measures ANOVA was performed on the probabilities of responding "yes" to words from the visual study phase, with factors of Test Instruction and Level of Processing (Semantic vs. Perceptual). The probability of responding "yes" was higher under inclusion (.65) than under exclusion (.29) instructions, indicating that control participants were able to follow the instructions (main effect of Test Instruction, $F(1,5) = 47.68$, $p < .001$). The probability of responding "yes" was higher following semantic (.53) than following perceptual (.41) encoding (main effect of Level of Processing, $F(1,5) = 12.10$, $p < .05$). The interaction was not reliable ($F(1,5) = 2.44$, $p > .17$).

M.S. demonstrated a pattern of responding similar to that of controls, with his performance falling within one SD of the mean of the control participants on all measures. M.S. responded "yes" more often under inclusion (.87) than under exclusion (.24) instructions. The probability of responding "yes" was similar following semantic (.57) and perceptual (.54) encoding. Finally, M.S. was more likely to include and to exclude items following semantic encoding.

Recollection and Familiarity

Unbiased estimates of the contributions of recollection and familiarity across Level of Processing were derived for the control participants and for M.S. using the dual-process signal-detection method (Yonelinas et al., 1995). Separate one-factor ANOVAs were performed to examine the effects of Level of Processing on recollection and familiarity in control participants (Figure 3). Recollection was greater following semantic than following perceptual encoding, although this difference failed to reach significance ($F(1,5) = 2.81$, $p = .15$). Similarly, familiarity was non-significantly greater following semantic than following perceptual encoding ($F(1,5) = 1.57$, $p > .26$). Although not statistically significant, this pattern of greater recollection and familiarity following semantic encoding is consistent with previous reports (Toth, 1996; Wagner and Gabrieli, 1998).

Importantly, M.S.'s process estimates fell within one SD of the mean of those from control participants for both measures of familiarity and both measures of recollection. M.S. demonstrated the same pattern of greater familiarity and recollection following semantic encoding. Thus, as in Experiment 1, M.S. demonstrated intact recognition familiarity.

GENERAL DISCUSSION

The present studies examined whether the perceptual nondeclarative memory that mediates perceptual priming also subserves familiarity-based recognition judgments. In two experiments the status of recognition familiarity was evaluated in M.S., who has a well documented impairment of visual repetition priming due to a right occipital cortex lesion (Fleischman et al., 1995, 1997; Gabrieli et al., 1995; Vaidya et al., 1997). In both experiments, M.S.

demonstrated levels of recognition familiarity comparable to those of control participants. In Experiment 1, recognition familiarity for read items and for anagram-solved items were similar for both M.S. and control participants (although M.S.'s estimate in the anagram condition was constrained). Likewise, Experiment 2 revealed similar recognition familiarity for M.S. and control participants following semantic and perceptual encoding. Thus, M.S. demonstrated intact recognition familiarity on all measures despite his known impairment of visual nondeclarative memory.

These results extend previous reports by demonstrating that M.S.'s preserved recognition is supported by intact familiarity and recollection processing. It is not surprising that M.S. demonstrates intact recollection-based recognition as his lesion is restricted to his right occipital cortex, sparing the medial-temporal regions that are critical for declarative memory. However, demonstration that familiarity-based recognition is intact in M.S. despite his visual repetition priming deficit might be unexpected given suggestions that perceptual priming and recognition familiarity share a common nondeclarative underpinning (e.g., Cermak and Verfaellie, 1992; Cermak et al., 1992; Dorfman et al., 1995; Gardiner, 1988; Jacoby and Dallas, 1981; Johnston et al., 1991; Mandler, 1991). This dissociation between intact recognition familiarity and impaired perceptual priming strongly argues against the idea that these memory abilities reflect the operations of the same perceptual nondeclarative memory system. Visual repetition priming, but not recognition familiarity, depends on a nondeclarative memory system in right occipital cortex.

This anatomic dissociation between impaired perceptual priming and intact recognition familiarity complements the report of a reverse anatomic dissociation between perceptual priming and recognition memory. Hamann and Squire (1997) describe a patient (E.P.) with global amnesia resulting from extensive medial-temporal lobe damage. As is typical in amnesia, E.P.'s perceptual priming on word identification and word-stem completion tasks is intact. To the extent that the nondeclarative memory that supports perceptual priming also mediates recognition familiarity, then it might be expected that E.P. would demonstrate some recognition abilities. To the contrary, E.P. fails to demonstrate above chance performance on recognition tests. Collectively, M.S. and E.P. demonstrate an anatomic double dissociation between perceptual priming and recognition familiarity, indicating that perceptual priming and recognition familiarity are mediated by entirely separable mnemonic substrates.

In addition to being anatomically dissociable, the present and prior studies indicate that recognition familiarity and perceptual priming are functionally dissociable (Wagner and Gabrieli, 1998; Wagner et al., 1997). Recognition familiarity is either similar for read and anagram-solved items (the present Experiment 1; Jennings and Jacoby, 1993) or is greater for anagram-solved items (Jacoby, 1991; Verfaellie and Treadwell, 1993), whereas perceptual priming is greater for read items (e.g., Allen and Jacoby, 1990; Schwartz, 1989). Further, although Experiment 2 did not demonstrate a statistically significant increase in recognition familiarity with increased conceptual encoding, prior studies indicate that recognition familiarity typically is greater with increased conceptual encoding (Toth, 1996; Wagner and Gabrieli, 1998; Wagner et al., 1997). These

results sharply contrast with demonstrations that perceptual priming is typically unaffected by conceptual encoding (Jacoby and Dallas, 1981).

Collectively, the present and previous studies demonstrate that visual repetition priming is functionally and anatomically distinct from the familiarity process supporting visual recognition memory. In contrast to the assertions of some dual-process theorists, recognition judgments do not appear to be based on the same perceptual nondeclarative memory that subserves perceptual priming. It is important to note these results do not rule out the possibility that some form of nondeclarative memory contributes to recognition. One possibility is that conceptual nondeclarative processes – processes that are mediated by temporal, parietal, and frontal regions (e.g., Fleischman et al., 1995; Gabrieli, Desmond, Demb et al., 1996; Keane, Gabrieli, Fennema et al., 1991; Salmon, Shimamura, Butter et al., 1988; Wagner, Desmond, Demb et al., 1997) and that are preserved in M.S. (Fleischman et al., 1995, 1997; Gabrieli et al., 1995) – support recognition familiarity (Toth, 1996; Wagner et al., 1997). Alternatively, nondeclarative memory processes may make no contribution to recognition, with recognition familiarity entirely reflecting declarative memory operations (Knowlton and Squire, 1995; Squire and Knowlton, 1994; for a review see, Wagner and Gabrieli, 1998). Future studies may serve to clarify the relationship between recognition familiarity and conceptual nondeclarative memory.

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