The visual paired-comparison task as a measure of declarative memory

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Performance on the visual paired-comparison task depends on the integrity of the hippocampal formation in humans, monkeys, and, for an analogous task, in rats. The present study sought additional evidence in healthy volunteers concerning the nature of this task. We found that performance on the visual paired-comparison task was predictive of subsequent recognition memory performance whereas perceptual priming was unrelated to subsequent recognition memory performance. The results are consistent with the data from lesions and suggest that performance on the visual paired-comparison task measures a form of declarative memory.

Human memory can be divided into two major forms: declarative (explicit) and nondeclarative (implicit) (1–3). Declarative memory depends on the hippocampus and anatomically related structures in the medial temporal lobe and diencephalon and supports the capacity for conscious recollection of facts and events. Nondeclarative memory supports a collection of nonconscious learning abilities that are independent of the medial temporal lobe and are expressed in skills, habits, simple forms of conditioning, and the phenomenon of priming.

A well-studied example of nondeclarative memory is perceptual priming (4–7). Perceptual priming refers to an improvement in the ability to detect or identify a stimulus as a result of its recent presentation. For example, an object that has been seen recently can be detected or named more quickly and accurately than a novel object (8–10). Perceptual priming is fully intact even in severely amnesic patients with bilateral damage to the medial temporal lobe who have no detectable capacity for declarative memory (11, 12). Perceptual priming is also independent of recognition memory in healthy individuals (13–16) and appears to depend on changes within posterior cortical areas that are specialized for perceptual operations (7).

In contrast to perceptual priming, recognition memory is a well-studied example of declarative memory and depends on the integrity of the medial temporal lobe and diencephalic structures (17, 18). Although it has been proposed that recognition memory includes a nondeclarative component derived from the phenomenon of perceptual fluency (19–21), several findings argue against this idea. First, the severely amnesic patient E.P. (22) performs at chance on recognition memory tests despite performing normally on many tasks of nondeclarative memory, including perceptual priming (11, 12). E.P. scored at chance even when methods were used to discourage reliance on episodic memory and to encourage reliance on the kind of information that has been proposed to be available from perceptual fluency (12). Second, although improved perceptual fluency can increase the probability that healthy controls (e.g., refs. 23 and 24) and amnesic patients (25) will endorse an item as familiar during a recognition memory test, the increase is similar for both studied and nonstudied items. That is, improved perceptual fluency can shift response bias but does not reliably increase recognition memory accuracy (26). Third, recognition memory in healthy individuals is independent of perceptual priming (13–16). Thus, recognition memory performance appears to provide a relatively pure measure of declarative memory capacity.

Although perceptual priming and recognition memory can be accommodated readily by the distinction between declarative and nondeclarative memory, there are other ways in which experience can modify behavior that resist easy classification. For example, in the visual paired-comparison task (27, 28), two identical pictures are presented side by side for a brief viewing period (e.g., 5 sec). After a delay (e.g., 5 min), one of the previously viewed pictures is presented along with a new picture. The phenomenon of interest is that individuals will look more at the new picture than the old picture. The question naturally arises: What kind of memory is being exhibited in the visual paired-comparison task? On the one hand, the task has many of the features of implicit memory. No reference is made to a study episode, and performance appears to have an automatic quality that is reminiscent of habituation. On the other hand, the direction of gaze is voluntary, and a preference for the new picture could be guided by the same recollective processes that support recognition memory.

Evidence from rats, monkeys, and humans with bilateral lesions of the hippocampus and related structures suggest that the visual paired-comparison task depends on declarative memory. In monkeys and humans, performance on the visual paired-comparison task is markedly impaired after hippocampal damage (29–32) just as other tasks of declarative memory are impaired after hippocampal damage. Further, in the rat, hippocampal lesions impair performance on an object-exploration task that is analogous to the visual paired-comparison task (33). Yet, the concept of declarative memory is meant to be based not just on the importance of the hippocampal formation but also on a particular kind of information processing and on particular operating principles. For example, conscious recollection is important, as well as the achievement of flexible representations based on relationships among stimuli (34, 35). Accordingly, it should be possible to obtain independent evidence from healthy individuals about the kind of information being processed in a task and about the kind of memory that a task requires.

One approach to determining the extent to which a task assesses declarative memory is to ask how well performance on the task predicts (is correlated with) performance on a well studied task of declarative memory (for example, see ref. 13). In the present study, we sought to determine whether performance on the visual paired-comparison task was correlated with performance on a task of recognition memory and whether this correlation was higher than the correlation between a task of nondeclarative memory (perceptual priming) and recognition memory. Participants were tested on two consecutive days. On the first day, half the participants were given the visual paired-comparison task and half were given a parallel task of perceptual

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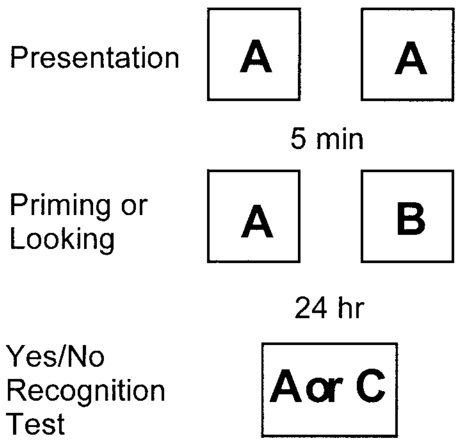

Fig. 1. The experimental procedure. In the presentation phase, all participants saw 24 pairs of identical pictures (A), which appeared simultaneously on two computer screens. Five minutes later, in either the priming test (for the priming group) or the looking phase (for the looking group), participants saw 24 old–new (A–B) pairs of pictures. Finally, 24 h later, participants took a 48-item, yes–no recognition memory test in which the old pictures (A) were targets and completely new pictures (C) were foils. Old and new pictures were seen equally often on the left and right.

priming. On the second day, all participants were given a recognition memory test for the material presented on the previous day. Recognition performance was assessed with three different measures: recognition accuracy, the confidence ratings associated with recognition decisions, and the reaction times for recognition decisions. These measures are generally well correlated with each other (8, 36).

Methods

Participants. The participants were volunteers or employees at the San Diego Veterans Affairs Medical Center or respondents to an advertisement placed in the local newspaper. The priming group (n = 19, 5 men and 14 women) was given a priming task on the first day of testing. These participants averaged 66.1 years of age (range, 49–78), had an average of 15.7 years of education, and obtained WAIS-R (Wechsler Adult Intelligence Scale–Revised) Information and Vocabulary subscale scores of 22.8 and 58.7, respectively. The looking group (n = 20, 7 men and 13 women) was given the visual paired-comparison task on the first day of testing. These participants averaged 68.4 years of age (range, 55–77), had an average of 15.4 years of education, and obtained WAIS-R Information and Vocabulary subscale scores of 21.6 and 56.8, respectively.

Materials and Procedure. Participants were seated approximately 0.7 m in front of two identical laptop computers that were spaced 0.5 m apart and 0.75 m above the floor. The visual angle from the center of one screen to the other was approximately 50°. Testing consisted of three phases: a presentation phase, a test phase (priming or looking), and a recognition test (Fig. 1).

Priming group. In the presentation phase, 24 pairs of identical color photographs of common objects were presented simultaneously on both computer screens for 5 sec each with an interstimulus interval of 5 sec. The order of the pictures was different for each subject. Participants were instructed to say aloud, once and as quickly as possible, the word that named the object on the two screens. Naming latencies were recorded with a tie-clip microphone that was connected to a voice key.

After a 5-min pause, the priming test began. Participants again saw 24 pairs of pictures, 5 sec for each pair (interstimulus interval = 5 sec). One picture appeared on each screen. For each pair of pictures, one was repeated from the first 24 pairs and one was new. The left–right location of the old and new pictures was counterbalanced across the 24 pairs. The order of presentation was pseudorandom, such that a new picture never appeared on the left or right computer screen more than three times in succession. The order of presentation was different for each participant. Before each pair of pictures was presented, and at the end of the 5-sec interstimulus interval, a white cross appeared on either the left or the right computer screen. After 2 sec, the cross disappeared and both photographs appeared simultaneously. Participants were instructed to name, as quickly as possible, the object that appeared on the screen that had displayed the white cross and then to name the object appearing on the other screen. The cross appeared equally often on the left or right computer screen and was followed equally often by an old or new picture. Naming latencies were recorded for the first object named, i.e., the object cued by the white cross.

Approximately 24 h later, participants were given a 48-item recognition memory test. Half the items were the old pictures that had been viewed twice on the previous day (targets). The other half of the items were new pictures that had the same name as an object in one of the old pictures but had not been seen before (foils). All 48 pictures were presented one at a time on a single laptop computer screen and remained on the screen until participants made a yes–no response. The order of the pictures was pseudorandom, such that no more than three old or three new pictures were presented in succession. After participants pressed a key to indicate their decision, the computer screen cleared and was replaced with the question "How sure are you?" Participants then rated their response from 1 ("pure guess") to 5 ("very sure"). No feedback was provided during the recognition test.

In total, each participant saw 72 different photographs: 24 (the old pictures; A in Fig. 1) that appeared in the presentation phase, the priming test, and the recognition memory test; 24 that appeared only as new pictures in the priming test (B in Fig. 1); and 24 that depicted objects with the same name as the old pictures and appeared only as foils in the recognition test (C in Fig. 1). Which pictures were old or new (A and B in Fig. 1) was counterbalanced across participants. Additionally, for half the participants within each counterbalanced group, the pictures used as recognition test foils (C) and the pictures used as old photographs (A) were reversed.

Looking group. Testing involved the same two sets of pictures that were used for the priming group and consisted of three phases: presentation, a looking phase, and a recognition test (Fig. 1). For the presentation phase, 24 pairs of identical pictures were presented in exactly the same manner as for the priming group, except that participants were asked simply to view the pictures rather than to name them. Five minutes later, in the looking phase, participants saw 24 old–new pairs of pictures (5 sec/pair; interstimulus interval = 5 sec) and again were instructed simply to look at them. Approximately 24 h later, a 48-item recognition memory test was given in exactly the same manner as for the priming group. Assignment of the pictures was balanced across participants as described for the priming group.

Data Analysis. Priming scores were based on the naming latencies for the pictures that were named first in each of the 24 pairs during the priming test, i.e., the 12 new pictures and the 12 old pictures that were cued by the white cross. The 12 old pictures that were cued by the white cross represented the primed pictures. The priming score for each participant was the mean naming latency for the 12 new pictures minus the mean naming latency for the 12 old pictures. A positive score indicates priming.

For the looking group, a frame-by-frame analysis of videotape (30 frames per sec) determined the percentage of the 5-sec looking phase during which gaze was directed toward the left or right computer screen. The looking score was the percent time spent looking at the new pictures (and away from the old pictures). Viewing not directed at either screen was not included in the score. Participants almost always maintained their gaze toward one of the two screens (>94% of the time).

In addition to obtaining priming scores for the priming group and looking scores for the looking group, we carried out three analyses to determine how priming and looking related to performance on the next day's recognition memory test. First, for each participant, we compared priming scores and looking scores for pictures that were recognized correctly to priming and looking scores for pictures that were not recognized correctly. Second, for the priming group, we calculated an item-by-item correlation for each participant between the priming score for pictures that were recognized correctly on the next day and the confidence ratings (1 to 5) that were assigned to these same pictures in the recognition test. Similarly, for the looking group, we calculated an item-by-item correlation for each participant between the looking score for pictures that were recognized correctly on the next day and the confidence ratings (1 to 5) assigned to these same pictures in the recognition test.

Finally, for the priming group, we calculated an item-by-item correlation for each participant between the priming score for the primed pictures and reaction times when recognition decisions were made for the same pictures on the next day. Similarly, for the looking group, we calculated an item-by-item correlation for each participant between the looking score and reaction times when recognition decisions were made for the old pictures on the next day. For all item-by-item correlations, a Pearson correlation coefficient (r) was calculated for each participant, converted to a standardized z score (Fisher r-to-z transformation; ref. 37, p. 649), and then averaged across the participants within each group.

Priming scores and looking scores were calculated such that in each case a numerically larger score indicated a stronger effect of the old pictures on behavior. That is, a high priming score reflected strong priming, and a high looking score reflected a strong tendency to look at the new pictures (and away from the old pictures).

Results

On the first day of testing, participants in the priming group demonstrated a robust priming effect (mean ± SEM = 208.3 ± 42 msec; naming time for new pictures = 1,573 ± 48 msec; naming time for old pictures = 1,365 ± 40 msec). The mean priming score was well above 0 ($t[18] = 4.94$, $P < 0.001$).

On the first day of testing, participants in the looking group spent more time looking at the new pictures than the old pictures (mean percent time spent viewing the new pictures ± SEM = 58.8 ± 1.3%; $t[19] = 6.55$, $P < 0.001$). Fig. 2 shows the cumulative percent time spent viewing the new pictures across the 5-sec viewing period. A tendency to look at the new pictures was first detectable ($P = 0.05$) at 1.23 sec into the 5-sec viewing interval. A preference for new pictures over old pictures is the expected finding in this paradigm (e.g., ref. 29).

Recognition scores were similar for the two groups (mean percent correct ± SEM = 84.0 ± 2.3% and 82.1 ± 1.4% for the priming and looking groups, respectively; mean d′ ± SEM = 2.3 ± 0.2 and 2.0 ± 0.1 for the priming and looking groups, respectively). The mean confidence ratings were also similar (mean ± SEM = 4.5 ± 0.1 and 4.3 ± 0.1 for the priming and looking groups, respectively). In addition, for both groups, the mean confidence rating for correctly recognized pictures was higher than the mean confidence rating for incorrectly recognized pictures (4.6 ± 0.1 vs. 4.0 ± 0.2 for the priming group and 4.4 ± 0.1 vs. 3.8 ± 0.1 for the looking group; $t > 3.8$, $P < 0.01$). Finally, the time needed to make recognition memory judgments for correctly recognized old pictures (for the looking group) and primed pictures (for the priming group) was faster than the reaction times for incorrectly recognized old and primed pictures (mean reaction time ± SEM = 3,150 ± 204 msec vs. 6,484 ± 532 msec for the priming group and 3,272 ± 165 msec vs. 5,184 ± 454 msec for the looking group; $t > 4.1$, $P < 0.01$). These results indicate that both confidence ratings and recognition reaction times served as indicators of recognition memory accuracy.

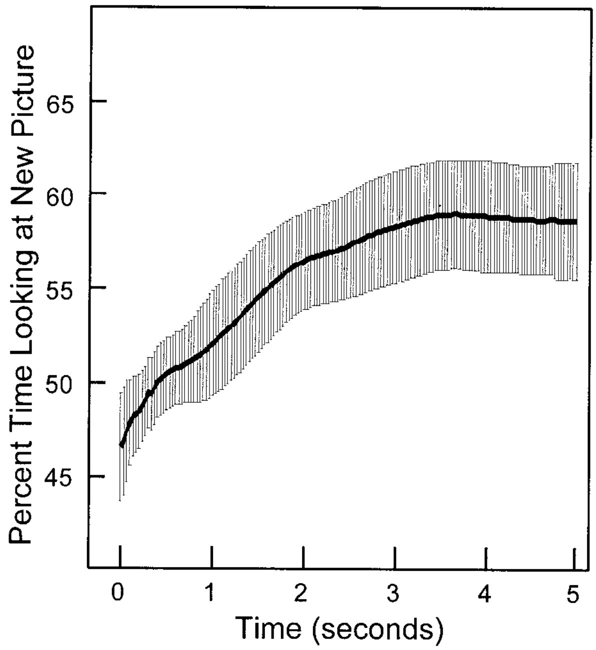

Fig. 2. Mean cumulative percent time spent looking at the novel picture during the 5-sec viewing interval. Thirty data points are plotted per sec. Brackets show 95% confidence intervals.

We next examined the correlation between priming and subsequent recognition performance (in the priming group) and between looking behavior and subsequent recognition memory performance (in the looking group). For the priming group, we found that the priming score was unrelated to recognition performance. For the looking group, we found that a strong tendency to look at the new pictures (and away from the old pictures) during the looking phase was positively correlated with subsequent recognition memory performance. These correlations were significant in the case of the confidence ratings assigned to recognition judgments and in the case of reaction times for recognition memory decisions, but not in the case of recognition accuracy. In addition, the correlations between looking performance and recognition memory performance were significantly higher than the correlations between priming and recognition memory.

Priming, Looking, and Percent Correct Recognition Scores. As predicted, priming was unrelated to recognition performance. The priming score for primed pictures that subsequently were recognized correctly (186 ± 55 msec) was nearly the same as for primed pictures that subsequently were not recognized (196 ± 92 msec; $t[11] = 0.12$, $P > 0.1$). Seven participants correctly recognized all of the primed pictures (mean priming score for these participants = 248 ± 63 msec) and were not included in this comparison.

In the looking group, the tendency to look away from old pictures that were subsequently recognized was only slightly stronger (59.3 ± 1.0% preference for the new pictures) than the tendency to look away from old pictures that later were not recognized (56.3 ± 2.3%). This difference, although in the hypothesized direction, was not reliable ($t[18] = 1.17$, $P = 0.26$).

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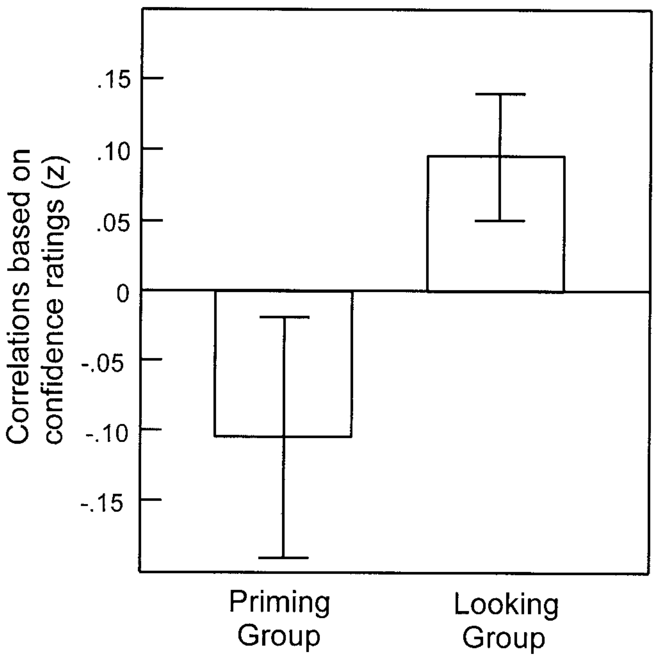

Fig. 3. Mean *z* scores of correlations between recognition confidence ratings and priming scores (*Left*, $n = 19$) and between recognition confidence ratings and percent time spent viewing the novel picture (*Right*, $n = 20$). A positive *z* score indicates a positive correlation. Brackets show SEM.

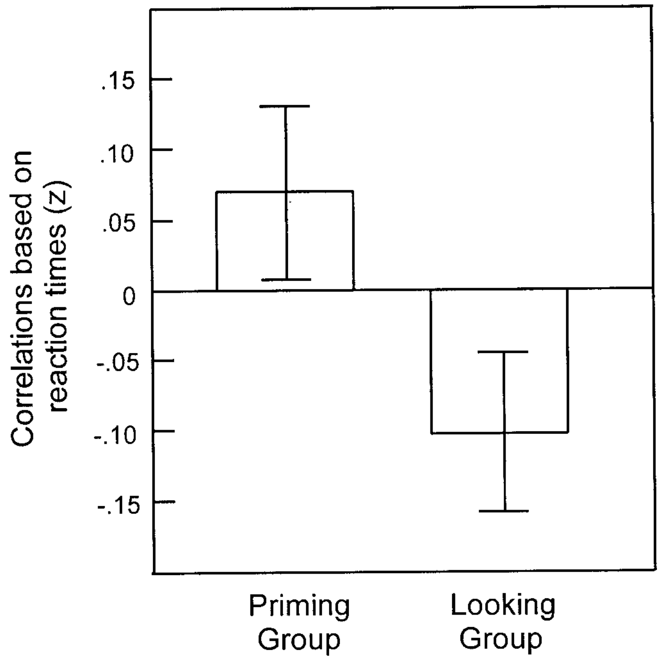

Fig. 4. Mean *z* scores of correlations between recognition reaction times and priming scores (*Left*, $n = 19$) and between recognition reaction times and percent time spent viewing the novel picture (*Right*, $n = 20$). A positive *z* score indicates a positive correlation. Brackets show SEM.

(One participant correctly recognized all of the old pictures and was not included in this comparison.)

Priming, Looking, and Confidence Ratings. We next examined the relationship between the priming score or the looking score and the confidence ratings that were given by participants during the subsequent recognition memory test. First, for each participant in the priming group, we calculated an item-by-item correlation between the priming score and the confidence ratings (1 to 5) assigned to correctly recognized, primed pictures on the next day (see *Data Analysis*). The priming score was unrelated to confidence ratings (mean *z* score of correlations ± SEM = −0.10 ± 0.09; $t[15] = 1.21, P > 0.1$) (Fig. 4). Indeed, the direction of the effect was that a higher priming score was associated with somewhat lower confidence ratings on the next day. [The data from three participants were not included because they selected the highest confidence rating (a rating of 5) for all of the primed pictures that were correctly recognized.]

For the looking group, we hypothesized that a strong tendency to look away from an old picture during the looking phase reflected a strong memory for that picture and, therefore, would predict a high confidence rating when that same picture was recognized correctly on the next day. The results confirmed this expectation. The tendency to look away from old pictures (and toward new pictures) was correlated with high confidence ratings for the same pictures on the subsequent recognition test (mean *z* score of correlations ± SEM = 0.10 ± 0.05, $t[19] = 2.14, P < 0.05$). In addition, the correlation between the looking score and confidence ratings was higher than the correlation between the priming score and confidence ratings ($t[34] = 2.18, P < 0.05$) (Fig. 3).

For both groups, only confidence ratings for correctly recognized pictures were used to calculate correlations because it seemed difficult to interpret confidence ratings associated with incorrect recognition decisions. Nevertheless, the results were the same when the correlations were based on the data for all of the old pictures, whether or not they were recognized correctly (mean *z* score ± SEM = −0.15 ± 0.09 and 0.08 ± 0.03 for the priming and looking groups, respectively; $t[35] = 2.65, P < 0.05$).

Priming, Looking, and Recognition Reaction Times. Finally, we examined the relationship between the priming score or the looking score and the reaction times associated with recognition responses. For each participant in the priming group, we calculated an item-by-item correlation between the priming score for each of the primed pictures and the reaction times when recognition decisions were made for the same pictures on the next day. The results were that priming scores were unrelated to recognition memory reaction times (mean *z* score ± SEM = 0.07 ± 0.06; $t[18] = 1.19, P > 0.1$). In fact, the direction of the correlation indicated that participants tended to make recognition decisions a little more slowly for pictures that were associated with higher priming scores on the previous day.

Finally, for the looking group, we calculated for each participant the correlation between the looking score (the percent time looking at the new pictures and away from the old pictures) and the reaction times when recognition decisions were made for the old pictures on the next day. We hypothesized that a strong tendency to look away from an old picture during the looking phase might be associated with a faster reaction time when that same picture appeared on the recognition test. The results were that participants did tend to make decisions more quickly about pictures that they had spent less time viewing on the previous day. Although this correlation was only marginal (mean *z* score ± SEM = −0.10 ± 0.06; $t[19] = 1.79, P = 0.09$), the correlation between looking and reaction times in the looking group was significantly different from the correlation between priming and reaction times in the priming group ($z = -0.10$ vs. $z = 0.07$; $t[37] = 2.05, P < 0.05$) (Fig. 4).

Discussion

The 19 participants in the priming group exhibited robust priming of picture naming and then on the next day scored 84.0%

correct on the recognition memory test for the pictures they had seen. Similarly, the 20 participants in the looking group exhibited a robust tendency to look at the new pictures in the visual paired-comparison task and then on the next day scored 82.1% on the recognition memory test for the pictures they had seen. The finding of interest was that performance on the visual paired-comparison task was predictive of subsequent recognition memory performance in terms of confidence ratings and reaction times for recognition judgments. In contrast, performance on the priming test was not related to recognition memory performance.

Thus, looking scores were correlated with the confidence ratings that were given when the same pictures appeared later on the recognition memory test. That is, the more one looked away from the old picture in the visual paired-comparison task, the higher the confidence rating assigned to that picture when it appeared on the recognition memory test. In addition, looking scores were correlated with recognition reaction times. That is, the more one looked away from the old picture in the visual paired-comparison task, the faster the reaction time when the same picture was presented for a recognition decision on the next day. Finally, looking scores were only weakly, and not significantly, related to recognition accuracy.

In contrast, priming was unrelated to recognition memory. First, priming scores were nearly the same for pictures that were or were not recognized on the next day. Second, the priming scores were not correlated with the confidence ratings that were assigned to the same pictures on the recognition memory test. Third, the priming scores were not correlated with the reaction times when the same pictures were presented for recognition decisions on the next day. Finally, the correlation between performance on the visual paired-comparison task and performance on the recognition memory task (as measured by both confidence ratings and reaction times) was stronger than the correlation between priming and recognition memory.

Although the findings from the current study were consistent, the effects were quite small. Yet, small effect sizes perhaps are not surprising, considering the nature of the experiment. First, the priming effect and the looking effect are themselves quite small. Previous studies typically have found a priming effect of 50–200 msec for picture naming and looking scores of 60–65%, effect sizes similar to what we observed. These small effect sizes and the variability associated with each measure make it difficult to obtain large correlations with measures of recognition memory performance (accuracy, confidence ratings, and reaction times). Second, for the looking group, the looking effect would seem to work against finding a strong positive correlation between looking scores and recognition memory performance. The finding was that old pictures that were viewed for less time were recognized more quickly and with higher confidence ratings than old pictures that were viewed for more time. Presumably, this correlation emerged because the pictures that were best remembered from the presentation phase were viewed for the least time during the looking test and then were recognized more readily in the recognition test. Nevertheless, it seems reasonable to suppose that less viewing during the looking test worked against good recognition memory and that larger correlations between looking scores and recognition memory performance might have been observed if this presumably counteractive effect of looking time on recognition memory had not been present.

Perceptual priming is a well-studied example of nondeclarative memory and is independent of the hippocampal formation (11, 12). As expected from earlier work (16), participants in our study named old pictures more quickly than new pictures, and this decrease in naming latency for old pictures was unrelated to recognition memory performance on the next day. Indeed, the direction of the observed correlations was such that stronger priming predicted slightly worse recognition memory performance.

In contrast to perceptual priming, performance on the visual paired-comparison task is known to depend on the hippocampal formation in humans, monkeys, and, for an analogous task, in rats (29–33). However, no other information has been available about the nature of the visual paired-comparison task. The findings of the present study suggest that the operating characteristics and the kind of information being processed in the visual paired-comparison task bear some similarity to the characteristics of recognition memory. Moreover, this similarity is stronger than the similarity between perceptual priming and recognition memory. Nevertheless, in view of the small effect sizes we observed, the present study can provide only a first step at clarifying the nature of the visual paired-comparison task, independent of evidence from lesions. The kind of approach described here could be useful in exploring the nature of other tasks as well.

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1. Schacter, D. L. & Tulving, E. (1994) *Memory Systems* (MIT Press, Cambridge, MA).
2. Squire, L. R. & Zola, S. M. (1997) *Philos. Trans. R. Soc. London B* **352,** 1663–1673.
3. Gabrieli, J. D. E. (1998) *Annu. Rev. Psychol.* **49,** 87–115.
4. Richardson-Klavehn, A. & Bjork, R. A. (1988) *Annu. Rev. Psychol.* **39,** 475–542.
5. Roediger, H. L. & McDermott, K. (1993) in *Handbook of Neuropsychology*, eds. Boller, F. & Grafman, J. (Elsevier Science, Amsterdam), vol. 8, pp. 63–132.
6. Tulving, E. & Schacter, D. L. (1990) *Science* **247,** 301–306.
7. Schacter, D. L. & Buckner, R. L. (1998) *Neuron* **20,** 185–195.
8. Cave, C. & Squire, L. R. (1992) *J. Exp. Psychol. Learn. Mem. Cognit.* **18,** 509–520.
9. Jacoby, L. L. & Dallas, M. (1981) *J. Exp. Psychol. Gen.* **3,** 306–340.
10. Schacter, D. L. (1994) in *Memory Systems*, eds. Schacter, D. L. & Tulving, E. (MIT Press, Cambridge, MA), pp. 233–268.
11. Hamann, S. B. & Squire, L. R. (1997) *Behav. Neurosci.* **111,** 850–854.
12. Stark, C. E. L. & Squire, L. R. (2000) *Behav. Neurosci.* **114,** 459–467.
13. Hayman, C. G. & Tulving, E. (1989) *J. Exp. Psychol.* **15,** 228–240.
14. Tulving, E., Schacter, D. L. & Stark, H. A. (1982) *J. Exp. Psychol. Learn. Mem. Cognit.* **8,** 336–342.
15. Stark. C. E. L. & McClelland, J. L. (2000) *J. Exp. Psychol. Learn. Mem. Cognit.* **26,** 945–972.
16. Mitchell, D. B. & Brown, A. S. (1988) *J. Exp. Psychol. Learn. Mem. Cognit.* **14,** 213–222.
17. Reed, J. M. & Squire, L. R. (1997) *Behav. Neurosci.* **111,** 667–675.
18. Manns, J. R. & Squire, L. R. (1999) *Hippocampus* **9,** 495–499.
19. Gardiner, J. M. & Java, R. I. (1993) in *Theories of Memory*, eds. Collins, A., Gathercole, S., Conway, M. & Morris, P. (Erlbaum, Hillsdale, NJ), pp. 163–188.
20. Jacoby, L. (1991) *J. Mem. Lang.* **30,** 513–541.
21. Mandler, G. (1980) *Psychol. Rev.* **87,** 252–271.
22. Stefanacci, L., Buffalo, E. A., Schmolck, H. & Squire, L. R. (2000) *J. Neurosci.* **20,** 7024–7036.
23. Johnston, W. A., Dark, W. J. & Jacoby, L. L. (1985) *J. Exp. Psychol. Learn. Mem. Cognit.* **11,** 3–11.
24. Whittlesea, B. W. A. (1993) *J. Exp. Psychol. Learn. Mem. Cognit.* **19,** 1235–1253.
25. Cermak, L. S., Verfaellie, M. & Chase, K. A. (1999) *Neuropsychology* **9,** 281–290.
26. Reber, P. J. & Squire, L. R. (1999) *Mem. Cognit.* **27,** 501–511.
27. Fantz, R. L. (1964) *Science* **146,** 668–670.
28. Fagan, J. F. (1970) *J. Exp. Child Psychol.* **9,** 217–226.
29. McKee, R. D. & Squire, L. R. (1993) *J. Exp. Psychol. Learn. Mem. Cognit.* **19,** 397–404.
30. Bachevalier, J., Brickson, M. & Hagger, C. (1993) *Learn. Mem.* **4,** 77–80.
31. Pascalis, O. & Bachevalier, J. (1999) *Hippocampus* **9,** 609–616.
32. Zola, S. M., Squire, L. R., Teng, E., Stefanacci, L., Buffalo, E. A. & Clark, R. E. (2000) *J. Neurosci.* **20,** 451–463.
33. Clark, R. E., Zola, S. M. & Squire, L. R. (2000) *J. Neurosci.,* in press.
34. Squire, L. R. (1992) *Psychol. Rev.* **99,** 195–231.
35. Eichenbaum, H. (1997) *Annu. Rev. Psychol.* **48,** 547–572.
36. Juslin, P., Olsson, N. & Winman, A. (1996) *J. Exp. Psychol. Learn. Mem. Cog.* **22,** 1304–1316.
37. Hays, W. L. (1994) *Statistics* (Harcourt Brace, Fort Worth, TX).