An Electrophysiological Signature of Unconscious Recognition Memory

Joel L. Voss[*] and **Ken A. Paller**

Interdepartmental Neuroscience Program and Department of Psychology Northwestern University 2029 Sheridan Rd Evanston, Il 60208

Abstract

Contradicting the common assumption that accurate recognition reflects explicit-memory processing, we describe evidence for recognition lacking two hallmark explicit-memory features: awareness of memory retrieval and facilitation by attentive encoding. Kaleidoscope images were encoded in conjunction with an attentional diversion and subsequently recognized more accurately than those encoded without diversion. Confidence in recognition was superior following attentive encoding, though recognition was remarkably accurate when people claimed to be unaware of memory retrieval. This "implicit recognition" was associated with frontal-occipital negative brain potentials at 200-400 ms post-stimulus-onset, which were spatially and temporally distinct from positive brain potentials corresponding to explicit recollection and familiarity. This dissociation between behavioral and electrophysiological characteristics of "implicit recognition" versus explicit recognition indicates that a neurocognitive mechanism with properties similar to those that produce implicit memory can be operative in standard recognition tests. People can accurately discriminate repeat stimuli from new stimuli without necessarily knowing it.

Keywords

explicit memory; implicit memory; memory systems; forced-choice recognition; familiarity; recollection; event-related brain potentials; ERP

The dramatic differences between *explicit memory* and *implicit memory* have shaped memory research ever since their seminal descriptions in patients with amnesia.[1-5] Explicit memory is commonly measured in tests of recall and recognition, and is intimately linked with the conscious awareness of memory retrieval. In contradistinction, implicit memory can guide behavior without the awareness of memory retrieval, and is measured in priming tests and other tests that make no reference to prior learning (implicit memory tests). We sought answers to a set of fundamental questions regarding explicit and implicit memory: can

Address correspondence to: Joel L. Voss Phone (847) 467-3370 Fax (847) 491-7859 joelvoss@illinois.edu.
[*]Current address: The Beckman Institute for Advanced Science and Technology University of Illinois Urbana-Champaign Urbana, Il 61801 USA

implicit-memory processes guide responses in an explicit recognition test, and if so, under what circumstances and by means of what neural mechanisms?

Many researchers have explored cognitive and neurophysiological distinctions between explicit memory and perceptual implicit memory. A consensus view is that they rely on distinct brain networks and that only explicit memory is disrupted in amnesia.[2, 4-7] Explicit memory depends on coordinated processing in the hippocampus and cerebral cortex, whereas perceptual implicit memory is thought to result from repetition-related processing fluency within cortical networks involved in perception.[8-11] Furthermore, electrophysiological and brain-imaging studies indicate that explicit memory and implicit memory can be dissociated in intact brains.[12-19]

Nevertheless, some evidence supports the notion that implicit-memory processes can influence explicit memory, or, more specifically, that enhancing the perceptual fluency that supports implicit memory can sometimes bias performance on recognition tests.[20-24] Although these influences have been characterized as negligible,[20] it is possible that implicit-memory processes exert appreciable influences on recognition in particular circumstances. Identifying the neural basis of these influences, and the experimental factors that serve to emphasize or deemphasize them, is thus vital to investigations of the neurocognitive basis of both explicit memory and implicit memory, and of possible interactions between the two.

We recently described behavioral evidence for explicit recognition based on an implicit perceptual-fluency signal in the visual modality.[25] Recognition for kaleidoscope images learned under the challenge of a concomitant attentional diversion was superior to that with no attentional challenge at study. Given that dividing attention at encoding reduces explicit memory,[26] this result was opposite to the predicted outcome if explicit memory had guided recognition. Critically, this surprising influence of attention occurred only when repeat items (targets) and similar novel items (foils) were presented with temporal proximity sufficient to permit comparison of their relative visual fluency during two-alternative forced-choice recognition testing. In this testing format, repetition-induced perceptual fluency can provide a reliable and valid memory cue. Indeed, divided attention during encoding was harmful to subsequent recognition accuracy when targets and foils were temporally segregated in yes-no format tests, as well as when each target was not paired with a visually-similar foil in forced-choice tests. We thus inferred that implicit-memory processing contributed to forced-choice recognition. However, further evidence is needed to demonstrate whether retrieval processing responsible for this novel influence of visual fluency on recognition can be dissociated from the explicit-memory mechanisms generally thought to support recognition.

In the present study, we sought a neural validation of *implicit recognition* (recognition based on implicit-memory processes) using event-related potential (ERP) methods for recording brain activity. As in the experiments reported by Voss and colleagues,[25] we examined memory for kaleidoscope images using forced-choice recognition testing with a highly similar foil in each trial. We analyzed neural signals of memory processing as a function of encoding conditions and of the level of awareness of memory retrieval. Generally, recognition accompanied by remembering of specific details from the learning context is

referred to as *recollection*, whereas recognition accompanied only by a vague feeling of "knowing" is referred to as *familiarity*. We compared brain potentials associated with these two types of explicit recognition, as measured using a modified "remember/know paradigm,"27-29 to those of recognition without retrieval awareness. We were thus able to determine the extent to which these theoretically different memory phenomena occur in conjunction with signals of distinct neural mechanisms.

Results

Kaleidoscope images were studied with either full attention or divided attention, and then the same images (targets) were discriminated from visually similar foils during forced-choice recognition testing (Fig. 1). Accuracy was higher for targets studied with divided attention than for targets studied with no attentional diversion [Fig. 2A; $t(11)=2.4$, $p=0.03$]. Although divided attention did not disrupt recognition accuracy, it did disrupt metamemory (Fig. 2B). *Remember* and *know* decisions made after the recognition response signified the explicit-memory experiences of recollection and familiarity, respectively, and *guess* decisions signified the absence of retrieval awareness. Although subjective ratings of awareness are notoriously limited by subjects' abilities to introspect accurately, meaning that the guess condition may actually include some low-level retrieval awareness, this concern is mitigated by the divergence between findings for know trials and guess trials, as described below.

Recognition responses accompanied by remember decisions were more common following full- compared to divided-attention encoding [$t(11)=6.7$, $p<0.01$], whereas recognition responses accompanied by guess decisions were more common following divided- compared to full-attention encoding [$t(11)=8.5$, $p<0.01$]. Taken together, recognition accuracy and recognition awareness were influenced by encoding conditions in an apparently counterintuitive manner—stimuli encoded when attentional resources were diverted were subsequently recognized more accurately, despite less awareness of retrieval.

An analysis of accuracy for each metamemory category (Fig. 2C) indicated that guess decisions were highly accurate. The accuracy of guess decisions was higher than the accuracy of know decisions for both full-attention encoding [$t(11)=2.3$, $p=0.05$] and divided-attention encoding [$t(11)=7.9$, $p<0.01$]. Interestingly, guess accuracy was higher for items encoded with divided-attention compared to items encoded with full-attention [$t(11)=3.5$, $p<0.01$], suggesting that the efficacy of the retrieval processing that produced guess decisions was enhanced by impoverished attention during encoding. It thus appears that higher recognition accuracy following encoding with divided- compared to full-attention resulted from highly accurate guess decisions, which predominated in the divided-attention condition.

The pattern of behavioral results in Fig. 2C indicates that retrieval processes operative during guess decisions were distinct from those responsible for recognition with retrieval awareness (i.e., either recollection or familiarity). A reasonable expectation is that guess decisions, to the extent that they show any evidence of accuracy, result from a weaker

expression of the same retrieval processes that produce recognition with retrieval awareness. On the contrary, we found that guess decisions were more accurate than know decisions.

ERP results shed further light on the neurocognitive foundations of responding based on remembering, knowing, and guessing. For the half of the trials in which testing concerned an item encoded with full attention, Fig. 2D contrasts ERPs for three conditions: old items correctly endorsed with remember decisions, old items correctly endorsed with know decisions, and their corresponding correctly rejected foils (including all trials with either a remember or know metamemory decision).

ERPs at approximately 180-220 ms displayed a positive potential that was least positive for new items, most positive for remember, and intermediate for know (correct trials only). A linear trend for these three conditions was statistically significant for the anterior and posterior electrode clusters indicated in Fig. 2D [$F(1.6,18.0)=10.8$, $p<0.01$ and $F(1.9,21.1)=15.3$, $p<0.01$, respectively]. This latency interval captured the first observed positive ERP deflection at anterior and central recording sites, and we refer to this linear trend as a graded P200 effect.

A second old/new ERP difference following full-attention encoding encompassed late-onset positive potentials with a posterior-maximum distribution, referred to as the late positive complex (LPC). ERP amplitudes to remember and to know items were more positive than to new items from 600-900 ms at the anterior and posterior electrode clusters [condition main effects $F(1.2,13.6)=5.8$, $p=0.03$, and $F(1.3,14.0)=18.9$, $p<0.01$, respectively; $p<0.05$ for pairwise old/new comparisons], without significant differences between remember and know [anterior $F(1,11)=0.12$, ns; posterior $F(1,11)=0.23$, ns]. To summarize, we observed a P200 old/new difference and an LPC old/new difference; whereas P200 amplitudes were also greater for remember compared to know conditions, LPC amplitudes were approximately the same for these two conditions.

Fig 2E shows old/new ERP differences following encoding with divided attention. The key contrast was between old items correctly endorsed with guess decisions and new items from the same test trials. Strikingly, ERPs from 200-400 ms were more negative for guess items compared to new items for both anterior and posterior electrode clusters [$F(1,11)=10.8$, $p<0.01$ and $F(1,11)=15.5$, $p<0.01$, respectively]. This old/new ERP difference averaged -0.9 µV over this time interval for the two electrode clusters, and appeared to begin as early as about 175 ms after stimulus onset. This early-onset negative repetition effect was distinct from ERP correlates of remember and know decisions, which were both positive during the same time interval.

The ERP analyses above were advantageous because ERPs to old and new items in each old/new contrast derived from the same test trials. However, one possible shortcoming is that old/new contrasts for remember and know conditions came from full-attention encoding trials whereas old/new contrasts for the guess condition came from divided-attention encoding trials. We also computed ERPs by first collapsing trials from the two encoding conditions together. Given that the relative proportion of full- versus divided-attention trials varied systematically as a function of metamemory response (Fig 2A), it is possible that

old/new ERP contrasts collapsed across encoding condition could obscure the potential influence of encoding condition on these effects. This concern could be obviated if the different types of old/new ERP effects described thus far (P200 and LPC vs. early negativity) could be ascribed more directly to retrieval processing rather than to encoding condition per se. To address this issue, data were analyzed from a subset of subjects with a suitable number of trials for assessing ERPs for guess responses to stimuli studied with full attention (Supplementary Fig. 1) and likewise for ERPs for know responses to stimuli studied with divided attention (Supplementary Fig. 2). In both cases, ERPs were highly similar to the main findings presented in Fig. 2. For example, for the early-onset negative shifts for guess trials, the mean old/new amplitude difference was -0.7 μV following full-attention encoding, compared to -0.8 μV following divided-attention encoding in these same eight subjects and -0.9 μV for the whole group (for both electrode clusters from 200-400 ms). For the LPC for know trials, the mean old/new amplitude difference was 1.2 μV following divided-attention encoding, compared to 1.1 μV following full-attention encoding in these same eight subjects and 0.8 μV for the whole group (for the posterior electrode cluster from 600-900 ms). This indicates that ERP dissociations between know and guess responses did not result from the encoding manipulation per se, even though encoding condition clearly influenced the outcome of recognition and metamemory decisions The essential variable to take into account was whether recognition was accompanied by a remember, know, or guess response.

Topographic maps of the old/new ERP differences appear in Fig. 3 for correct remember, know, and guess decisions, all relative to correctly rejected new items. In this analysis, the same correct-rejection baseline ERPs were used in all old/new contrasts so that they could be compared with each other. Thus, new items came from correct trials, regardless of whether the target was encoded with full attention or divided attention, and regardless of the metamemory decision. Likewise, encoding conditions were collapsed for targets. Qualitative differences were readily apparent between ERP correlates of guess-recognition and remember/know-recognition, whereas a high degree of qualitative similarity was evident for the remember and know contrasts. The reliability of these observations was assessed via the vector-normalization procedure, in which a significant condition-by-electrode interaction term following the removal of overall amplitude differences indicates distributional differences for two conditions. Analyses included consecutive 100-ms intervals from 0 ms to 800 ms. The guess old/new distribution differed significantly from both the remember and know old/new distributions from 200-400 ms [$F(7.1,78.5)=2.4$, $p=0.02$ and $F(7.3,80.0)=2.5$, $p=0.02$ for remember and know, respectively] and from 600-700 ms [$F=(6.9,76.6)=2.2$, $p=0.04$ and $F(8.7,95.7)=2.5$, $p=0.01$, respectively]. Topographies did not differ significantly for other intervals (interaction term p value range was 0.14-0.53). In contrast, the remember and know old/new distributions did not differ reliably for any 100-ms interval (interaction term p value range was 0.28-0.71). Fig. 3 thus indicates a topographic dissociation between ERP old/new effects for guess decisions versus remember and know decisions.

Relationships among neural mechanisms supporting remember, know, and guess decisions were further explored via a correlational analysis of averaged ERP difference values. A finding that two retrieval-awareness categories (i.e., remember and know) are associated

with qualitatively different neural correlates would suggest that these two categories are manifestations of different neural mechanisms. Alternatively, the conclusion that two retrieval-awareness categories are manifestations of the same basic memory processing would be consistent with evidence that they are indexed by similar electrophysiological signatures. In this analysis, electrodes were divided into seven clusters covering major scalp regions. For each subject, difference ERP amplitudes for each of the three metamemory categories were computed relative to a new-item baseline (collapsing across the two encoding conditions for targets, and for corresponding foils collapsing across the two encoding conditions and the three possible metamemory decisions for correct recognition of corresponding targets). Amplitude values were averaged for consecutive 100-ms intervals from 0 ms to 800 ms and for each electrode cluster. Across-subject correlations were then computed between the *remember-minus-new and the know-minus-new* difference, between the *guess-minus-new and know-minus-new* difference, and between the *remember-minus-new and the guess-minus-new* difference for each cluster/interval. As indicated in Fig. 4, difference values were positively correlated for remember and know conditions for every electrode cluster and latency interval from 100-200 ms onward, indicative of the activity of a common retrieval process. In contrast, guess and remember/know conditions were not systematically related, indicative of distinct retrieval processes.

Discussion

Behavioral and electrophysiological indications of explicit memory were exhibited in conjunction with correct recognition of abstract visual images in a two-alternative forced-choice test. Correct recognition decisions in these cases were accompanied by a metamemory decision designated either remember or know. Subjects were asked to indicate a remember decision when they recognized a stimulus and also felt able to recall specifics concerning the earlier episode when they first viewed the stimulus; know decisions signified recognition with a feeling of familiarity and without retrieval of the study-phase context. Remember decisions were more accurate than know decisions, and remembering was less likely following encoding with divided than with full attention, as expected.[26, 30]

In contrast, properties commonly associated with explicit memory were not found in conjunction with correct recognition when designated a guess, rather than remember or know. One hallmark feature of implicit memory is that it can occur without the awareness of memory retrieval, precisely the circumstances of correct recognition guesses in the present experiment. In addition, attentive encoding apparently did not facilitate recognition with correct guessing. Rather, guess responses were more accurate following divided- compared to full-attention encoding. Moreover, recognition responses for guesses were surprisingly accurate, even more accurate than those accompanied by know decisions—a pattern opposite to the outcome expected if guesses merely reflected a weaker version of the explicit retrieval driving know responses. Guess responses were also about twice as prevalent following divided- compared to full-attention encoding, such that overall recognition accuracy was higher with divided-attention encoding compared to full-attention encoding.

Recognition accompanied by subjective reports of recollection or familiarity was indexed by positive shifts in LPC and P200 potentials. Previously, LPC potentials have been

consistently associated with successful retrieval based on explicit memory,31-34 and possibly reflect the concerted involvement of parietal cortex and medial temporal structures. 35 Recollection and familiarity were associated with LPC effects of similar magnitude, indicating consistent influences of these processes across both conditions. P200 potentials, though seldom observed in ERP studies of recognition memory, have been linked to the matching of immediately-available visual information to perceptual representations stored in memory.36-39 Larger P200 potentials for recollection versus familiarity therefore might indicate that the extent of perceptual matching correlates with the efficacy of explicit retrieval and its subsequent phenomenological salience. We did not identify qualitatively distinct neural signatures for recollection and familiarity, which is consistent with the proposition that these metamemory measures tap differing degrees of the same explicit retrieval process rather than distinct retrieval processes.40,41

Critically, accurate recognition without retrieval awareness triggered none of the ERP old/new effects commonly linked with explicit memory or found here for remember and know decisions. Instead, correct guesses were indexed by rapid-onset, negative old/new effects with foci at occipital and left frontal recording sites. Whereas ERP indices of recollection and familiarity were highly correlated across space and time, ERP indices of implicit recognition were essentially uncorrelated with those of recollection and familiarity.

We thus conclude that recognition was supported by explicit-memory processing when accompanied by recollection and familiarity, whereas highly accurate guess decisions were not supported by explicit-memory processing. By dissociating the neural signature of highly accurate guesses from that of familiarity memory, we provide an unprecedented demonstration of the distinctive nature of overt recognition derived from unconscious memory—a phenomena we describe as "implicit recognition."

Not only do these behavioral and electrophysiological results imply that explicit memory did not underlie this implicit recognition, but a further speculation is that implicit recognition was derived from neural events typically responsible for repetition-based perceptual fluency enhancements in perceptual implicit memory tests. The finding of negative old/new ERP effects at 200-400 ms for correct guesses prompts an intriguing connection across experiments. Similar negative ERPs have been attributed to perceptual implicit memory observed in the absence of explicit memory18 and also in association with corresponding encoding events,14 though facial stimuli were used in the former study and verbal stimuli in the latter study. Furthermore, the spatial distribution of ERP correlates of implicit recognition observed here is consistent with a recent framework proposed by Schacter and colleagues.10 In this framework, negative repetition effects in early visual cortex reflect stimulus-specific perceptual fluency enhancements,11 and negative repetition effects in left prefrontal cortex mediate the behavioral ramifications of this visual processing fluency on priming measures during implicit memory tests. Temporary neurodisruptive interference of left prefrontal processing42 could be used to test its causal role in implicit recognition in future studies. Further leverage for interpreting the functional significance of occipital negative repetition effects could be gained if these effects could be related to behavioral manifestations of fluency, such as priming, although it has been argued that occipital fluency effects are generally not strongly related to behavioral measures of priming.10 Although

evidence of this sort could provide a closer connection between implicit recognition and priming in implicit memory tests, physiological data from the present experiment are sufficient to demonstrate that the mechanisms responsible for implicit recognition were distinct from those responsible for explicit memory, in keeping with previous neuroanatomical dissociations between implicit and explicit memory.4, 6, 7, 43

It is important to note that, despite long-standing suggestions from cognitive psychology that perceptual fluency can cue recognition,28, 44, 45 it has never previously been shown that implicit-memory mechanisms can exert powerful influences on recognition. Our novel paradigm and neuroimaging measures thus provide the first neural validation for the role of implicit visual fluency in recognition. Furthermore, these findings indicate that recognition memory derives from multiple memory systems, including those that operate both explicitly and implicitly.

The current experiment provides several advantages over our previous description of implicit recognition.25 Because items studied with full attention and divided attention were intermixed at test, it is possible to dismiss the notion that our previous use of blocked study/ test conditions led to implicit recognition only as an artifact of retrieval orientation. In addition, the use of remember/know metamemory measurements expanded the sense in which implicit recognition could be contrasted with explicit memory. However, the experiments diverged in several ways, including (a) the number of experimental blocks, (b) the numbers of items in each block, (c) the use of metamemory measurements, and (d) the combination of tests (repeated two-interval forced-choice recognition testing in the current experiment vs. two-alternative forced-choice testing and yes-no testing in the prior experiments). Whereas the finding of higher recognition accuracy with divided-attention encoding than with full-attention encoding has now been replicated in multiple experiments, indicating its robustness, the difference was somewhat reduced in the current experiment (71% vs. 67%, respectively, as opposed to 72% vs. 59% and 73% vs. 61% in Experiments 1 and 2 of Voss et al.26), perhaps due to the need to memorize so many more stimuli.

In the present experiment, recognition accuracy restricted to guess responses was higher for items studied with divided versus full attention. Elaborative encoding may have been relatively more feasible for images presented without the concurrent working-memory task, and may have led to a greater tendency to rely on explicit-memory processes. In contrast, differential accuracy as a function of encoding condition was not observed in Experiment 2 of Voss et al.26 That experiment, however, included far fewer trials than the present experiment, such that for many subjects there were only one or two guess responses in the full-attention condition. A further analysis of those data, including only subjects with three or more such trials, revealed a trend for higher accuracy for divided-attention versus full-attention encoding [81.4% versus 72.1%; $t(7)=2.3$, $p=0.05$]. High trial counts for both conditions in the current experiment provided sufficient power for revealing a robust effect of encoding condition on recognition accuracy for guess trials.

Several features of these experiments, by design, likely served to enhance the contribution of implicit-memory processing to recognition. One factor may be the reduced potential for explicit-memory processing. Semantically elaborative encoding and semantic retrieval

strategies are strongly associated with explicit-memory processing[29, 30] but could not easily be deployed for kaleidoscope images. Furthermore, the high perceptual similarity between targets and foils should have enhanced the utility of stimulus-specific perceptual fluency. Indeed, behavioral evidence for implicit recognition was eliminated in previous experiments by reducing target/foil similarity.[25]

Our results indicate that nominally "explicit" memory tests can be constructed such that they are preferentially sensitive to influences from implicit memory. Forced-choice testing, high similarity between targets and corresponding foils, low usefulness of conceptual or contextual information, and procedures that discourage analytic or prolonged retrieval strategies are key features that promote implicit influences.[25] The current findings thus provide indirect evidence for the notion that recognition testing in nonhuman animals might in some cases not provide valid indices of explicit memory,[46, 47] given that these tests frequently include such features. In investigations of human amnesia, forced-choice recognition tests with high target/foil similarity have been used to probe the neuroanatomical foundations of explicit familiarity memory,[48-50] and so further evidence is also needed to determine the extent to which these tests assess implicit recognition. Moreover, our findings hint at the possibility that implicit recognition could be operative even in recognition tests that do not include all these features, perhaps just on a subset of trials.

Because previous studies have been premised on the widely accepted assumption that recognition performance is based only on explicit-memory processing, our results complicate, but also enrich, the search for the neural and cognitive mechanisms of memory. Implicit memory must be taken into account in studies of recognition. We envision future explorations of implicit recognition leading to a better understanding of the multiple neurocognitive influences that determine memory performance.

Methods

Visual stimuli included 336 kaleidoscope images created by overlaying three opaque hexagons of different color and performing three rounds of side bisection and random deflection on each. These images were divided into 168 pairs. High similarity between the members of each pair was achieved by using the same three colors and deflecting each matching-color hexagon at similar random angles ($<10°$ difference). Pairs were further subdivided into 14 sets, such that a different selection of three hexagon colors was used for each set.

Kaleidoscope stimuli were presented to individuals (*N*=12, all right-handed, 5 male, 18 to 26 years old, provided informed written consent) during 14 study-test blocks. All stimuli in a given block were created with the same three hexagon colors. During each study session, subjects viewed 12 target images that later appeared again during the corresponding recognition test. Each target comprised one member, assigned randomly for each subject, from each of the 12 stimulus pairs from a set. Matching-color stimulus sets were randomly assigned to study-test blocks for each subject.

Each study session was divided in half, with six targets studied with full attention during one half and six with divided attention during the other half (Fig 1AB). Each target was presented one time for 2000 ms with a variable 1500-2000 ms interstimulus interval, in randomized order. Divided-attention encoding included a concomitant 1-back task involving odd/even judgments to spoken digits. A 1000-ms prompt presented 3000 ms before the first divided-attention trial was used to notify the subject of the divided-attention task. Spoken digits were presented only for divided-attention trials. For each divided-attention trial (except the first), subjects pressed a button to indicate whether the digit spoken on the previous trial was odd or even. There were eight stimuli in each full- and divided-attention portion, as the six targets were bracketed by primacy and recency buffers, each one a unique, similar-format kaleidoscope image that did not appear during the recognition test. The order of the full- and divided-attention portions was alternated across study-test blocks.

A forced-choice recognition test followed each study session after a 45-s delay during which subjects performed mental arithmetic for 30 s and then were reminded of test instructions. Each trial included one of the 12 studied targets and its corresponding visually-similar foil, presented in an alternating stimulus train that allowed subjects to compare the two stimuli while maintaining visual fixation (Fig 1C). Targets and foils each appeared three times during a trial, for 500 ms per presentation with a variable 800-1200 ms interstimulus interval. Targets were randomly assigned to the first or second position with the constraint that the target was first in six trials in each test session. Subjects were instructed to indicate the position of the stimulus they thought was the target. A recognition prompt was presented at a delay of one interstimulus interval from the last stimulus in the train, and was accompanied by an alerting tone. All response times were less than 700 ms (mean=462 ms, *SEM*=112). Subjects then reported on their awareness of memory retrieval via a modified remember/know paradigm. A *remember* response indicated that recognition was accompanied by retrieval of some contextual detail regarding the initial study-session encounter with the recognized stimulus. A *know* response indicated selection confidence but with no details retrieved. Subjects were instructed to make this response if they experienced any feeling of familiarity for the selected item. A *guess* response was made when there was no confidence in the selection and no contextual details were retrieved. Subjects were instructed to make this response when they experienced "absolutely no feeling of familiarity for the selected item" and were "guessing because they were forced to select one kaleidoscope or the other." The metamemory prompt immediately followed the recognition decision, and the average response time was 532 ms (*SEM*=155 ms). The next trial began after a variable delay of 1000-1500 ms. Trial order was randomized such that trials containing targets studied with full attention were intermixed with those containing targets studied with divided attention. Subjects practiced performing the 1-back odd/even task and an abbreviated study-test block prior to experimental blocks.

Stimulus-locked event-related potentials were extracted from continuous electroencephalographic recordings made during test sessions. Recordings were made from 59 evenly distributed scalp locations using tin electrodes embedded in an elastic cap. Five additional recording locations included the left mastoid and four locations for monitoring eye movements in horizontal and vertical directions. Recordings were referenced to right

mastoid, and rereferenced offline to average mastoids. Electrode impedance was 5 kΩ. Signals were amplified with a band pass of 0.05 to 200 Hz and sampled at 1000 Hz. Stimulus-locked activity was extracted for 1000-ms epochs beginning 100 ms prior to the onset of each item during the test session. Baseline correction was performed using mean prestimulus amplitudes. Epochs contaminated by artifacts were discarded. The mean trial count (±*SEM*) for each condition (corresponding to ERPs in Figures 2 and 3) was as follows: 55±5 for full-attention encoding/remember, 37±4 for full-attention encoding/know, 70±6 for full-attention encoding/new with remember and know metamemory decisions collapsed, 51±4 for divided-attention encoding/guess, 68±5 for divided-attention encoding/new with guess metamemory decisions, 77±9 for remember with encoding condition collapsed, 59±7 for know with encoding condition collapsed, 89±6 for guess with encoding condition collapsed, and 195±4 for new with encoding condition and type of metamemory decision collapsed (for new items, encoding condition refers to that of the corresponding target in that trial and type of metamemory decision refers to the response to that target).

Single-trial ERPs were averaged for each condition of interest, which included targets and foils segregated by response accuracy and metamemory judgment. Only trials with correct responses were considered in the main ERP analyses (i.e., approximately 70% of all trials). In a subsidiary analysis, we examined all the incorrect trials and found that ERPs were virtually indistinguishable for old versus new items, even when taking metamemory judgment into account.

Whereas ERP averages in the main analysis were derived from all three presentations of a stimulus during each recognition test trial, ERP differences among the three presentations were negligible for all conditions for the subset of subjects with suitable trials counts to examine these effects (*N*=9). Furthermore, the pattern of ERP differences across metamemory condition was qualitatively similar to that in the main analysis when ERP computations included first presentations only, as indicated in Supplementary Fig. 3 (*N*=10).

Statistical comparisons were made using repeated-measures ANOVA for amplitudes averaged over latency intervals and electrode clusters, with Geisser-Greenhouse corrections when necessary. Temporal filtering included a 45-Hz low-pass zero-phase-shift Butterworth filter for presentation purposes only.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

References

1. Claparede, E. Recognition and 'me-ness'. In: Rapaport, D., editor. Organization and pathology of thought. Columbia University Press; New York: 1951. p. 58-75.

2. Gabrieli JD. Cognitive neuroscience of human memory. Annu Rev Psychol. 1998; 49:87–115. [PubMed: 9496622]

3. Scoville WB, Milner B. Loss of recent memory after bilateral hippocampal lesions. J Neurol Neurosurg Psychiatry. 1957; 20:11–21. [PubMed: 13406589]

4. Squire LR. Memory systems of the brain: A brief history and current perspective. Neurobiol Learn Mem. 2004; 82:171–177. [PubMed: 15464402]

5. Schacter DL. Implicit memory: History and current status. J Exp Psychol Learn Mem Cogn. 1987; 13:501–518.

6. Hamann SB, Squire LR. Intact perceptual memory in the absence of conscious memory. Behav Neurosci. 1997; 111:850–854. [PubMed: 9267663]

7. Stark CE, Squire LR. Recognition memory and familiarity judgments in severe amnesia: No evidence for a contribution of repetition priming. Behav Neurosci. 2000; 114:459–467. [PubMed: 10883797]

8. Henson RN. Neuroimaging studies of priming. Prog Neurobio. 2003; 70:53–81.

9. Schacter DL, Buckner RL. Priming and the brain. Neuron. 1998; 20:185–195. [PubMed: 9491981]

10. Schacter DL, Wig GS, Stevens WD. Reductions in cortical activity during priming. Curr Opin Neurobiol. 2007; 17:171–176. [PubMed: 17303410]

11. Wiggs CL, Martin A. Properties and mechanisms of perceptual priming. Curr Opin Neurobiol. 1998; 8:227–233. [PubMed: 9635206]

12. Donaldson DI, Petersen SE, Buckner RL. Dissociating memory retrieval processes using fMRI: Evidence that priming does not support recognition memory. Neuron. 2001; 31:1047–1059. [PubMed: 11580903]

13. Rugg MD, et al. Dissociation of the neural correlates of implicit and explicit memory. Nature. 1998; 392:595–598. [PubMed: 9560154]

14. Schott B, Richardson-Klavehn A, Heinze HJ, Duzel E. Perceptual priming versus explicit memory: Dissociable neural correlates at encoding. J Cogn Neurosci. 2002; 14:578–592. [PubMed: 12126499]

15. Schott BH, et al. Redefining implicit and explicit memory: The functional neuroanatomy of priming, remembering, and control of retrieval. Proc Natl Acad Sci U S A. 2005; 102:1257–1262. [PubMed: 15657126]

16. Voss JL, Paller KA. Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. J Neurosci. 2006; 26:926–933. [PubMed: 16421312]

17. Paller KA, Gross M. Brain potentials associated with perceptual priming vs explicit remembering during the repetition of visual word-form. Neuropsychologia. 1998; 36:559–571. [PubMed: 9705066]

18. Paller KA, Hutson CA, Miller BB, Boehm SG. Neural manifestations of memory with and without awareness. Neuron. 2003; 38:507–516. [PubMed: 12741996]

19. Voss JL, Reber PJ, Mesulam MM, Parrish TB, Paller KA. Familiarity and conceptual priming engage distinct cortical networks. Cereb Cortex. 2008; 18:1712–1719. [PubMed: 18056085]

20. Conroy MA, Hopkins RO, Squire LR. On the contribution of perceptual fluency and priming to recognition memory. Cogn Affect Behav Neurosci. 2005; 5:14–20. [PubMed: 15913004]

21. Jacoby LL, Whitehouse K. An illusion of memory: False recognition influenced by unconscious perception. J Exp Psychol Gen. 1989; 118:126–135.

22. Johnston WA, Hawley KJ, Elliott JM. Contribution of perceptual fluency to recognition judgments. J Exp Psychol Learn Mem Cogn. 1991; 17:210–223. [PubMed: 1827829]

23. Keane MM, Orlando F, Verfaellie M. Increasing the salience of fluency cues reduces the recognition memory impairment in amnesia. Neuropsychologia. 2006; 44:834–839. [PubMed: 16157355]

24. Verfaellie M, Cermak LS. Perceptual fluency as a cue for recognition judgments in amnesia. Neuropsychology. 1999; 13:198–205. [PubMed: 10353371]

25. Voss JL, Baym CL, Paller KA. Accurate forced-choice recognition without awareness of memory retrieval. Learn & Mem. 2008; 15:454–459.

26. Mulligan NW. The role of attention during encoding in implicit and explicit memory. J Exp Psychol Learn Mem Cogn. 1998; 24:27–47. [PubMed: 9438952]

27. Gardiner JM, Java RI. Forgetting in recognition memory with and without recollective experience. Mem Cognit. 1991; 19:617–623.

28. Mandler G. Recognizing: The judgment of previous occurrence. Psychol Rev. 1980; 87:252–271.

29. Yonelinas AP. The nature of recollection and familiarity: A review of 30 years of research. J Mem Lang. 2002; 46:441–517.

30. Yonelinas AP. Consciousness, control, and confidence: The 3 Cs of recognition memory. J Exp Psychol Gen. 2001; 130:361–379. [PubMed: 11561915]

31. Mecklinger A. Interfacing mind and brain: A neurocognitive model of recognition memory. Psychophysiology. 2000; 37:565–582. [PubMed: 11037034]

32. Paller KA, Voss JL, Boehm SG. Validating neural correlates of familiarity. Trends Cogn Sci. 2007; 11:243–250. [PubMed: 17475539]

33. Rugg MD, Curran T. Event-related potentials and recognition memory. Trends Cogn Sci. 2007; 11:251–257. [PubMed: 17481940]

34. Voss, JL.; Paller, KA. Neural substrates of remembering: Electroencephalographic studies. In: Byrne, JH., editor. Learning and memory: A comprehensive reference. Elsevier; Oxford: 2008. p. 79-97.

35. Vincent JL, et al. Coherent spontaneous activity identifies a hippocampal-parietal memory network. J Neurophysiol. 2006; 96:3517–3531. [PubMed: 16899645]

36. Curran T, Dien J. Differentiating amodal familiarity from modality-specific memory processes: An ERP study. Psychophysiology. 2003; 40:979–988. [PubMed: 14986851]

37. Evans KM, Federmeier KD. The memory that's right and the memory that's left: Event-related potentials reveal hemispheric asymmetries in the encoding and retention of verbal information. Neuropsychologia. 2007; 45:1777–1790. [PubMed: 17291547]

38. Luck SJ, Hillyard SA. Electrophysiological correlates of feature analysis during visual search. Psychophysiology. 1994; 31:291–308. [PubMed: 8008793]

39. Misra M, Holcomb PJ. Event-related potential indices of masked repetition priming. Psychophysiology. 2003; 40:115–130. [PubMed: 12751809]

40. Squire LR, Wixted JT, Clark RE. Recognition memory and the medial temporal lobe: A new perspective. Nat Rev Neurosci. 2007; 8:872–883. [PubMed: 17948032]

41. Wixted JT. Dual-process theory and signal-detection theory of recognition memory. Psychol Rev. 2007; 114:152–176. [PubMed: 17227185]

42. Wig GS, Grafton ST, Demos KE, Kelley WM. Reductions in neural activity underlie behavioral components of repetition priming. Nat Neurosci. 2005; 8:1228–1233. [PubMed: 16056222]

43. Levy DA, Stark CE, Squire LR. Intact conceptual priming in the absence of declarative memory. Psychol Sci. 2004; 15:680–686. [PubMed: 15447639]

44. Jacoby LL, Dallas M. On the relationship between autobiographical memory and perceptual learning. J Exp Psychol Learn Mem Cogn. 1981; 110:306–340.

45. Whittlesea BW, Williams LD. The source of feelings of familiarity: The discrepancy-attribution hypothesis. J Exp Psychol Learn Mem Cogn. 2000; 26:547–565. [PubMed: 10855417]

46. Clayton NS, Bussey TJ, Dickinson A. Can animals recall the past and plan for the future? Nat Rev Neurosci. 2003; 4:685–691. [PubMed: 12894243]

47. Hampton RR, Schwartz BL. Episodic memory in nonhumans: What, and where, is when? Curr Opin Neurobiol. 2004; 14:192–197. [PubMed: 15082324]

48. Aggleton JP, et al. Sparing of the familiarity component of recognition memory in a patient with hippocampal pathology. Neuropsychologia. 2005; 43:1810–1823. [PubMed: 16154457]

49. Holdstock JS, Mayes AR, Gong QY, Roberts N, Kapur N. Item recognition is less impaired than recall and associative recognition in a patient with selective hippocampal damage. Hippocampus. 2005; 15:203–215. [PubMed: 15390152]

50. Mayes AR, et al. Associative recognition in a patient with selective hippocampal lesions and relatively normal item recognition. Hippocampus. 2004; 14:763–784. [PubMed: 15318334]
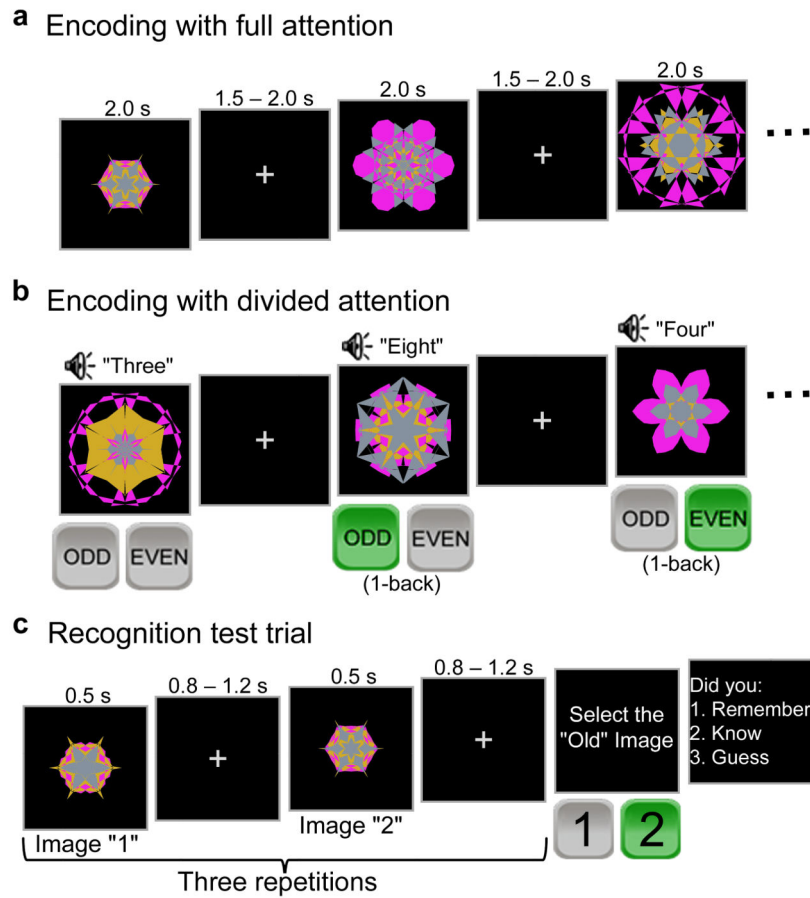
Figure 1. Schematic representation of experimental design

A Kaleidoscope images were presented individually (with the indicated timing parameters) during the full-attention portion of the study session. **B** The divided-attention portion of the study session included a distracting task that was performed concomitantly. Subjects pressed a button on each trial (except the first) to indicate whether the auditory digit presented during the previous trial was odd or even (a "1-back" response). Buttons shown in green indicate the correct response. **C** Trials during the recognition test included three presentations of the repeated target and its visually-similar novel foil in a *1-2-1-2-1-2* stimulus train, such that target and foil ERPs could be segregated within a forced-choice format test. Then, a button response was made to select the target (image "1" or "2"). Next, a metamemory decision was entered: "remember," "know," or "guess," to signify recollection, familiarity, or a lack of retrieval awareness, respectively. Recognition trials for items studied with full attention and divided attention were intermixed.
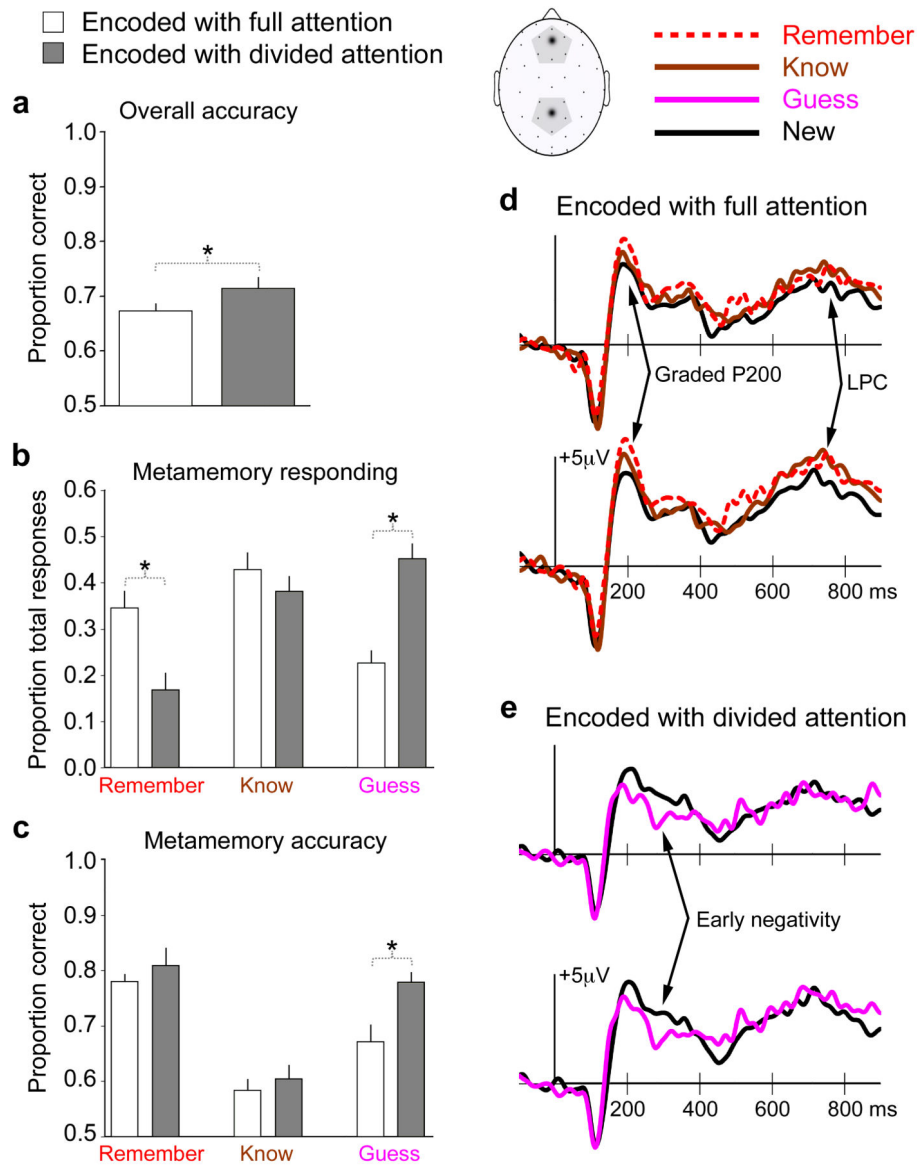
Figure 2. Behavioral and ERP results

A Recognition was superior following divided-attention encoding compared to full-attention encoding. **B** The proportion of metamemory decisions in each category indicates that awareness of retrieval was lower for divided-attention encoding compared to full-attention encoding. **C** The accuracy in each metamemory category indicates that guess responses were more accurate than know responses. **D** ERPs recorded during the recognition test are displayed for the remember and know categories for items studied with full attention, and for their corresponding foils (correct responses only). Waveforms, beginning 100 ms prior to stimulus onset, derive from the two electrode locations marked with large circles on the diagram of the top of the head (approximately Fz and Pz). The shaded regions encompass the anterior and posterior electrode clusters used in statistical tests. Graded P200 and LPC effects are indicated on the waveforms with arrows. ERPs for old and new items when recognition responses were endorsed with guess decisions were not included here because of

low trial counts (<20 trials for one-third of subjects), but these data are shown in Supplementary Figure 2. **E** Recognition-test ERPs for the same two electrode locations are displayed for the guess category for items studied with divided attention, and their corresponding foils (correct responses only). The early negative effect is indicated with arrows. Remember and know conditions were not included here because of the low trial counts (<20 trials for remember in almost all subjects and for know in one-third of subjects), but these data are shown in Supplementary Figure 1. (Asterisks indicate p<0.05, error bars indicate *SEM*.)
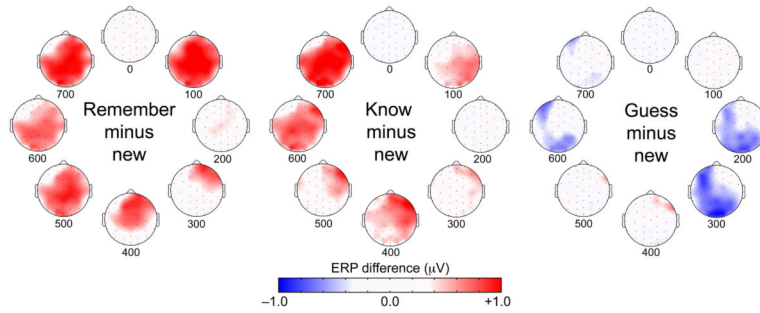
Figure 3. Distinct temporal and topographic ERP patterns for accurate guess decisions compared to remember and know decisions

Distributions of ERP old/new differences are plotted for the remember minus new, know minus new, and guess minus new contrasts (correct responses only), averaged for successive 100-ms intervals starting at 0 ms. Intervals progress clockwise. Items for each condition were included regardless of whether encoding was with full or divided attention, and the new condition was formed by collapsing foils for all three metamemory categories. Thus, these analyses produced different waveforms than those presented in Fig. 2. Coloration indicates difference amplitudes as shown.
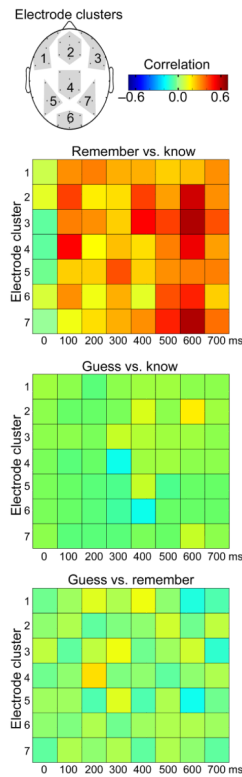
Figure 4. Relationships between ERP correlates of recognition accompanied by remember, know, and guess decisions

ERP difference values were calculated for each of the seven electrode clusters indicated on the map of the head, averaged over consecutive 100-ms latency intervals beginning at 0 ms. Difference values came from old/new subtractions for remember, know, and guess conditions (as in Figure 3), and only trials with correct recognition responses were included. Color values indicate the correlation magnitude across subjects for each electrode cluster and latency interval for the indicated comparisons.