Redefining implicit and explicit memory: The functional neuroanatomy of priming, remembering, and control of retrieval

Björn H. Schott*†‡, Richard N. Henson‡§, Alan Richardson-Klavehn*‡∥, Christine Becker*, Volker Thoma‡, Hans-Jochen Heine*, and Emrah Düzel*

*Center for Advanced Imaging, Magdeburg University, Leipziger Strasse 44, 39120 Magdeburg, Germany; †Medical Research Council Cognition and Brain Sciences Unit, Cambridge CB2 2EF, United Kingdom; ‡Goldsmiths College, London University, London SE14 6NW, United Kingdom; and ¶Thames Valley University, London W5 5RF, United Kingdom

Communicated by Endel Tulving, Rotman Research Institute of Baycrest Centre, North York, Ontario, Canada, December 13, 2004 (received for review August 6, 2004)

We used event-related functional MRI to study awareness of prior episodes during memory retrieval and its relationship to the intention to retrieve memories. Participants completed cues with words from a prior list (intentional test) or with the first words that came to mind (incidental test). During both tests, explicit memory was separated from priming in the absence of explicit memory. Priming was associated with hemodynamic decreases in left fusiform gyrus and bilateral frontal and occipital brain regions; explicit memory was associated with bilateral parietal and temporal and left frontal increases. Retrieval intention did not change these patterns but was associated with activity in right prefrontal cortex. Our results provide firm evidence that implicit and explicit memory have distinct functional neuroanatomies, and that strategic control of retrieval engages brain structures distinct from those involved in both implicit and explicit memory. They have critical implications for theories of memory and consciousness, which often equate consciousness with control.

The neuroscience of human memory has been dominated by distinctions between forms of memory that involve different kinds of consciousness. Foremost is the distinction between explicit and implicit memory (1). Explicit memory involves conscious remembering of prior episodes, often by means of intentional retrieval of those episodes, whereas implicit memory involves influences of prior episodes on current behavior without intentional retrieval, and sometimes without conscious remembering of those prior episodes. Many studies of implicit memory have focused on priming, the facilitated processing of stimuli as a function of prior exposure, an important mechanism by which memory facilitates perception.

Tulving and Schacter (2) proposed that priming and explicit memory depend on distinct neural systems. Although there is support for this view (3–7), a separation at the level of functional neuroanatomy has not yet been firmly established, owing to conceptual and methodological ambiguities in prior neuroimaging studies (6, 8). These studies have either compared incidental tests (in which participants respond with the first item coming to mind) with intentional tests (in which participants try to retrieve studied items) or have only used incidental tests (6). Brain activity in incidental tests can, however, reflect not only priming but also unintentional conscious remembering of prior episodes (unintentional or involuntary explicit memory) (4, 8–13), and sometimes contamination by intentional retrieval of prior episodes. Moreover, brain activity in intentional tests reflects not only explicit memory for specific episodes but also the general intention to retrieve prior episodes, or retrieval mode (14–18). Addressing these ambiguities has awaited a theoretical approach (8, 12) that distinguishes (i) implicit and explicit memory for specific episodes from retrieval intention, and, more specifically, (ii) unintentional implicit memory from unintentional and intentional explicit memory. The approach prescribes a behavioral paradigm that permits this separation (4, 8–11), which we here implemented for functional MRI. Our results provide firm evidence that priming and explicit memory are neuroanatomically separable, and that retrieval intention engages brain structures distinct from those involved in both priming and explicit memory.

Participants completed three-letter word stems, either with words from a prior study list (intentional test), or with the first word that came to mind (incidental test). In both cases, they indicated whether the completion was from the prior study list. They completed stems covertly, and responded orally with their completions between trials. Stems of studied words completed with words judged not to be from the study list were defined as primed items, and stems of studied words completed with studied words judged to be from the study list were defined as remembered items. Stems of unstudied words completed with unstudied words judged not to be from the study list were defined as correct rejections (CRs), thus providing comparison items for which there was no memory. The primed items gave a measure of priming that was far less likely to be contaminated by either unintentional or intentional explicit memory, as compared with priming measures used in prior neuroimaging studies.

Experiment 1 used only an intentional test (4, 10) to gain large numbers of primed, remembered, and CR observations. Prior studies (6, 19, 20) suggest that priming is associated with hemodynamic response decreases in occipital (extrastriate), inferior temporal, and prefrontal cortices, perhaps reflecting improved perception and identification processes, whereas explicit memory is associated with response increases in medial temporal, parietal, and prefrontal brain regions (21, 22). We used these data to guide our imaging contrasts. Experiment 2 compared intentional and incidental tests to assess whether the neural correlates of priming and explicit memory interacted with retrieval intention, and whether retrieval intention and explicit memory for specific episodes engaged similar brain regions. Experiment 2 also used fixation periods that permitted neural responses to CRs alone to be contrasted across the intentional and incidental tests, allowing the purest assessment possible of the correlates of retrieval intention (11, 18, 23).

Methods

Experiment 1. Participants. Twenty-five healthy right-handed native German speakers (18–36 years of age, with 19 being female) volunteered for paid participation with written informed consent.

Abbreviations: CR, correct rejection; BA, Brodmann area; MTL, medial temporal lobe.
†To whom correspondence should be addressed. E-mail: bschott@neuro2.med.uni-magdeburg.de.
∥B.H.S., R.N.H., and A.R.-K. contributed equally to this work.
© 2005 by The National Academy of Sciences of the USA

www.pnas.org/cgi/doi/10.1073/pnas.0409070102

PNAS | January 25, 2005 | vol. 102 | no. 4 | 1257–1262
were discarded. The experimental session was also divided into two test phases (i.e., the stem- and were acquired in an interleaved manner (1–23 in steps of two, data categories.

target vs. nontarget words. Fig. 5, which is published as supporting 3,200 ms, and a cue of three exclamation marks (‘’!!!’’) for 2,000 ms, fixation cross for 1,000 ms, a word stem for 300 ms, an asterisk for judgments was discouraged. Each test trial consisted of a central speech cue appeared. Making false-positive study-list membership completed each stem with a studied or an unstudied word (left and studied word. Participants indicated by pressing a button if they had the first word that came to mind if they could not remember a ms, and a further fixation cross for 1,200 ms.

In the test phases, participants were instructed to complete each stem with a word from the preceding study list, if possible, but with the first word that came to mind if they could not remember a studied word. Participants indicated by pressing a button if they had completed each stem with a studied or an unstudied word (left and right index fingers for studied and unstudied, respectively, counterbalanced across participants), but did not respond orally until a cue appeared. Making false-positive study-list membership judgments was discouraged. Each test trial consisted of a central fixation cross for 1,000 ms, a word stem for 300 ms, an asterisk for 3,200 ms, and a cue of three exclamation marks (“!!!”) for 2,000 ms, which prompted participants to respond orally with the word they had used to complete the stem. Oral responses were recorded with a microphone at the bottom end of the head coil and scored as target vs. nontarget words. Fig. 5, which is published as supporting information on the PNAS web site, shows the test trial structure and data categories.

MRI scanning. Echo-planar images were acquired on a GE Medical Systems Signa 1.5-T MRI scanner (repetition time = 2.0 s; echo time = 35 ms). Images consisted of 23 axial slices [64 × 64, voxel size = 3.13 × 3.13 × 6 mm (slice thickness = 5 mm with 1 mm gap)] and were acquired in an interleaved manner (1–23 in steps of two, 2–22 in steps of two, from bottom to top). A total of 788 volumes were acquired during each of two test sessions (i.e., the stem-completion test phases). The first three volumes of each session were discarded.

Data processing and analysis. Data analysis was performed by using statistical parametric mapping (SPM2, Wellcome Department of Imaging Neuroscience, London). Echo-planar images were corrected for acquisition delay, realigned, normalized (voxel size: 3 × 3 × 3 mm), and smoothed (Gaussian kernel: 8 × 8 × 8 mm). A high-pass filter (cutoff period = 128 s) was applied to the data and model. Statistical analysis was performed in two stages of a mixed-effects model. In the first stage, neural activity was modeled by a delta function at stimulus onset. The ensuing hemodynamic response was modeled by convolving these delta functions with a canonical hemodynamic response function (HRF) (24). The resulting time courses were down-sampled each scan to form covariates in a general linear model. Separate covariates were modeled for the conditions of interest, one time-locked to each speech event, six for the rigid-body movement parameters determined from realignment, and a single covariate representing the mean (constant) over scans. Contrasts of the parameter estimates for each covariate comprised the data for the second-stage analyses, which treated participants as a random effect. Specifically, images of each contrast of interest for the canonical HRF were entered into one-sample Student’s t tests.

The critical events at test were the onsets of (i) stems of studied words completed with studied target words judged to be from the study list (remembered items), (ii) stems of studied words completed with studied target words judged not to be from the study list (primed items), and (iii) stems of unstudied words completed with unstudied words judged not to be from the study list (CRs). For imaging purposes, the CRs included stems completed with nontarget as well as target words. The one-tailed Student t test planned comparisons were as follows: to isolate the neural correlates of priming, responses to primed items were subtracted from responses to CRs; to isolate the neural correlates of explicit memory, responses to primed items were subtracted from responses to remembered items. The significance level was set to 0.001 (uncorrected), with a minimum of five adjacent voxels. Coordinates of local maxima of activation were converted into the Talairach reference frame (25).

Experiment 2. Participants. Sixteen healthy right-handed native German speakers (20–41 years of age, with eight being female) volunteered for paid participation, with written informed consent. Scanning occurred at the Wellcome Department of Imaging Neuroscience, London, in accordance with local ethics approval.

Paradigm. The experiment resembled experiment 1 (see Fig. 5), including the use of the same counterbalancing procedures and German materials; only the differences from experiment 1 are described. The main difference was that the two test phases had different instructions: One test phase used intentional test instructions as in experiment 1; the other test phase used incidental test instructions, that is, participants completed each stem with the first

| Table 1. Mean word-stem completion proportions at test (relative to total number of word stems; with SDs in parentheses) in experiments 1 and 2 |
|---|---|---|---|
| **Exp.** | Stems of studied words | Stems of unstudied words |
| | **Overall** | **Remembered target** | **Primed target** | **Forgotten (nontarget)** | **Overall** | **CR target** | **CR nontarget** |
| Experiment 1 | | | | | | | |
| Intentional | 0.93 (0.05) | 0.32 (0.11) | 0.32 (0.11) | 0.23 (0.05) | 0.87 (0.07) | 0.36 (0.08) | 0.39 (0.06) |
| Intentional | 0.31 (0.10) | 0.33 (0.13) | 0.33 (0.13) | 0.31 (0.10) | 0.33 (0.13) | 0.33 (0.13) | 0.33 (0.13) |
| Incidental | 0.92 (0.05) | 0.20 (0.11) | 0.41 (0.12) | 0.28 (0.07) | 0.86 (0.08) | 0.36 (0.10) | 0.45 (0.11) |

Overall, total proportion of completed stems; remembered, stem completed with studied target word judged as studied; primed, stem completed with studied target word judged as unstudied; forgotten, stem completed with unstudied (i.e., nontarget) word; CR target, stem completed with unstudied target word judged as unstudied; CR nontarget, stem completed with unstudied nontarget word judged as unstudied. Differences of overall completion proportions from the sum of the individual response categories (remembered plus primed plus nontarget for studied; CR target plus CR nontarget for unstudied) are because of small proportions of false alarms (items completed with unstudied words judged as studied).
word that came to mind, then indicated by pressing a button if they happened to remember it from the study phase (9, 10). Order of intentional and incidental tests was counterbalanced across participants. This procedure, together with the counterbalancing procedure of experiment 1, ensured that all words and stems appeared in both the intentional and the incidental tests across participants. The test trial timing differed from experiment 1, so that speech occurred only during a 1-s gap between volume acquisitions, reducing movement artifacts in the data owing to oral responses (26).

Following the central fixation cross for 1,000 ms and word stem for 300 ms, the asterisk was presented for 3,700 ms, and then the speech cue ("!!!") was presented for 1,000 ms during the gap between image acquisitions. A final difference was the insertion of 18 s of fixation every eight trials.

**MRI scanning.** Echo-planar images were acquired on a Siemens 1.5-T Sonata scanner with an echo time of 50 ms. Images consisted of 22 axial slices \([64 \times 64, \text{voxel size}=3 \times 3 \times 5 \text{ mm (slice thickness = 3 mm with 2 mm gap)}]\) and were acquired in a sequential, descending manner (excluding cerebellum). The volume acquisition time was 2.0 s and the volume repetition time was 3.0 s, resulting in a 1.0-s gap between acquisitions to accommodate the speech (26). A total of 605 volumes were acquired during each of two test sessions (i.e., the stem-completion test phases). The first five volumes of each session were discarded.

**Data processing and analysis.** These resembled experiment 1, except that interactions of the planned comparisons used in experiment 1 with the new factor of retrieval intention were tested (ANOVA). Also, the fixation periods in experiment 2 allowed more efficient estimation of the main effect of events vs. baseline (27), permitting a contrast (two-tailed Student’s \(t\) test) of the hemodynamic response for CRs alone across the intentional and incidental tests.

**Results**

**Behavioral Results.** Table 1 shows, for test stems corresponding to studied and unstudied words, the proportions completed with target and nontarget words, broken down by study-list membership judgment. Table 2, which is published as supporting information on the PNAS web site, shows reaction times for the study-list membership judgments. In experiment 1, collapsing across list-membership judgment, stems of studied words yielded a higher mean proportion of target completions than did stems of unstudied words (studied words: 0.64, SD = 0.06; unstudied words: 0.41, SD = 0.07). \(t(24) = 16.0, P < 0.001\). In experiment 2, collapsing across list-membership judgment, stems of studied words also yielded higher mean proportions of target completions (incidental test: 0.61, SD = 0.08; intentional test: 0.64, SD = 0.06) than did stems of unstudied words (incidental test: 0.36, SD = 0.08; intentional test: 0.37, SD = 0.07), and two-way (incidental vs. intentional \(\times\) studied vs. unstudied) ANOVA revealed only a main effect of prior study, \(F(1, 15) = 367.4, P < 0.001\). To examine priming in the absence of explicit memory, we restricted analysis to stems completed with words judged as unstudied, and computed, separately for stems of studied and unstudied words, the proportions of each stem type completed with target words. In experiment 1, stems of studied...
words yielded a higher mean proportion of target completions than did stems of unstudied words (studied words: 0.57, SD = 0.09; unstudied words: 0.47, SD = 0.07), t(24) = 6.3, P < 0.001. In experiment 2, stems of studied words also yielded higher mean proportions of target completions (incidental test: 0.59, SD = 0.12; intentional test: 0.58, SD = 0.12) than did stems of unstudied words (incidental test: 0.43, SD = 0.13; intentional test: 0.43, SD = 0.10), and two-way (incidental vs. intentional × studied vs. unstudied) ANOVA revealed only a main effect of prior study, F(1, 15) = 76.1, P < 0.001. The results for both experiments demonstrate priming in the absence of explicit memory in both intentional and incidental tests. In experiment 2, intentional test instructions resulted in a higher proportion of remembered words than did incidental test instructions (see Table 1, second column), t(15) = 3.4, P < 0.01, which is consistent with prior behavioral data (10, 11).

**Experiment 1 fMRI Results.** Compared with CRs, primed items elicited significantly decreased hemodynamic responses in several brain regions, including the left inferior temporooccipital junction (fusiform gyrus and inferior temporal gyrus), parts of the medial occipital cortex (bilateral cuneus and bilateral lingual gyrus), and the left and right inferior frontal gyrus (Fig. 1A). There was also a decreased hemodynamic response for primed items in the left medial temporal lobe (MTL) (Fig. 3). Table 3, which is published as supporting information on the PNAS web site, summarizes local maxima of activation in the CRs minus primed contrast in experiments 1 and 2. Fig. 2A displays significant increases in hemodynamic responses for remembered items in comparison with primed items. Remembered items were associated with extensive activation of bilateral parietal regions, including the precuneus, the superior and inferior parietal lobule, and the posterior cingulate; other regions that showed activations included the left superior and middle frontal gyri, bilateral temporal cortices, and the left MTL. Table 4, which is published as supporting information on the PNAS web site, shows the local maxima of activation in the remembered minus primed contrasts of experiments 1 and 2. A decreased hemodynamic response for remembered items compared with CRs was observed in several areas that also showed a decreased response for primed items compared with CRs, including prefrontal and occipital brain regions, and the left fusiform and inferior temporal gyr (data not shown).

**Experiment 2 fMRI Results.** The comparison of primed items with CRs, collapsing across incidental and intentional tests, revealed a pattern very similar to that in experiment 1 (Figs. 1B and 3). None of the regions that were revealed showed a significant interaction with retrieval intention, with the exception of lingual gyrus [−18, −90, −2; Brodmann area (BA) 17], which showed a priming-related deactivation in the incidental, but not in the intentional, test. The comparison of remembered and primed items, collapsing across incidental and intentional tests, also revealed a pattern of lateral and medial parietal activations similar to that in experiment 1 (Fig. 2B). Tables 3 and 4 show voxels with local activation maxima that were also activated significantly in experiment 1 (P < 0.001, uncorrected). None of these regions showed a significant interaction with retrieval intention. However, four other regions showed a significant interaction: Right middle frontal gyrus (42, 22, 29; BA 9), left middle occipital gyrus (−15, −87, 18; BA 18), right anterior superior temporal gyrus (45, −17, 1; BA 22), and right posterior superior temporal gyrus (50, −55, 14; BA 39). All four regions showed greater activation for primed than remembered items in the intentional test, and little evidence of a difference in the incidental test (Fig. 4 Left).

The comparison of incidental and intentional tests restricted to
CRs only revealed three regions: Left and right posterior superior frontal gyrus (−18, 11, 55, and 15, 3, 63; BA 6), and right medial anterior prefrontal cortex (12, 50, −2; BA 10). The former two regions showed greater activation for CRs in the intentional compared with the incidental test, whereas the latter region showed greater activation for CRs in the incidental compared with the intentional test (Fig. 4 Right).

Discussion

Our results provide firm evidence that priming and explicit memory have distinct neuroanatomical correlates, by comparing the hemodynamic activity correlates of priming in the absence of explicit memory with those of explicit memory, a behavioral approach that has proven fruitful in electrophysiological studies (3–5). Moreover, the results show that retrieval intention has little influence on these distinct activation patterns. Instead, differences between intentional and incidental retrieval occur in other brain regions. Consequently, neurocognitive theories of memory retrieval must distinguish levels of theoretical description relating to awareness of memory (i.e., implicit vs. explicit memory for specific study episodes) and to strategic control of retrieval (i.e., intentional vs. incidental retrieval). Current theories and models of memory retrieval (e.g., refs. 28 and 29) often conflate these levels of description. Prior studies of the functional neuroanatomy of priming and explicit memory have also suffered from this conflation (6), because they simply compared incidental and intentional memory tests, or used only incidental tests. Consequently, brain activity attributed to priming could have reflected unintentional (or involuntary) explicit memory (4, 6, 8, 13), or even contamination by intentional retrieval, and brain activity attributed to explicit memory could have reflected both explicit memory for specific episodes and the general intention to retrieve prior episodes (18). Our conceptual and methodological approach (4, 8–12) overcomes these ambiguities.

Priming was evident in higher proportions of target completions for stems of studied words as compared with stems of unstudied words, even when those words were not judged as studied, and was associated with decreased hemodynamic responses in several brain regions (Fig. 1 and Table 3). The robustness of these findings is indicated by their replication across two experiments performed in different laboratories and using different scanners and acquisition parameters. As in previous studies (6, 20), priming-related response decreases were found in bilateral occipital and inferior temporal regions. The current results show that response decreases in these brain regions occur in the absence of awareness of the previous study episode, and thus reflect true implicit memory, rather than unintentional or intentional explicit memory. Response decreases in these areas also occurred for remembered items (data not shown), as well as primed items, demonstrating that priming-related response decreases occur irrespective of awareness of the study episode, which is consistent with the notion that priming sometimes or always accompanies explicit memory. Prefrontal regions (BA 9, 44, and 46 bilaterally, and BA 6, 8, and 47 on the left) also showed response decreases for primed items (and for remembered items). Left frontal decreases have been related to conceptual priming (30). The current frontal deactivations may also reflect phonological priming (31), in view of behavioral evidence that word-stem completion priming involves perceptual and lexical processing, but not conceptual processing (10, 11, 32).

A further region that showed a greater response to CRs than to primed items was the left MTL (hippocampus in experiment 1 and hippocampus/perirhinal cortex in experiment 2; Fig. 3 and Table 3). Whereas left hippocampal activation during conscious remembering has been reported previously (33), and was observed in experiment 1 (Table 4), the MTL has not typically been implicated in priming. However, some argue that MTL pathology produces implicit memory impairment that often goes undetected (34–36), so that the present result might implicate the MTL in priming. An alternative explanation, accommodating the more common view that priming does not involve the MTL (6), is that this result reflects novelty detection without awareness. The MTL is known to play a role in novelty detection (37, 38), and parahippocampal regions can respond differentially to novel vs. repeated stimuli in absence of conscious awareness (39).

Regions that showed greater responses to remembered items than to primed items (Fig. 2 and Table 4) included bilateral parietal, posterior cingulate, and anterior prefrontal brain regions that have been previously linked with explicit memory (21, 22). However, the current results extend prior findings by showing that activations in these regions occur even when remembered items are compared with primed items, and not just with unstudied items. This comparison allows for the possibility that priming may accompany
explicit memory, and thus links the activations more closely with explicit memory, rather than with priming.

In experiment 2, only one region implicated in priming showed an interaction with retrieval intention (i.e., lingual gyrus, BA 17), and no interaction was observed for the clusters of BA 10 that showed an interaction between retrieval intention and awareness of prior study (remembered vs. primed) was also observed in experiment 2 in four brain regions that were different to those implicated in explicit memory. In these regions, including the right middle frontal gyrus (BA 9), a response increase was observed for primed items (and CRs) relative to remembered items, but only in the intentional test (Fig. 4 Left). This pattern mirrors that of the reaction times for the study-list-membership judgments in the intentional test (Table 2). Intentional test instructions resulted in a larger increase in reaction times for primed items and CRs than for remembered items. The most likely explanation is that in an intentional test there is greater generation and rejection of candidate completions for primed items and CRs than for remembered items. Activity in these regions, therefore, may be related to postretrieval monitoring (18). Such a role has been previously hypothesized for the right dorso-lateral prefrontal region (17, 22, 26). This account again suggests that the processes and brain regions involved in strategic control of retrieval are separable from those involved in priming and explicit memory.

In summary, we show that priming-related hemodynamic response decreases in occipital, inferior temporal, and prefrontal cortices occur in both the absence and presence of explicit memory, and independent of attempts to retrieve studied items. Parietal, temporal, and prefrontal activations associated with explicit memory are also observed regardless of retrieval intention. Retrieval intention and postretrieval monitoring are associated with responses in right prefrontal regions distinct from those implicated in priming and explicit memory. Neurocognitive theories of memory must therefore distinguish the processes involved in the strategic control of retrieval from the processes involved in explicit memory for specific prior episodes, which is in contrast to many current theoretical approaches that conflate these levels of description. Consciousness of memory in the sense of intended vs. unintended retrieval of prior episodes should not be conflated with consciousness of memory in the sense of awareness vs. absence of awareness of specific prior episodes.