

Neuroanatomical Dissociation of Encoding Processes Related to Priming and Explicit Memory

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Priming is a facilitation of cognitive processing with stimulus repetition that can occur without explicit memory. Whereas the functional neuroanatomy of perceptual priming at retrieval is established, encoding processes that initiate priming and explicit memory have not yet been anatomically separated, and we investigated them using event-related functional magnetic resonance imaging. Activations predicting later explicit memory occurred in the bilateral medial temporal lobe (MTL) and left prefrontal cortex (PFC). Activity predicting later priming did not occur in these areas, but rather in the bilateral extrastriate cortex, left fusiform gyrus, and bilateral inferior PFC, areas linked with stimulus identification. Surprisingly, these regions showed response reductions. Our results demonstrate that priming and explicit memory have distinct functional neuroanatomies at encoding, with MTL activations being specific for explicit memory, and suggest that priming is initiated by sharpness of neural responding in stimulus identification areas, consistent with recent electrophysiological evidence regarding priming-related neural oscillations at encoding. We tentatively suggest that this sharpened responding at encoding may set the stage for increased neural processing efficiency at retrieval, with these different neural mechanisms both leading to observed priming-related hemodynamic decreases, and argue that neural measurements at encoding, and not just at retrieval, will be critical in resolving the debate about the neural mechanisms of learning that underlie priming.

Key words: priming; explicit memory; encoding; event-related fMRI; medial temporal lobe; extrastriate cortex; fusiform gyrus; prefrontal cortex

Introduction

The implicit–explicit memory distinction (Graf and Schacter, 1985) is fundamental to the cognitive neuroscience of memory. One important form of implicit memory is perceptual priming, the facilitated processing of a stimulus as a result of previous exposure to that stimulus, which can occur in the absence of explicit memory for the previous exposure (Richardson-Klavehn et al., 1994a; Richardson-Klavehn and Gardiner, 1995, 1996). Tulving and Schacter (1990) argued that perceptual priming reflects the inbuilt memory capabilities of perceptual representation systems that do not support explicit memory. Consistent with this notion, at retrieval, priming has been associated with hemodynamic response decreases in occipital, temporal, and prefrontal brain regions (Schacter et al., 1996; Henson, 2003; Lustig and Buckner, 2004; Schott et al., 2005), whereas explicit memory has been associated with hemodynamic response in-

creases in prefrontal, parietal, and medial temporal regions (Schacter et al., 1996; Henson et al., 1999; Eldridge et al., 2000; Schott et al., 2005). At encoding, activations in the medial temporal lobe (MTL) and left prefrontal cortex (PFC) predict later explicit memory (Brewer et al., 1998; Wagner et al., 1998; Buckner et al., 2000b; Otten et al., 2002; Reber et al., 2002; Schott et al., 2004), but the functional neuroanatomy of priming-related encoding processes is unknown. Here, we provide firm evidence that priming and explicit memory have distinct functional neuroanatomies at encoding.

A particular concern in adapting priming measures for neuroimaging is that retrieval of primed items by healthy participants can be accompanied by involuntary explicit memory (Schacter, 1987; Richardson-Klavehn et al., 1994a,b, 2002; Richardson-Klavehn and Gardiner, 1995, 1996), contaminating the neural measure of priming-related activity (Henson, 2003). Consequently, we have developed a version of the word-stem completion test (Graf et al., 1984; Richardson-Klavehn and Gardiner, 1998; Richardson-Klavehn et al., 1999) in which participants complete three-letter word stems (e.g., GAR), some of which can be completed with previously studied words (e.g., GARDEN), and make an “on-line” study-list-membership judgment after competing each stem (Richardson-Klavehn and Gardiner, 1995, 1996). In this test, after a shallow encoding task, such as counting the syllables in words, there is priming for studied words that

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participants judge as nonstudied, yielding priming-related neural activity measures at encoding and retrieval that are much less likely to be contaminated by explicit memory (Schott et al., 2005). In electrophysiological studies of encoding, this measure has shown that priming-related neural processes occur earlier than explicit-memory-related processes (Schott et al., 2002) and that priming-related modulations of α and γ oscillations occur in ventral visual stream regions during the time window of stimulus identification (Düzel et al., 2005). Here, we used functional magnetic resonance imaging (fMRI) to obtain precise neuroanatomical information about the neural correlates of priming at encoding. We hypothesized that MTL activation at encoding would predict only later explicit memory, not later priming, and that later-primed words, compared with later-forgotten words, would elicit hemodynamic response increases in ventral visual stream regions involved in stimulus identification, such as the bilateral extrastriate cortex and left fusiform gyrus, which show priming-related hemodynamic response decreases at retrieval (Schott et al., 2005).

Materials and Methods

The fMRI data reported here were collected during the study phases of an experiment from which the test-phase fMRI data are published (Schott et al., 2005).

Participants. Twenty-five healthy right-handed volunteers (age range, 18–36 years; 19 females) participated in the experiment in return for payment. The experiment was performed at the Faculty of Medicine, Otto von Guericke University (Magdeburg, Germany) in accordance with the guidelines of its ethics committee.

Behavioral tasks. At test, we used an adapted version of the word-stem completion task, which is well established in studies of both amnesic patients (Graf et al., 1984; Graf and Schacter, 1985) and healthy participants (Richardson-Klavehn and Gardiner, 1998; Richardson-Klavehn et al., 1999). The materials were 480 unique German word stems (the first three letters of words) and corresponding target words, developed on the basis of normative data (Schott et al., 2002, 2005), with 160 words being presented in each of two study phases and 240 stems (including 80 stems of nonstudied words) being presented in each of two test phases. Test phases followed their respective study phases. For 160 stems, the target word was studied, and for 80 stems, the target word was nonstudied. Across participants, items were counterbalanced across studied/nonstudied status and across use in the first study and test phase versus the second study and test phase.

Stimuli were presented visually on a back-projection screen that participants viewed via a mirror. On each study trial, a ready cue (“?”) appeared on the screen for 400 ms, followed by a central fixation cross for 150 ms, a word for 1000 ms, and a central fixation asterisk for 1200 ms. These timings resulted in intervals of 2750 ms between word onsets. Participants counted the syllables of each word, responding by key press with either their right or left index finger for one or two syllables versus more than two syllables (response hands counterbalanced across participants). They were instructed not to try to memorize the words because doing so would interfere with the syllable-counting task, and these instructions were reinforced before the second study phase. On each test trial, participants completed the word stem with a word from the preceding study list, or with the first word coming to mind if they could not. Participants indicated by key press whether they had completed each stem with a studied or a nonstudied word (left and right index fingers for studied and nonstudied, respectively, counterbalanced across participants). Then a speech cue appeared prompting participants to respond orally with the completed word. They were discouraged from making false positive judgments regarding study-list membership and were told not to respond at all if they had been unable to complete the stem. Oral responses were recorded via a microphone and scored by a native German speaker as target versus nontarget words. The trial timings and relevant data categories are summarized in Figure 1.

The critical events at study were the onsets of words that were later

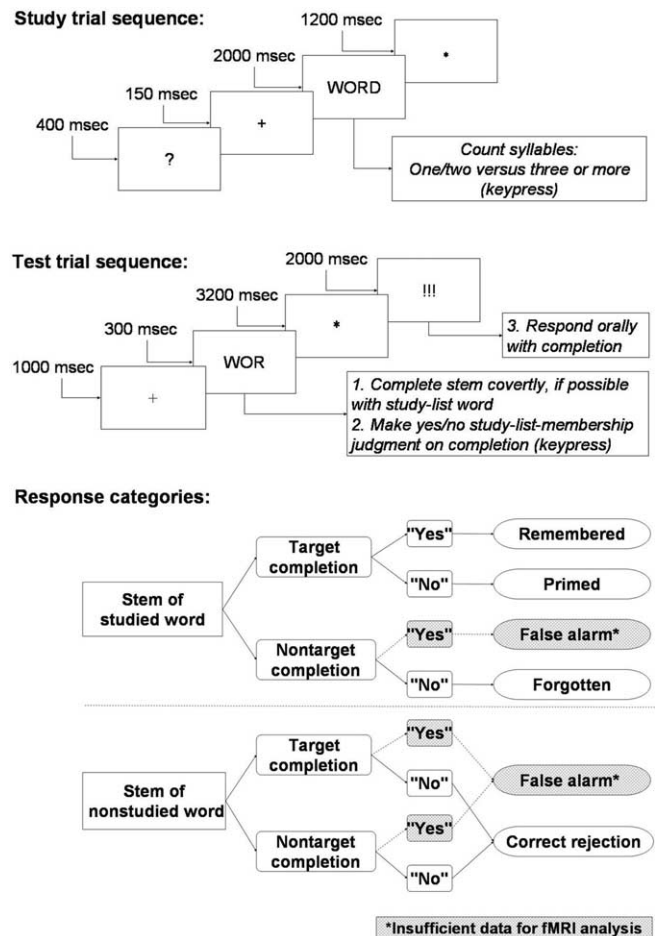


Figure 1. Trial structure and timing at study and test and behavioral response categories from the combination of stem-completion responses and study-list-membership judgments. The relevant contrasts at study were between remembered-and-forgotten and primed-and-forgotten response categories. The relevant contrast at test (used for an inclusive masking analysis of the study-phase data) was between the correct-rejection and primed response categories (Schott et al., 2005). False alarms were rare and did not yield enough observations for fMRI analysis.

remembered (stems of studied words at test completed with studied words judged as studied), later primed (stems of studied words at test completed with studied words judged as nonstudied), and later forgotten (stems of studied words at test completed with nonstudied words judged as nonstudied). The primed items gave a measure of priming at test that was unlikely to be contaminated by involuntary explicit memory, which is ubiquitous in healthy participants in standard tests of priming (Richardson-Klavehn et al., 1994a,b, 2002; Richardson-Klavehn and Gardiner, 1995, 1996; Schott et al., 2005). The corresponding measure of neural activity at study therefore was unlikely to be contaminated with neural activity relating to encoding processes that support later involuntary explicit memory (Schott et al., 2002; Düzel et al., 2005).

Note that priming for studied words judged nonstudied occurs in the word-stem completion task even when participants are instructed to try to retrieve a studied completion before responding with the first word coming to mind, as they were in the present experiment (Richardson-Klavehn and Gardiner, 1995, 1996; Schott et al., 2002, 2005; Düzel et al., 2005). Moreover, with the kind of retention interval used in the present experiment, studied words judged nonstudied are not accompanied by familiarity, but rather are not accompanied by any awareness of previous presentation in the experiment (Richardson-Klavehn et al., 1994a, 2002; Richardson-Klavehn and Gardiner, 1995).

fMRI scanning. fMRI scanning was performed with a General Electric (Milwaukee, WI) 1.5T Signa neurovascular system using a standard

quadrature head coil. T2*-weighted echoplanar functional images were acquired continuously [repetition time (TR), 2000 ms; echo time, 35 ms; flip angle, 90°]. Each volume consisted of 23 axial slices (64 × 64 voxels; voxel size, 3.13 × 3.13 × 6 mm; slice thickness, 5 mm; gap, 1 mm), and slices were acquired in an interleaved manner (1–23 in steps of 2, 2–22 in steps of 2, from bottom to top). During each study phase, 228 volumes were acquired, with the first three volumes of each phase being discarded. The volume-acquisition TR of 2000 ms, in conjunction with the interval between word onsets of 2750 ms, resulted in a jittering of volume acquisition relative to word onset, sufficient to permit the event-related hemodynamic response to later-remembered, later-primed, and later-forgotten words to be extracted from the fMRI time series (Josephs and Henson, 1999; Henson, 2004).

fMRI data analysis. Data analysis was performed using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, University College, London, UK). Echoplanar images were corrected for acquisition delay, realigned, normalized (voxel size, 3 × 3 × 3 mm), and smoothed (Gaussian kernel, 8 × 8 × 8 mm). Before model estimation, a high-pass filter of 64 s was applied. Statistical analysis was performed in two stages of a mixed-effects model. In the first stage, neural activity was modeled by a δ function at stimulus onset. The ensuing hemodynamic response was modeled by convolving these δ functions with a canonical hemodynamic response function (HRF) and its temporal derivative, which captures the majority of the variability in the blood-oxygen level-dependent (BOLD) impulse response (Henson, 2004). The resulting time courses were downsampled each scan to form covariates in a general linear model. Separate covariates were modeled for the event types of interest at study, plus one for each of the six rigid-body-movement parameters determined from realignment (to capture residual movement-related effects). To account for possible differences in reaction time (RT) between words with one or two syllables versus words with three or more syllables, RT was included as a response-locked regressor for each study trial in which participants actually responded (in one participant, for whom the RTs of the first study phase were not available, the mean RTs of the second study phase were used to generate the response regressor). Finally, a single covariate represented the mean (constant) over scans. Parameters for each covariate were estimated by a least-squares fit to the data. Note that whereas speech was involved in the test phases of the current experiment (Schott et al., 2005), speech-related movement artifacts were not of concern during the study phases, which involved only key-press responses.

Contrasts of the parameter estimates for the hemodynamic response to the onsets of remembered, primed, and forgotten words at study comprised the data for the second-stage analyses, which treated participants as a random effect. More specifically, images of each contrast of interest on the canonical HRF (later-remembered words vs later-forgotten words, later-primed words vs later-forgotten words, and later-remembered words vs later-primed words) were entered into two-tailed, one-sample *t* tests. Given that the hemodynamic correlates at encoding of later priming had not been examined previously, a significance threshold of 0.005 (uncorrected, extent threshold $k = 5$ adjacent voxels) was adopted as a reasonable trade-off between the statistical conservativity of two-tailed (rather than one-tailed) analysis, regarding type I errors, and the likelihood of making type II errors (i.e., failing to statistically detect brain-activity differences that are of theoretical interest). Coordinates of significant voxels were transformed into Talairach space (Talairach and Tournoux, 1988).

The reported activations and deactivations reflect relative changes of the hemodynamic response across the three event types of interest, because no baseline fixation periods (i.e., null events) were included at study. Fixation periods were avoided because they would have resulted in the isolation of words before and after the fixation periods, leading to Von Restorff (i.e., distinctiveness) effects (Richardson-Klavehn and Bjork, 2002). Additionally, during fixation periods, participants might have continued to think about the words directly preceding those periods, leading to differences in effective study time between words. Both of these factors would have been undesirable sources of variability in the imaging data.

Null events would have permitted estimation of the main effect of

events versus baseline (Josephs and Henson, 1999; Henson, 2004); however, the purpose of the current study was not to assess hemodynamic responses to words per se but only to compare hemodynamic responses to words based on their later memory fate (remembered, primed, forgotten), and the absence of a fixation baseline does not limit conclusions about response differences across these word types (Josephs and Henson, 1999; Henson, 2004). Assuming the BOLD impulse responses to successive events summate in a linear manner (as is assumed by nearly every analysis method used conventionally), there is no need for null events, because the fMRI time series is deconvolved with an assumed response shape; moreover, inclusion of null events would have reduced statistical power for comparisons between the different event types (Josephs and Henson, 1999; Henson, 2004). There is good evidence that the degree of nonlinearity is minimal for interstimulus intervals of approximately ≥ 3000 ms, as used here (Henson, 2004).

To examine a possible regional overlap of priming-related activity at study and test, the relevant SPM at test (i.e., correct rejections of nonstudied words minus primed words) (Fig. 1) (Schott et al., 2005) was used as an inclusive mask. This mask image was applied to the primed-minus-forgotten and forgotten-minus-primed contrasts of the study phase, to identify activations and deactivations at study in brain regions that showed response decreases at test. The significance threshold for the mask was 0.001 (uncorrected, one tailed, extent threshold $k = 5$ adjacent voxels) (Schott et al., 2005), but the threshold for the masking analysis was 0.005 (uncorrected, two tailed, extent threshold $k = 5$ adjacent voxels), as in the other encoding contrasts. The theoretical purpose of this analysis was to test our hypothesis that priming-related response decreases in the ventral visual stream at test would be mirrored by priming-related response increases in the same regions at study.

Results

Behavioral results

There were a total of 10 behavioral data categories at test created by the combinations of stem status (stem of studied vs stem of nonstudied word), completion status (target word vs nontarget word vs no completion), and study-list-membership judgment status (studied vs nonstudied). For stems of studied words, these were targets judged as studied (remembered category), targets judged as nonstudied (primed category), nontargets judged as nonstudied (forgotten category), nontargets judged as studied (false alarm category), and uncompleted stems. For stems of nonstudied words, these were targets judged as studied (false-alarm category), targets judged as nonstudied (correct rejection category), nontargets judged as studied (false-alarm category), nontargets judged as nonstudied (correct rejection category), and uncompleted stems. A preliminary multivariate ANOVA indicated no significant differences in the profile of mean response proportions across these 10 behavioral response categories at test as a function of study-test phase (first vs second), with no main effect of study-test phase ($F_{(1,24)} = 0.2$; Wilks's $\lambda = 0.99$; $p > 0.65$) and no interaction of response category and study-test phase ($F_{(9,16)} = 0.63$; Wilks's $\lambda = 0.74$; $p > 0.75$). These results provided no evidence of differing encoding and/or retrieval strategies between the two study-test phases, and the data were therefore collapsed across the two study-test phases for further analysis.

The overall mean proportions of stems successfully completed with words at test were 0.93 (SD, 0.05) for stems of studied words and 0.87 (SD, 0.07) for stems of nonstudied words. Collapsing across study-list-membership judgment, stems of studied words yielded a higher mean proportion of target completions than did stems of nonstudied words (studied: 0.64; SD, 0.06; nonstudied: 0.41; SD, 0.07; $t_{(24)} = 16.0$; $p < 0.001$). For the nonstudied target words, a mean of 0.36 (SD, 0.08) was correctly rejected as nonstudied. For the studied target words, a mean of 0.32 (SD, 0.11) was judged studied (remembered words), and a mean of 0.32

Table 1. Anatomical locations of activations and deactivations at study related to later explicit memory ($p < 0.005$, uncorrected, two tailed, extent threshold $k = 5$ adjacent voxels)

Structure	x	y	z	Z score
Remembered > forgotten				
Left inferior frontal gyrus, BA 47	-36	29	-4	2.94
Left middle frontal gyrus, BA 9 and 46	-47	30	21	3.77
	-39	27	26	3.43
Left superior frontal gyrus, BA 10	-27	56	5	2.92
Left precentral gyrus, BA 9	-42	8	35	3.34
Right inferior frontal gyrus, BA 47	30	20	-16	3.36
Left parahippocampal gyrus, BA 30 and 35	-18	-32	-6	3.54
	-18	-24	-11	3.64
Left middle temporal gyrus, BA 22	-56	-38	5	3.58
Left superior temporal gyrus, BA 39	-39	-46	5	2.95
Left cingulate gyrus, BA 24	-15	-10	39	3.76
Right hippocampus	33	-24	-9	3.95
Right parahippocampal gyrus	21	-6	-10	3.30
	36	-4	-20	2.87
Right parahippocampal gyrus, BA 30	24	-35	4	3.48
Right temporal lobe, BA 20	42	-13	-20	3.23
Right cingulate, BA 31	21	-34	27	2.82
Left superior parietal lobule, BA 7	-30	-68	45	3.86
	-39	-59	53	2.65
Left inferior occipital gyrus, BA 18	-42	-84	-1	3.10
Right middle occipital gyrus, BA 19	36	-70	3	3.18
Left caudate	-21	-37	16	2.99
Left brainstem	-3	-36	-23	3.55
Left cerebellum, anterior lobe	-32	-42	-23	3.54
Right caudate	21	-34	13	3.34
Right cerebellum, anterior lobe	30	-39	-21	3.04
Forgotten > remembered				
Right superior frontal gyrus, BA 6, 9	9	51	22	4.62
	21	15	63	3.30
Right medial frontal gyrus, BA 6	3	48	34	3.80
Right subcallosal gyrus, BA 47	21	20	-9	4.23
Left fusiform gyrus, BA 18	-21	-80	-21	3.03
Right superior temporal gyrus, BA 22	62	-54	22	3.37
Right anterior cingulate, BA 32	12	38	12	3.83
Right caudate	18	12	10	3.67
Right putamen	21	11	-3	4.26
Left cerebellum, posterior lobe	-30	-80	-26	3.45

All coordinates are given in Talairach space (Talairach and Tournoux, 1988). The structures are gray-matter structures closest to the local maxima.

(SD, 0.11) was judged nonstudied (primed words), yielding means of 102.4 observations per participant for each of these word categories. For stems of studied words, a mean of 0.23 (SD, 0.05) was completed with nontarget (nonstudied) words judged nonstudied, yielding a mean of 73.6 observations per participant in the forgotten category. (A small mean proportion of false alarms accounts for the difference between the sum of the three response proportions just given and the total mean stem-completion proportion of 0.93.) For stems of nonstudied targets, a mean of 0.36 (SD, 0.08) was completed with nonstudied target words judged nonstudied, and a mean of 0.39 (SD, 0.06) was completed with nonstudied nontarget words judged nonstudied. (A small mean proportion of false alarms accounts for the difference between the sum of these two proportions and the overall stem-completion proportion of 0.87.)

Considering only completions judged nonstudied, target completions formed a higher mean proportion (0.57; SD, 0.09) of completions for stems of studied words (primed words) than for stems of nonstudied words (0.47; SD, 0.07; $t_{(24)} = 6.3$; $p < 0.001$), demonstrating priming at test. Additionally, the mean RT at test for creating a completion and judging it nonstudied was faster for

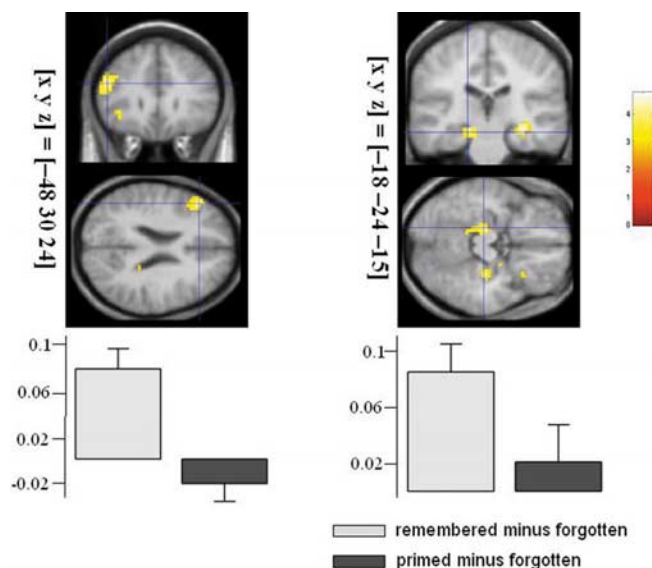


Figure 2. Brain-activity differences at encoding related to conscious remembering (explicit memory). Compared with later-forgotten items, later-remembered items showed greater activation in the left PFC (left) and bilateral MTL (right). The significance threshold was 0.005 (uncorrected, two tailed, extent threshold $k = 5$ adjacent voxels). Bar plots display the peak percentage signal differences of the best-fitting canonical HRF for remembered/primed items relative to forgotten items. The error bars here and in Figure 4 indicate SE of the difference in means between remembered/primed items and forgotten items.

the primed response category (i.e., studied words used to complete stems of studied words; 1660 ms; SD, 336) than it was for the forgotten response category (i.e., nonstudied words used to complete stems of studied words; 1821 ms; SD, 327; $t_{(24)} = 8.6$; $p < 0.001$). Because both of these word categories were judged nonstudied, the only difference being the production of a studied word in the former case but not the latter, the RT advantage for the primed category also reflected priming of word-stem completion (Schott et al., 2002; Düzel et al., 2005). Note that any increased difficulty in judging the word nonstudied for the studied words (primed category) compared with the nonstudied words (forgotten category) would have worked against this priming-related RT advantage. For additional details of the behavioral data, see Schott et al. (2005).

At study, the mean RTs for the syllable judgments were 980 ms (SD, 380) for later-remembered words, 973 ms (SD, 374) for later-primed words, and 990 ms (SD, 382) for later-forgotten words, which were not significantly different in a one-way ANOVA ($F_{(2,48)} = 1.5$; $p > 0.20$). Moreover, consistent with previous research using this procedure (Schott et al., 2002), there was also no significant difference in mean normative word frequency per million words of printed text (Schott et al., 2002) between later-remembered words (38.8; SD, 12.9), later-primed words (43.9; SD, 14.3), and later-forgotten words (36.7; SD, 14.5; $F_{(2,48)} = 1.6$; $p > 0.20$). (The overall means reported are means of individual-participant median word frequencies, in view of positively skewed distributions of word frequencies within participants, as is typically observed.) There was also no significant difference in the mean number of syllables between later-remembered words (2.1; SD, 0.1), later-primed words (2.0; SD, 0.1), and later-forgotten words (2.1; SD, 0.1 ($F_{(2,48)} = 0.35$; $p > 0.70$)). However, the mean number of possible completions to the stems of the three word types, as indicated by normative data (Schott et al., 2002, 2005), did differ significantly between stems of later-remembered words (6.3; SD, 0.5), stems of later-primed

words (6.4; SD, 0.5), and stems of later-forgotten words (8.6; SD, 0.7; $F_{(2,48)} = 116.1$; $p < 0.001$). The difference was created by a greater number of completions to the stems of later-forgotten words compared with those of later-remembered and later-primed words, with later-remembered and later-primed words not differing significantly from each other ($t_{(24)} = 0.9$; $p > 0.3$). The mean word length (in number of letters) also differed significantly between later-remembered words (5.7; SD, 0.2), later-primed words (5.8; SD, 0.2), and later-forgotten words (5.9; SD, 0.2; $F_{(2,48)} = 4.6$; $p < 0.025$). The significant difference was created by a slightly greater mean length for later-forgotten words compared with later-remembered words ($t_{(24)} = 2.9$; $p < 0.01$), with later-primed and later-forgotten words ($t_{(24)} = 2.0$; $p > 0.05$), and with later-remembered and later-primed words ($t_{(24)} = 1.2$; $p > 0.20$), not differing significantly from each other.

Three observations are in order, given the greater number of possible completions and greater word length for later-forgotten words compared with later-remembered and later-primed words. First, for the fMRI imaging contrasts of later-remembered words with later-forgotten words and of later-primed with later-forgotten words, these item differences for the forgotten words were a constant across the two imaging subtractions and cannot account for differing patterns of activations and deactivations across the two subtractions. Second, the direct imaging contrast of later-remembered and later-primed words was conducted across word types that did not differ in the number of completions or word length and revealed results broadly consistent with those of the contrasts of later-remembered with later-forgotten words and of later-primed with later-forgotten words. Third, any experiment examining brain activity at encoding as a function of the later memory fate of the studied items (Wagner et al., 1998), which is inherently a random variable and not an experimentally controlled variable, must inevitably leave some item characteristics or participant–item interactions uncontrolled, which correlate with, or may be responsible for, differences in later memory. Indeed, these may be part and parcel of the phenomena of interest and should not be regarded as detracting from the fruitfulness of this approach.

fMRI results

Tables 1–3 show, respectively, activations and deactivations at study for later-remembered words compared with later-forgotten words, for later-primed words compared with later-forgotten words, and for later-remembered words compared with later-primed words. Compared with later-forgotten and later-primed words, later-remembered words were associated with relatively higher hemodynamic responses in the bilateral MTL (left and right parahippocampal gyrus and hippocampus) and in the left PFC [Brodmann's area (BA) 9, 10, 46, and 47] at study (Fig. 2; Tables 1, 3), consistent with results from previous studies of memory encoding (Brewer et al., 1998; Wagner et al., 1998; Buckner et al., 2000b; Otten et al., 2002; Reber et al., 2002; Schott et al., 2004).

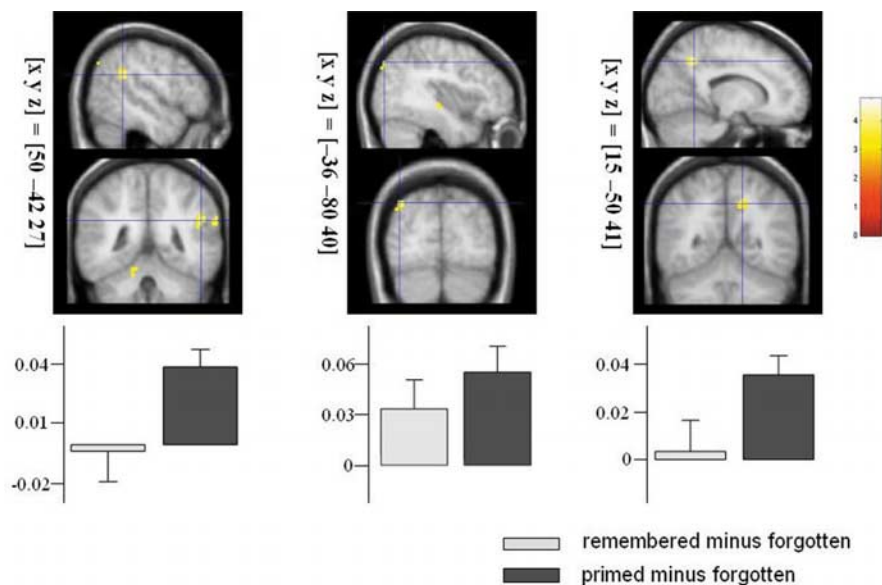


Figure 3. Hemodynamic response increases at encoding related to priming (implicit memory). Compared with later-forgotten items, later-primed items showed greater activation in the right temporoparietal junction (supramarginal gyrus, inferior parietal lobule) (left panel), in the left (and right) lateral precuneus (middle panel), and in the right medial precuneus (right panel). See Figure 2 legend for more details.

Table 2. Anatomical locations of activations and deactivations at study related to later priming ($p < 0.005$, uncorrected, two tailed, extent threshold $k = 5$ adjacent voxels)

Structure	x	y	z	Z score
Primed > forgotten				
Right inferior frontal gyrus, BA 47	36	20	-16	2.90
Right middle frontal gyrus, BA 10	27	44	12	3.42
Left insula, BA 13	-39	-21	-4	2.76
Right supramarginal gyrus, BA 40	65	-42	27	3.20
Left precuneus, BA 19	-36	-80	40	3.19
Right inferior parietal lobule, BA 40	50	-42	27	3.80
Right precuneus, BA 7 and 19	15	-50	41	3.72
	45	-71	42	3.41
Left cerebellum, anterior lobe	-15	-47	-15	2.91
Forgotten > primed				
Left inferior frontal gyrus, BA 46	-39	30	12	3.24
Left precentral gyrus, BA 6	-48	-7	34	2.90
Right inferior frontal gyrus, BA 9 and 46	48	-2	25	3.31
	53	33	9	3.20
Right subcallosal gyrus, BA 47	21	20	-11	3.31
Left fusiform gyrus, BA 37	-45	-47	-10	2.87
Left anterior cingulate, BA 24	-9	32	7	2.85
Right middle temporal gyrus, BA 19, 20, and 39	50	-38	-6	3.12
	53	-69	23	2.75
	50	-63	17	2.70
Right temporal lobe	39	-32	-1	4.07
Corpus callosum/anterior cingulate	0	15	10	3.33
Left superior parietal lobule, BA 7	-21	-70	59	2.77
Left precuneus, BA 31	-6	-69	20	2.75
Right precuneus, BA 31	18	-72	23	3.41
Right putamen	21	11	-11	2.74
Right cerebellum, anterior lobe	12	-57	-27	2.84

All coordinates are given in Talairach space (Talairach and Tournoux, 1988). The structures are gray-matter structures closest to the local maxima. Boldface type denotes brain regions that also showed significant deactivations at test.

Compared with later-forgotten words, later-primed words were associated with a complex pattern of regional hemodynamic response increases and decreases at study that was strikingly different from that observed in the contrast of later-remembered

Table 3. Anatomical locations of differential activations for remembered and primed items ($p < 0.005$, uncorrected, two tailed, extent threshold $k = 5$ adjacent voxels)

Structure	x	y	z	Z score
Remembered > primed				
Left middle frontal gyrus, BA 11, 46, and 47	−42	27	18	3.78
	−50	39	15	3.59
	−27	35	−7	3.44
	−24	37	−14	2.90
Left inferior frontal gyrus, BA 46, 47	−42	32	4	3.00
	−36	31	−12	3.01
Left precentral gyrus, BA 9	−39	5	33	2.97
Right middle frontal gyrus, BA 46	53	36	15	3.57
Right inferior frontal gyrus, BA 47	24	32	−7	2.87
Left anterior cingulate, BA 24	0	24	7	3.63
Right anterior cingulate, BA 33	3	10	22	2.85
Right cingulate gyrus, BA 31	24	−25	34	3.12
Left hippocampus	−33	−18	−14	2.92
Left parahippocampal gyrus, BA 35	−18	−24	−9	2.90
Left uncus, BA 20	−33	−13	−27	3.12
Right hippocampus	33	−24	−9	3.71
Right parahippocampal gyrus, BA 37	15	−9	−12	3.06
Right insula, BA 13	33	−22	29	3.19
Left fusiform gyrus, BA 37	−48	−44	−8	3.23
Right fusiform gyrus, BA 20	36	−39	−18	3.04
Left superior parietal lobule, BA 7	−33	−62	50	3.90
Left precuneus, BA 7	−21	−73	56	3.38
Left middle occipital gyrus, BA 19	−45	−79	1	3.39
Left cerebellum, anterior lobe	−6	−36	−23	3.06
Primed > remembered				
Right medial frontal gyrus, BA 9 and 10	9	42	34	3.78
	9	47	11	3.34
Right superior frontal gyrus, BA 6, 9, and 10	21	18	63	3.76
	12	62	22	3.57
	12	51	22	3.32
	27	47	14	2.88
Right middle frontal gyrus, BA 8	39	22	40	3.64
	24	31	37	2.90
	30	40	37	2.80
Right superior temporal gyrus, BA 13, 22	48	−42	24	3.09
	62	−54	22	2.81
Right supramarginal gyrus, BA 40	56	−46	22	3.34
Right precuneus, BA 31	12	−54	36	3.21
Right caudate	18	12	10	2.99

All coordinates are given in Talairach space (Talairach and Tournoux, 1988). The structures are gray-matter structures closest to the local maxima.

with later-forgotten words. Priming-related hemodynamic increases were mostly observed in parietal brain regions, namely in the right temporoparietal junction (supramarginal gyrus, inferior parietal lobule), in the lateral precuneus bilaterally, and in the right medial precuneus (Fig. 3, Table 2). Portions of the right PFC (BA 10 and 47) also showed priming-related response increases at study compared with both forgotten items (Table 2) and remembered items (Table 3). None of these regions showed priming-related hemodynamic response decreases at test (i.e., none survived masking with the correct rejections-minus-primed contrast from the test phase) (Schott et al., 2005) (Fig. 1).

In the left fusiform gyrus (BA 37) and in the bilateral inferior frontal gyrus (BA 46) and extrastriate cortex (BA 19 and 31), brain regions usually linked with perception and identification, primed words elicited smaller hemodynamic responses than forgotten words at study (Fig. 4, Table 2). Masking these results with the correct rejections-minus-primed contrast from the test phase (Schott et al., 2005) (Fig. 1) revealed an overlap of priming-related deactivations at study and test in left fusiform gyrus and

bilateral inferior frontal gyrus (Table 2). Although there were priming-related hemodynamic deactivations in the extrastriate cortex bilaterally at both study and test, these deactivations did not statistically overlap: the masking analysis revealed that the decreases at study occurred in “higher” visual areas (BA 19 and 31) than the decreases at test, which occurred in “lower” visual areas (BA 17, 18, and 19).

The precuneus showed a pattern of significant activations and deactivations for primed words relative to forgotten words, with a similar pattern being apparent (albeit not significantly so at $p = 0.005$) for remembered words relative to forgotten words (Figs. 3, 4). Although a lateral portion of the left precuneus (BA 19; Talairach coordinates: $x = -36$, $y = -80$, $z = 40$) was associated with increased activation for primed (and remembered) words relative to forgotten words (Fig. 3, middle; Table 2), a more medial region of the right precuneus (BA 31; Talairach coordinates: $x = 18$, $y = -72$, $z = 23$) showed a deactivation for primed (and remembered) words relative to forgotten words (Fig. 4, right; Table 2). A different pattern emerged in the left PFC (Fig. 4, left; Tables 1–3) and left fusiform gyrus (Fig. 4, middle; Tables 1–3). These regions showed an increased activation for remembered relative to forgotten words but a deactivation for primed relative to forgotten words, leading to strong activation differences between later-remembered and later-primed words in these regions in direct contrast of these word types (Table 3).

Discussion

Our results show that priming and explicit memory are anatomically distinct during encoding. Whereas encoding for later explicit memory was associated with hemodynamic increases in the bilateral MTL and left PFC, encoding for later priming was associated with a complex pattern of hemodynamic increases and decreases, but not with MTL activity. The hemodynamic decreases occurred in some regions associated with perception and identification that are implicated in priming at retrieval (Schott et al., 2005).

Later-remembered items elicited activations of the left PFC and bilateral MTL (Fig. 2; Tables 1, 3), including both the hippocampus and the parahippocampal gyrus, replicating previous studies (Brewer et al., 1998; Wagner et al., 1998; Buckner et al., 2000b; Otten et al., 2002; Reber et al., 2002; Schott et al., 2004). Our results, especially because they show activations in these regions for remembered compared with both forgotten and primed items, extend those findings by showing that these MTL activations are specific to encoding for later explicit memory and not priming. They are also consistent with the finding of intact priming despite MTL pathology (Schacter, 1987; Richardson-Klavehn and Bjork, 1988).

Brain activity predicting priming differed from that predicting explicit memory. As predicted, priming-related activity occurred in ventral visual stream areas (bilateral extrastriate cortex, inferior frontal gyrus, and left fusiform gyrus) implicated in perception and identification. These findings are consistent with electrophysiological evidence that neural activity relating to encoding for later priming occurs earlier than neural activity relating to explicit memory encoding (Schott et al., 2002). Together, this evidence supports the notion that brain systems, the function of which are perception and identification, have inbuilt learning mechanisms that operate during the initial experimental encounter with later-primed stimuli (Tulving and Schacter, 1990; Schacter et al., 2000; Bowers and Marsolek, 2003) and questions “unitary” theories of memory that view implicit and explicit

memory as reflecting different access modes, at retrieval, to the same encoded episodic memory traces (Jacoby, 1983a,b).

Although, as predicted, priming-related responses occurred in ventral visual stream areas, responses in these areas were deactivations rather than activations, contrary to prediction. Moreover, masking analysis revealed that deactivations occurred in two areas also showing priming-related deactivations at test (Schott et al., 2005), the bilateral inferior frontal gyrus and left fusiform gyrus (Fig. 4; Table 2). This finding is counterintuitive because of behavioral data linking priming at test with increased cognitive processing efficiency (Richardson-Klavehn and Bjork, 1988; Kirsner et al., 1993) and because of the view that priming-related hemodynamic decreases at test reflect increased neural processing efficiency (for review, see Henson, 2003). Previous behavioral studies indicate that items processed less efficiently at study show greater priming at test. For example, low-frequency words show more later priming than do high-frequency words. The latter, attributable to frequent pre-experimental exposure, are already efficiently processed on initial experimental exposure and often show no later priming (Hall, 1954; Jacoby, 1983a). Additionally, studying a word in the context of a related word (e.g., FLOWER-GARDEN), thus priming its initial identification, reduces later perceptual priming compared with studying the word in isolation (e.g., XXXXXX-GARDEN) (Jacoby, 1983b). In summary, items already efficiently processed at study (e.g., as a result of pre-experimental exposures) would be less likely to be later primed and more likely to be selected into the later-forgotten category, and not the later-primed category, than would items not efficiently processed at study. Consequently, if priming-related neural response decreases at test reflect increased neural processing efficiency, the intuitive prediction is of priming-related response increases at study, reflecting reduced processing efficiency for later-primed compared with later-forgotten words. Our results disconfirm this prediction.

An interpretation that reconciles the encoding and retrieval findings is that different neural mechanisms underlie priming at encoding and retrieval. At encoding, priming may be initiated by a more precise (or “sharp”) and coordinated response of the neural word identification hierarchy for primed compared with unprimed words, creating better conditions for Hebbian learning within that hierarchy (Düzel et al., 2005). Sharpened cortical responding (Desimone, 1996) means that the tuning curves of neurons are narrower, so that only neurons best representing the stimulus features respond and fewer neurons respond. Regional hemodynamic responses reflect both the number of responsive neurons and their level of synaptic and spiking activity (Logothetis and Wandell, 2004); thus, a sharper cortical response for later-primed compared with later-forgotten words implies priming-related hemodynamic decreases rather than increases. The perceptual learning enabled by this sharpened responding could enable later increases in neural processing efficiency for primed compared with nonrepeated stimuli at retrieval, implying lower synaptic and spiking activity, again leading to hemodynamic decreases. Increased processing efficiency might be medi-

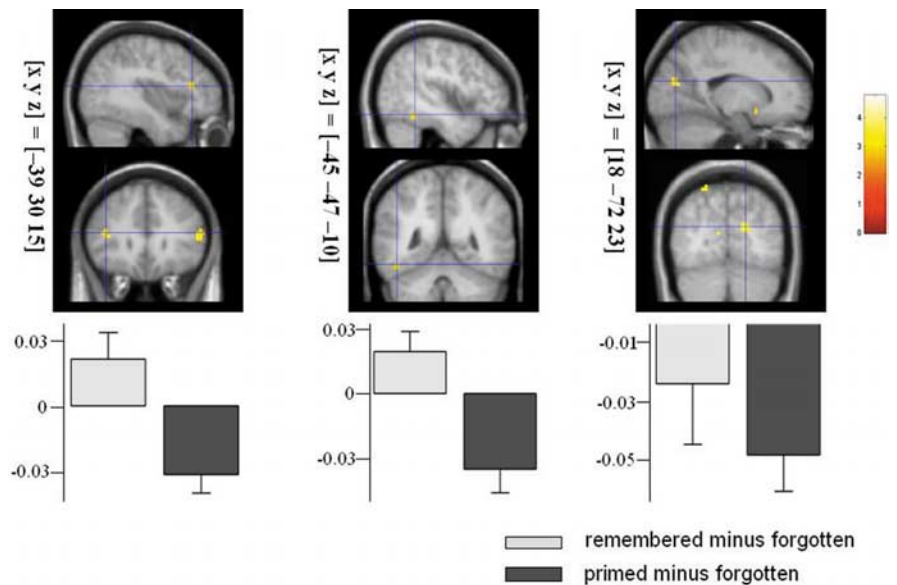


Figure 4. Hemodynamic response decreases at encoding related to priming (implicit memory). Compared with later-forgotten items, later-primed items showed decreased activation in the left (and right) PFC (left panel), in the left fusiform gyrus (middle panel), and in the right (and left) extrastriate cortex (right panel). See Figure 2 legend for more details.

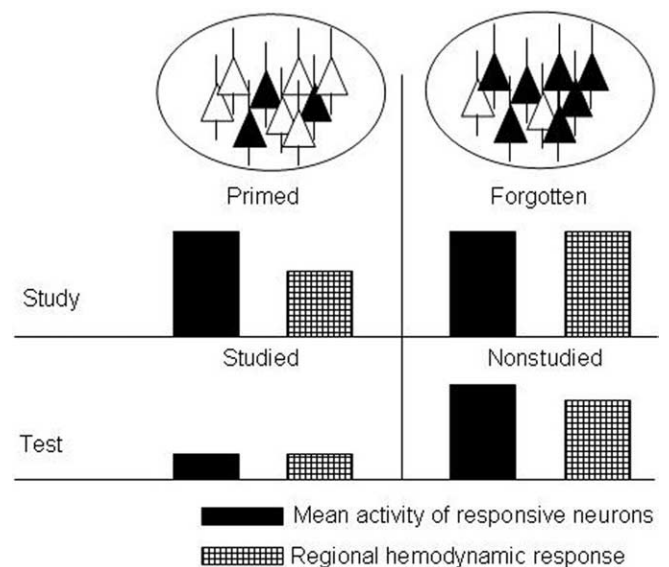


Figure 5. Illustration of different neural mechanisms for priming-related hemodynamic decreases in the ventral visual stream at encoding and retrieval (in the top row, filled nodes represent responsive neurons and unfilled nodes represent nonresponsive neurons). Hemodynamic responses are influenced by the number of responsive neurons as well as their level of synaptic and spiking activity. At study, the priming-related hemodynamic decrease reflects fewer responsive neurons (i.e., sharper or more precise cortical responding), whereas at test it reflects a repetition-related decrease in the activity of responsive neurons (i.e., increased neural processing efficiency).

ated in part by top–down feedback from higher to lower stimulus identification areas (Henson, 2003), consistent with our finding that priming-related extrastriate deactivations at encoding occurred in higher visual areas (BA 19 and 31) than those that showed deactivations at retrieval (BA 17, 18, and 19) (Schott et al., 2005). [However, it should be noted that the stimuli at study were entire words, whereas those at test were word stems, which could also explain these differences (Buckner et al., 2000a).] Our two-factor view of priming-related neural processes at encoding and retrieval is illustrated schematically in Figure 5.

The view that verbal priming is initiated by a more precise and coordinated neural response in word identification areas is supported by magnetoencephalographic data concerning priming-related neural oscillations at encoding during the time window of word identification (within 250 ms of word presentation) (Düzel et al., 2005). Compared with later-forgotten words, later-primed words elicited reduced amplitude γ (and β_2) oscillations (~ 20 – 45 Hz), which were, however, better phase aligned to stimulus onset across trials (suggesting a more precise cortical response). Source analysis of these γ oscillations located them in the ventral visual stream areas (including the bilateral extrastriate cortex and left fusiform gyrus) implicated by the current hemodynamic response decreases at encoding. The priming-related γ amplitude decreases were accompanied by increased amplitude α oscillations (~ 8 – 13 Hz), again source localized to ventral visual stream areas, coupled with increased synchrony of the α oscillations across these areas, suggesting more coordinated responding in the word identification hierarchy for later-primed compared with later-forgotten words. These findings are highly consistent with the current priming-related hemodynamic decreases, because of the location and early onset of the oscillatory modulations, and because γ oscillation amplitudes correlate positively with the strength of the hemodynamic signal (Logothetis and Wandell, 2004).

There were response increases at encoding for later-primed compared with later-forgotten words (Fig. 3, Table 2), which might be taken as neural correlates of decreased cognitive processing efficiency. However, the parietal and right frontal locations of these activations might also suggest a role for attention (Culham and Kanwisher, 2001; Behrmann et al., 2004). Priming is often thought to be independent of attention (Jacoby et al., 1993). However, there is, in fact, strong evidence that priming is enhanced by stimulus-specific attention at encoding (Richardson-Klavehn and Bjork, 1988; Mulligan and Stone, 1998; Richardson-Klavehn and Gardiner, 1998; Stone et al., 1998, 2000). Furthermore, some priming-related oscillatory modulations at encoding reported by Düzel et al. (2005), particularly increased α synchrony across word-identification areas, commenced just before stimulus onset, suggesting that prestimulus attentional state influences the coordination of responding in the word-identification hierarchy and consistent with evidence concerning attentional modulation of oscillatory synchrony (von Stein et al., 2000; Engel et al., 2001; Fries et al., 2001). Clearly, future research should explore these apparent neural links at encoding between attention, perception, and later priming (Zago et al., 2005). Another issue meriting additional research is whether priming-related activations and deactivations at study occur for both remembered items and primed items, as suggested, for example by activations and deactivations in the precuneus that occurred for primed items relative to forgotten items, with a similar (nonsignificant) trend for remembered items (Fig. 3, middle; Fig. 4, right). Other areas, such as the left fusiform gyrus (Fig. 4, middle) and PFC (Fig. 4, left), showed activations for remembered items and deactivations for primed items, raising the question of whether priming-related deactivations in these areas occur for remembered items as well as primed items but are obscured by the activations related to explicit memory encoding.

In conclusion, there has been considerable speculation about neural mechanisms that underlie priming-related hemodynamic response decreases at retrieval (Schacter and Buckner, 1998; Wiggs and Martin, 1998; Henson, 2003; Henson and Rugg, 2003; Zago et al., 2005), including increased neural processing efficiency, sharpened cortical representations, and sparser cortical

representations. Some theorizing has focused on neural mechanisms during initial experimental exposure (encoding) of later-primed stimuli (Zago et al., 2005), but before the current study, hemodynamic evidence has been obtained only at retrieval, and no theorizing has considered that different neural processes may underlie priming at encoding and retrieval. Our two-factor interpretation of priming at encoding and retrieval is highly tentative. However, our results do indicate that future research should focus not only on neural measurements at retrieval but also on neural measurements at encoding, when the learning occurs that underlies later priming.

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