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Linking Implicit and Explicit Memory: Common Encoding Factors and Shared Representations

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Summary

Dissociations between implicit and explicit memory have featured prominently in theories of human memory. However, similarities between the two forms of memory have been less studied. One open question concerns whether implicit and explicit memory share encoding resources. To explore this question, we employed a subsequent memory design in which several novel scenes were repeated once during an fMRI session and explicit memory for the scenes was unexpectedly tested afterward. Subsequently remembered scenes produced more behavioral priming and neural attenuation—two conventional measures of implicit memory—than did subsequently forgotten scenes. Moreover, brain-behavior correlations between these two implicit measures were mediated by subsequent memory. Finally, tonic activity, possibly reflecting the natural time course of attention, was predictive of subsequent memory. These results suggest that implicit and explicit memory are subject to the same encoding factors and can rely on similar perceptual processes and representations.

Introduction

A fundamental tension in the study of human memory is how a single moniker can encompass such diverse phenomena as priming, familiarity, recollection, skill acquisition, and knowledge. Cognitive psychologists have cleaved these behaviors in many ways based on their features and constraints. The most influential of these divisions is that of implicit versus explicit memory (Graf and Schacter, 1985). Implicit memory refers to the retrieval of stored representations without the need for conscious awareness or intent (also known as nondeclarative memory; Squire, 1987). Explicit memory, on the other hand, results from conscious reflection of previous experiences or knowledge (also known as declarative memory; Cohen and Squire, 1980).

One basic question about implicit and explicit memory concerns whether they recruit multiple different memory systems and subsystems (e.g., Schacter and Tulving, 1994) or whether they reflect different types of processing by a single memory system (e.g., Ratcliff and McKoon, 1988). There is now substantial evidence for multiple memory systems, much of it coming from *behavioral dissociations*. Lesion studies demonstrated that certain types of brain damage only impair implicit performance, while others only impair explicit performance (Gabrieli et al., 1995; but see Jernigan and Ostergaard, 1993; Kinder and Shanks, 2003). In normal adults, experimental manipulations, such as levels of processing, have differential effects on implicit and explicit performance (for a review, see Tulving and Schacter, 1990; but see Blaxton, 1989; Moscovitch and Bentin, 1993).

Neuroimaging techniques have also been used to emphasize differences between implicit and explicit memory. These *neural dissociations* were based on findings of distinct neural correlates of implicit and explicit retrieval. For example, event-related potentials (ERPs) have revealed different spatiotemporal components of implicit and explicit retrieval (e.g., Paller et al., 2003; Rugg et al., 1998; Schott et al., 2002). Functional magnetic resonance imaging (fMRI) has helped localize neuroanatomical differences between implicit and explicit memory: in one study, for example, implicit retrieval recruited prefrontal, fusiform, and extrastriate regions, while explicit retrieval recruited the posterior cingulate, precuneus, and inferior parietal lobule (Schott et al., 2005); many other studies have reported frontal involvement in explicit retrieval as well (e.g., Buckner and Koutstaal, 1998).

While behavioral and neural dissociations convincingly demonstrate that implicit and explicit memory must have independent components, the scope of this independence is unclear. At one extreme, stochastic dissociations suggest that implicit and explicit memory are completely independent: "Perfect stochastic independence implies complete absence of…overlap [of information, stages, processes, mechanisms]" (Tulving, 1985, p. 395); however, the methodological and statistical techniques used to obtain stochastic dissociations have been questioned (for a review, see Poldrack, 1996). Another possibility is that while implicit and explicit memory have independent components, they might additionally have shared components. There is some evidence for this hybrid view. For example, the neural correlates of implicit and explicit retrieval of verbal information are very similar, but explicit retrieval recruits additional brain regions, including anterior prefrontal and medial temporal cortices (Buckner and Koutstaal, 1998). Similarly, priming-related right posterior reductions in neural activity have been observed during both implicit and explicit retrieval, with additional left frontal and hippocampal activation during explicit retrieval (e.g., Badgaiyan and Posner, 1997). Moreover, some areas that show greater activity for novel than repeated items (neural priming or attenuation; Henson, 2003; Schacter and Buckner, 1998; Wiggs and Martin, 1998) also show greater activity for items that are later remembered in an explicit memory test (Kirchhoff et al., 2000). Finally, signatures of implicit retrieval were observed under conditions of explicit retrieval in the study on neural dissociations discussed earlier (Schott et al., 2005); the authors suggest that implicit retrieval may sometimes or always accompany explicit retrieval (p. 1261).

In addition to evidence that implicit and explicit memory may share neural circuitry, they may also be subject

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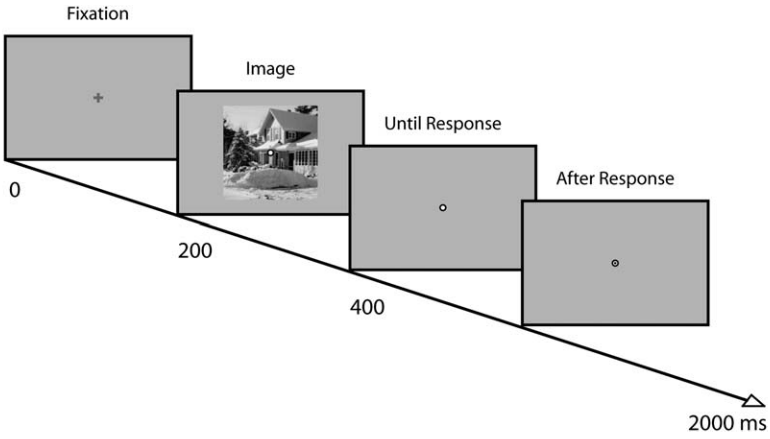

Figure 1. Trial Sequence

Trials consisted of a green fixation cross for 200 ms, followed by the scene for 200 ms, and then a blank screen with a fixation dot that was filled-in after response. During the first phase of the experiment, subjects decided as quickly and accurately as possible whether the scene occurred indoors or outdoors. The trial sequence was identical at test, except subjects now determined whether the scene had been previously studied and indicated their confidence.

to the same encoding factors. In one study (Yi and Chun, 2005), subjects were presented with composite images of scenes and faces and were required to attend to either the scene or face. Neural attenuation was observed in the parahippocampal place area, a scene-selective region of visual cortex (PPA; Epstein and Kanwisher, 1998), only when subjects attended to scenes; later, only attended scenes were recognized in a memory test (see also Vuilleumier et al., 2005; Yi et al., 2006). Behaviorally, attention modulates both conceptual and perceptual priming, as well as the explicit tests paired with these tasks (e.g., Bentin et al., 1998; Mulligan, 1998). Thus, there is some reason to believe that implicit and explicit memory are not completely independent.

The present experiment explores the neural and behavioral relationship between implicit and explicit memory by analyzing fMRI BOLD responses associated with repetition priming as a function of subsequent memory. Subjects viewed 120 novel scenes, each repeated once, while performing an indoor/outdoor judgment task (Figure 1). The difference in response time between the first and second exposure of each scene provided a measure of behavioral priming. Neural attenuation was calculated as the difference in activation between the first and second exposure of each scene at the peak of the hemodynamic response (Epstein et al., 2003; Yi and Chun, 2005). These two measures have been conventionally used as evidence of implicit retrieval. Fifteen minutes after the last scan, subjects were given a surprise recognition test, including all 120 old scenes and 60 new ones. Based on the subsequent memory design (Brewer et al., 1998; Wagner et al., 1998), fMRI trials were sorted by explicit memory response, allowing us to conditionalize measures of implicit memory. A crucial difference between this study and Kirchhoff et al. (2000) is that we repeated many more stimuli, allowing us to directly assess how behavioral priming and neural attenuation for individual items varies according to subsequent memory.

Results

Recognition Performance

Based on responses during the surprise recognition test, old scenes were assigned to high confidence hits ("high confidence studied"), low confidence hits ("low confidence studied"), and misses ("new"), and new scenes were assigned to high confidence false alarms, low confidence false alarms, and correct rejects, for the same responses. Figures 2A shows the results of the recognition test. Collapsing across confidence, the hit rate was greater than the false alarm rate, $t(15) = 8.51$, $p < 0.0001$. Upon further inspection, subjects showed greater sensitivity for making high confidence responses than low confidence responses, $t(15) = 5.79$,

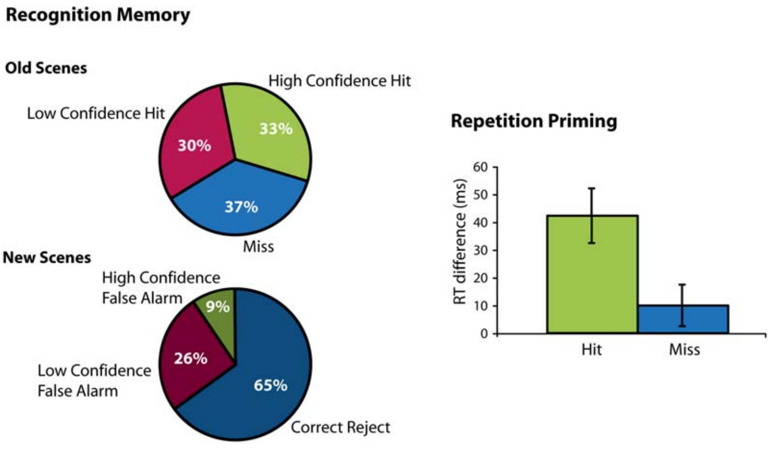

Figure 2. Behavioral Responses

(A) Mean percentage of each type of response during test. Trials were categorized as hits or misses, depending on responses to old scenes, and as false alarms or correct rejects, depending on responses to new scenes. Hits and false alarms were further subdivided by confidence. All subsequent uses of "hit" refer to high confidence responses (see Wagner et al., 1998).

(B) Repetition priming. Differences in indoor/outdoor response time to the first versus second exposure of a scene, as a function of subsequent memory. Error bars correspond to the standard error of the difference between hits and misses.

$p < 0.0001$; accordingly, the high confidence hit rate was robustly greater than the high confidence false alarm rate, $t(15) = 10.24$, $p < 0.0001$, but the difference between the low confidence hit rate and the low confidence false alarm rate only approached significance, $t(15) = 2.01$, $p = 0.06$. This suggests that a significant proportion of low confidence responses were guesses. For this reason, we will focus our analyses on high confidence hits as remembered items and misses as forgotten items (as in previous subsequent memory studies; e.g., Wagner et al., 1998). A post hoc analysis of low confidence hits is reported in the Supplemental Data available online.

An item analysis revealed no differences in the proportion of hits across indoor and outdoor images, $t < 1$. In addition, the distribution of hits and misses over items did not differ from a normal distribution, $t(391) = 1.47$, $p = 0.14$, suggesting that there was little consistency in the particular items that subjects remembered. In addition, the lag between the first and second exposure of each image in the scanner did not vary by hit or miss, neither in terms of the number of items (5.37 versus 5.37; $t < 1$) nor the amount of time (19.30 versus 19.38 s; $t < 1$).

Behavioral Responses

Indoor/outdoor responses during the two functional runs were sorted by whether the scene was subsequently remembered (high confidence hit) or forgotten (miss). Response times were analyzed with a 2 (subsequent memory: remembered, forgotten) × 2 (exposure: first, second) repeated-measures analysis of variance (ANOVA). There was no significant main effect of subsequent memory on response time, $F < 1$. There was, however, a strong effect of exposure, $F(1,15) = 14.28$, $p = 0.002$, with faster responses to the second exposure than to the first (614.7 versus 640.8 ms). Importantly, there was a robust interaction between subsequent memory and exposure, $F(1,15) = 11.25$, $p = 0.004$, with more priming for remembered [42.3 ms; $t(15) = 4.45$, $p = 0.0005$] than for forgotten [10.0 ms; $t(15) = 1.39$, $p = 0.19$] scenes (Figure 2B).

Response accuracies were analyzed in the same manner as response times. There was no main effect of memory on accuracy, $F < 1$, with very high accuracy for both remembered (96.3%) and forgotten (96.6%) scenes. There was also no main effect of exposure, $F < 1$, and no interaction between memory and exposure, $F(1,15) = 1.44$, $p = 0.25$. These results indicate that the priming reported above cannot be attributed to speed-accuracy tradeoffs. Only scenes that were correctly responded to at both exposures were included in brain analyses.

Neural Attenuation

Attenuation was assessed by comparing peak activity for the first versus second exposure of each scene (e.g., Epstein et al., 2003; Yi and Chun, 2005; Yi et al., 2004), as a function of subsequent memory. Peak activity was determined by all time points in the peristimulus time course that did not statistically differ from the time point with the greatest activation (see Experimental Procedures).

For the PPA ROIs (Figure 3A), the BOLD signal peaked at a single time point (6 s). Peak activity in the PPA was analyzed using a 2 (hemisphere) × 2 (memory) × 2 (exposure) repeated-measures ANOVA. There was no main effect of hemisphere, $F(1,15) = 1.11$, $p = 0.31$, and hemisphere did not interact with any combination of the other factors, $ps > 0.54$. The main effect of subsequent memory approached significance, $F(1,15) = 4.06$, $p = 0.06$, with higher peak response for remembered scenes, collapsed across exposure. There was also a main effect of repetition, $F(1,15) = 27.94$, $p < 0.0001$, evidence of neural attenuation. Importantly, there was an interaction between subsequent memory and exposure, $F(1,15) = 5.65$, $p = 0.03$. To further explore this interaction, two planned follow-up analyses were conducted. In response to the first exposure, peak activation was greater for remembered scenes (0.43%) than for forgotten scenes (0.37%), $t(15) = 2.51$, $p = 0.02$, replicating previous findings (e.g., Brewer et al., 1998). Second, more neural attenuation (first exposure minus second exposure) was observed for remembered scenes [0.086%; $t(15) = 4.79$, $p = 0.0002$] than for forgotten scenes [0.026%; $t(15) = 1.76$, $p = 0.10$], $t(15) = 2.38$, $p = 0.03$.

It is crucial to note that the lack of attenuation for forgotten scenes is not a result of a floor effect. First, Yi and Chun (2005), who experimentally addressed this concern, continued to obtain strong attenuation effects when the amplitude of their PPA responses was reduced by approximately 40% with blurring (for similar results with a contrast manipulation see Turk-Browne et al., 2006; Yi et al., 2006). Second, an analysis of low confidence hits revealed robust neural attenuation (0.080%), $t(15) = 3.31$, $p = 0.005$, but identical peak amplitude to forgotten scenes (0.37%), $t < 1$. This suggests that the lack of attenuation for forgotten scenes cannot be attributed to the lower overall amplitude per se.

There are conflicting reports about whether the PPA attenuation effects reported above are specific to scenes. In support of such specificity, attenuation is not observed in the PPA when faces are repeated (Epstein et al., 1999; Yi et al., 2006). However, repetition attenuation is observed in similar parahippocampal cortex when other non-scene stimuli, such as words and objects, are repeated (Kirchhoff et al., 2000; Kohler et al., 2005; O'Kane et al., 2005). This, combined with evidence that parahippocampal cortex contributes to episodic encoding of words (e.g., Kirchhoff et al., 2000; Wagner et al., 1998), suggests that in memory tasks, PPA specificity to scenes may be limited.

The finding of greater priming and attenuation for subsequently remembered scenes may seem to contradict evidence that priming hinders subsequent memory (Wagner et al., 2000). However, the purpose of that study was to consider the effect of priming *at encoding* on subsequent memory. In other words, they were interested in how processes at the second exposure impacted subsequent memory. The present study is primarily concerned with how processes at the first exposure impact subsequent priming and subsequent recognition. In fact, while subsequent recognition was the only measure of explicit memory in Wagner et al. (2000), we were also able to examine the relationship between priming and neural signatures of explicit memory during initial encoding (in their study, all items were encoded outside of the scanner). Moreover, one

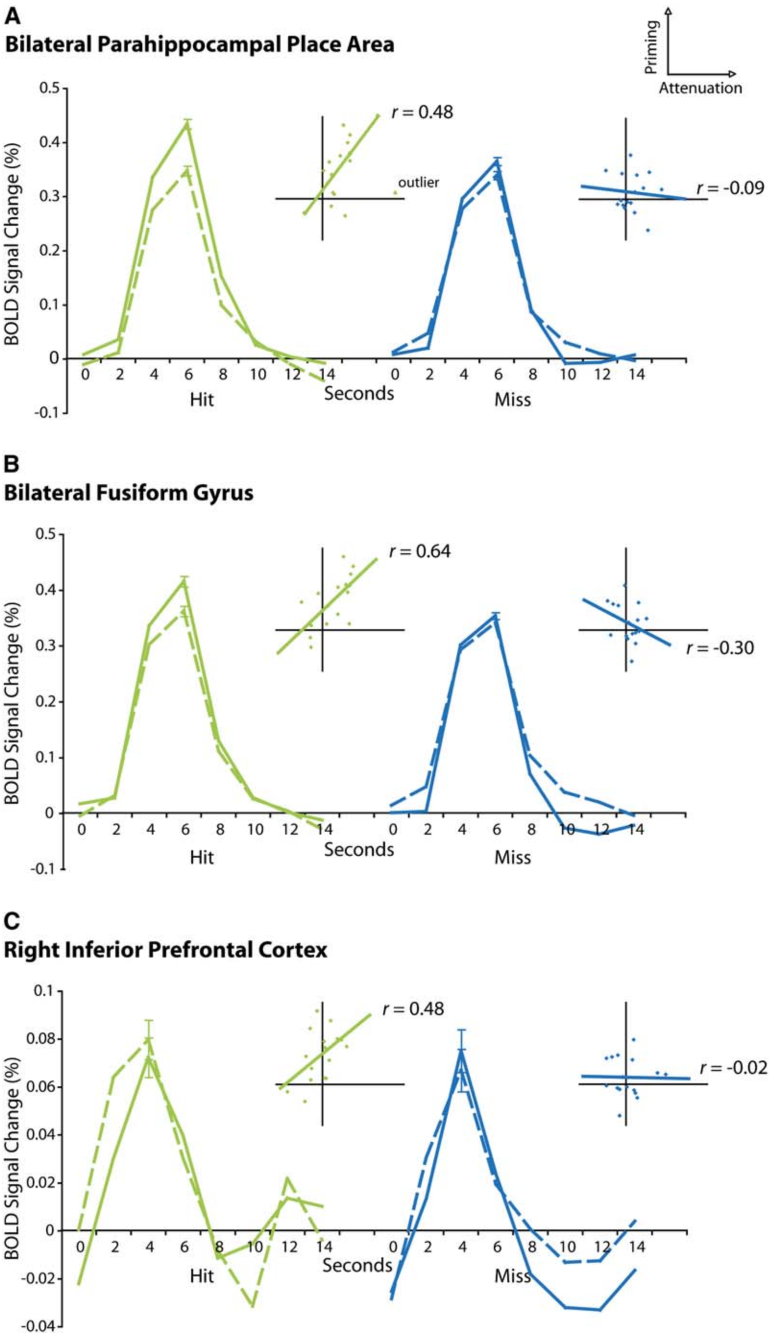

Figure 3. Neural Attenuation

Finite impulse responses for the first (solid) and second (dashed) exposures of each scene. In the left and right PPA (−28, −45, −7; 29, −43 −8), scenes that were subsequently remembered showed both a greater peak response for their first exposure and greater neural attenuation (first minus second exposure) than scenes that were forgotten. Peak error bars correspond to the standard errors of the difference between first and second exposure. Correlations between behavioral priming and neural attenuation in the PPA, left and right fusiform gyrus (−28, −55, −9; 34, −49, −12), and right inferior prefrontal cortex (43, 3, 37) were mediated by explicit memory. On the scatterplots, the x axis corresponds to attenuation and the y axis corresponds to priming. An outlier on the PPA hit scatterplot has been excluded from the displayed correlation.

conclusion of our study—that implicit and explicit memory share resources—is an untested assumption in the hypothesis that priming hinders recognition. Thus, rather than conflicting with each other, the studies explore different questions and may even be complementary.

Correlations between Priming and Attenuation

The relationship between priming and attenuation was examined in fusiform and inferior frontal regions, based on Maccotta and Buckner (2004). Since they used word stimuli, we obtained anatomical coordinates for bilateral fusiform gyrus and right inferior prefrontal cortex from Kirchhoff et al. (2000), who used scene stimuli. One difference between the two studies is that words led to stronger attenuation in left frontal regions, while scenes led to stronger attenuation in right frontal regions.

To examine the relationship between priming and attenuation in the present data, subjects' behavioral priming effects were correlated with their neural attenuation effects in each ROI (data from left and right fusiform gyrus were collapsed because there were no hemispheric differences, Fs < 1). Surprisingly, whereas Maccotta and Buckner (2004) found no correlation between priming and attenuation in the fusiform gyrus (r = 0.17), when the present data were sorted by subsequent memory, we observed a stronger correlation for remembered scenes (r = 0.64, p = 0.007) than for forgotten scenes

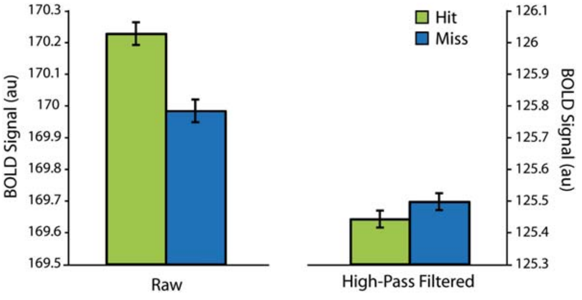

Figure 4. Tonic Activity

Greater raw BOLD signal immediately prior to the onset of the first exposure of a scene was associated with an increased likelihood of remembering the scene. High-pass filtering removed the baseline difference, suggesting that it might be attributable to slow shifts in encoding factors, such as attention. Error bars correspond to the standard errors of the difference between hits and misses.

($r = -0.30$, $p = 0.26$) using Fisher's r-to-z transformation, $z = 2.72$, $p = 0.007$. In addition, the fitted time course data for the fusiform ROIs were consistent with the PPA data reported above (Figure 3B).

The relationship between attenuation and priming was examined in bilateral PPA as well, because of the large attenuation effect there. Similar to bilateral fusiform gyrus, there was no correlation for forgotten items, $r = -0.09$, $p = 0.75$; however, there was also no correlation for remembered items, $r = 0.06$, $p = 0.82$. As can be seen in the scatterplot in Figure 3A, however, there is an outlier with 3.14 standard deviations more attenuation than the mean. The correlation without this subject approached significance for remembered items, $r = 0.48$, $p = 0.07$, but was nonsignificant for forgotten items, $r = -0.12$, $p = 0.67$; the difference between these correlations was not significant, $z = 1.64$, $p = 0.10$. Importantly, the outlying individual did not drive the attenuation effects discussed earlier, since all effects remained significant with the outlier removed.

The correlation between priming and attenuation in right inferior prefrontal cortex (Figure 3C) approached significance for remembered scenes, $r = 0.48$, $p = 0.06$, but not for forgotten scenes, $r = -0.02$, $p = 0.94$; the difference between these two correlations was not significant, $z = 1.38$, $p = 0.17$. In contrast to previous studies, there was no attenuation in this frontal ROI, which could be due to differences in experimental protocol: repeated stimuli were pre-exposed five times in Maccotta and Buckner (2004) and ten times in Kirchhoff et al. (2000); moreover, in the latter study, repeated stimuli were presented 100 times during scanning. It is worth noting that although some of the brain-behavior correlations reported above are only marginally significant, they were obtained with a small sample size relative to Maccotta and Buckner (2004), who used 54 subjects.

Intuitively, one would predict that any relationship between attenuation and priming should be based on subjects who exhibited positive effects. In other words, it is unclear what to predict for subjects who had greater activation and/or response times for repeated than for novel stimuli (although, see James and Gauthier, 2005; Vuilleumier et al., 2005). Thus, it is worthwhile to consider the stability of our correlations when the scatterplots in Figure 3 are restricted to the upper-right quadrant (positive attenuation and positive priming). While statistical power was reduced because of smaller sample sizes, the magnitude of the correlations for remembered items remained stable in all three regions: bilateral fusiform, $r = 0.54$, $df = 9$, $p = 0.09$; PPA (outlier removed), $r = 0.66$, $df = 11$, $p = 0.01$; right inferior prefrontal cortex: $r = 0.39$, $df = 7$, $p = 0.30$. Even though the frontal correlation was not statistically significant, it remained comparable to the effect ($r = 0.31$) reported by Maccotta and Buckner (2004). These results demonstrate more conclusively that behavioral priming can be positively associated with neural attenuation across subjects. A similar analysis for forgotten items was impossible, since it would involve restricting the correlations to six or fewer subjects in all three regions. Overall, these correlations mesh well with a recent TMS study (Wig et al., 2005) showing that activity in left inferior frontal gyrus during encoding (which has previously been implicated in subsequent memory) is necessary for observing behavioral priming and neural attenuation in frontal and middle temporal regions.

Tonic Activity

The analyses reported thus far support a positive association between measures of implicit and explicit memory. This association could be explained if both forms of memory are affected by similar factors at encoding, such as selective attention. While we did not directly manipulate attention as in other studies (e.g., Yi and Chun, 2005), we may be able to measure the natural state of attention by looking at tonic or sustained activity (Chawla et al., 1999). For example, stimuli from intentional encoding blocks with greater tonic activity are more likely to be subsequently recalled (Fernandez et al., 1999) and recognized (Otten et al., 2002); tonic activity has also been linked to retrieval (Donaldson et al., 2001; Rugg et al., 2002).

To explore the effect of tonic activity on encoding, the raw BOLD signal in bilateral PPA was extracted 2 s *prior* to the onset of the first exposure of each scene as a function of subsequent memory (Figure 4). There was reliably greater baseline activity for remembered items (170.23 arbitrary units; au) than for forgotten items (169.99 au), $t(15) = 3.39$, $p = 0.004$. Interestingly, tonic deactivations have been observed in the parahippocampal cortex during retrieval (Donaldson et al., 2001). The baseline difference between remembered and forgotten items was eliminated [remembered = 125.44 au, forgotten = 125.50 au; $t(15) = 1.03$, $p = 0.32$] when low temporal frequencies in the signal were filtered out by a conventional method (SPM high-pass filter, 128 s period cutoff).

Although high-pass filtering serves to remove noise such as drift from the raw signal, it may remove a global variable of interest from analysis. More specifically, attention, by way of tonic activity, may increase the sensitivity of neuronal populations, influencing the nature of phasic responses (Chawla et al., 1999; see also Hyder et al., 2002). It is worth noting that, as is inherent to designs that employ *post hoc* coding of trials, it was impossible to control trial history; differences in history could therefore explain the effect observed in the raw signal, although fixation trials and onset jittering likely helped. Moreover, given that high-pass filtering eliminated the baseline asymmetry, it is unlikely that differences in local trial history can totally explain the results.

The present study extends prior findings about tonic activity in three ways. First, the use of an event-related design allowed us to study the influence of tonic activity at encoding on memory for particular stimuli, rather than for blocks of stimuli. Second, earlier studies employed intentional encoding tasks, and therefore tonic activity may reflect motivation to remember items; in the current experiment, subjects were unaware of the recognition test, and thus any task-related or strategic influences on tonic activity were incidental to subsequent memory. Finally, while Otten et al. (2002) removed phasic effects from their estimations of tonic activity, the block-level responses in Fernandez et al. (Fernandez et al., 1999) may have been contaminated by stimulus-specific responses. The elevated levels of baseline activity reported here cannot be attributed to stimulus features, since this activity was recorded prior to the appearance of each stimulus.

Whole-Brain Analyses

Random-effects analyses revealed significant ($p < 0.001$ uncorrected, cluster threshold = 5 voxels) attenuation effects (first > second exposure) for remembered scenes (Talairach coordinates; Talairach and Tournoux, 1988): left and right PPA (−33, −38, −11; 33, −41, −8), left inferior temporal gyrus (−48, −61, −4), and left and right angular gyrus near the intraparietal sulcus (−42, −80, 32; 45, −77, 29). The same analysis for forgotten items revealed significant neural attenuation in anterior cingulate cortex (9, 46, −5). No significant neural enhancement effects (second > first exposure) were observed for either remembered or forgotten scenes. In addition, no regions showed greater activity for remembered than forgotten scenes at first exposure. Brewer et al. (1998) may have observed robust frontal activations in this contrast because of stronger signal resulting from 2.88 s stimulus exposures (versus 200 ms here). In line with this view, a slightly more liberal threshold ($p < 0.005$ uncorrected, cluster threshold = 5 voxels) replicated the frontal activations reported in previous subsequent memory studies: left and right inferior frontal gyrus (−33, 34, −9; 50, 29, 1), and left and right precentral sulcus (−30, 9, 18; 39, 15, 30). At the more conservative threshold, there were three regions that showed greater activity for forgotten than remembered scenes at first exposure: anterior cingulate cortex (ACC; 6, 32, −9), left precuneus (−9, −56, 36), and right precuneus (15, −54, 36).

Encoding Deactivations

It was initially believed that regions showing greater activity for forgotten than remembered items were involved in computations that, by way of draining processing resources, impaired episodic encoding (Otten and Rugg, 2001; Wagner and Davachi, 2001). For example, computations related to incidental task(s) during encoding impair subsequent memory (Reynolds et al., 2004). Such explanations might predict that greater activity for forgotten than remembered items results from greater *activation* during the presentation of subsequently forgotten items relative to baseline. Alternatively, greater activity for forgotten than remembered items could result from greater *deactivation* during the presentation of subsequently remembered items relative to baseline. Such deactivations (fixation > remembered) have been observed in dorsolateral prefrontal cortex, temporoparietal cortex, and posterior midline regions, while activations (forgotten > fixation) have been observed in the insula and thalamus (Daselaar et al., 2004).

To examine whether the effects observed in the current experiment reflect activation during the presentation of forgotten items or deactivation during the presentation of remembered items, responses in the three regions that exhibited whole-brain effects (first exposure: forgotten > remembered) were judged relative to fixation. In the ACC (Figure 5A), remembered scenes elicited lower responses than fixation at first exposure, $t(15) = 2.55$, $p = 0.02$; forgotten scenes did not differ from fixation, $t < 1$. Deactivation relative to fixation was also observed in left precuneus (Figure 5B) for remembered scenes at first exposure, $t(15) = 4.13$, $p = 0.0009$, but not for forgotten scenes, $t < 1$. In right precuneus (Figure 5C), the deactivation was not significant for remembered scenes at first exposure, $t(15) = 1.75$, $p = 0.10$, and there was a trend in the opposite direction for forgotten scenes, $t(15) = 1.30$, $p = 0.21$. Similar effects were observed at second exposure for subsequently remembered scenes in the ACC, $t(15) = 2.40$, $p = 0.03$, and approached significance in the left precuneus, $t(15) = 1.83$, $p = 0.09$; but not in the right precuneus, $t < 1$. There were no significant differences from fixation for the second exposure of subsequently forgotten scenes, $ps > 0.24$.

Interestingly, the precuneus and ACC are central components of the network of brain regions that are spontaneously active during rest (e.g., Mazoyer et al., 2001; McKiernan et al., 2003; Shulman et al., 1997); this network may be responsible for *automatically* gathering and evaluating information about our environment (Raichle et al., 2001). Deactivations in these regions may then correspond to the reallocation of resources from default/general processes to task-specific processes, as demonstrated by manipulations of task difficulty (McKiernan et al., 2003). For example, Daselaar et al. (2004) reported greater deactivations for subsequently remembered than forgotten items, possibly reflecting the fact that more resources were available to complete their intentional encoding task.

The present results extend prior findings in two important ways. First, since our indoor/outdoor task was equally difficult for subsequently remembered and forgotten items (in terms of both response time and accuracy), the observed association between deactivations and subsequent memory cannot be attributed to task difficulty per se (cf. Lustig et al., 2003). Second, our deactivations were directly related to encoding rather than to differences in strategy or motivation that can accompany intentional encoding tasks (cf. Daselaar et al., 2004). Taken together, these two features of our study suggest that natural variation in the “harmful” engagement of default processes is an important encoding factor. Along with the finding that neither older adults nor Alzheimer’s patients exhibit deactivations in posterior midline regions during encoding (Lustig et al., 2003),

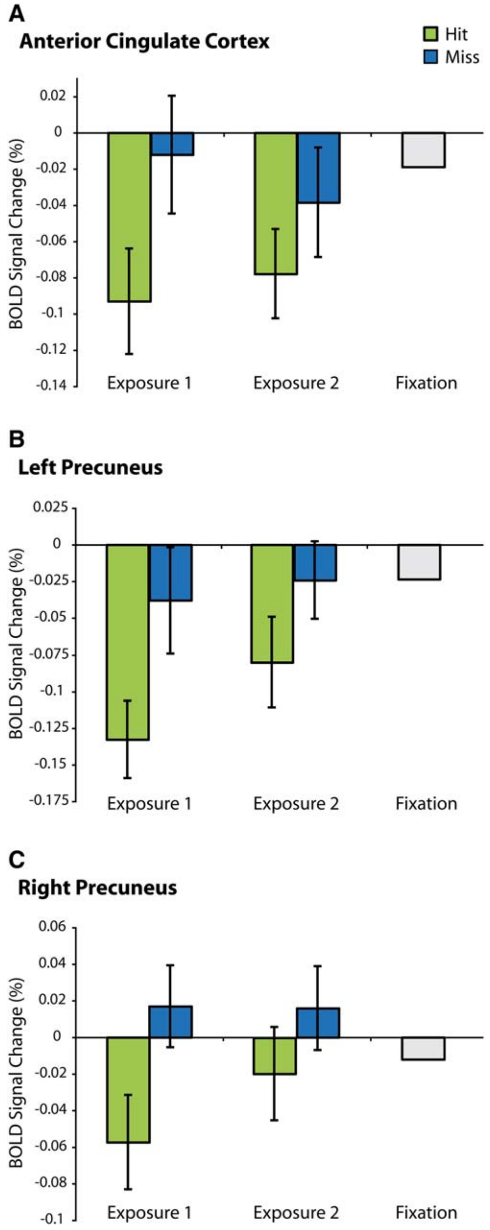

Figure 5. Encoding Deactivations

Regions demonstrating greater activity for forgotten than remembered scenes at first exposure. Relative to fixation and misses, HRF-modeled responses to the first exposure of hits were deactivated in the ACC (6, 32, −9) and left precuneus (−9, −56, 36); there was also a trend for right precuneus (15, −54, 36). Responses to the second exposure of hits were deactivated in the ACC and left precuneus. Error bars correspond to the standard errors of the difference between each condition and fixation.

our results support the interesting conjecture that memory deficits may result from the inability to appropriately allocate processing resources.

Discussion

By repeating stimuli during an fMRI session, we were able to compare behavioral and neural signatures of implicit and explicit memory as a function of subsequent memory. At first exposure, subsequently remembered items produced two correlates of episodic encoding: greater peak activation in medial temporal and frontal regions, and greater deactivation in anterior cingulate cortex and precuneus. Upon second exposure, these same items resulted in two correlates of implicit memory: behavioral priming and neural attenuation in medial temporal regions. Moreover, brain-behavior correlations between these two implicit measures were observed for subsequently remembered items, but not for subsequently forgotten items. In summary, we found evidence that while implicit and explicit memory can be dissociated, they can also be related in several ways. Four possible explanations for these results are explored below.

Implicit and explicit memory may be linked in terms of encoding factors. One such factor could be selective attention. Although we did not manipulate attention, tonic activity can serve as a measure of sustained attention (Chawla et al., 1999). Accordingly, greater tonic activity at initial encoding was observed for subsequently remembered items, which, given that measures of implicit and explicit memory were mediated by subsequent memory, suggests that attention at encoding benefited both forms of memory. This may be analogous to the attentional enhancement observed when subjects are explicitly instructed to attend (O'Craven et al., 1999; Yi and Chun, 2005). Moreover, these results fit parsimoniously with the finding that attention modulates behavioral and neural forms of implicit and explicit memory (Baker et al., 2004; Bentin et al., 1998; Eger et al., 2004; Ishai et al., 2004; Jiang and Chun, 2001; Jiménez and Méndez, 1999; Mulligan, 1998; Murray and Wojciulik, 2004; Turk-Browne et al., 2005; Vuilleumier et al., 2005; Yi and Chun, 2005). The relationship between tonic activity, attention, and memory deserves further study, as the effects are complex. For example, different cortical regions not only show task-specific responses, but they also differ in showing either positive or negative correlations with subsequent memory (Otten et al., 2002).

Another complementary explanation for the link between implicit and explicit memory is based on shared representational or processing resources (Buckner and Wheeler, 2001). In the current data, we observed neural signatures of implicit and explicit memory in the same scene-selective region of visual cortex for the same items. This extends prior results that colocalized neural responses related to implicit and explicit tasks in posterior sensory regions of the brain (Badgaiyan and Posner, 1997; Buckner and Koutstaal, 1998; Kirchhoff et al., 2000; Schott et al., 2005). This overlap may reflect perceptual processes common to the two forms of memory, such as *reinstatement* or *refreshing* (Johnson and Chalfonte, 1994). For example, while it is obvious that perceptual regions will be involved in perceptual priming, these same areas are activated in explicitly recalling visual information (e.g., O'Craven and Kanwisher, 2000). Another possibility is that output from a perceptual representational system (PRS; Tulving and Schacter, 1990) underlying priming and attenuation could serve as input to episodic memory, as suggested previously (Schacter and Tulving, 1994). In support of this view, recognition of impossible objects, which cannot be represented in the PRS and do not prime, is impaired relative to possible objects (e.g., Schacter et al., 1991). The "encoding factors" and "shared resources" hypotheses can be neatly reconciled by positing that attention may play an important role in consolidating perceptual representations, which can then be accessed during both implicit and explicit retrieval.

The notion of perceptual fluency can provide yet another explanation for the relationship between implicit and explicit memory. By definition, stimuli that are more quickly perceived upon repetition lead to more priming. Similarly, stimuli that are more quickly processed lead to lower BOLD responses and, hence, more attenuation (Henson and Rugg, 2003). However, it has also been observed that such perceptual fluency contributes to feelings of familiarity (e.g., Johnston et al., 1991), which may have formed the basis of responses in our recognition test and could explain the observed association. However, when explicit memory is available during recognition (because of previous study or under normal circumstances), the contribution of perceptual fluency to recognition is minimal (Johnston et al., 1991; Verfaellie and Cermak, 1999). In fact, a recent study suggests that perceptual fluency does not boost recognition much above chance, even when explicit memory is impaired (Conroy et al., 2005). Thus, it does not appear that perceptual fluency mediates the positive association between implicit and explicit memory.

Finally, one could argue that our measures of implicit memory—priming and attenuation—were contaminated by incidental explicit recognition. In other words, the indoor/outdoor and recognition tasks may have been correlated, possibly even sharing encoding factors and resources, because they were both tests of explicit memory. It is certainly possible that repeated scenes were recognized; however, we do not believe that such explicit contamination can account for the observed pattern of results. One relevant aspect of our results is the lack of priming and attenuation for forgotten items. This finding places an important burden on the "explicit contamination" hypothesis: the large priming and attenuation effects for remembered items must have been entirely caused by explicit recognition. In other words, one would have to argue that there was no implicit component of either the priming or attenuation effect to refute the claim that subsequent memory was correlated with implicit retrieval.

Evidence suggests that the strong attenuation effect for remembered items was not caused by explicit recognition. For example, it has been demonstrated that when completely novel stimuli are repeated, explicit recognition is associated with enhancement in ventral visual areas, rather than attenuation (Henson et al., 2000). In contrast, other studies have reported that explicit retrieval is accompanied by attenuation (e.g., Gonsalves et al., 2005; Henson et al., 2005; Weis et al., 2004). However, these attenuation effects may reflect implicit rather than explicit components of the retrieval process. In support of this, all attenuation effects observed during explicit retrieval in Schott et al. (2005) were also observed during purely implicit retrieval; explicit retrieval was only uniquely associated with enhancement effects. In fact, attenuation may track perceived (hence explicit) memory strength (Gonsalves et al., 2005) as a result of increased involvement of implicit processes. Finally, and perhaps most relevant to the current results, attenuation effects in parahippocampal cortex, as measured by depth electrodes, occur irrespective of whether stimuli are being implicitly or explicitly retrieved (Grunwald et al., 2003). The causal link between attenuation and priming (Wig et al., 2005) thus suggests that the behavioral priming effect for remembered items also had an implicit component.

To reconcile our findings with work showing dissociations between implicit and explicit memory, we propose a common-encoding independent-retrieval hypothesis. On one hand, the two memory systems may be dependent on common perceptual representations constructed during the encoding of novel visual stimuli. Factors that influence encoding, such as attention, may modulate both implicit and explicit memory by affecting the fidelity and durability of these representations. The strength of the encoding dependence may also vary as a function of the direct (Buckner and Wheeler, 2001) or indirect (Schacter and Tulving, 1994) contribution of perceptual (versus conceptual) representations to specific episodic memories. On the other hand, implicit and explicit memory are dissociable in terms of how they access these representations, reflecting different retrieval mechanisms. Implicit retrieval is typically stimulus driven, resulting from the reactivation of existing perceptual representations by repeated stimuli in the environment, while explicit retrieval relies on conscious reflection, elaboration, and association. In line with such a view, the occipital lobe is critical for implicit retrieval, while the medial temporal lobe is critical for explicit retrieval (e.g., Gabrieli et al., 1995). To conclude, our results demonstrate that studying the overlap between implicit and explicit memory can complement work on dissociations, helping to advance our understanding of human memory systems.

Experimental Procedures

Subjects

Sixteen subjects (ten women, four left handed; mean age, 22.6 years old; range, 18–30 years old) with normal or corrected-to-normal vision participated in this study. Informed consent was obtained from all subjects, and the study protocol was approved by the Human Investigation Committee of the School of Medicine and the Human Subjects Committee of the Faculty of Arts and Sciences at Yale University.

Procedure

Subjects viewed a series of grayscale photographs, presented one at a time for 200 ms. Their task was to classify, as quickly and accurately as possible, whether the scene depicted in the photograph occurred indoors or outdoors by pressing one of two buttons. The mapping of responses to buttons was counterbalanced across subjects. Subjects were also instructed to remain fixated at the center of the screen where there was always a cross or dot. Eye movements were unlikely in this design because image durations were too short for a saccade to be completed. A short practice block consisting of ten scenes was administered to subjects before they entered the scanner.

There were two runs of the indoor/outdoor task, each with 136 2 s trials: 1 filler trial, 60 novel images, their 60 repetitions, and 15 fixation trials. The fixation trials, in addition to jittering trial onsets (2, 4, or 6 s), served to improve estimation of event-related responses. The stimulus presentation order was randomized, while the lag between the first and second exposure of scenes varied from 2 to 11 items, which amounted to, on average, 19.5 s or 5.4 items. While shorter than some studies of long-term repetition priming, this lag was chosen to maximize attenuation effects. It is unclear whether priming and attenuation at this lag are the result of the same mechanism as at longer lags of one or more days (e.g., Wagner et al., 2000).

The trial sequence is depicted in Figure 1. Each trial began with a green fixation cross subtending 0.5° × 0.5° of visual angle, presented in the center of a gray background. After 200 ms, the cross was removed and replaced with a 13° × 13° of visual angle grayscale photograph of an indoor or outdoor place. A fixation dot was superimposed at the center of the scene to help fixation. The scene was removed after 200 ms, and the fixation dot remained on the screen. After the response was recorded, the fixation dot turned black. Subjects had up to 1700 ms to respond to each image, but were instructed to respond as quickly and accurately as possible. If they failed to respond or responded incorrectly to either exposure of a scene, the scene was excluded from analysis. Fixation trials were opaque to subjects; the fixation dot simply remained on the screen.

After completing two experimental runs, subjects were told about the surprise recognition test. They were then instructed about the PPA localizer run and were told that none of the scenes in the localizer would be tested. The purpose of informing subjects about the surprise memory test at this stage was to reduce the effect of retroactive interference. Pilot data revealed that other ways of reducing interference, such as running the PPA localizer first or changing the color tint of the localizer scenes, were less effective.

The PPA localizer involved alternating blocks of faces and scenes. During the scene blocks, subjects performed the same indoor/outdoor judgment as in the previous runs. All scenes in the localizer were completely novel. During face blocks, subjects performed a gender discrimination task. Faces were grayscale and cropped to exclude hair information. There were seven blocks of each type, and block order was counterbalanced. Each block lasted for 30 s, including an instruction screen and 12 scenes or faces, each presented for 200 ms. In addition, because subjects tend to saccade to the eyes of a face, the fixation dot was placed directly between the eyes for faces, and at the corresponding location for scenes in this run (~2° above center).

Subjects were removed from the scanner after completing the localizer run and were moved to an adjacent testing room to perform the recognition test. The lag between the end of the last encoding run and the start of the test phase was ~15 min. The recognition test involved evaluating 180 scenes: 120 old and 60 new. Subjects responded to each scene in one of three ways (based on Wagner et al., 1998): "new" if they did not recognize the scene, and either "low confidence studied" or "high confidence studied" if they recognized the scene, depending on their confidence level. The recognition task was self-paced, with most subjects finishing in fewer than 15 min. When finished, subjects were debriefed about the purpose of the experiment. No subject reported being aware that their memory would later be tested for the scenes while performing the indoor/outdoor task.

fMRI Acquisition

All scans took place in a Siemens Trio 3T scanner with a standard birdcage head coil. Functional images were acquired with a T2*-weighted gradient-echo sequence (TR = 2000 ms, TE = 25 ms, flip angle = 80°, 7 × 3.75 × 3.75 mm resolution, no gap); each volume contained 19 axial slices parallel to the anterior commissure/posterior commissure line, covering the entire brain. The main experiment was conducted in the first two functional scans, each acquiring 261 volumes. The final scan was for the PPA localizer and acquired 220 volumes. Visual stimuli were presented by a liquid crystal display projector on a rear-projection screen, which was viewed with an angled mirror attached to the head coil. An MRI-compatible button box was used to collect subjects' responses.

fMRI Analyses

Preprocessing and statistical analyses were conducted using Statistical Parametric Mapping (SPM2; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). After the first six volumes of each functional scan were discarded to allow for T1 equilibration effects, each remaining volume was slice time corrected and aligned to the first volume in each scan to correct for head motion (INRIAlign toolbox, Alexis Roche, EPIDAURE Group, INRIA Sophia Antipolis, France). The volumes were then normalized to a standard stereotaxic space (MNI; Montreal Neurological Institute, Montreal, Canada), interpolated to 3 mm isotropic voxels, and spatially smoothed with an 8 mm full-width half-maximal (FWHM) Gaussian kernel. The signal time course in each voxel was high-pass frequency filtered (128 s period cutoff) and corrected for auto-correlation.

Bilateral PPA ROIs were functionally localized in each subject based on the independent localizer scan. Blocks of faces and scenes were separately modeled with a canonical hemodynamic response function (HRF) and used as regressors in a multiple regression analysis. The six movement parameters from motion correction were entered as covariates of no interest. The linear contrast of scene block > the face block created a statistical parametric map of t values with a strict threshold ($p < 0.001$, corrected for family-wise error rate; cluster threshold = 5 voxels). A maximally scene-selective voxel was localized for each hemisphere within the ventral visual stream including the parahippocampal gyrus and the collateral sulcus (average coordinates: left PPA, −28, −45, −7; right PPA, 29, −43, −8).

Individual subject coordinates were entered into the MarsBar toolbox (Brett et al., 2002) to create spherical ROIs (4 mm radius). The experimental conditions were modeled using 13 finite impulse response (FIR) functions in these ROIs, one for each peristimulus time point (trial window = 26 s). To determine which time points should be included in random-effects ANOVAs, the time courses were averaged across conditions and hemispheres, and the numerical peak was statistically compared to each of the other time points. The peak response in the PPA occurred 6 s after trial onset; this time point was significantly greater than all others (t test, $p < 0.05$ one-tailed).

A similar technique was used to examine regional responses within the three other ROIs: left and right fusiform gyrus and right inferior prefrontal cortex. The motivation for including these ROIs comes from a recent study (Maccotta and Buckner, 2004) that examined the relationship between neural and behavioral repetition effects in similar areas. These researchers, however, used word stimuli, and so their ROIs were not suitable for present purposes. Instead, the anatomical coordinates from another experiment (Kirchhoff et al., 2000) were used as the center of spherical ROIs (left fusiform, −28, −55, −9; right fusiform, 34, −49, −12; right inferior prefrontal cortex, 43, 3, 37). Hemodynamic responses were modeled with FIR functions. The peak response in the fusiform ROIs occurred between 4 and 6 s after trial onset, while the peak response in right inferior prefrontal cortex occurred at 4 s.

Exploratory whole-brain analyses were conducted to study attenuation and subsequent memory effects outside of our ROIs. The fMRI data were modeled with an HRF including time derivatives and used as regressors in a multiple regression analysis, along with regressors for the six movement parameters. Comparisons of interest include: novel high confidence hit versus repeated high confidence hit, novel miss versus repeated miss, and novel high confidence hit versus novel miss. Within-subject contrasts were combined into group random-effects analyses using SPM2 ($p < 0.001$ uncorrected; cluster threshold = 5 voxels).

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/49/6/917/DC1/.

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