Decreased demands on cognitive control reveal the neural processing benefits of forgetting

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Remembering often requires the selection of goal-relevant memories in the face of competition from irrelevant memories. Although there is a cost of selecting target memories over competing memories (increased forgetting of the competing memories), here we report neural evidence for the adaptive benefits of forgetting—namely, reduced demands on cognitive control during future acts of remembering. Functional magnetic resonance imaging during selective retrieval showed that repeated retrieval of target memories was accompanied by dynamic reductions in the engagement of functionally coupled cognitive control mechanisms that detect (anterior cingulate cortex) and resolve (dorsolateral and ventrolateral prefrontal cortex) mnemonic competition. Strikingly, regression analyses revealed that this prefrontal disengagement tracked the extent to which competing memories were forgotten; greater forgetting of competing memories was associated with a greater decline in demands on prefrontal cortex during target remembering. These findings indicate that, although forgetting can be frustrating, memory might be adaptive because forgetting confers neural processing benefits.

Remembering the past is fraught with competition. Given the associative nature of memory, remembering a goal-relevant memory often involves selecting it against several competing memories, placing demands on effortful cognitive control mechanisms that detect and resolve competition[1–3]. Fortunately, memory can be adaptive[4–7], as acts of selective remembering seem to regulate mnemonic competition. Specifically, although selective remembering facilitates future retrieval of the same target memories[8,9], it also produces a cost—forgetting—for selected-against competing memories (a phenomenon termed 'retrieval-induced forgetting')[1,10,11]. Such forgetting of competing memories is hypothesized to reflect their weakening (or suppression)[1,5,10,12]. A crucial question is whether forgetting is indeed adaptive, such that it confers processing benefits precisely because it reduces competition during future attempts to retrieve target memories[4,5]. To the extent that this is the case, it predicts that the forgetting (suppression) of competing memories will be associated with a beneficial decline in demands on the cognitive control mechanisms that are typically required for remembering in the face of competition.

Our functional magnetic resonance imaging (fMRI) experiment tested this hypothesis by examining the relationship between the engagement of prefrontal cognitive control mechanisms during repeated acts of selective retrieval and later behavioral evidence that competing memories were forgotten. The experiment was divided into three phases: study, selective retrieval practice and test (**Fig. 1a**). During the study phase, participants encoded a series of cue-associate word pairs, encoding multiple associates of each cue word. Next, participants engaged in selective retrieval practice, repeatedly retrieving some of the associates of some of the cues. Crucially, of the associates that were not

practiced, some competed during retrieval practice (that is, they shared cues with practiced associates) whereas others did not. Finally, about 15 min after retrieval practice, memory for all of the initially encoded cue-associate pairs was tested to assess the consequences of selective retrieval practice for both practiced and unpracticed memories.

To test our hypothesis, we examined the relationship between fMRI measures of prefrontal cortical (PFC) activation during repeated selective retrieval practice and a behavioral measure of competitor forgetting. First, we predicted that unpracticed memories that competed with targets during selective retrieval practice would suffer a greater rate of forgetting than would unpracticed memories that did not compete[10]. Second, we predicted that repeated selective retrieval would yield benefits for practiced memories, reflected in both behavioral measures of retrieval efficiency and neural measures of reduced demands on PFC-mediated cognitive control mechanisms during repeated retrieval. Finally, and most important, we predicted that the behavioral measure of long-term competitor forgetting (which putatively reflects memory suppression) would correlate with fMRI measures of reduced demands on PFC-mediated control mechanisms during repeated selective retrieval. The data support each of these predictions, providing functional neurobiological evidence that mnemonic suppression occurs when competing memories conflict with target memories during retrieval, and that the successful suppression of competing memories yields immediate benefits—namely, reduced demands on neural mechanisms that detect conflict (in the anterior cingulate cortex; ACC)[13–15] and overcome competition through selection and inhibition (right dorsolateral and ventrolateral PFC)[2,3,16–24].

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RESULTS

Behavioral performance

Consistent with the expectation that retrieval efficiency should increase with repeated selective retrieval, retrieval success was higher on third practice attempts than first ones (52.4% versus 44.5%; $F_{1,19} = 35.93$, $P < 0.001$), and reaction times decreased across repeated successful retrieval (**Fig. 1b**; $F_{1,19} = 168.04$, $P < 0.001$). Crucially, performance on the final memory test revealed the long-term benefits and costs of selective retrieval practice[10]. Specifically, subjects remembered practiced items (Rp+) better than baseline non-practiced items (Nrp) (**Fig. 1c**; $F_{1,19} = 90.85$, $P < 0.001$). By contrast, subjects forgot non-practiced items associated with a practiced cue (Rp–; the competitors during the retrieval practice phase) more often than they forgot baseline Nrp items (**Fig. 1c**; $F_{1,19} = 13.52$, $P < 0.005$). We calculated the proportion of the magnitude of this retrieval-induced forgetting of Rp– items for each subject [(Nrp – Rp–)/Nrp], yielding a subject-specific measure of forgetting relative to baseline retrieval levels. We used this 'suppression score' to assess how neural activation during selective retrieval practice correlates with subsequent long-term forgetting of competing memories.

fMRI analyses

Evidence provided by fMRI during the retrieval practice phase bears on our predictions. First, we assessed how activation varied with retrieval outcome (successful versus unsuccessful) and how the recruitment of PFC-mediated control mechanisms dynamically changed with repeated selective retrieval. Subsequently, and most crucially, we assessed whether these dynamic changes in PFC activation during selective retrieval tracked the magnitude of long-term competitor forgetting (as indexed by the suppression score). Such an outcome would provide functional neurobiological evidence that suppressing competing memories produces immediate benefits—namely, decreased reliance on effortful cognitive control processes during the retrieval of target memories.

Neural correlates of successful associative recall

Previous electrophysiological and neuroimaging data indicate that the neural correlates of retrieval success are at least partially separable from those associated with the engagement of cognitive control during attempts to retrieve[25–29]. We found that there was greater activation during successful associative retrieval than during unsuccessful retrieval in a set of frontoparietal regions[28,30] (**Fig. 2**, **Supplementary Results** online and **Supplementary Fig. 1** online), including the bilateral dorsolateral PFC (DLPFC), spanning the anterior to posterior extent of middle frontal cortex; the left frontopolar cortex (FPC); and the medial PFC, extending to the ACC. As discussed below, we also found effects of retrieval success in the medial temporal lobe.

PFC activation decreases with repeated selective retrieval

During retrieval practice, retrieved targets are strengthened, whereas competitors are weakened (putatively through suppression). We predicted that this dynamic change in target-competitor competition should result in a reduction in demands on PFC control mechanisms during subsequent attempts to selectively retrieve the targets. As a first step in testing this prediction, we contrasted activation between first and third successful retrieval practice trials (subsampling the retrieval practice events to control for serial position; see **Supplementary Methods** online). This contrast revealed reductions in activation in a set of frontoparietal regions, including bilateral ventrolateral PFC (VLPFC), spanning the anterior to posterior extent of the inferior frontal cortex, and right DLPFC (**Fig. 2**; **Supplementary Table 1** online). The regions that were modulated by repeated selective retrieval
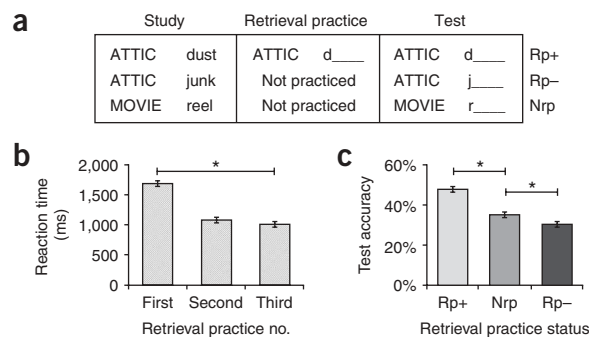

Figure 1 Experimental protocol and behavioral results. (**a**) During study, participants learned cue-associate word pairs, studying six associates for each cue. During retrieval practice, participants were shown cue words with the first letter of a studied associate. Participants practiced retrieving half of the associates of half of the cues, with each practiced associate repeated three times. This retrieval practice phase divided associates into three conditions: practiced target associates (Rp+); unpracticed associates of practiced cues (Rp–); and baseline items for which neither the associates nor the cues received retrieval practice (Nrp). Finally, participants were tested on all studied associations, using the same cued-recall procedure as during retrieval practice. See Methods. (**b**) Reaction times during retrieval practice revealed that successful retrieval was accomplished more quickly with repetition. (**c**) Practiced associates (Rp+) were remembered better than unpracticed baseline associates (Nrp). Unpracticed competitors (Rp–) of practiced associates were more poorly remembered than unpracticed baseline associates (Nrp), reflecting the retrieval-induced forgetting of competing memories. *Ps < 0.05; error bars reflect within-subject standard error.

were largely distinct from those associated with retrieval success, with the overlap within PFC being limited to the caudal extent of the left FPC, bilateral anterior VLPFC (inferior frontal pars orbitalis) and the inferior extent of the left mid-VLPFC (inferior frontal pars triangularis; **Supplementary Results, Supplementary Discussion** and **Supplementary Fig. 1** online).

Neural markers of memory suppression

Although the above analyses indicated that the PFC was decreasingly engaged with repeated selective retrieval, our central objective was to ask whether there are neural processing benefits of forgetting. That is, do these reduced demands on the PFC reflect the benefits of having suppressed (forgotten) competing memories? We reasoned that, to the extent that competitor suppression reduces mnemonic conflict, this would decrease demands on PFC control mechanisms that are needed to detect competition (in the ACC)[13–15] and to overcome it through selection or inhibition (in the DLPFC and VLPFC)[2,3,16–24]. Accordingly, we predicted that the magnitude of repetition-related decreases in activation in these PFC subregions should correlate with the magnitude of subsequent competitor forgetting. Such a finding would constitute the first evidence that neural changes during selective retrieval track memory suppression, thus revealing the neural processing benefits of forgetting.

Consistent with our prediction, a between-participant regression analysis using the suppression score as a covariate revealed that repetition-related reductions in activation in the dorsal ACC (~Brodmann's area 32; small volume corrected, $P_{svc} < 0.05$) and right VLPFC (~Brodmann's area 47; $P_{svc} < 0.05$) positively correlated with long-term forgetting of competitors (**Fig. 3a,b**; **Supplementary Table 2** online). That is, to the extent that competing memories were suppressed, demands on PFC-mediated control processes declined across repeated acts of successful selective retrieval. Importantly, because we
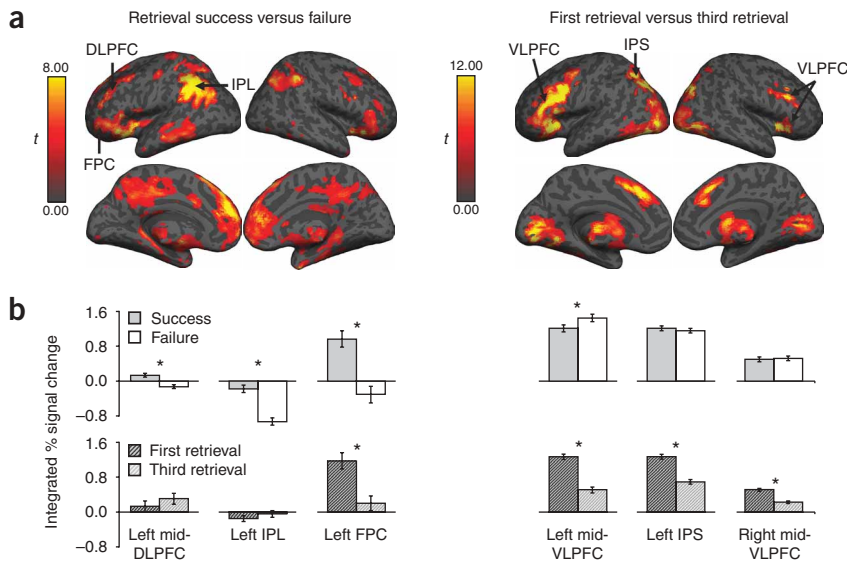
Figure 2 Dissociable neural correlates of retrieval success and repetition-related changes in the demands on cognitive control. (**a**) Left, contrast of retrieval success versus retrieval failure, restricted to first retrieval practice attempts (a full set of coordinates are available upon request); right, contrast of first successful retrieval practice versus third successful retrieval practice, matched for average serial position (coordinates in **Supplementary Table 1**). (**b**) Targeted regions of interest from the retrieval success and retrieval repetition contrasts: left mid-DLPFC (~Brodmann's area (BA) 9/46; MNI coordinates of −41, 41, 30); left IPL, inferior parietal lobule (~BA 40; −54, −54, 36); left FPC (~BA 10; −49, 44, −5); left mid-VLPFC (~BA 45; −45, 18, 21); left IPS, intraparietal sulcus (~BA 7; −30, −63, 45); right mid-VLPFC (~BA 45; 39, 21, 24). *$Ps < 0.05$; error bars reflect within-subject standard error.

did not observe such a relationship across repeated unsuccessful retrieval attempts (**Supplementary Results**), this link between decreasing engagement of the ACC and right VLPFC across successful retrieval attempts and subsequent competitor forgetting does not reflect a global reduction in task engagement. Moreover, these declines in PFC activity across successful retrieval attempts accounted for between 45% and 55% of the variance in the magnitude of competitor suppression.

To investigate whether these activation changes in the ACC and right VLPFC were specifically associated with competitor suppression, we conducted three additional analyses. First, to verify that the ACC and right VLPFC were sensitive to changes in the strength of competing, but not target (practiced), memories, we calculated a proportionalized facilitation score for each subject [(Rp+ − Nrp)/Nrp], representing the increase in the strength of target memory traces. Importantly, memory facilitation did not correlate with activation changes in the ACC or right VLPFC ($Ps > 0.5$). Second, although reaction time decreased across successful retrieval practice trials, changes in reaction time did not predict the magnitude of long-term competitor suppression ($P > 0.5$), nor did these changes correlate with the decreases in ACC and right VLPFC activation ($Ps > 0.2$). Third, when reaction time was included as a regressor (either between-subjects or as a trial-by-trial parametric modulator), we again observed a relationship between reductions in PFC activation and competitor suppression (**Supplementary Results**). The last two analyses indicated that the correlations between PFC activation reductions and competitor forgetting cannot be explained in terms of reaction time effects.

Dorsal ACC and competition-dependent suppression
The correlation between the repetition-related decrease in dorsal ACC activity and the magnitude of competitor suppression is consis-

tent with the putative role of ACC in detecting conflict[13–15]. That is, as competitor strength decreases, so too should conflict; this decline in conflict was putatively indexed by the reduction in ACC signal. Importantly, although the observed correlation linked the ACC with between-participant differences in competitor suppression, there remains the question: why did participants differ in the magnitude of their suppression scores?

Previous behavioral studies have indicated that retrieval-induced forgetting occurs only when non-target memories actually interfere (compete) during attempts to selectively retrieve target memories[10,12,31]. Accordingly, to the extent that ACC activation marks the presence and magnitude of conflict, the competition-dependent hypothesis of suppression predicts that 'high suppressors' should differ from 'low suppressors' not only in the degree to which they demonstrated reductions in ACC activation across retrieval practice, but also in terms of the degree to which the ACC was initially activated. Specifically, if competition triggers suppression, then high suppressors should have experienced greater competition than low suppressors during initial retrieval attempts, and this difference should be apparent in their initial ACC activity levels.

To test this prediction, we median-split participants into two groups (high and low suppressors) on the basis of the magnitude of their behavioral suppression score. By definition, this resulted in the suppression score being markedly greater for high suppressors (27.9%) than for low suppressors (1.5%), with the latter group not showing a reliable retrieval-induced forgetting effect ($F < 1$). Importantly, other than this difference in the magnitude of observed competitor suppression, the high and low suppressors did not differ in any other behavioral measure (for example, memory for Rp+ and for Nrp items did not differ between groups; $Fs < 1$).

For each group, we extracted the ACC response on the first and third successful retrieval practice trials from the ACC region revealed in the regression analysis (**Fig. 3a**). Importantly, these data supported the competition-dependent hypothesis. In particular, a significant Group × Repetition interaction ($F_{1,18} = 7.97$, $P < 0.05$) revealed that high suppressors showed significantly greater activation than low suppressors during first retrieval practice trials ($F_{1,18} = 8.71$, $P < 0.01$), as well as a reliable decrease in ACC activation with repetition ($F_{1,9} = 10.23$, $P < 0.05$). By contrast, low suppressors did not display above baseline ACC activation during first retrieval practice trials, nor did they show a decrease in ACC activation with repetition ($Fs < 1$). These data are consistent with the interpretation that ACC activation marked the presence of conflict; initial conflict was robust for the high suppressors and was weak for the low suppressors; and high suppressors resolved the conflict through suppression of the competitors, thus decreasing the presence of conflict on later retrieval practice trials.

Right VLPFC
Given the putative role of the right VLPFC in mediating response selection or inhibition[19–24], the correlation between the repetition-related decrease in right VLPFC activation and the magnitude of
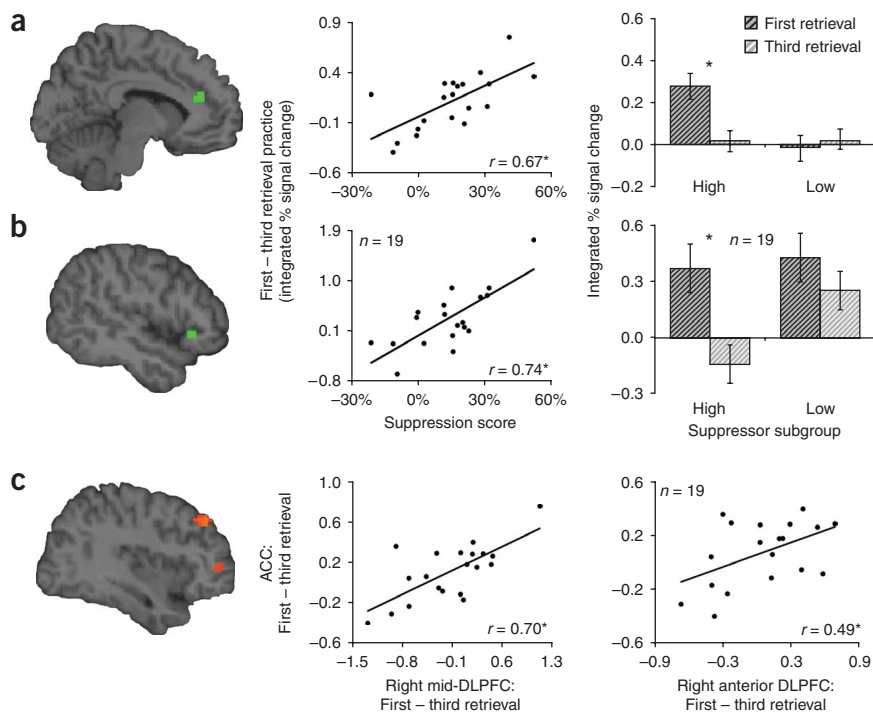
Figure 3 Neural predictors of mnemonic suppression. A whole-brain regression analysis showed that memory suppression at test was predicted by repetition-related activation decreases in (**a**) left dorsal ACC (~BA 32; –9, 36, 18), and (**b**) right anterior VLPFC (~BA 47; 48, 27, –6), as shown in scatter plots (middle). In the ACC and right VLPFC, high suppressors showed reliable decreases in activation from first to third retrieval practice trials, whereas low suppressors did not. High suppressors showed greater initial ACC activation than low suppressors, but comparable initial right VLPFC activation. (Note: For right VLPFC, one participant was an outlier ($Z > 3.5$) and was removed from the regression plot and the high versus low suppressors analyses (indicated by $n = 19$). In all subsequent analyses, functional data from this participant were excluded when they exceeded $Z = 3.5$ (indicated by $n = 19$). Inclusion or exclusion of this participant did not change the significance of any statistical tests reported.) (**c**) A whole-brain regression analysis showed that the repetition-related activation decline in the right DLPFC covaried with that in the ACC, showing a functional coupling between ACC and right DLPFC (~BA 10/46 and 9/46; 39, 48, 3 and 39, 37, 41) that specifically relates to changes in demands on cognitive control across retrieval repetitions.

retrieval-induced forgetting lends further support to our hypothesis that one benefit of memory suppression is a reduction in the demands on cognitive control. However, analyzing this correlation for the two suppression subgroups revealed that the activation pattern in the right VLPFC differed from that in the ACC (**Fig. 3b**). Specifically, whereas high suppressors showed a reliable decrease in right VLPFC activation from first to third retrieval practice trials ($F_{1,8} = 6.67$, $P < 0.05$), and low suppressors did not ($F_{1,9} = 1.72$, $P > 0.20$), high and low suppressors did not differ in activation during first retrieval practice trials ($F < 1$). These results indicate that the initial engagement of the right VLPFC was not exclusively driven by the strength of competing memories, as both low and high suppressors showed comparable initial right VLPFC activation, despite marked differences in ACC-detected conflict. Rather, given that initial retrieval attempts represented a situation of under-determined responding[32], the right VLPFC might have been initially engaged in the service of response selection or inhibition, regardless of the strength of competing memories. However, importantly, subjects who suppressed competing memories ultimately showed a clear neural processing benefit in the form of robust reductions in the demands placed on the right VLPFC during subsequent acts of target memory retrieval.

DLPFC recruitment and demand for control

The preceding analyses indicated that the dorsal ACC might have a unique role in detecting the initial presence of mnemonic competition. However, the detection of competition is thought to be only the initial step in the implementation of cognitive control, with conflict detection triggering the recruitment of other PFC mechanisms that directly implement control[13–15,33]. Within the context of episodic associative recognition, activity in the ACC correlates with activity in the right DLPFC under circumstances where retrieval targets are weak[34]. Similarly, the right DLPFC and ACC have been implicated in stopping the act of retrieval, with a recent report placing particular emphasis on the potential role of the DLPFC in directly contributing to memory suppression[17]. Given these findings, we predicted that the ACC

might functionally couple with the right DLPFC during selective retrieval practice.

To assess this hypothesis, we regressed the magnitude of repetition-related activation change in dorsal ACC against repetition-related activation change elsewhere in the brain. Strikingly, the only PFC foci that showed repetition-related activation changes that covaried with changes in ACC activity were two clusters in the right DLPFC (**Fig. 3c**; $P_{svc} \le 0.05$). These data suggest that the function of the right DLPFC was influenced by conflict signals generated by the ACC, and as a consequence, that the right DLPFC had an important role in implementing control in the presence of mnemonic competition. This correlation raises the possibility that the right DLPFC mediates either the direct suppression of strong mnemonic competitors[1,17], or, conversely, the selection of target memories[35–37].

To differentiate between these two possibilities, we further examined the response within these right DLPFC clusters. Notably, neither the magnitude of initial right DLPFC activation nor the repetition-related change in right DLPFC activation correlated with the magnitude of competitor suppression ($Ps > 0.5$). Thus, although the right DLPFC was modulated by conflict detection in the ACC, there was no evidence that it responded to, or influenced, the strength of competing memories. Strikingly, however, activation of the right DLPFC did correlate with the facilitation of target memories, as evidenced by right DLPFC activation during initial successful retrieval practice attempts ($r = 0.47$, $P < 0.05$). This was also true when we considered right DLPFC activation across all successful retrieval practice attempts ($r = 0.58$, $P < 0.01$), but not when considering unsuccessful retrieval practice attempts ($P > 0.2$). Moreover, activation across successful trials was a significantly better predictor of facilitation than was activation across unsuccessful trials ($t = 7.54$, $P < 0.001$). Thus, although the recruitment of right DLPFC was coupled with, and was presumably triggered by, conflict detection by the ACC, the essential contribution of the right DLPFC seems to have been to bias retrieval toward task-relevant representations[35–37], thereby contributing to the long-term facilitation of these target memories.
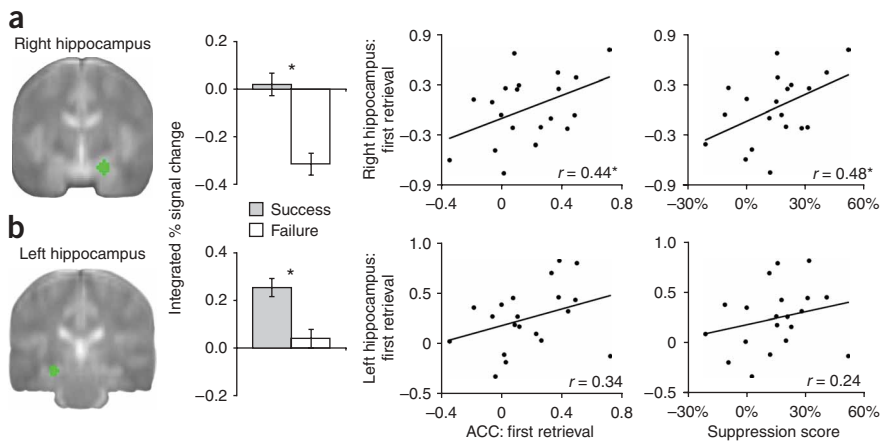
Figure 4 MTL contributions to selective retrieval practice. Both (**a**) right anterior hippocampus (21, –6, –21) and (**b**) left hippocampus (–26, –27, –12) showed retrieval success effects during first retrieval practice attempts. Right hippocampal activation during initial successful retrieval positively correlated with initial ACC activation and with the magnitude of mnemonic suppression at test. A qualitatively similar, though not reliable, pattern was observed in the left hippocampus.

Selective retrieval and the medial temporal lobe

So far, we have focused on the control mechanisms that respond to, and regulate, mnemonic competition. However, to the extent that the robust ACC activity shown by high suppressors on initial retrieval practice trials reflected mnemonic conflict, the initial conflict signal in the ACC should be correlated with activation in neural systems that directly mediate episodic memory retrieval, such as the medial temporal lobes (MTL)[38–40]. Specifically, robust retrieval-related MTL responses might reflect activation of both relevant and irrelevant memories, thus producing the mnemonic conflict detected by the ACC.

To test this hypothesis, we explored how MTL activation during selective retrieval practice related to retrieval success and to subsequent levels of conflict detection and competitor suppression. We found two important results. First, as alluded to above, we found retrieval success effects in the MTL, including the bilateral hippocampus (**Fig. 4**). This finding builds on earlier fMRI observations of greater hippocampal activation during successful associative recognition[41–43], extending retrieval success effects in the hippocampus to interference-laden associative recall. Second, given the competition-dependent hypothesis of suppression, we predicted that high MTL activation during initial retrieval attempts would be associated with, and presumably give rise to, the initial conflict response in the ACC, and, as a consequence, would trigger the suppression of competing memories. Consistent with this prediction, activation in the right hippocampus during first retrieval practice trials was positively correlated with initial ACC activity, as well as with the behavioral measure of competitor suppression (**Fig. 4a**). Within the left hippocampus, we observed a qualitatively similar pattern, though the correlations were not significant (**Fig. 4b**; Ps > 0.1). Collectively, these data support the hypothesis that initial mnemonic conflict emerges through MTL-dependent retrieval, and, once detected, triggers the recruitment of control mechanisms that ultimately implement memory suppression.

DISCUSSION

Our study tested the hypothesis that forgetting confers benefits—namely, decreased demands on cognitive control mechanisms that detect and resolve mnemonic conflict during selective retrieval. We obtained three main findings. First, the magnitude of competitor

forgetting correlated with reduced activation in the ACC and right VLPFC across repeated selective retrieval of target memories, indicating that dynamic changes in demands on these PFC regions reflected the benefits of having successfully suppressed competing memories. Notably, compared with low suppressors, high suppressors showed neural evidence of robust initial mnemonic conflict, as detected by the ACC, supporting the competition-dependent hypothesis of suppression. Second, changes in activation in the right DLPFC during repeated selective retrieval covaried with changes in ACC activation, indicating that these regions might be functionally coupled, and that the detection of competition by the ACC triggered the engagement of control implemented by the DLPFC. Finally, hippocampal activation during initial retrieval correlated with initial engagement of the ACC and later competitor forgetting, providing evidence that the competition detected by the ACC was mnemonic in nature and that this mnemonic competition triggered memory suppression.

Our findings that ACC engagement changed dynamically as conflict from competing memories declined bear on theoretical models of ACC function. On the one hand, our findings extend ACC conflict detection theory beyond the domain of response conflict, suggesting a broader role for ACC[44]—in this case, in the detection of conflict between competing mnemonic representations. Importantly, although conflict detection theory can account for the present findings, a related, and perhaps superordinate, account of ACC function holds that the ACC serves to predictively signal the likelihood of errors[45]. By this view, the dynamic changes in ACC activation observed here might track changes in the strength of competing memories because the strength of competing memories influences the likelihood that retrieval will fail. Interestingly, error likelihood theory might predict that, in this study, ACC activation would increase across repeated unsuccessful retrieval practice attempts. Although ACC activation did numerically increase across repeated unsuccessful retrieval attempts, this change did not approach significance (P > 0.1). Thus, our findings do not clearly favor either conflict detection theory or error likelihood theory. Rather, they are broadly consistent with the notion that the ACC is sensitive to the strength of competing, goal-irrelevant, representations, which accords with both theories of ACC function. Moreover, and most importantly, our data provide new evidence that as the strength of competing memory representations declines through selective retrieval of target memories, there is a neural processing benefit—decreased demands on the ACC.

Whereas our findings highlight the sensitivity of the ACC to the strength of competing memories, they also indicate that the right lateral PFC functionally couples with the ACC to implement control. Specifically, our regression analysis revealed that changes in ACC activation are tightly correlated with the engagement of the right DLPFC, extending prior observations of correlated ACC–DLPFC activation during response selection[18,33] and associative recognition[34] to situations of selective recall in the face of competition. Moreover, the engagement of the right DLPFC was associated with a specific behavioral consequence—the strengthening of target memories—and this provides direct evidence for the functional utility of DLPFC engagement in response to conflict detection by the ACC. This observation is

also consistent with the notion that the DLPFC biases processing toward task-relevant representations[35–37,46]. In addition, the right VLPFC showed a modest functional coupling with the ACC across retrieval practice trials ($r = 0.44$, $P < 0.06$), with changes in activation in both the right VLPFC and the ACC tracking the suppression of competing memories. Although the right VLPFC has consistently been implicated in response selection or inhibition[19–24], our findings extend such observations to the domain of competitive remembering. Together, these results indicate that the ACC functionally couples with multiple lateral PFC regions (in this case, the right DLPFC and right VLPFC), with these anatomically separable subregions of the lateral PFC subserving distinct forms of cognitive control[47]. Moreover, it seems that the demands on these PFC control processes decline as competing memories are forgotten (suppressed), revealing a neural processing benefit of forgetting.

Although we have described the observed retrieval-induced forgetting effects in terms of competitor suppression, it is possible to formulate alternative accounts of such instances of forgetting. Specifically, although behavioral studies provide empirical support for the construct of competitor suppression[1,5,10,12], thereby motivating our framework, models of associative memory might attribute the observed forgetting effect to associative interference (blocking) arising at test[48]. That is, given that Rp+ and Rp– items share the same retrieval cues, the observed forgetting of Rp– items could be explained, in theory, in terms of strengthened Rp+ items that 'block' access to Rp– items (rather than to the suppression of Rp– items). However, there are three arguments against such an interpretation. First, previous studies show that retrieval-induced forgetting of Rp– items is observed even when Rp+ and Rp– items do not share retrieval cues at test (that is, retrieval-induced forgetting is cue-independent)[12]. Second, in our study, the high and low suppressor subgroups did not differ in terms of Rp+ recall, indicating that differences in Rp– recall probably do not reflect differences in the strengthening of Rp+ items, but rather reflect the weakening of these competitors. Third, whereas our fMRI data accord with competitor suppression, these data are difficult to integrate with a blocking view. Specifically, although the magnitude of initial hippocampal activation and of repetition-related changes in ACC activation predicted the magnitude of retrieval-induced forgetting, these neural measures did not predict the magnitude of Rp+ facilitation ($Ps > 0.5$). Together, these data indicate that the observed competitor forgetting was predominantly the consequence of competitor suppression, with the decline in demands on the ACC and right lateral PFC during repeated selective retrieval revealing the immediate processing benefits of such suppression.

Collectively, our results show that forgetting is associated with decreasing demands on ACC and right lateral PFC function during repeated selective retrieval. These dynamic changes reveal the adaptive nature of memory[4–7], wherein initial acts of resolving mnemonic conflict result in both costs (forgetting) and benefits (reduced demands on cognitive control). Viewed through the lens of cognitive control and prefrontal function, forgetting is advantageous, such that the costs are the benefits.

METHODS

Participants. Twenty healthy participants (12 female, ages 18–32 years) took part in this study. All were right-handed, native English speakers. We excluded data from one additional participant owing to a failure to respond on a high percentage of trials ($>25\%$) during the second phase of the experiment. Participants received $20 per h, with the experiment lasting approximately 3 h. We obtained informed written consent from all participants in accordance with procedures approved by the institutional review board at Stanford University.

Procedure. During fMRI, all responses were covert, wherein subjects pressed one of two buttons to indicate successful or unsuccessful retrieval of the target associate. A separate behavioral experiment, as well as an overt post-scanning test included in the present experiment, revealed comparable performance across covert and overt procedures (**Supplementary Results**).

The fMRI experiment was divided into four phases: study, during which participants encoded cue-associate word pairs; retrieval practice, during which we cued participants to covertly recall some of the previously studied associates; a 15-min visuospatial filler task; and test, during which we cued participants to covertly recall each of the initially studied associates (**Fig. 1**). We collected fMRI data during all phases except the filler task; only the imaging data from the retrieval practice phase are considered here.

In the study phase, each 4-s encoding trial consisted of a 1-s fixation cross, followed by a cue-associate word pair presented centrally for 3 s. Cue words appeared in uppercase letters; associate words, presented to the right of cue words, appeared in lowercase letters. We instructed participants to intentionally encode the presented cue-associate pairs for a later memory test; no response was required. We distributed study trials in an event-related manner, with variable-duration null events (0–16 s) intermixed with study trials. During null events, left or right arrows were presented, 1 per s; participants pressed the left or right key on a button box to indicate the arrow direction.

In the retrieval practice phase, each 4-s trial began with a cue word presented along with the first letter of a previously studied associate word for 3 s. As in the study phase, the cue was presented in uppercase letters, and the first letter of the associate was presented to the right in lowercase. Participants tried to covertly recall the associate that fit the cue word and letter stem, and pressed one of two keys on a button box to indicate successful or unsuccessful retrieval of the cued associate. As in the study phase, we distributed retrieval practice trials in an event-related manner, intermixed with null events. The test phase was identical, in procedure, to the retrieval practice phase, differing only in the set of items tested.

Stimuli. Stimuli consisted of 40 cues, each with 6 associates (240 total word pairs). Cues and associates were nouns ranging in length from 3 to 11 letters. See **Supplementary Methods** for further details.

Materials. For counterbalancing purposes, we divided the stimuli into 4 subsets of word pairs: the 40 cues were divided into 2 sets of 20, with half of the associates from each of these sets constituting a subset. At study, we presented each of the 240 cue associate word pairs once, creating 240 study trials. At retrieval practice, one subset of word pairs (half of the associates of half of the cues) received retrieval practice. Each of these associates was practiced three times. Thus, the retrieval practice phase consisted of 180 trials (3 repetitions of 3 of the associates of 20 cues). The test phase consisted of the same number of trials as the study phase. See **Supplementary Methods** for further details.

During study, retrieval practice, and test, the total time allotted for null events was equal to 1/3 of the scan time. We optimized the duration and distribution of null events for estimation of rapid event-related fMRI responses[49].

fMRI data acquisition. Whole-brain imaging was conducted on a 3.0T Signa MRI system (GE Medical Systems). Structural images were collected using a T2-weighted flow-compensated spin-echo pulse sequence (TR = 3 s; TE = 70 ms; 24 contiguous 5-mm-thick slices parallel to the AC-PC plane). Functional images were collected using a T2*-weighted two-dimensional gradient echo spiral-in/out pulse sequence (TR = 2s; TE = 30 ms; 1 interleave; flip angle = 70°; FOV = 20 cm; 64 × 64 voxels)[50].

fMRI data analysis. Image preprocessing was performed using SPM2 (Wellcome Department of Cognitive Neurology, London). Functional images were corrected for differences in slice acquisition timing and then corrected for head motion. Each participant's structural images were co-registered to their functional images and segmented into gray matter, white matter and cerebrospinal fluid. The gray matter images were then stripped of any remaining skull and normalized to a gray matter MNI template image. This normalized gray matter image was used for normalization of the structural and functional images. Images were resampled to 3-mm cubic voxels and smoothed with a Gaussian kernel (8 mm at full-width half-maximum).

Data were analyzed using SPM2, under the assumptions of the general linear model. Trials were modeled as an event, using a canonical hemodynamic response function and its first-order temporal derivative. Correct and incorrect trials were modeled separately. The resulting functions were entered into a general linear model with session treated as a covariate. Linear contrasts were used to obtain participant-specific estimates for each effect. These estimates were then entered into a second-level analysis, treating participant as a random effect, using a one-sample t-test against a contrast value of zero at each voxel. With the exception of the contrast of retrieval success (correct > incorrect), all contrasts were restricted to correct trials (see **Supplementary Results** for analyses of unsuccessful trials). Effects in *a priori* predicted PFC and MTL regions were considered significant if they exceeded an uncorrected threshold of $P < 0.001$ and consisted of 5 or more contiguous voxels, as our experience has revealed that this threshold for *a priori* regions yields highly replicable effects. The regression analyses were thresholded with the same criteria, though to be conservative, *a priori* targeted regions observed in the regression analyses were small-volume corrected using anatomical masks for these regions of interest (**Supplementary Methods**).

Region of interest (ROI) analyses were conducted to investigate effects revealed by voxel-based comparisons. ROIs included all significant voxels within a 6-mm radius of a maximum. Deconvolution of the signal within ROIs was performed using a finite impulse response function implemented with MarsBar (http://marsbar.sourceforge.net), allowing comparison of the integrated percent signal changes (summed across 2–10 s post-trial onset) associated with conditions.

Note: Supplementary information is available on the Nature Neuroscience website.

COMPETING INTERESTS STATEMENT
The authors declare no competing financial interests.

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