

Fidelity of neural reactivation reveals competition between memories

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Remembering an event from the past is often complicated by the fact that our memories are cluttered with similar events. Though competition is a fundamental part of remembering, there is little evidence of how mnemonic competition is neurally represented. Here, we assessed whether competition between visual memories is captured in the relative degree to which target vs. competing memories are reactivated within the ventral occipitotemporal cortex (VOTC). To assess reactivation, we used multivoxel pattern analysis of fMRI data, quantifying the degree to which retrieval events elicited patterns of neural activity that matched those elicited during encoding. Consistent with recent evidence, we found that retrieval of visual memories was associated with robust VOTC reactivation and that the degree of reactivation scaled with behavioral expressions of target memory retrieval. Critically, competitive remembering was associated with more ambiguous patterns of VOTC reactivation, putatively reflecting simultaneous reactivation of target and competing memories. Indeed, the more weakly that target memories were reactivated, the more likely that competing memories were later remembered. Moreover, when VOTC reactivation indicated that conflict between target and competing memories was high, frontoparietal mechanisms were markedly engaged, revealing specific neural mechanisms that tracked competing mnemonic evidence. Together, these findings provide unique evidence that neural reactivation captures competition between individual memories, providing insight into how well target memories are retrieved in the present and how likely competing memories will be remembered in the future.

forgetting | pattern classification

Our ability to remember an event from the past is powerfully influenced by competition arising from memories of similar or overlapping events (1–3). For example, in searching for today's parking space, we may find ourselves standing where we parked yesterday. Though competition between memories is almost ubiquitous, and a primary reason why we forget, there is surprisingly little evidence of how competition between memories is neurally represented. In part, the lack of evidence reflects a methodological challenge of how to measure neural competition between memories. Here, we consider whether competition between memories can be measured by, and understood in terms of, the relative degree to which memories are neurally reactivated—that is, the degree to which patterns of neural activity present during event encoding are reinstated at retrieval. By this view, competitive remembering may strongly parallel competitive perception (4)—a domain that has been more extensively studied.

When competition exists between visual stimuli, responses within the ventral occipitotemporal cortex (VOTC) are strongly modulated by how attention is allocated. For example, when faces and scenes are concurrently or sequentially presented, increased activity is observed in fusiform or parahippocampal gyri according to whether faces or scenes are attended, respectively (5–9). Similarly, VOTC responses are tightly correlated with both spontaneously fluctuating perceptions (10, 11) and misperceptions (12) of visual stimuli. VOTC responses also scale with gradations in the strength of visual stimuli (13–15), thus reflecting the quality of perceptual events. Importantly, perceptual evidence emerging from the VOTC is also correlated with the engagement of fron-

toparietal structures (15–19), putatively reflecting the translation of perceptual evidence to goal-relevant behavior.

Building on the literature relating competitive perception to VOTC responses, we used a memory task in which subjects learned cue-associate pairs for which the cues were words and the associates were images of faces or scenes. Competition between individual memories was created through AB/AC learning: subjects first encoded and retrieved novel cue-associate pairs (noncompetitive, AB pairs) and subsequently encoded and retrieved overlapping pairs that contained a repeated cue paired with a novel associate (competitive, AC pairs; Fig. 1). A separate set of novel cue-associate pairs (noncompetitive, DE pairs) were not followed by overlapping pairs, thus functioning as a control condition. To allow for separation of VOTC reactivation related to target vs. competitor memories, the B and C images for a given AB/AC set were always from distinct visual categories (i.e., a face and a scene). During the critical retrieval phase, subjects were presented with word cues and attempted to covertly recall target associates, indicating by button press whether they were able to recall the specific image vs. a more general memory for the category of the image (face/scene). The scanned encoding and retrieval rounds were followed by a behavioral posttest that reassessed memory for AB and DE pairs, allowing for measurement of the impact that AC learning had on memory for previously learned AB pairs.

Reactivation was assessed via multivoxel pattern analysis (MVPA)—a technique well-suited to measuring reactivation (20–22). Accordingly, we first trained a pattern classifier to discriminate patterns of activity within the VOTC that were associated with the encoding of words paired with faces vs. scenes; we then applied the classifier to retrieval trials to estimate the degree to which VOTC responses reflected face vs. scene reactivation—that is, the fidelity with which target memories were retrieved. Importantly, because the classifier measured the relative evidence for face vs. scene reactivation, here, fidelity of reactivation refers to the relative strength of target reactivation. We predicted that competitive remembering would be associated with reactivation of both target and competitor memories, thereby reducing the fidelity of VOTC reactivation. Moreover, we predicted that measures of competitive reactivation would be related to both how well target memories were retrieved in the present and how likely competing memories would be remembered in the future. Finally, we predicted that neural evidence of competitive reactivation would correspond to the engagement of frontoparietal structures that evaluate mnemonic—and perhaps perceptual—evidence.

Results

Behavioral Results. Retrieval rounds. Responses during the scanned retrieval rounds were separated according to whether subjects

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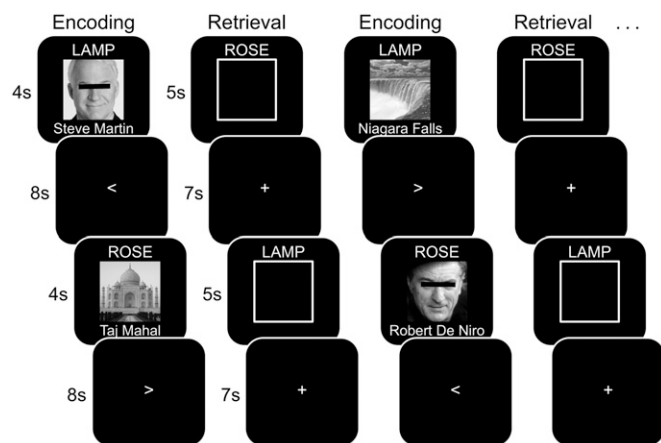


Fig. 1. Encoding and retrieval rounds. During encoding, subjects viewed nouns (cues) paired with images of well-known faces or scenes (associates). The name of each face/scene was presented below the image. During retrieval, subjects were presented with cues and instructed to recall the corresponding associate, indicating the category (face/scene) via button press. Encoding and retrieval rounds alternated for a total of seven rounds each. Half of the cues were paired with one associate (DE pairs), and half of the cues were paired with two associates (one face, one scene). If a cue was paired with two associates, the first associate (AB pair) was encoded and retrieved before encoding and retrieval of the second associate (AC pair). During retrieval, subjects were instructed to recall the most recent associate for each cue. Images of faces were not obscured in the actual experiment.

correctly indicated the category (face/scene) of the target image (hit); indicated that they did not remember the target image (don't know); or incorrectly classified the category of the target image (error). Hits were further subdivided according to whether subjects reported remembering specific or general details of the image. Because errors were relatively infrequent, they were not subdivided into specific and general errors.

Overall, subjects were fairly successful at retrieving target images: specific hit = 53.2% (mean); general hit = 23.5%; don't know = 14.7%; error = 6.4%; no response = 2.1% (Fig. 2). Critically, competition significantly impacted retrieval success, as evidenced by a robust reduction in the rate of specific hits ($t_{17} = 5.10, P < 0.001$; Fig. 2). Though the reduction in the rate of specific hits necessarily corresponded to a higher rate of responses in the remaining bins—and thus nonindependence of additional tests—competition increased general hits ($t_{17} = 2.22, P < 0.05$), don't knows ($t_{17} = 2.23, P < 0.05$), and errors ($t_{17} = 2.38, P < 0.05$). The rate of specific hits, general hits, don't knows, and errors did not differ for faces vs. scenes (all P 's > 0.4).

Posttest. Recall performance at posttest probed memory for AB and DE pairs from the scanned encoding/retrieval rounds. Posttest trials were coded as successful (recalled) if subjects retrieved at least some detail of the target image beyond the category. As with

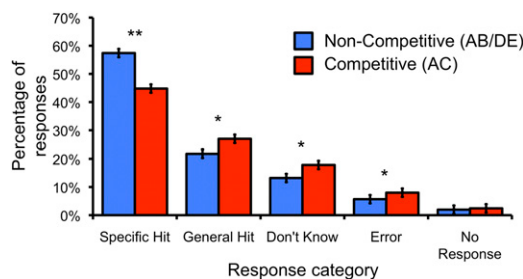


Fig. 2. Behavioral accuracy during retrieval rounds as a function of retrieval competition. Error bars indicate within-subject SEM.

the retrieval rounds, competition negatively impacted performance at posttest, evidenced by a lower rate of recalled AB pairs than DE pairs (mean = 52.4% vs. mean = 57.2%; $t_{17} = 2.32, P < 0.05$; *SI Results*).

fMRI Results. Category-selective encoding. Univariate analysis of the encoding data revealed robust category-sensitive neural responses within VOTC (Fig. S1), including greater responses to face trials within fusiform gyrus and greater responses to scene trials in parahippocampal cortex, confirming category-sensitivity within the VOTC. To next permit quantification of the fidelity of cortical reactivation at retrieval, we trained a pattern classifier to discriminate face vs. scene encoding trials using the encoding data from all voxels within an anatomically defined VOTC mask (*SI Methods* and Fig. S2A). MVPA of encoding trials confirmed highly robust sensitivity to face- vs. scene-related encoding responses in the VOTC (*SI Results*).

Cortical reactivation at retrieval. To assess reactivation at retrieval, pattern classification of retrieval trials was performed using the encoding data as the training set and the retrieval data as the testing set. Because the training set was restricted to the encoding data, classification of retrieval data could only succeed to the extent that neural responses that differentiated faces vs. scenes at encoding were reactivated at retrieval.

Considering all retrieval trials, irrespective of the subject's response or condition, trial-by-trial classification accuracy of the target associate's perceptual category (i.e., whether a retrieved item was a face vs. scene) was well above chance (mean = 66.6%, $t_{17} = 7.70, P < 0.001$), providing strong evidence that encoding-related activity within VOTC was reactivated at retrieval. This cued-recall result builds on prior evidence of neural reactivation of episodic memories revealed by MVPA, including during free recall (22), source memory (21), and item recognition (20). Notably, classification accuracy scaled with the number of voxels included in the VOTC mask (Fig. S2B), consistent with the idea that the representation of visual stimuli is distributed across the VOTC (23).

We next considered classifier performance in several additional ways. First, by computing classifier performance at each volume [i.e., repetition time (TR)-by-TR classification], we confirmed that classification accuracy generally conformed to the pattern of a hemodynamic response function, with peak accuracy achieved 4–8 s poststimulus onset (Fig. S2C). Second, the distribution of classifier evidence revealed that trials varied considerably in the strength of evidence for target reactivation (Fig. S2D). Finally, this distribution of evidence allowed for generation of receiver operating characteristic (ROC) curves (Fig. S2E); the area under these curves (AUC) provides another useful index of classifier performance (24, 25).

Cortical reactivation and retrieval strength. Having confirmed the approach, our first fundamental objective was to determine whether cortical reactivation scales with retrieval performance. Supporting this possibility, classification accuracy for specific hits, general hits, don't know, and error trials revealed a significant main effect of retrieval performance ($F_{3,51} = 21.70, P < 0.001$; Fig. 3A–D). Though classification accuracy for don't know trials did not differ from chance ($t_{17} = 0.27, P = 0.79$), classification accuracy for general hit trials was significantly above chance ($t_{17} = 6.48, P < 0.001$) and significantly greater than accuracy for don't know trials ($t_{17} = 3.45, P < 0.005$). Moreover, as the specificity of retrieval increased, so did the fidelity of cortical reactivation: classification accuracy for specific hit trials was well above chance ($t_{17} = 10.19, P < 0.001$) and significantly greater than accuracy for general hit trials ($t_{17} = 2.80, P < 0.05$). Finally, classification accuracy for error trials was numerically, but not significantly, below chance ($t_{17} = -1.53, P < 0.14$). Measures of AUC mirrored these results (Fig. 3E).

Mnemonic competition and cortical reactivation. Our second fundamental objective was to determine whether and how competition impacts the reactivation of target memories during retrieval. To this end, we first computed mean classification accuracy separately for noncompetitive DE/AB trials and for competition-

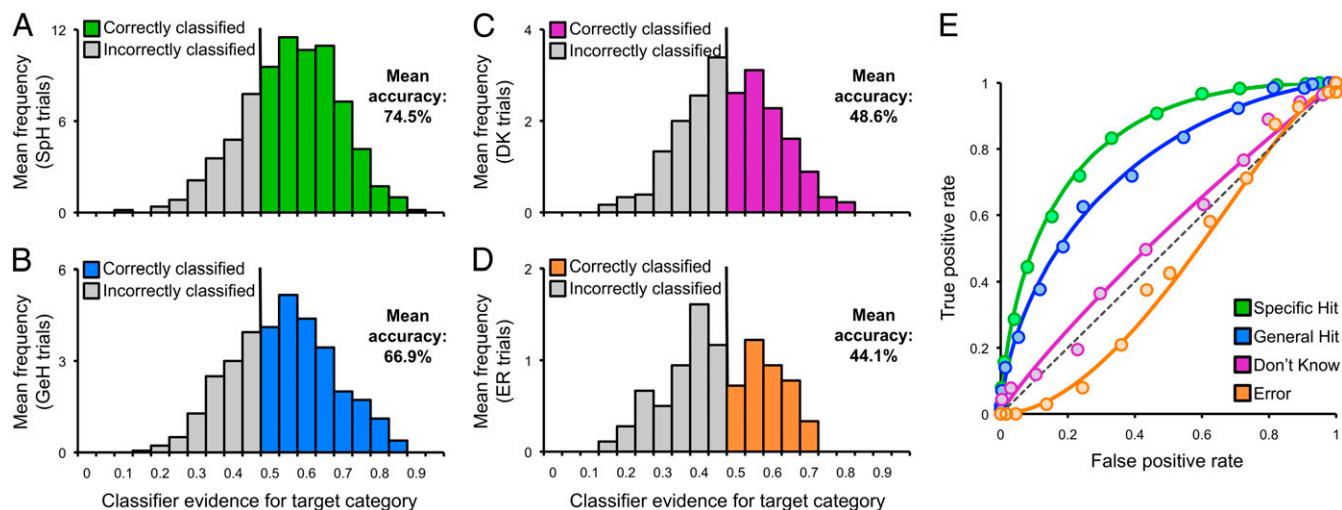


Fig. 3. Classification performance as a function of behavioral response. (A–D) Distribution of classifier evidence for target category and mean classification accuracy for (A) specific hits, (B) general hits, (C) don't knows, and (D) error trials. Individual trials were correctly classified if target evidence exceeded 0.5. (E) ROC curves for each response type; data are based on 14 of the 18 subjects (four subjects excluded due to an insufficient number of trials in at least one of the response bins). AUCs for fitted ROC curves: specific hit = 0.832; general hit = 0.745; don't know = 0.544; error = 0.427.

laden AC trials, irrespective of behavioral performance. Critically, classification accuracy—and thereby evidence for neural reactivation—was lower for competitive retrieval trials than noncompetitive retrieval trials ($t_{17} = 2.39, P < 0.05$), consistent with worse behavioral retrieval success for competitive retrieval trials. Notably, classification accuracy for AB and DE trials did not differ ($t_{17} = 0.49, P = 0.63$), whereas AB vs. AC classification accuracy differed significantly ($t_{17} = 2.61, P < 0.05$; Fig. 4). For subsequent comparisons of competitive vs. noncompetitive classification, we focus exclusively on AB vs. AC trials, as these conditions shared a common retrieval cue (A term).

Though the above data indicate that competition reduced both retrieval success and the fidelity of neural reactivation, it is possible that neural evidence of competition was present even when retrieval performance was matched across AB and AC trials. To this end, we conducted an ANOVA with factors of trial type (AB vs. AC trials) and retrieval specificity (specific vs.

general hit trials), allowing for a comparison of the degree of target reactivation as a function of competition while controlling for subjects' responses. Indeed, there was a trend toward poorer classification success for AC than AB retrieval trials ($F_{1,17} = 3.99, P = 0.06$), and no evidence that this effect interacted with retrieval success level (specific vs. general hits; $F < 1$). Together, these results indicate that competitive retrieval events were associated with lower-fidelity reactivation of retrieval targets.

Critically, we next sought to determine whether reductions in the fidelity of target reactivation provided insight into the long-term fate of competing memories. Specifically, we considered whether trial-by-trial measures of classifier evidence for AC reactivation were predictive of posttest memory for AB pairs (i.e., the associations that competed during AC retrieval). To address this, we separated AC retrieval trials according to whether they corresponded to AB pairs that were subsequently remembered vs. forgotten at posttest and according to behavioral measures of AC memory during the scanned retrieval rounds (specific vs. general hits), thus controlling for behavioral evidence of AC learning. This analysis indicated that lower-fidelity reactivation of C terms—or, conversely, greater evidence for reactivation of competing B terms—was associated with a greater likelihood of subsequently remembering the corresponding AB pair at posttest ($F_{1,17} = 8.00, P < 0.05$; Fig. 5). Though the magnitude of this effect was numerically greater for general hit trials, the effect did not interact with AC retrieval performance (specific vs. general hits, $F_{1,17} = 1.10, P = 0.31$). It is important to emphasize that this analysis was based only on AC trials for which subjects correctly identified the category of the C term (i.e., specific and general hit trials), indicating that although there was behavioral evidence that the target category was successfully retrieved, there was nonetheless variance in the fidelity of reactivation that was predictive of subsequent AB memory. Indeed, this relationship was still evident when the analysis was further restricted to only those AC trials that both the subject and the classifier categorized correctly ($F_{1,15} = 5.80, P < 0.05$; two subjects were excluded due to empty cells). Thus, the diminished AC reactivation on trials where subjects went on to later remember the corresponding AB pair cannot be wholly attributed to subjects occasionally reactivating the B associate more strongly than the C associate. Additionally, the relationship did not simply reflect how well AB pairs were initially learned, as the fidelity of initial AB reactivation was not related to the fidelity of AC reactivation (mean r across subjects = $-0.04, P > 0.20$). Together, these data indicate that reduced-fidelity re-

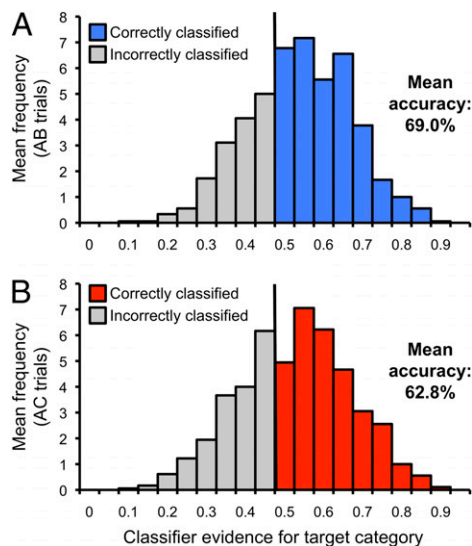


Fig. 4. Classification performance as a function of retrieval competition. Distribution of classifier evidence for target category and mean classification accuracy for (A) AB retrieval trials and (B) AC trials.

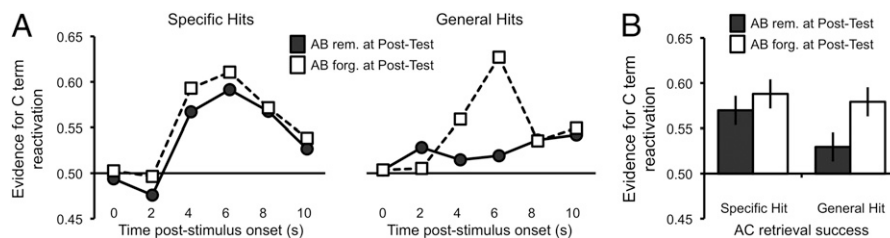


Fig. 5. Relationship between fidelity of reactivation during AC retrieval and subsequent memory for AB pairs. (A) Mean classifier evidence for C term reactivation during AC retrieval as a function of acquisition volume (2 s per volume), behavioral measures of AC retrieval success (specific hit vs. general hit), and subsequent memory for corresponding AB pairs at posttest (remembered vs. forgotten). (B) Mean classifier evidence for C term reactivation during AC retrieval as a function of AC retrieval success (specific hits vs. general hits) and subsequent memory for corresponding AB pairs at posttest [recalled vs. forgotten (don't know or error)]. Error bars indicate within-subject SEM.

membership of new associations corresponded to better subsequent memory for previously encoded, competing associations.

Frontoparietal mechanisms and low-fidelity reactivation. The preceding analyses indicate that low-fidelity remembering of AC pairs is positively associated with later memory for AB pairs. One interpretation of this relationship is that past associations (B terms) are reactivated during the retrieval of newer associations (AC pairs), and this coactivation of B and C terms yields low-fidelity reactivation (i.e., ambiguous classifier evidence) but ultimately benefits AB retention. By this account, low-fidelity AC trials can be characterized in terms of high, but conflicting, mnemonic evidence. Alternatively, it is possible that when AC pairs are weakly reactivated, memory for AB pairs is less likely to be disrupted, thus accounting for the inverse relationship between AC reactivation and subsequent AB memory. By this account, low-fidelity AC trials can be characterized in terms of low, but not necessarily conflicting, evidence.

To differentiate between these competing accounts, we first identified frontoparietal regions that positively tracked retrieval evidence, and then assessed how responses in these regions related to the fidelity of AB vs. AC reactivation. Specifically, we performed a conjunction analysis of two independent contrasts: (i) a contrast to identify regions that tracked behavioral expressions of mnemonic evidence, and (ii) a contrast to identify regions that were differentially related to the fidelity of reactivation across AB vs. AC trials. To first identify regions that tracked mnemonic evidence, we contrasted specific hit trials against general hit and don't know trials. Importantly, we restricted this contrast to only DE pairs, so as to obtain a contrast that was independent of the critical AB/AC trials (Table S1). To next identify regions that were differentially engaged in relation to the fidelity of reactivation across AB vs. AC retrieval events, we first separated AB and AC trials according to the fidelity of classifier-based evidence for VOTC reactivation. AB trials were sorted into three bins of equal size: low-, medium-, and high-fidelity reactivation, and likewise for AC trials. It should be emphasized that these bins only represented the relative strength of target evidence; strong reactivation of both face and scene representations would correspond to low-fidelity reactivation because of the lack of evidence selectively favoring the target category. Using these binned data, we then tested for a voxel-level interaction between the fidelity of reactivation (high vs. low) and pair type (AB vs. AC), with the prediction being that AC trials associated with low-fidelity reactivation would elicit relatively high engagement of regions that tracked mnemonic evidence.

A conjunction analysis of the two contrasts (each thresholded at $P < 0.005$) revealed overlapping activation in several regions, including the dorsolateral prefrontal cortex (DLPFC), medial prefrontal cortex, and lateral and medial parietal cortex (Fig. 6A and Fig. S3A). Critically, these regions were characterized by relatively high activation during low-fidelity AC retrieval events (Fig. 6B). Indeed, a direct contrast of low-fidelity AC retrieval events vs. low-fidelity AB retrieval events revealed highly similar frontoparietal regions (Table S2). These data are particularly striking considering that, following our trial binning procedure,

low-fidelity AC retrieval events were associated with even lower-fidelity reactivation (mean = 0.41) than low-fidelity AB retrieval events (mean = 0.43; $P < 0.01$). High-fidelity AB (mean = 0.70) vs. AC (mean = 0.70) trials did not differ ($P = 0.73$). Thus, whereas low-fidelity AC retrieval events were associated with weaker classifier-based evidence that target memories were reactivated, they were associated with elevated frontoparietal responses, suggesting that a relatively high amount of episodic information was nonetheless retrieved. Together, these data strongly favor the interpretation that low-fidelity reactivation during AC retrieval reflected robust but nonselective retrieval—that is, reactivation of both target and competitor memories.

Discussion

Emerging evidence indicates that neural reactivation is a fundamental component of event remembering (26). The present results provide unique evidence that reactivation reflects not only how successfully memories are retrieved but also how competition impacts remembering—namely, that competitive remembering of visual memories is associated with lower-fidelity

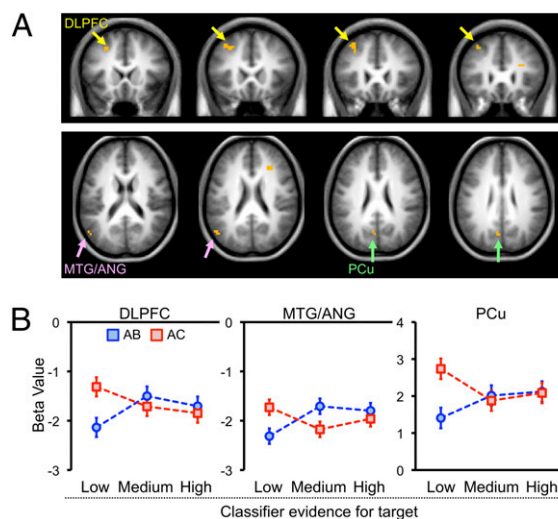


Fig. 6. Frontoparietal regions that tracked mnemonic evidence and fidelity of reactivation. (A) Conjunction analysis: regions that tracked retrieval of specific event details (specific hit trials > general hit/don't know trials; DE pairs only; $P < 0.005$) and displayed an interaction between fidelity of reactivation (low vs. high) and trial type (AB vs. AC; $P < 0.005$). DLPFC, dorsolateral prefrontal cortex; MTG, middle temporal gyrus; ANG, angular gyrus; PCu, precuneus. For complete set of implicated regions, see Fig. S3. (B) Responses in several regions of interest drawn from the conjunction analysis revealed that the interaction between fidelity of reactivation and trial type was characterized by marked activation for AC trials associated with low-fidelity reactivation. Error bars indicate within-subject SEM.

responses within VOTC, regardless of whether these responses are driven by current visual input or memory-based reactivation of visual events. These functional interactions between the prefrontal cortex and the VOTC putatively enable perceptual or mnemonic evidence to be translated to goal-relevant behavioral responses (15, 17, 18). Importantly, these interactions are thought to be fundamental to the implementation of cognitive control in service of competitive remembering (*SI Discussion*).

Collectively, the present results constitute unique evidence relating patterns of neural reactivation elicited during competitive remembering to the quality of information retrieved in the present and to memory outcomes experienced in the future. These results parallel findings from studies of visual perception, indicating that VOTC structures are modulated by current mnemonic goals while reflecting the costs associated with mnemonic competition. Importantly, our results also point to overlap in frontoparietal mechanisms that operate upon perceived vs. remembered representations. More broadly, our results reveal that reactivation provides unique insight into understanding competitive dynamics between memories, and is central to both the experience and consequences of episodic remembering.

Methods

Procedure. The experiment was comprised of four phases: encoding, retrieval, a face/scene localizer task (not considered here), and a posttest. All phases except the posttest were conducted during fMRI scanning. Seven encoding rounds and seven retrieval rounds occurred in alternation. During encoding rounds, subjects studied words (cues) paired with either faces or scenes (associates) for 4 s each. Subjects encoded a total of 48 pairs in each of three conditions (AB, AC, DE). AB and DE pairs appeared in encoding rounds 1–6 (eight pairs per condition per round); AC pairs appeared in rounds 2–7 (eight pairs per round). AB pairs and corresponding AC pairs always appeared in encoding rounds n and $n + 1$, respectively. Encoding trials were separated by

an 8-s active baseline period (Fig. 1). During retrieval rounds, subjects' memory was tested for each pair from the immediately preceding encoding round. Subjects were presented with cues and instructed to covertly recall the corresponding associate. Each trial lasted 5 s, and subjects indicated their retrieval success by making one of five responses using a five-key button box: (i) don't know, (ii) face-specific, indicating that they remembered the specific image and that it was a face, (iii) face-general, indicating that they had a nonspecific memory of a face, (iv) scene-specific, and (v) scene-general. Retrieval trials were separated by a 7-s baseline during which a fixation cross was presented. After exiting the scanner, subjects completed the posttest. For each posttest trial (5 s), subjects were presented with a cue along with the instruction to retrieve either the face or the scene that was previously studied with that cue. For cues that had been associated with more than one image, subjects were always prompted to retrieve the first associate (B term). Subjects responded aloud during posttest. Each trial was followed by a 1-s fixation cross. For additional details of each phase, see *SI Methods*.

fMRI Data Analysis. fMRI scanning was conducted at the Lucas Center at Stanford University on a 3.0T GE Signa MRI system (GE Medical Systems). Functional images were obtained using a T2*-weighted 2D gradient echo spiral-in/out pulse sequence; TR = 2 s; echo time (TE) = 30 ms; flip angle = 75°; 30 slices, $3.4 \times 3.4 \times 4$ mm; axial oblique sequential acquisition. Encoding rounds corresponded to seven functional scans (940 volumes total), and likewise for retrieval rounds. Image preprocessing and data analysis were performed using SPM5 (Wellcome Department of Cognitive Neurology, London). Pattern classification analyses were conducted using the Princeton Multi-Voxel Pattern Analysis Toolbox (<http://code.google.com/p/princeton-mvpa-toolbox/>) and custom code implemented in MATLAB (MathWorks).

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