Competition between associations in memory

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Abstract

If two associations share an item, one may be remembered at the expense of the other (BC recalled but not AB). Here we identify the neural processes by which this competition materializes and is resolved. We analyzed fMRI signal while participants studied sets of pairs that reliably induced pair-to-pair associative interference, but which participants could not fully resolve. Precuneus activity tracked retrieval of previous pairs during study of later overlapping pairs. This retrieval apparently produced interference by diverting study resources from the currently displayed pair. However, when activity in ventromedial prefrontal cortex, as well as anterior subregions of the hippocampus, was present while the earlier pair had been studied, interference was reversed, and both pairs were likely to be recalled. Angular gyrus and mid-frontal activity were related to interference-resolution once the participant had seen both pairs. Taken together, associations compete via precuneus-mediated competitive retrieval, but vmPFC may neutralize this by ensuring that when the earlier association is remembered while studying the later pair, memories of the two pairs can overcome interference likely via activity in mid-frontal cortex and angular gyrus.

Keywords: associative memory, interference, hippocampus, ventromedial prefrontal cortex, precuneus

Introduction

Knowledge often demands that we remember associations that share an item. Suppose you are learning about animals. You first find out that chickadees eats seeds, an association, A**B**, between seeds (A) and chickadees (B). Later you find out that chickadees

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(B), in turn, are eaten by hawks (C), the association **B**C (boldface is used here to highlight the shared item). In a second example, you are keeping track of which teams have played each other in a children's sports tournament, to be able to plan future games. Team A ("Trojans") played against Team B ("United") who played against Team C ("Strikers") in a later game. Again, this entails remembering both the A**B** and **B**C associations; there is no sense in which the later association replaces the earlier association. However, the repeated item (B) in two pairs introduces associative interference. Without mechanisms to specifically address this interference, mathematical models predict a somewhat mutually exclusive relationship between the A**B** and **B**C memories (e.g., Caplan et al., 2014). That is, if A**B** is remembered, **B**C is less likely to be remembered and vice versa. This formal argument seems different than our daily experience. Clearly we can remember new information related to B without losing the previous memories. Our overarching question is whether this competition ever materializes in human memory tasks and is then resolved, or possibly is never a challenge to begin with. Note that in these examples, the order of the two associations relative to each other might or might not be known. Here we are focused on whether both associations can be remembered, or just one at the expense of the other, whether or not their relative-order is also known.

Most associative interference studies have been modelled not on the A**B**/**B**C arrangement but on **A**B/**A**C learning, where the left-hand item is always the shared item (note that AB/AC is also an associative interference paradigm, but the shared item is always the cue, whereas in AB/BC, the cue switches positions). Moreover, most of the theory of associative interference has been developed with two-list procedures, where list 1 contains unambiguous pairs (all the $\boldsymbol{A}_iB_i$ plus control pairs) and list 2 introduces interference (all the $\boldsymbol{A}_iC_i$ plus more control pairs). One can look for evidence of competition by comparing accuracy, on average, of memory for interference pairs compared to control pairs with no repeated items. But it has long been pointed out that there can be a general effect, where for example, the interference pairs as a set are remembered worse than the control pairs as a set (e.g., Kliegl & Bäuml, 2021; Martin, 1971b; Postman et al., 1968; Underwood & Schulz, 1960). With two lists, this could be as simple as participants inhibiting all the response-items of interference-pairs in list 2 (or similarly in list 1), regardless of their specific pairings. Returning to our situation, where the overlapping item switches position ($A_i\boldsymbol{B}_i$ and $\boldsymbol{B}_iC_i$), if interference occurs directly between pairs sharing an item, what is needed is a test of whether a particular $A_i\boldsymbol{B}_i$ pair competes with a particular $\boldsymbol{B}_iC_i$ pair— in other words, a correlation across overlapping pairs indexed by i. If $A_i\boldsymbol{B}_i$ and $\boldsymbol{B}_iC_i$ compete, then if one pair is remembered, it will often be at the expense of the other, producing a negative correlation between the pairs. If there is no competition at the level of pairs, we might instead find zero correlation, indicating independence (accuracy of $\boldsymbol{B}_iC_i$ is unrelated to accuracy of $A_i\boldsymbol{B}_i$), or a positive correlation, indicating facilitation ($A_i\boldsymbol{B}_i$ and $\boldsymbol{B}_iC_i$ tend to both be remembered or both be forgotten). Empirical results actually show correlations of zero, indicating no competition but independence of the memories, or even positive correlations, indicating a facilitatory relationship between the memories (Burton et al., 2017; Delprato, 1972; Greeno et al., 1971; Martin, 1971a, 1971b; Tulving & Watkins, 1974; Wichawut & Martin, 1971). This could mean that contrary to the intuition of many researchers, as well as memory models with competitive retrieval, pairs sharing an item never, in fact, compete in memory. Alternatively, some characteristics of the tasks may have enabled participants

to overcome and sometimes even reverse competition between overlapping memories by the time memory is tested. In support of the latter, Caplan et al. (2014) were able to show unambiguous evidence for the presence of competition between overlapping pairs. The key was to construct lists of the form AB, BC, CD, DE, EF, FA (shuffled). In such "double-function" lists (Primoff, 1938), each item is a left-hand item of one pair and a right-hand item of another pair. When ambiguous pairs are segregated to different lists, as is frequently done with AB/AC paradigms, participants can use list-membership to resolve interference (Kliegl & Bäuml, 2021). However, with the double-function paradigm, which we adopt here (Fig. 1), list-discrimination cannot be used because interfering pairs are studied within a single list. Pairs were tested with a two-response procedure.[1] For example, given B as a cue, participants attempt to recall A and C. In response to **B** as a cue, accuracy for **B**C was negatively correlated with accuracy for A**B** ("same-probe" correlation, where accuracies of AB and or BC were derived from the two responses to a single (B) cue; see Fig. 1b,c). Follow-up data-analyses showed that it was not just the two responses (A and C) competing to be retrieved, but the memories for the A**B** and **B**C where associations were stored with somewhat mutually competitive strengths (the distinct-probe correlation described in the methods and elaborated in Caplan et al., 2014).

If the range of interference resolution is book-ended by this competition effect and classic independence with AB/AC learning, this suggests that associative competition is, indeed, present initially (evidence: negative correlation with the one-list double-function task), but is often resolved by the time researchers test memory (evidence: independence with the two-list AB/AC task). The single list in the double-function paradigm prevents participants from using list-membership to protect against associative ambiguity. In addition, the long chains of double-function pairs might explain why this task produces pair-specific competition whereas double-function lists with shorter, three-item chains has produced pair-to-pair independence or even net facilitation (Horner et al., 2015; Horner & Burgess, 2013, 2014). Because interference was present but not complete, this paradigm is well positioned to investigate neural processes underlying both the materialization and resolution of competition between associations.

Previous studies of neurocognitive mechanisms of associative interference, mostly using AB/AC tasks, have reported interference on average but not tested for pair-to-pair competition. Those that have tested for pair-level effects have produced results consistent with the behavioural literature, confirming near-zero or positive correlations in pair-specific analyses (for example, in AB/AC lists, Kuhl et al., 2010, and in short, three/four-element double-function lists, Horner et al., 2015). These studies have therefore focused on understanding how the brain produces good memories of both pairs, but a clear view of processes by which competition initially materializes has remained elusive. Here we investigate the initial piece of the story when competition first emerges, by studying brain activity in a one-list double-function associative interference paradigm that does show evidence of competition at the level of pairs. Also, whereas most neuroimaging studies of associative interference have recorded only during retrieval and encoding of the later-studied pairs, we also recorded and analyzed activity during encoding of the earlier-studied pairs. Even in our paradigm interference is resolved for a substantial proportion of pairs. This might occur during study

[1] This was confusingly called "modified modified free recall" in the past; see for example, Barnes and Underwood (1959), Burton et al. (2017), and Tulving and Watkins (1974).

of the later pair. However, a hypothesis that has not yet been tested is that processes, already during encoding of the earlier pair, might make it more likely that later interference can be resolved.

The present experiment. We scanned participants while they studied double-function lists, tested with two-response cued recall (Fig. 1). We sought activity related to interference and its resolution during study of the later pair, but also prospectively, during study of the earlier pair linked by a common item ($A_i\boldsymbol{B}_i$ and $\boldsymbol{B}_iC_i$; due to randomization, the earlier pair could be either $A_i\boldsymbol{B}_i$ or $\boldsymbol{B}_iC_i$). We tested the following non-mutually exclusive hypotheses, that build on and connect with prior studies that have traced what are presumably the later interference-resolution stages (reviewed in more detail in the Discussion). These analyses specifically take advantage of the fact that we recorded brain activity during the earlier-, as well as later-studied pairs.

Regarding the source of interference, our first hypothesis was that neurocognitive processes that lead to good memory also lead the pair to compete, which falls out of models that assume retrieval is competitive. Thus, if encoding strength is indicated by brain activity that shows a subsequent-memory effect (greater activity during later-remembered versus later-forgotten pairs; Kim, 2011), that same activity should also be associated with competition between two pairs. In other words, the neurocognitive processes that lead to good memory also lead the pair to compete. Next, consider that associative interference studies have found evidence that participants remember the previous pair when presented with a pair with a repeated item (e.g., Horner et al., 2015; Kuhl et al., 2011; Kuhl et al., 2010; Richter et al., 2016). Extending these findings to explain pair-specific competition in our paradigm, our second hypothesis was that retrieval during study produces interference, consistent with behavioural effects found by Caplan et al. (2014). Thus, retrieval-related activity during the later pair, such as is found in the precuneus in related paradigms (e.g., Brodt et al., 2016; Himmer et al., 2019; Phillips & Niki, 2002; Wimber et al., 2008), may be associated with mutually exclusive memory— one pair remembered at the expense of the other. Moreover, activity during the earlier pair that reflects this propensity to reactivate may then produce proactive interference. The two hypotheses are not mutually exclusive and might coexist. As elaborated in detail in the Results section, the former would be supported if regions showing the simple subsequent-memory effect contrast also appear in the interference contrast during the earlier-studied pair. Otherwise, the hypothesis will not be supported, but also not strictly rejected, since there could be activity beyond the sensitivity of our measure. The latter will be supported if regions that appear in the contrast aimed to isolate reactivation also appear in the interference contrast during the later-studied pair.

Regarding the resolution of interference, our first hypothesis was inspired a different body of work, associative *inference*. This paradigm has similar task design but very different research goals. In studies of associative *inference*, having studied A**B** and **B**C, participants must infer the association AC. Given the major role ascribed to the hippocampus in transitive and associative inference (e.g., Bunsey & Eichenbaum, 1996; Zeithamova & Bowman, 2020; Zeithamova et al., 2012), our first hypothesis was that activity in the hippocampus overcomes competition between associations and can possibly even reverse it. Our second hypothesis, which could coexist with the first, was that interference may be resolved when the participant thinks about (i.e., retrieves) the earlier-studied pair while

viewing the later-studied pair. Simply retrieving the earlier pair, as mentioned in the previous paragraph, would be expected to exacerbate a negative correlation between encoding strengths of the two pairs, so for interference to be resolved, additional processes should be present. Previous studies have implicated ventromedial prefrontal cortex (vmPFC) in associative inference (e.g., Kumaran et al., 2009; Spalding et al., 2018; Zeithamova & Bowman, 2020; Zeithamova et al., 2012). A third hypothesis is possible, and testable with data recorded during the earlier-studied pairs. That is, there might be cognitive processes during the earlier-studied pair that make its representation in memory conducive to resolution with the later-studied pair, reminiscent of prior-knowledge effects (Sommer, 2017; Sommer et al., in press). These three hypothesis are not mutually exclusive, and might all coexist. They are each tested in their own right. The first interference-resolution hypothesis would be supported if hippocampal regions were isolated in the resolution contrasts during the later-studied pair. The second hypothesis would be supported if the same region or set of regions were found to be significant in both the reactivation and resolution contrasts during the later-studied pair. The third hypothesis would be supported if a region or regions showed robust effects in the resolution contrast during the earlier-studied pair.

Finally, once we obtained activity consistent with reactivation of the earlier pair while studying the later pair, we sought convergent evidence that reactivation was, in fact, occurring, using representational similarity analysis (RSA; Kriegeskorte et al., 2008) and single-voxel correlations across trials. We also interrogated the nature of that reactivated activity, testing the hypothesis that later reactivation of memory of a pair reactivates different, higher-order, activity (non-overlapping areas; Favila et al., 2020) than the original online processing of the stimuli.

Methods

Participants

Thirty (20 F, 10 M, age 28.8 $\pm$ 3.5 years; target sample size was set in advance based on related studies with similar expected sensitivity; Caplan and Madan, 2016) healthy participants were recruited from the university community. Participants had normal or corrected-to-normal vision, and reported no past or present psychiatric or neurological disorders. The study was approved by the local ethics committee, Board of Physicians, Hamburg, Germany. All participants gave written informed consent and received monetary reimbursement (10 €/h).

Behavioural methods

We first adapted the verbal paradigm used by Caplan et al. (2014) to pictures, similar to our previous studies on emotional associates (Caplan et al., 2019; Fujiwara et al., 2021; Madan et al., 2017). The task is illustrated in Fig. 1. To increase power for the fMRI analyses, we omitted the single-function (control) pairs that were in the original design. There were twelve double-function pairs per list, an inter-pair active-baseline task, only one test per item, vocal responses instead of typed, and changes to the timing. The experiment was implemented with home-grown MATLAB code and the PsychToolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and CogToolbox (Fraundorf et al., 2014) libraries. The testing session began with practice outside the scanner (not analyzed), to familiarize the

participant with the procedures. The experimenter ensured that the participants understood their tasks and were able to recognize the practice-list stimuli. Most participants then did 18 runs (full procedure relevant to a given study set; 1 with only 17 runs and 2 with only 16 runs due to failure to start the scanner, and 1 with 14 runs due to withdrawing early) with scanning during the study phase only.

Materials

Stimuli were nameable, coloured line-drawing object images from Rossion and Pourtois (2004), with some stimuli removed by the authors when they were thought to be difficult for German participants to identify. A stimulus was never used on more than one list (including the practice list) and a fresh full random assignment of stimuli to lists was done for each participant. In each study set, twelve objects were randomly assigned to a set of twelve pairs, with the restriction that they comprised a ring structure (AB, BC, CD, DE, EF, FG, GH, HI, IJ, JK, KL, LA) wherein every word was the left-hand member of one pair and the right- hand member of another pair (related to the stimulus structure of Horner et al., 2015, closed-loop triads, but differing in that here, the "loop" is longer and all items are of the same material, objects). The classic finding of associative symmetry of cued recall of pairs explains some important aspects of our task design. That is, in a standard list of non-overlapping pairs, when the left-hand and right-hand items are treated the same (Horowitz et al., 1966), forward (given A, recall B) and backward (given B, recall A) cued-recall accuracies are equal (Asch, 1969). Moreover, in past experiments, if each pair is tested twice, cued recall of a given pair in the forward and backward direction nearly always produces the same accuracy; in other words, there is a very high correlation between forward and backward cued recall, computed across pairs (Kahana, 2002; Rizzuto & Kahana, 2000, 2001). Both the equivalence of mean accuracy and high correlation were also confirmed with the double-function list-structure we use here (Caplan et al., 2014).

Procedure

Study phase. Pairs were presented sequentially in random order. The items of each pair were displayed simultaneously, with the two items separated by a space in the centre of the screen. Each pair was displayed for 3960 ms (2 × TR=1,980 ms), followed by a 150-ms blank interpair interval. Following the blank ISI, participants completed an active baseline task (described below), lasting from 2 to 4 integer multiples of 2/3 TR (step size 1.32 s; range: 2640–5280 ms) to introduce randomly selected jitter into the timing. Note that the onset of the picture was not always at the same time with respect to the scanner pulse.

Test phase. Scanning halted during the test phase so that vocal responses could be recorded. Each item served as a cue exactly once, requesting up to two responses, presented in random order. Each test trial, preceded by a block of the active baseline arrow task as in the study phase, consisted of a cue word centred on the screen. The phrase "Bild #1" (translation: "Picture #1") was displayed centered, underneath the cue object while the participant was asked to vocally recall a word or phrase describing one of the two images that were targets of the cue object. The vocal response was recorded for 7850 ms into a sound file, but also scored in real time by the experimenter and a research assistant on a scoring sheet printed out in advance of the session. The recording was voice-activated,

and the onset time was logged as well. A second response was collected the same way, with "Bild #2" displayed. Following previous implementations of the two-response procedure, participants were told they could give the two responses in any order they chose (Barnes & Underwood, 1959; Caplan et al., 2014). Accuracy was determined by matching the response with stimuli in the word pool. A response was considered correct if it was one of the two responses given, regardless of the other response and regardless of whether it was the first or second response given to the cue.

We were able to confirm that our task produced associative interference that could not be entirely resolved by the time memory was tested, replicating the central findings of Caplan et al. (2014) with the changes described above (see Results).

Active baseline: arrow task. To suppress rehearsal and reduce rest-related hippocampal activity (Stark & Squire, 2001), participants viewed an arrow pointing left or right, and responded with the button box with the button congruent with the arrow direction. Each arrow-task trial lasted a fixed duration (2/3 TR) and the number of trials was selected to fill the inter-pair jitter interval.

Behavioural data analysis

Correlations between pairs of accuracy outcomes were evaluated with Yule's $\mathcal{Q}$, equivalent to a gamma correlation for bivariate data (Kahana, 2002), but can otherwise be interpreted much like Pearson correlation; $\mathcal{Q} = 0$ indicates statistical independence, $\mathcal{Q} > 0$, positive coupling between the variables, and $\mathcal{Q} < 0$, negative coupling, or some level of mutual exclusion (one memory tends to be recalled at the expense of the other). Statistics were conducted on log-odds-transformed $\mathcal{Q}$ values (logits), for which residuals are theoretically approximately Gaussian, thus appropriate for parametric tests, and resulting p values are the same as if one conducted a χ^2 test on the same contingency table (Bishop et al., 1975; Hayman & Tulving, 1989).

Yule's $\mathcal{Q}$ is computed from 2×2 contingency table comprised of tallies. As illustrated in Fig. 1c, accuracy of one pair is in rows and accuracy of the other pair is in columns. If we label the four cells such that cell a counts the number of trials for which both pairs are correct, cell b when the first pair is correct and the second is incorrect, cell c when the first pair is incorrect but the second is correct, and cell d when both pairs are incorrect, $\mathcal{Q} = (ad - bc)/(ad + bc)$. The main relationship we are interested in is $\mathcal{Q}_{\text{same-probe}}$, where accuracy of two pairs sharing an item is derived from the test trial where the common item was the cue (for pairs AB and BC, we would use accuracy from the trial for which B was the cue, and both A and C were requested as responses). An example where the earlier pair was evaluated in what would be equivalent to a forward probe in a non-interference list of pairs (given B, did the participant recall C?) and the later pair was evaluated in a backward probe (given B, did the participant recall A?) is illustrated in Fig. 1c. If associative interference is present, $\mathcal{Q}_{\text{same-probe}}$ would be expected to be negative. If the interference between the earlier and later pairs is reversed, we would expect $\mathcal{Q}_{\text{same-probe}}$ to be positive. Following Caplan et al. (2014), we also compute $\mathcal{Q}_{\text{distinct-probe}}$, where accuracy of the earlier pair is derived from a different test-cue trial than accuracy of the later pair. This exploits the fact that each item was given as a cue one time, with spaces for two valid responses. Consequently, each pair is tested twice, once in the forward direction, on the trial where its left-hand item is the cue, and once in the backward direction, on a different trial where

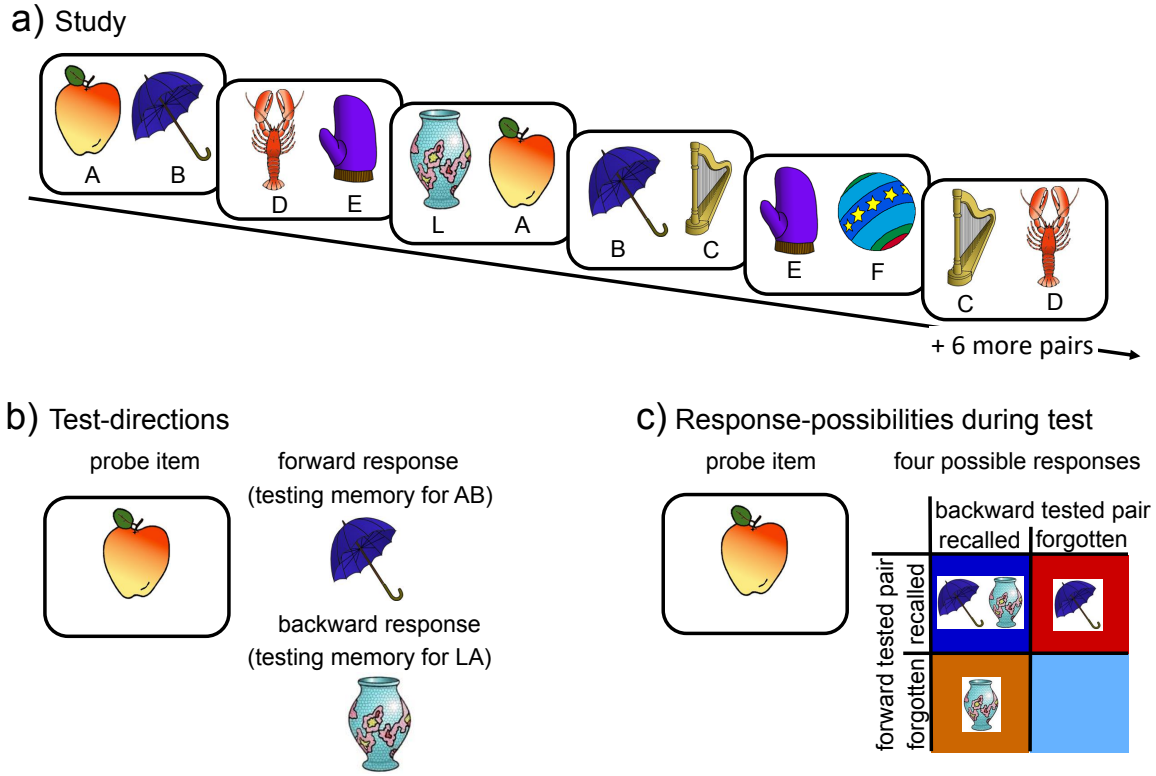

Figure 1

The double-function list procedure. (a) In each cycle of the task, participants study a sequentially presented set of 12 pairs, where each item appears in the left position of one pair and the right position of another pair. After a distractor task (not depicted), each item appears one single time as a cue, where participants attempt to vocally recall both associates. The procedure affords several ways of scoring accuracy, to assess the relationship between two overlapping pairs in memory. (b) An example test trial, where A (the apple) is the cue item and the participant can (vocally) respond with the umbrella, which would indicate memory of AB (tested in the forward direction) and/or with the vase, which would indicate memory for LA (tested in the backward direction). (c) Four combinations of responses (accuracies) are possible, and tallied as in the depicted 2×2 contingency table to compute the "same-probe" correlation. ("Forward" here indicates that scoring is done for pairs of pairs considering the forward-probe direction for the current pair and consequently, the backward-probe direction for the competing pair). When analyzing brain activity, we standardize such that the pair that is tested forward on a given test trial is the "current" pair and the pair that is tested backward on the same trial is the "competing" pair. Thus, the brain-activity analyses are subdivided depending on whether the current pair was the earlier-studied pair or later-studied pair, respectively. Note that the color coding in the contingency tables is maintained across the other figures.

its right-hand item is the cue (Fig. 2a). Thus, the distinct-probe correlation is computed from a contingency table assembled from the relationship between pairs sharing an item, where accuracy of one pair was evaluated on a different test trial than accuracy of the other pair (Fig. 2b). For example, we can assess memory for AB on the trial with A as the cue (correct if B was one of the two responses given and incorrect otherwise, corresponding to the forward response (Fig. 2a). This would be yoked to the assessment of memory for BC on the trial with B as the cue (correct if C was one of the two responses given and incorrect otherwise; Fig. 2a). In this example, both pairs were tested in the forward direction (on different trials). This pair of pairs would thus increment, in the contingency table, cell a if both were correct, cell d if both were incorrect, and cells b and c if one were correct and the other incorrect (Fig. 2b). The other relevant cases are where both pairs were tested in the backward direction (on different trials). Thus, $\mathcal{Q}_{\text{distinct}-\text{probe}}$ also measures competition between memories of two associations sharing an item, but it eliminates the contribution of immediate competition between two candidate responses to a single cue, since memory accuracy is evaluated based on two different test-cue trials. Finally, we compute a control correlation, $\mathcal{Q}_{\text{control}}$, which is a bootstrap, computed on a contingency table composed of pairs from the same list that do not share an item (e.g., AB and CD). This estimates the positive correlation expected due to variability across lists (Caplan et al., 2014; Hintzman, 1980). If response candidates compete in response to a single cue, $\mathcal{Q}_{\text{same}-\text{probe}}$ would be more negative than $\mathcal{Q}_{\text{control}}$. If in addition, memories of two pairs sharing an item have been encoded in a competitive relationship, as found by Caplan et al. (2014), $\mathcal{Q}_{\text{distinct}-\text{probe}}$ will also be more negative than $\mathcal{Q}_{\text{control}}$; otherwise, $\mathcal{Q}_{\text{distinct}-\text{probe}}$ would be equivalent to $\mathcal{Q}_{\text{control}}$.

fMRI methods

Data acquisition and preprocessing

Functional magnetic resonance imaging (fMRI) was performed on a 3 T system (Siemens Trio) with a 32-channel head coil. An echo planar imaging T2*-sensitive sequence in 64 contiguous axial slices (2×2×2 mm); TR, 1.98 s; TE, 26 ms; Multiband 2; parallel acquisition techniques (PAT) factor 2; flip angle, 70°; matrix 64×64) was employed. High resolution ($1 \times 1 \times 1$ mm voxel size) T1-weighted structural MRIs were acquired for each subject using a 3D MPRAGE sequence. Functional imaging data were processed using the Statistical Parametric Mapping 12 software (SPM12, Wellcome Department of Cognitive Neurology, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Functional images were realigned and unwarped to correct for susceptibility-by-movement artefacts. For quality control, it was then checked whether individual participants had excessively moved within run and the normalization was checked via comparison of the template and normalized T1 using the contour-function in SPM. The anatomical images were coregistered to the mean functional image of that participant. The anatomical images were then segmented and transformed into standard stereotaxic MNI space using Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL) as implemented in SPM12 and the deformation field applied to the functional images of the same participant. Functional images were smoothed with full-width at half-maximum of 6 mm.

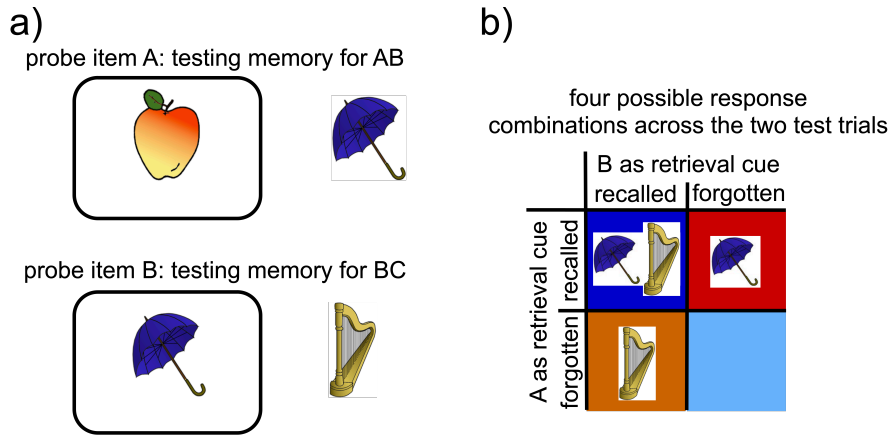

Figure 2

The distinct-probe correlation. (a) As indicated by our terminology, the "distinct-probe" correlation is computed between two different trials, each of which tests a different one of two pairs sharing an item. One example is depicted here. (b) The "distinct-probe" correlation is then computed by the contingency table tallied across such pairings; one example is illustrated here. Note that the color coding in the contingency tables is maintained across the other figures.

Univariate fMRI analyses

Individual subjects and group level data were analyses using the general linear model (GLM) as implemented in SPM 12 in a mass univariate approach. Here we describe the full first-level model, with 8 regressors of interest. In the Results, we describe, in turn, each second-level model that is derived from those 8 regressors.

First-level model. For the first-level model, we sorted the encoding trials according to the subsequent performance in the same probe forward test, i.e., current and competing pair remembered, only current but not competing pair, not the current but only the competing, and neither of the pairs remembered (Fig. 1c). In other words, we sorted trials according to their Yule's $\mathcal{Q}$ cell in the same-probe forward/backward relationship (Fig. 1c). We focused on the forward/backward relationship (that is, the cue that tests the current pair in the forward direction and the competing pair in the backward direction) because of the expected high associative symmetry (Kahana, 2002) which was previously confirmed for this paradigm using verbal stimuli (Caplan et al., 2014) and— foreshadowing our current results— also observed in this experiment (Fig. 3b). The symmetry charac-

teristic ensures that the results of one test direction generalise to the other. Although the same-probe and distinct-probe correlations were significantly different from one another (Fig. 4), we focused on the same-probe relationship for two reasons. First, the number of trials differentiating the same- and distinct-probe pairings was too small to be able to reliably identify brain activity that might be unique to the same-probe activity. Second, when we reran the analyses based on the distinct-probe relationship, activation maps were quite similar to those based on the same-probe relationship. We present only the same-probe results, as they should include both competition both at the item level (competition between the two response candidates to the cue item) and at the association level (competition between memories of two associations sharing an item).

Moreover, we dissociated 'earlier-studied' pairs from 'later-studied' pairs. 'Earlier-studied' pairs were studied before the competing pair had been studied (AB, in the case of A as a probe in the example illustrated in Fig. 1c). 'Later-studied' were studied after the competing pair had been studied (LA, in the case of A as a probe). [2] Based on these considerations, the first-level model included 8 regressors (earlier- vs- later-studied pair × 4 Yule's $\mathcal{Q}$ cells) that were created by convolving the onsets of the conditions with the canonical hemodynamic response function (hrf). The Yule's $\mathcal{Q}$ cells were the four cells of the contingency table used to compute $\mathcal{Q}$ (see Fig. 1c). In addition, six movement regressors were added as nuisance variables. The encoding runs of each participants were concatenated with appropriate adjustments to the runs-specific constant, the autocorrelation structure, and the high-pass filter.

Second-level model. On the second level we contrasted the parameter-estimates of the these regressors with participant as a random factor in order to identify brain areas where activity exhibited contrasts consistent with (re-)encoding, interference and resolution during processing of earlier- and later-studied pairs. The non-sphericity correction for violation of the independent and identically distributed (i.i.d.) assumption was applied. The particular contrasts applied will be detailed in the results section (see also Table 1). The fourth cell of the Yule's $\mathcal{Q}$ contingency table (both pairs incorrect) is ambiguous. Both pairs could be forgotten because neither was studied well, or because both were studied well but the two pairs competed such that neither response could be produced in response to the cue. For this reason, this fourth cell was usually left out of the contrasts, but beta values nonetheless plotted alongside the beta values for the other cells when illustrating the results.

It is important to note that the presence of competition, its neutralization or reversal are evaluated by computing correlations across pairs. We cannot infer whether competition between memory of any *one* AB pair was resolved with memory of its corresponding BC pair. The way we have structured our analyses should be viewed in terms of working on the assumption that, for example *more cases* for which both pairs are remembered reflect resolution of interference than cases for which one, but not the other, pair is remembered. No different than other contrast-based analyses of neuroimaging data, the results should be viewed with this limitation in mind. If two conditions in a contrast were truly sampling from a single distribution and differed only due to random noise, the contrast would usually

[2] In the familiar AB/AC procedure, earlier- and later-studied pairs would correspond to AB and AC, respectively, but in the current paradigm, pairs could appear in any order (i.e., LA could just as likely precede AB in our example).

be non-significant.

Psycho-Physiological-Interaction analyses. As a follow-up analysis, we conducted four Psycho-Physiological-Interactions (PPI; Friston et al., 1997) analyses using the results of the second level resolution contrast, namely, left and right angular and mid frontal gyri (from Fig. 6b) as seeds (thresholded $p < 0.05$, corrected) and compared coupling during resolution (condition 1) with retro- and proactive interference (condition 2 and 3). Parameter estimates of the individual PPIs were tested on the second level using a one-sample t-test. Because we did not *a priori* select which areas to use as seed regions, these PPIs should be viewed as exploratory.

Trial-to-trial variability: multi-voxel and single-voxel effects related to visual perception and reactivation

Whereas the analyses just described identify changes in mean activity across conditions, the following set of analyses identify activity that varies across trials within-condition. Our first question was whether we could find convergent evidence in support of the idea that memory of the earlier-studied pair is, in any concrete sense, retrieved (reactivated) during the later-studied pair, as other neuroimaging studies have found. Then we asked whether later reactivation of memory of a pair reactivates the same or different activity (non-overlapping areas) as online processing of the stimuli (Favila et al., 2020).

In order to get activity estimates for each individual trial as input for these analyses, detailed in the following sections, for each trial we created an independent first-level model with one regressor containing only the corresponding trial, i.e., its onset convolved with the canonical hrf, and one for all other trials in that fMRI run (Mumford et al., 2012). Again, six movement regressors were added as nuisance variables, the correction for autocorrelation and a high-pass filter were applied. The t-maps testing the beta of the trial of interest in each model against the implicit baseline was used for the following RSA to reduce the influence of noisy voxels (Dimsdale-Zucker & Ranganath, 2018). To maintain consistency with the other fMRI analyses, we used smoothed single-trial data with the same 6 mm FWHM kernel because it has been shown that that smoothing does not decrease the sensitivity of RSA (Hendriks et al., 2017; Kriegeskorte et al., 2010; Op de Beeck, 2010).

Representational Similarity Analyses. We used RSA to evaluate voxel-pattern similarity between pairs of study trials. In contrast to the previous contrasts and the following single-voxel series of analyses, RSA analyses identify activity that produces a "voxel-pattern," that is, carrying information in the relative weightings across voxels (e.g., Haynes & Rees, 2005; Kriegeskorte et al., 2008) that would traditionally be considered close enough together comprise a single "region."

The first RSA was conducted to identify areas involved in online processing of the objects and the second to identify areas involved in successful reactivation from memory of earlier-studied pairs while studying the later pairs. In both RSAs we employed a whole-brain searchlight approach (radius 5 voxels) and correlated (Pearson correlation across voxels) the resulting vectors of trial-specific t-values across conditions of interest where only t-values of trials within the same run were correlated. These correlation coefficients were averaged after Fisher z-transform and were saved as value for the centre voxel of the current searchlight.

Perceptual processing. With the first RSA we aimed to identify areas involved in processing the objects based on perceptual similarity of the two trials sharing an object.

Therefore, we correlated activity patterns of pairs with one overlapping item (e.g., BC with AB and CD in Fig. 1a) and contrasted these against the correlation of each pair with all other pairs in that run (e.g., BC with DE, LA, EF, etc.; Fig. 1a). The correlation coefficients of both conditions were contrasted in a paired t-test as implemented in SPM12.

Successful reactivation. With the second RSA we aimed to identify areas involved in successful reactivation of the competing pair. The rationale of this RSA was to identify areas where the similarity of activity patterns during encoding of later- and its competing earlier-studied pairs was greater when reactivation was presumed to have taken place versus no evidence of reactivation. These two pairs (e.g., BC and AB in Fig. 1a) share the overlapping item (e.g., B) which will result in the same degree of similarity in all of the 4 Yule's $\mathcal{Q}$ cells. However, only when the competing pair is reactivated during processing the later-studied pair is there additional similarity expected in areas that are involved in processing and reactivation of these pairs (e.g., AB is reactivated during BC-studying resulting in similarity of brain activity with AB). The resulting correlation coefficients in each of the 4 Yule's $\mathcal{Q}$ conditions were contrasted on the second level using SPM12.

Pattern similarity and univariate activity differences. Pattern similarity can be caused not only by distributed patterns of activity but also by univariate activity differences between conditions because a stronger signal in a condition could lead to stronger correlations of their trials (Wagner et al., 2016). To rule out this confound we averaged the activity in spheres (radius 5 voxels) around the peaks identified by the RSAs. First we contrasted this mean activity between conditions to test for differences in univariate activity that would not have survived the correction for multiple comparisons applied to the univariate analyses described above. Then we correlated the individual difference in mean activity between conditions with the individual difference in pattern similarity.

Single-voxel activity correlations across trials. Finally, we conducted single-voxel analogues of the two RSAs. This series of analyses tests for regional activity that might reflect perceptual processing and reactivation regardless of whether that activity produces a "voxel-pattern." If a voxel reflects activity that is reactivated (whether high or low in value), even if there is no difference in mean activity between successful and unsuccessful reactivations, its activity may covary between pairs that are successfully reactivated. For each voxel individually, we correlated activity between the earlier and later pair sharing an item, across such pairings. We contrasted those correlations with correlations across pairings that did not share an item to identify voxels related to perceptual processing. We also contrasted correlations of voxel-activity between pairs sharing an item for which the earlier pair was later recalled versus not recalled, to assess possible reactivation of single-voxel activity. The larger the correlation the more within-condition variability of activity between pairs of trials. This across pair, within condition correlation analysis was done on the single-voxel level but also using a searchlight approach (radius 5 voxels) and averaging the correlation coefficients within the spheres. The resulting correlation maps were contrasted between conditions on the group level as in the RSAs using SPM12.

Statistical significance

Results of all fMRI analyses were considered significant at $p < 0.05$, family-wise-error (FWE) corrected for multiple comparisons across the entire scan volume or within the a priori defined anatomical regions of interest (ROIs). Based on the previous literature ROIs

for the univariate analyses were the hippocampus, precuneus, and vmPFC, for the muli-variate analyses in addition the inferior temporal and fusiform gyri. Bilateral hippocampus, bilateral precuneus, bilateral inferior temporal gyrus (all three sub-sections combined) and bilateral fusiform gyrus were computed from the Harvard-Oxford cortical and subcortical structural atlases. A vmPFC ROI was manually traced on the mean T1 image based on previously published post-mortem data (Mackey & Petrides, 2014) using ITK-SNAP 3.6.0 (Yushkevich et al., 2006).

Results

Behaviour

We first report behavioural results showing that the prior finding of pair-specific competition could be replicated with a pure double-function design (and thus, twice as many double-function pairs per list as in the mixed lists used by Caplan et al., 2014), with particular attention to whether associative interference is present, rather than being largely resolved. We also examined whether there was a predominance of proactive or retroactive interference in the behavioural data. Accuracy was in the middle of the allowable range (Fig. 3), comfortably far from ceiling and floor, conducive to examining modulation of accuracy by competing pairs. There was little effect on accuracy of test position (Fig. 3a) or direction (Fig. 3a,b), replicating symmetry of mean cued-recall accuracy (Asch & Ebenholtz, 1962; Kahana, 2002). Next, consider that each item was used as a recall cue just once, but two responses were collected. This means that for a single pair, BC, the outcome of forward cued recall of BC can be evaluated by checking whether the participant produced C in response to B as the cue. Backward cued recall is evaluated on a different test trial: given C as the cue, did the participant produce B as one of the responses? Tallied in this way, the correlation of forward and backward recall of individual pairs was high; $Q = .87$ (SEM interval: [–.017, +.015]), extending previously observed associative symmetry (e.g., Caplan, 2005; Kahana, 2002; Rizzuto & Kahana, 2001; Sommer et al., 2007; Sommer et al., 2008) to pairs of pictures. More importantly this shows that associative symmetry holds even in the presence of heightened competition (Caplan et al., 2014; Rehani & Caplan, 2011). Thus, we can safely collapse over test position and test direction in the remaining analyses. There were large effects of serial position on accuracy (Fig. 3b). However, plotted differently, Fig. 3c shows that the driving factor was not serial position, but rather, the amount of interference present while the pair was studied. Pairs that were presented before either constituent item had been studied were most accurate, followed by pairs for which one, but not the other item had been seen, and the lowest accuracy for pairs for which both items had previously appeared in other pairs. In other words, proactive interference is a major source of variability in accuracy in this task. Fig. 3d shows the breakdown of accuracy as a function of cell within the contingency table from which $\mathcal{Q}_{\text{same}-\text{probe}}$ is computed (Fig. 1c), i.e., between the earlier-studied and later-studied of two pairs sharing an item. The first and fourth conditions are cases where both pairs are recalled or both pairs are not recalled, respectively. The middle conditions indicate competition between memory for the two pairs. Inspection of those middle bars shows that it was more common for the earlier-studied pair to be remembered at the expense of the later-studied pair, than the other way around. Consistent with Fig. 3c, proactive interference was more common than

retroactive interference.

Analyses of the interference-related Yule's $\mathcal{Q}$ values (Fig. 4, explained in the Methods section and illustrated in Figs. 1 and 2) confirmed the presence of direct competition between pairs sharing an item. Namely, both $\mathcal{Q}_{\text{same-probe}}$ and $\mathcal{Q}_{\text{distinct-probe}}$ were significantly below $\mathcal{Q}_{\text{control}}$ ($t(29) = -6.57$, $p < 0.0001$ and $t(29) = -5.28$, $p < 0.0001$, respectively), replicating Caplan et al. (2014). $\mathcal{Q}_{\text{same-probe}}$ was also significantly more negative than $\mathcal{Q}_{\text{distinct-probe}}$, $t(29) = -3.25$, $p = 0.0029$, a novel finding suggesting the presence of both simultaneous competition at time of test between two candidate target items, and a competitive relationship between memory for the pairs, themselves.

The conceptual replication of the negative correlation between overlapping pairs extends the boundary conditions for this result. Modelled on the task used by Caplan et al. (2014), our paradigm differed in several ways: 1) The stimuli were drawings of objects instead of words. 2) Recall was vocal rather than typed. 3) To maximize data-yield to support the analyses of interest, we omitted single-function pairs and doubled the number of double-function pairs. Despite all these changes, recall of pairs sharing an item was negatively correlated, indicating that as in Caplan et al. (2014), pairs competed directly in memory. The correlation was significantly negative (differing from behavioural findings from associative interference paradigms as described in the introduction), but not as negative as possible (–1). This satisfied the initial conditions we sought: associative interference was present, and partly, but not completely resolved by the time memory was tested.

fMRI results: overview

As described in the methods, the first-level model included 8 regressors of interest (earlier- versus later-studied pair × 4 memory-outcome conditions corresponding to the quadrants of the Yule's $\mathcal{Q}$ table; Fig. 1c). Isolating activity during earlier-studied pairs identifies activity during encoding that results in either proactive interference (only the current but not the later-studied pair will be remembered) or in resolution of interference of the current pair with the later-studied pair (both associations will be remembered). Activity during encoding of later-studied pairs (similar to AC in classic paradigms) can be related to either proactive interference of the earlier studied pair, retroactive interference of the current pair, or resolution with the earlier-studied pair. We first report analyses of activity during the earlier-studied pair and then during the later-studied pair.

The order of the regressors representing the 4 Yule's $\mathcal{Q}$ conditions was always 1) current and competing pair remembered, 2) only current pair remembered, 3) only competing pair remembered, 4) neither pair remembered. In the text, because our main analyses are restricted either to the earlier- or to the later-studied pair, we use shorthand, noting only the first four (earlier-studied) or last four (later-studied) regressors.

It should be borne in mind that the following contrasts are not designed to be mutually exclusive, but rather, to identify particular relationships of regional activity to the task. As we will note, when a region appears in one contrast, whether it does or does not appear in another one may further specify its putative role in the task.

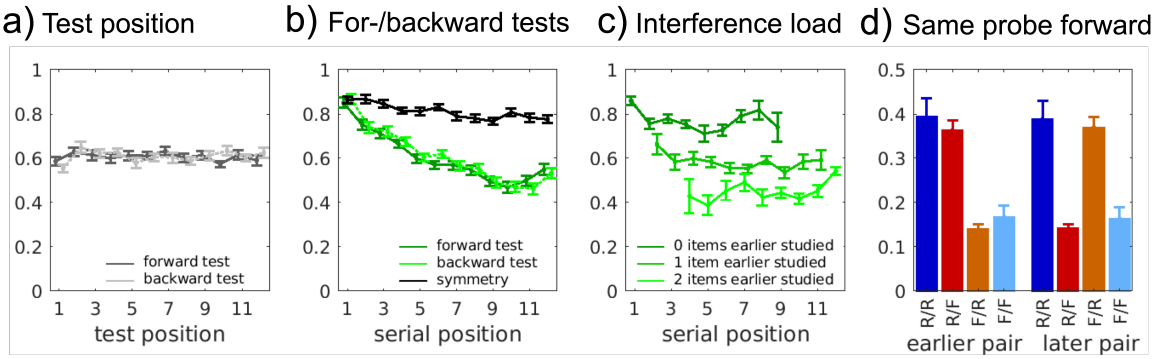

Figure 3

(a) Accuracy as a function of test position and probe direction, illustrating null effects of both factors. (b) Accuracy as a function of serial position and probe direction, as well as 'symmetry,' referring to the proportion of pairs for which either both directions were correct or both were incorrect. This illustrates that recall was largely symmetric, and serial position is a major factor. (c) Accuracy as a function of number of items within the pair previously studied (challenge due to interference) and serial position, showing that the steep serial-position effects in panel b are largely explained by the repetition of items. (d) Accuracy broken down by cell of the contingency table from which $\mathcal{Q}_{\text{same-probe}}$ *is computed. The high rates in the R/F and F/R outcome-conditions are responsible for the negative correlation. The predominance of R/F in the earlier pair and F/R in the later pair shows that the majority of the competition is proactive interference; the earlier pair is remembered at the expense of the later pair. The colours of the bars corresponds to the cells in Fig. 1c.*

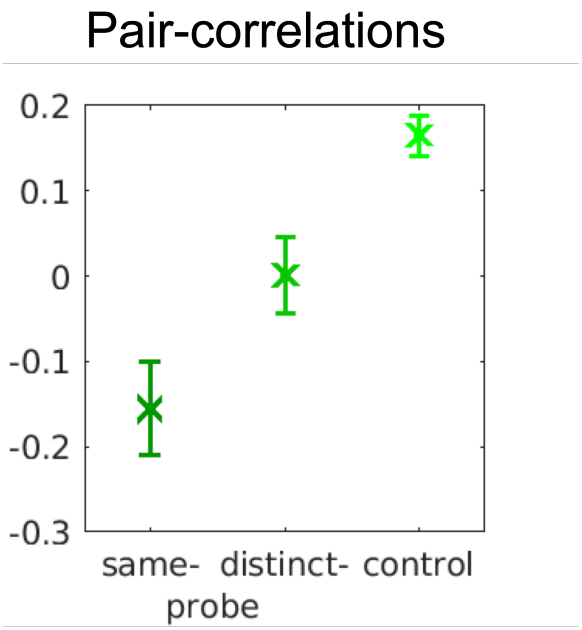

Figure 4

Correlations between pairs of pairs using response accuracy from a single cued-recall probe (same-probe) or from distinct probe trials (distinct-probe). Control is a bootstrap, controlling for independence by estimating the correlation due to list-to-list variability in accuracy. (See text for more detail.)

fMRI results: Activity during encoding of earlier-studied pairs

Subsequent memory of the earlier-studied pair. Before delving into effects specifically related to interference and its resolution, we conducted a simple subsequent-memory effect analysis, to identify the "basic" encoding regions. We identified areas showing a general subsequent memory effect for the current (earlier-studied) pair irrespective of memory for the competing (later-studied) pair by the contrast [1 1 –1 –1]. A set of regions comprising bilateral anterior hippocampus, vmPFC and visual areas showed a robust subsequent memory effect (Table 1, 'encoding').

Activity related to proactive interference. To identify areas where activity during encoding of the current pair resulted later in interference with the competing pair, i.e., that showed greater activity when the current pair was remembered but the competing pair was not remembered, the contrast [–1 2 –1 0] was applied. The case of both pairs forgotten was omitted from this contrast because it is ambiguous whether such cases are due to a failure of a resolution attempt or that one or both associations were individually not remembered. Regions within posterior hippocampus on both sides showed this effect (Table 1, 'interference', and Fig. 5a), suggesting that particular hippocampal-dependent

study processes produce a memory that eventually will compete with encoding of the later-studied pair. The inferior frontal and lingual gyri also showed this effect.

Following up on these findings, the contrast [–1 1 0 0] specifically tests for greater activity when only the current, and not both pairs, will be remembered. Only a right posterior hippocampal region showed this effect. We did not observe any areas showing activity related to retroactive interference from the later studied competing pair (contrast [–1 –1 2 0] as well as [0 –1 1 0]), consistent with the small corresponding behavioural effect (Fig. 3d).

Activity related to proactive resolution. Next, we ask if there is any activity present during processing the earlier-studied pair that later results in resolution with the competing pair (Table 1, 'resolution', and Fig. 5b), testing our third hypothesis about the cause of resolution. The contrast [2 –1 –1 0] isolates activity associated with both pairs being subsequently remembered, versus only one pair remembered but not the other. Again, hippocampal subregions bilaterally, most extensively in the anterior subdivision, showed greater activity during successful encoding of the earlier-studied pair when the later-studied competing pair was also successfully remembered. Numerous other regions, most importantly the vmPFC and ventral precuneus, showed a similar pattern of activity.

Following up on these findings, the contrast [1 -1 0 0] specifically tests for greater activity when both pairs were remembered versus the current pair remembered but the (later-studied) competing pair not. In other words, given that the current pair was remembered, was the competing pair also remembered or not? This contrast also isolates resolution-related brain activity during study of the earlier of the two pairs. Anterior hippocampus, vmPFC and precuneus were also found in this contrast.

fMRI results: Activity during encoding of later-studied pairs

Paralleling the analyses of the earlier-studied pairs, we first tested, for the later-studied pairs, which brain areas show a simple subsequent-memory effect contrast [1 1 –1 –1]), which revealed a set of regions comprising the supramarginal, middle temporal and fusiform gyri but not the hippocampus (Table 2, 'encoding'). However, this might be simply an effect of lower power because there was less successful encoding of the later-studied pairs, in particular whereas the proportions of later-studied pairs in the first regressors (Yule's $\mathcal{Q}$ cell 1) was similar to the earlier-studied pairs (Fig. 3d) there were substantially fewer in the second regressor due to proactive interference. Moreover, this contrast confounds interference effects with subsequent-memory effects, as we shall see below when we seek activity related to encoding or "re-encoding of earlier and encoding of later-studied pair."

Activity during the later-studied pair that might reflect memory of the earlier-studied pair. Next, we looked for regions that might reflect retrieval of the earlier-studied pair during study of the later pair (although this should be viewed not as conclusive; for convergent evidence, see the follow-up correlational analyses below). Areas that showed a reactivation-like pattern of activity were identified by the contrast [1 –2 1 0], on the logic that if the earlier pair was remembered while studying the later pair, it is more likely to be recalled correctly during the subsequent memory test than if the earlier pair were not remembered during the later pair. Moreover, reactivation offers more encoding time to the earlier pair, which should also increase the probability that the earlier pair would later be recalled. Regions showing this pattern included the the vmPFC, precuneus,

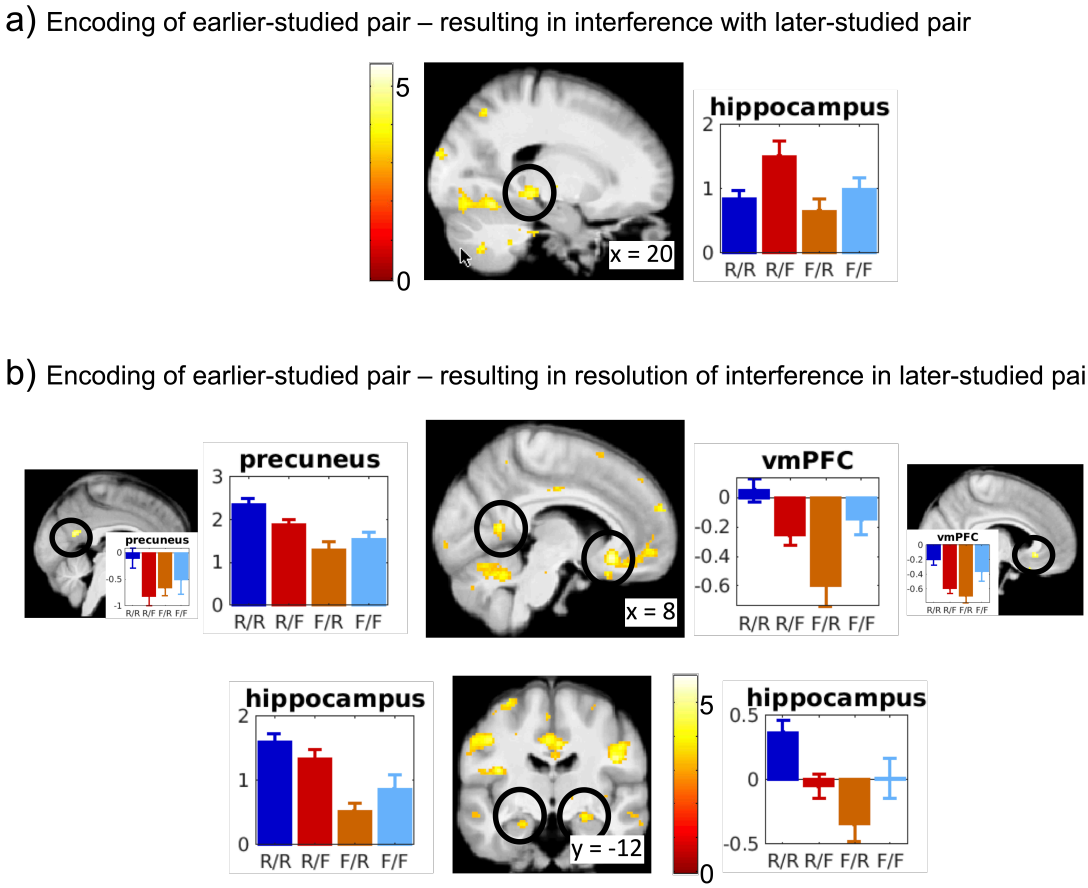

Figure 5

fMRI activity during encoding of earlier-studied pairs. (a) Among other areas (Table 1) activity in the bilateral posterior hippocampus during processing of earlier-studied pairs resulted in interference with the later-studied competing pair as identified by the contrast [–1 2 –1 0]. (b) Activity in the anterior hippocampus, vmPFC and precuneus (and other areas) during processing of the earlier-studied pairs resulted in resolution with the later encoded competing pair. The large plots of the parameters estimates of the four conditions reflect activity in the peak identified by the contrast [2 –1 –1 0]. The colours of the bars corresponds to the cells in Fig. 1c. The small plots of parameter estimates inserted in the precuneus and vmPFC represent activity in subregions showing also specifically greater activity when both pairs were remembered compared to when only the earlier-studied pair was remembered, i.e., [1 –1 0 0]. Statistical maps are overlayed on the mean normalised structural image of the participants. Visualisation threshold $p < .001$. Activity on the y-axis is in arbitrary units. Circles surround the local maxima from which activity is plotted. In these contrasts, the current pair is the earlier-studied pair and the competing pair is the later-studied pair.

contrast	area	xyz-coordinates	Z-value
encoding	anterior hippocampus	–20 –10 –18	4.73
[1 1 –1 –1]		22 –10 –18	4.11
	vmPFC	0 36 –24	5.29
		4 54 –6	4.51
	fusiform/lingual/inferior	22 –86 –10	7.40
	occipital gyri	–36 –74 –16	6.43
	temporal pole	40 6 –42	5.51
	middle cingulate gyrus	–2 –10 38	5.02
	superior temporal gyrus	–52 –20 –8	5.26
interference	lingual gyrus	8 –92 –10	5.37
[–1 2 –1 0]	posterior hippocampus	–20 –34 –6	3.76
		24 –40 2	4.43
		20 –32 –6	4.12
	inferior frontal gyrus	–54 12 6	5.14
[–1 1 0 0]	posterior hippocampus	24 –40 2	3.93
resolution	vmPFC	8 24- -12	5.21
[2 –1 –1 0]		–2 50 2	4.64
	posterior hippocampus	30 -26 -16	4.72
	anterior hippocampus	22 –12 –16	3.76
		–20 –10 –20	3.84
	precuneus	8 –54 10	4.39
	insula	–40 2 12	5.58
		–34 8 –10	5.42
	orbitofrontal cortex	–28 16 –24	5.33
	postcentral gyrus	–36 –28 54	4.96
	precentral gyrus	46 –8 24	5.29
	cerebellum	12 –56 –26	5.49
[1 –1 0 0]	vmPFC	6 26 –8	3.85*
	posterior hippocampus	–30 –24 –16	3.50*
	precuneus	–2 –56 20	3.74*

Table 1

*fMRI results during encoding of the earlier-studied pairs. xyz-coordinates of the peaks of clusters in MNI space. Correction for multiple comparisons was done on the whole-brain level or within pre-defined anatomical regions of interest, specifically the vmPFC, bilateral anterior hippocampus and precuneus. In the contrasts, the regressors are: 1) current (earlier-studied) and competing (later-studied) pair remembered, 2) only current pair remembered, 3) only competing pair remembered, 4) neither pair remembered. When two contrasts are listed for the same named contrast (here, 'interference' and 'resolution'), the contrasts should not be viewed as independent, but rather, the second as a follow-up refinement of the first, to test the robustness of the results. *trend toward significance* $p < .1$.

contrast	area	xyz-coordinates	Z-value
encoding	supramarginal gyrus	36 –34 40	5.29
[1 1 –1 –1]		-58 –36 34	5.77
	middle temporal gyrus	–56 –56 4	5.13
	temporal pole	–38 6 –38	5.04
	fusiform gyrus	30 -62 -6	4.89
reactivation	vmPFC	–2 32 2	4.47
[1 –2 1 0]		8 52 –12	4.30
	precuneus	4 –62 26	6.43
	angular gyrus	–40 –72 34	5.03
	thalamus	–4 –12 –6	5.53
	middle frontal gyrus	30 4 56	5.05
interference	vmPFC	–6 36 –2	4.50
[–1 –1 2 0]	precuneus	–8 –70 28	6.46
		12 –66 30	5.15
	ventral striatum	–16 6 –10	4.65
		24 10 -8	5.01
[–1 0 1 0]	precuneus	–8 –72 30	3.82*
		12 –68 30	3.75*
(re-)	posterior hippocampus	–28 –38 –6	3.74
encoding		34 –30 –6	3.92
[1 1 1 –3]	middle temporal gyrus	–50 –52 6	5.04
resolution	precuneus/	4 –62 26	4.59
[2 –1 –1 0]	posterior cingulate	–12 –48 26	5.64
	middle frontal gyrus	22 4 48	6.19
		–36 16 48	5.29
	angular gyrus	–46 –64 20	5.73
	temporal pole	58 8 –24	5.09
[1 -1 0 0]	precuneus/	4 –62 26	6.28
	posterior cingulate	–12 –56 24	5.18
	middle frontal gyrus	24 2 50	5.74
		–14 22 56	5.13
	angular gyrus	–46 –64 20	5.16
		40 –68 32	4.93
	temporal pole	58 8 –24	5.12

Table 2

*fMRI results during encoding of the later-studied pairs. xyz-coordinates of the peaks of clusters in MNI space. Correction for multiple comparisons was done on the whole-brain level or within pre-defined anatomical regions of interest, specifically the vmPFC, bilateral hippocampus and precuneus. In the contrasts, the regressors are: 1) current (later-studied) and competing (earlier-studied) pair remembered, 2) only current pair remembered, 3) only competing pair remembered, 4) neither pair remembered. When two contrasts are listed for the same named contrast (here, 'interference' and 'resolution'), the contrasts should not be viewed as independent, but rather, the second as a follow-up refinement of the first, to test the robustness of the results. *trend toward significance* $p < .1$.

middle frontal and angular gyri (Table 2, 'reactivation'). Because these analyses measure the amount of activity increase rather than the information-content of that activity, this set of putative 'reactivation' regions might reflect neural processes that evoke reactivation rather than the reactivated information, itself, which might be housed elsewhere. The RSA analyses will show some convergent support for this latter interpretation.

During study of a later pair, retrieval of the earlier pair could result either in interference with the current encoding or in resolution of interference, which we target in the next contrasts. Regions that appear in the current 'reactivation' contrast and the 'interference' contrast are candidate regions for introducing interference via reactivation. Likewise, regions that appear in the current 'reactivation' contrast and the 'resolution' contrast are candidate regions for resolving interference by acting on memory of the earlier pair.

A potential cause of proactive interference. We next asked if there is any activity present during processing the later-studied pair that reflects proactive interference from the earlier-studied pair (Table 2, 'interference,' and Fig. 6a). We applied the contrast [–1 –1 2 0] to identify areas where only the competing but not the current pair will be remembered, excluding the ambiguous case where both pairs are forgotten. In addition to the vmPFC and precuneus that also showed reactivation-like activity patterns, the bilateral ventral striatum showed greater activity when only the competing, earlier-studied but not the current pair was successfully encoded. Very similar precuneus regions also appeared in a follow-up contrast, [–1 0 1 0], although not reaching significance ($p < 0.1$), contrasting only the competing pair recalled versus both pairs recalled.

We pause here to emphasize how remarkable it is that precuneus, vmPFC and ventral striatum regions showed such robust activity differences that were primarily due to memory for a pair studied at an entirely different time in the study phase. This is compellingly consistent (although not conclusive) with the idea that these regions retrieve prior memories but if there is too much reactivation, this risks leaving little opportunity to resolve those retrieved memories with the current pair. Convergent evidence for the presence of reactivation is reported below, in the trial-to-trial correlational analyses. We did not observe any region where activity related to retroactive interference on the competing, earlier-studied pair (contrast [–1 2 –1 0]).

Resolution of the earlier-studied pair with the current later-studied pair. Next, we isolated areas where reactivation of the competing, earlier-studied pair resulted not in interference but possibly resolution with the currently processed pair (Table 2, 'resolution' and Fig. 6c). As with the earlier-studied pairs, the contrast [2 –1 –1 0] was used, contrasting both pairs recalled versus only one recalled. The precuneus/posterior cingulate as well as the middle frontal and angular gyri were active during probable resolution of interference. These regions also exhibited the simpler, follow-up contrast, [1 –1 0 0], both pairs recalled versus the current pair forgotten but the competing pair recalled. Our first resolution hypothesis, that the hippocampus produces resolved associations, was not supported (although it is possible that a hippocampal effect is present but under-powered). Rather, our second (although not mutually exclusive) resolution hypothesis was supported, namely, non-hippocampal regions more plausibly produce resolved associations.

Of the four PPIs, using the left and right angular and mid-frontal gyri as seed regions, only one reached significance individually ($p = .014$, $Z = 4.30$; but after a Bonferroni-correction, was only a trend). This was characterized by the left mid-frontal gyrus seed

region exhibiting stronger coupling with the precuneus during integration than interference ([–8 –50 36], arrow in Fig. 6c).

Re-encoding of earlier and encoding of later-studied pair. The suspected presence of reactivation raises the possibility that the earlier, retrieved pair could be encoded during study of the later pair, or both could be encoded at that time. We wondered if activity in the hippocampus might reflect this associative encoding, where sometimes the current (later-studied) pair is encoded, other times the competing pair (earlier-studied, retrieved during the current trial) is instead being encoded, or both. We collapsed together trials for which either the current or competing pair was correct, and contrasted those with trials for which both pairs were forgotten (Table 2, '(re-)encoding', and Fig. 6c). In other words, the contrast [1 1 1 –3] expresses the idea that activity in a particular brain region might reflect the total amount of encoding occurring, whether it is devoted exclusively to the current pair, exclusively to the (reactivated) competing pair, or split somehow between the two. A region within the posterior hippocampus on each side had an activity profile very much like this, as well as a region within the middle temporal gyrus. Thus, posterior hippocampal and middle temporal activity during the later-studied pair could reflect encoding of whatever is in mind— the current or competing pair or potentially both. It is interesting that anterior regions of the hippocampus showed neither the "naïve" subsequent-memory effect, nor this (re-)encoding effect during the later-studied pair.

Trial-to-trial variability analyses of fMRI: convergent evidence of reactivation

The set of regions that we identified with the 'reactivation' contrasts is consistent with the idea that reactivation occurs, but the link to this interpretation is still quite indirect. If reactivation is, in fact, taking place, then as in previous studies, we should be able to observe some similarity in brain activity between the earlier- and later-studied pairs when reactivation presumably succeeded. The regions identified in the previous contrasts more likely reflect control processes that identify the repetition, initiate or retrieve the information, rather than the information-content of the reactivated memory, itself. In fact, it is also possible that those 'reactivation' regions enhance later memory of the earlier-studied pair completely apart from any putative reactivation. Here we ask if we can obtain more concrete evidence that the earlier pair is sometimes remembered during study of the later pair? Namely, is there similarity of brain activity between earlier- and later-studied pairs that might reflect the memory that is first constructed and then later remembered? (See, for example, Koen and Rugg, 2016; Lee et al., 2011; Staresina et al., 2013 for this approach). And coupled to this: what is, in fact, reactivated? To tackle this question, we focused on a hypothesis from Favila et al. (2020), that reactivated information is different (non-overlapping regions) than online perceptual processing of the stimuli. In other words, what the participant remembers is at a different level of representation, presumably higher-order, than visual-processing of the object-pairs.

We therefore conducted analyses seeking brain activity that reflected the hypothetical reactivation, itself (described in the Methods). That is, we sought activity patterns, as well as individual voxels, that were common to the earlier and later pair sharing an item, when the earlier pair was subsequently remembered (presuming successful reactivation) versus not (less successful reactivation). We compared this to a control analysis that identified similarity of activity due to the common item being visually processed during both pairs.

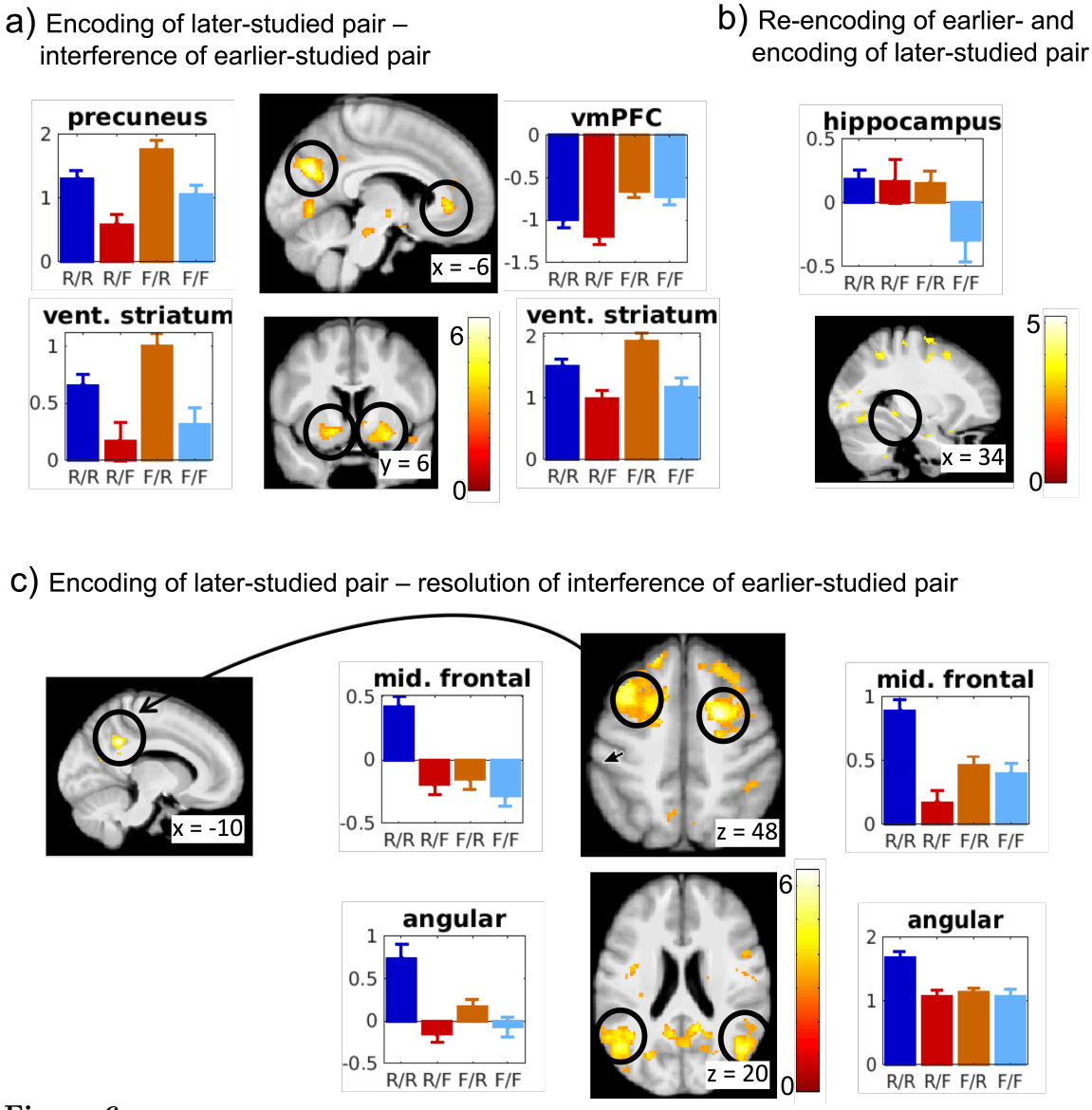

Figure 6

fMRI activity during encoding of later-studied pairs. (a) Activity in the vmPFC, precuneus and striatum during processing of later-studied pairs resulted in interference by the earlier-studied competing pair as identified by the contrast [-1 2 -1 0] (Table 2). (b) The hippocampus was involved when either the presumably reactivated competing pair, the current pair or both were (re-)encoded. (c) Activity in the middle frontal and angular gyri as well as the posterior cingulate showed greater activity if the competing earlier-studied pair was successfully resolved. The arrow in (c) illustrates the higher coupling of the left mid-frontal gyrus with precuneus during interference-resolution than interference (this exploratory PPI reached a trend toward significance when corrected for the 4 possible seeds shown in panel c). The large plots of the parameters estimates of the four conditions reflect activity in the peaks. The colours of the bars corresponds to the cells in Fig. 1c. Statistical maps are overlayed on the mean normalised structural image of the participants. Visualisation threshold $p < .001$. Circles surround the local maxima from which activity is plotted. In these contrasts, the current pair is the later-studied pair and the competing pair is the earlier-studied pair.

Representational Similarity Analysis. The maxima of the perceptual similarity RSA were in the inferior occipital ([–42 –88 –2], $Z = 5.82$; [46 –80 –6], $Z = 4.97$) and fusiform gyri ([–34 –54 –16], $Z = 4.80$; [40 –54 –16], $Z = 5.11$) where the fusiform cluster were the most anterior (Fig. 7a). This establishes the set of regions showing pattern-similarity likely due to visual processing of the item that was common between the earlier- and later-studied pair.

Reactivation was tested as in the univariate analyses with the contrast vector [1 –2 1 0]. This revealed a cluster in left inferior temporal gyrus ([–52 –32 –22], $Z = 4.42$) and vmPFC ([–4 40 –24], $Z = 3.96$; Fig. 7b). Thus, the reactivation regions were further in the ventral visual pathway, and did not include those whose voxel-patterns reflected visual processing of the shared stimuli, similar to Favila et al. (2020).

To test whether the reactivation RSA results were driven by univariate differences effects we first contrasted mean activity in the spheres around the peak voxels identified by the RSA between conditions 1 and 3 with condition 2. Second, we correlated the individual differences between these conditions with the corresponding differences in similarity (Wagner et al., 2016). (Note that this control analysis of mean activity within spheres is not sensible for the perceptual similarity RSA because of the fact that all trials are in both conditions lead to equal mean activity in both conditions.) In the inferior temporal gyrus, mean activity showed a trend toward a significant difference between conditions ($t(30) = 1.55$, $p = .065$), and this difference did not correlate with the individual difference in similarity between conditions ($r = .094$, $p = .612$). In the vmPFC a similar pattern emerged, namely, a trend toward a significant difference between conditions ($t(30) = 1.43$, $p = .082$) and no correlation of the individual differences with similarity difference ($r = .274$, $p = .136$).

Single-voxel correlations in activity across trials. For the perceptual similarity analysis the searchlight approach resulted in a very similar set of regions as the perceptual similarity RSA, i.e., bilateral early visual cortex (calcarine [–14 –96 –8], Z = 5.52; inferior occipital gyrus [–50 –72 –2], $Z = 5.72$; [52 –72 –2], $Z = 6.26$) and fusiform gyrus ([–32 –48 –10], Z = 3.73; [24 –46 –12], $Z = 4.56$) and in addition, the precuneus ([–6 –54 10], $Z = 4.09$). Without the searchlight, the single-voxel analysis produced less smooth results but were otherwise similar, also identifying the early visual cortex ([–12 –94 –8], $Z = 6.09$; [20 –88 –8], $Z = 5.87$) and the fusiform gyrus ([–28 –44 –12], $Z = 4.10$; [30 –40 –14], $Z = 4.58$).

For the reactivation analysis the searchlight approach converged with the RSA analysis, revealing clusters in the left inferior temporal gyrus ([–54 –32 –24], $Z = 3.35$; and vmPFC ([–4 34 –26], $Z = 4.34$). Without the searchlight, the single-voxel analysis also identified the left inferior temporal gyrus ([-54 –38 –24], $Z = 3.16$) and vmPFC ([0 34 –20], $Z = 3.4$). However, those clusters were not significant after correcting for multiple comparisons.

Thus, both distributed patterns (RSA analyses) and regional activity (single-voxel correlations) reflect pair-specific activity that is present during study of the earlier pair and then reactivated during study of the corresponding later pair. The regions showing these effects are different and higher-order than those reflecting perceptual processing of the displayed stimulus.

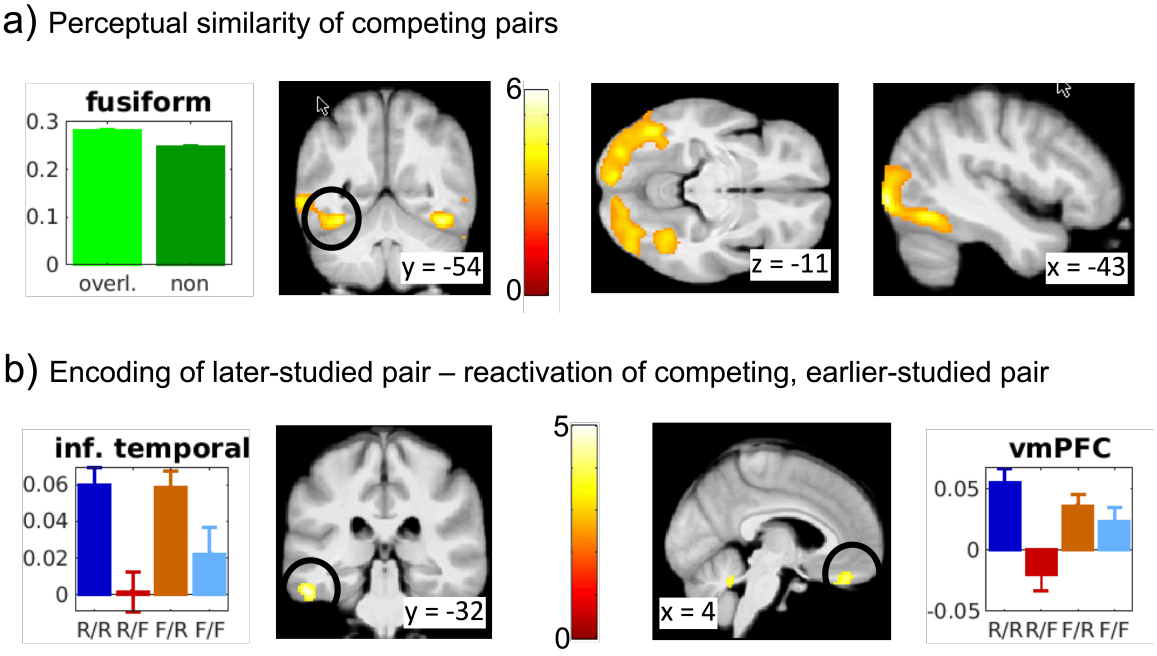

Figure 7

Representational similarity analysis. The measure (y axis and color scale) is similarity (Fisher z-transformed correlation coefficients). Note that the absolute values of the correlation coefficients cannot be directly interpreted, for instance the nearly zero correlation in condition 2 (R/F) in panel b does not necessarily mean that the patterns do not show any similarity (Dimsdale-Zucker & Ranganath, 2018). (a) Similarity greater between pairs sharing an item than pairs with no shared items. This presumably reflects similarity in visual-perceptual processing of the stimuli, caused by the common item. (b) For pairs sharing an item, similarity greater when the earlier pair was later remembered than when it was later forgotten, regardless of whether the later pair was recalled. This is presumably caused by memory of the earlier pair while studying the later pair, which results in additional encoding of the earlier pair. Note that the color coding in the bar graphs corresponds to that in the contingency tables in Fig. 1c.

Discussion

With the first behavioural paradigm in which participants are challenged by pair-specific associative interference but cannot fully resolve it, we identified neural processes that explain how competition between associations materializes, and how it can be overcome. We review these main findings and discuss how they dovetail with findings from prior studies in which pair-specific interference has been largely resolved.

The origin of associative interference. A rare feature of our paradigm, offering access to brain activity throughout the study phase, is that it allows us to follow proactive interference-related activity from the earlier-studied pair to the later-studied pair. Our first hypothesis, that simple competitive retrieval based on encoding strengths is the source of interference, was not supported; brain regions that led to good memory for the earlier-studied pair ('encoding' contrast in Table 1) did not show interference effects ('interference' contrasts). Consistent with the established importance of the hippocampus for associative memory (e.g., Caplan & Madan, 2016; Cohen et al., 1997; Davachi, 2006; Eichenbaum et al., 2007; Konkel & Cohen, 2009; Mayes et al., 2007; Nadel & Moscovitch, 1997; O'Keefe & Nadel, 1978; Rudy & Sutherland, 1989; Rudy & O'Reilly, 2001; Saksida & Bussey, 2010), hippocampal regions were associated with subsequent memory of the earlier-studied pair. However, different hippocampal subregions (more posterior) were related to future associative interference.

Instead, our second hypothesis was supported; the primary source of interference appeared to be retrieval of the earlier-studied pair while studying the later-studied pair. This echoes neuroimaging findings on pairs with repeated items. This includes associative interference paradigms for which pair-specific interference had been largely successfully resolved (e.g., Horner et al., 2015; Kuhl et al., 2011; Kuhl et al., 2010; Richter et al., 2016), as well as associative inference paradigms, where the participant's explicit goal is to combine information from both component pairs to answer inference questions (e.g., van Kesteren et al., 2020; Zeithamova & Bowman, 2020; Zeithamova et al., 2012; Zeithamova & Preston, 2010) and confirms behavioural evidence of such retrieval occurring in the one-list double-function paradigm (Caplan et al., 2014). Specifically, high activity in posterior hippocampus (Fig. 5a), with insufficient activity in vmPFC, precuneus and anterior hippocampus (Fig. 5b), lay the basis for interference with the later-studied pair.

During later-pair processing the 'reactivation' and 'interference' contrasts share regions with nearby peaks in a set of regions comprising vmPFC, precuneus and striatum (Table 2, Fig. 6). Precuneus and striatum have been implicated in memory retrieval (Clos et al., 2015; Huijbers et al., 2012; Schwarze et al., 2013). While studying the later-presented pair, right precuneus, along with bilateral vmPFC, left angular gyrus and thalamus and right middle frontal gyrus, were associated with good memory for the earlier-studied pair, regardless of memory of the current pair. This is remarkable, because the contrast completely omits brain activity during initial study of the earlier-studied pair.

Aligning these results with those from the interference contrast (later-studied pair), a left-sided vmPFC region and the right precuneus region recur in the interference contrast with nearby peaks. Although speculative, this pattern of findings reinforces our previous suggestion that strong encoding of the earlier-studied pair in posterior hippocampus together with weak encoding in the vmPFC-precuneus-anterior hippocampus might result in

subsequent reactivation via the striatum and precuneus that reduces encoding of the later, competing pair (cf. Long & Kuhl, 2019).

Resolution of interference. As with the origin of interference, our paradigm also allows us to track processes supporting resolution of interference across time, from the earlier- to the later-studied pair. Our first hypothesis, extrapolating from transitive/associative inference (e.g., Bunsey & Eichenbaum, 1996; Dusek & Eichenbaum, 1997; Heckers et al., 2004; Horner et al., 2015; Preston et al., 2004; Zeithamova et al., 2012), that the hippocampus supports successful resolution of the two pairs was unsupported. Perhaps the hippocampus was implicated in prior inference tasks for its role in supporting memory of the component associations (A→B and B→C), enabling a chained retrieval solution to the inference, or supporting encoding of the inferred A→C association during the B→C trial (Koster et al., 2018), without necessarily resolving any competition.

Our second hypothesis was supported. While reactivation can produce interference, if there is not too much reactivation, the participant might sometimes use extra-hippocampal processes (Fig. 6c) to resolve competition between the two co-activated associations, potentially producing facilitation between the memory for the two pairs (Burton et al., 2017; Jacoby & Wahlheim, 2013; Kuhl et al., 2010; Wahlheim & Jacoby, 2013; Wahlheim et al., 2014). Evidence for this can be seen in regions that appeared in both the 'reactivation' and 'resolution' contrasts (Table 2), which include a region within right precuneus, middle frontal and angular gyri. Consistent with this, it is interesting that the activity level when both pairs were recalled (Fig. 6a, R/R condition) was not the highest, but actually lower than when only the earlier (competing) pair was remembered and greater than when only the later (current) pair was remembered. Thus, if activity in the precuneus reflects the total amount of retrieval of the earlier pair while studying the later pair, this suggests that too much reactivation leaves too little opportunity for mid frontal and angular gyrus to resolve interference. The angular gyrus has been linked to integration and retrieval of supramodal complex semantic knowledge (Gilboa & Marlatte, 2017) and multimodal feature integration during episodic retrieval (Bonnici et al., 2021). The computations of the angular gyrus, as part of a wider lateral parietal system, enable the online dynamic buffering of multisensory spatiotemporally extended representations (Humphreys et al., 2021; Xie et al., 2019). The mid-frontal gyrus has been implicated in attention (Bourgeois et al., 2022), which may be this region's specific role in resolving interference here.

Finally, our third hypothesis, which we were for the first time able to investigate, was supported. That is, activity during the earlier-studied pair apparently set the initial conditions for future resolution of interference. Among the regions that exhibited this effect ('resolution' contrast in Table 1) were vmPFC bilaterally, anterior hippocampus bilaterally and precuneus. Similar regions were identified with the simple 'encoding' contrast. This suggests that (contrary to the first interference hypothesis discussed in the previous section), a well studied pair that is likely to be remembered is also one that has a good chance of being *reconciled with an overlapping association* in the future. This hippocampal activity was during the earlier-studied pair, so it does not reflect the resolution process, itself, but rather, the formation of a memory with favourable properties for future resolution. The role of vmPFC here is consistent with numerous prior studies implicating vmPFC in encoding (Fujiwara et al., 2021) and in forming integrated representations (Gilboa & Marlatte, 2017). But again, vmPFC is not apparently carrying out the resolution, itself, but laying down the

conditions for future resolution by other regions, namely, middle frontal and angular gyri and posterior cingulate, while the later competing pair is studied. Interestingly, an interplay of the vmPFC and hippocampus with the precuneus during encoding has been previously associated with incorporation of novel information into existing schemata (Sommer, 2017; Sommer et al., in press). Liu et al. (2017) found that an advantage for houses associated with famous faces versus non-famous faces was attributable to activity in anterior hippocampus, vmPFC and precuneus activity— similar to what we observed. The famous faces were presumed to provide richer representations to which the houses could be bound. In our task, this same set of regions may similarly provide additional details to the representation of the first pair, making it easier for the later pair to be reconciled with the earlier memory. This is in contrast to posterior hippocampus, which may produce a memorable association that is less amenable to resolution of competition with another pair. Importantly, participants do not simply resolve interference once it materializes, during the later-studied pair. Rather, at least as important, the way in which the earlier-studied pair is processed can be critical for subsequent successful resolution.

Cognitive mechanisms of resolution of interference

Having first identified the source of pair-specific interference and then identified brain activity related to the neutralization, or even reversal, of that interference, we now consider the cognitive processes that the latter activity might reflect.

First we note that the term "integration" arises repeatedly in the associative interference neuroimaging literature, but with several meanings, each of which might be related to the neurocognitive processes we identified here. Integration can refer to the formation of a composite representation of two pairs in memory, such as encoding not just AB and BC, but something like ABC. This is the idea behind instructions to participants to form integrative imagery as a way to resolve interference (e.g., Anderson & Bell, 2001; Anderson & McCulloch, 1999; Burton et al., 2017; Smith & Hunt, 2000). However, such integrated representations in memory are hard, if not impossible, to confirm. Correct recall of both pairs (or even a positive correlation across pairs of pairs; both pairs remembered or both forgotten, Burton et al., 2017) could conceivably result from such an integrated representation, but this kind of result could have other plausible causes. Strictly speaking, the positive correlation only tells us that memory for A_iB_i and B_iC_i have a source of shared variance.

Consider retrieval of the earlier pair while studying the later pair. If the earlier pair is well encoded, it might be retrieved with little effort and rapidly, thus displacing very little encoding time from the later pair. In this way, a highly recallable earlier pair might facilitate encoding and subsequent recall of the later pair without any direct integration. Conversely, a poorly studied earlier pair, itself less likely to be recalled correctly, may require more study time to be recalled, thus also obstructing encoding of the later pair, making it likely that both pairs will not later be recalled. Our findings are somewhat in line with this; hippocampal activity that produced a subsequent-memory effect during the earlier pair was associated with good memory for both pairs.

Second, drawing an analogy to associative inference, resolution and even reversal of interference in our task, when it does occur, might be caused by participants encoding the inferred association, AC, after retrieving the earlier pair while studying the later pair. This could positively couple the two pairs by adding a new retrieval route. Suppose that

given B as a probe, BC were not remembered. If AB was remembered, A could then be used as a retrieval cue for C, via the encoded inferred AC association. Inferring the indirect association might be one role of mid-frontal and angular gyrus activity during the later pair. Then, posterior hippocampal activity, which appears to be an agnostic (re-)encoder during the later pair, could then store the indirect association if it were successfully produced, or else the retrieved earlier association or the current association.

A different notion is that ambiguity between similar stimuli may be addressed in part by changing the representations so that they are more orthogonal, termed "pattern separation" (e.g., Marr, 1971; Norman & O'Reilly, 2003; O'Reilly & McClelland, 1994; Poppenk et al., 2013). Interestingly, Becker (2016) found that resolution of interference was solved by her model by making representations more similar rather than less similar (echoing the effects of strategy found by Burton et al., 2017), but the more general idea that representations may become more distinct (not necessarily orthogonal) when both associations are brought to mind together has been proposed by, for example, Kuhl et al. (2010), Kuhl et al. (2011) and Chanales et al. (2019). Representational Hierarchical Theory, which assumes no special role for the hippocampus in memory, per se, implicates the hippocampus precisely in offering the brain the ability to discriminate stimuli that would be processed as highly similar by more upstream regions (Bartko et al., 2010; Bussey & Saksida, 2002; Cowell et al., 2019; Cowell et al., 2010; Saksida & Bussey, 2010). This could neutralize interference by reducing the similarity-based ambiguity in encoded memories, but it might also reverse interference if the formation of distinctive representations were synergistic, likely to be successful for both pairs or unsuccessful for both pairs. The latter mechanism is, in fact, the antithesis of an integrated representation. The mid-frontal and angular gyrus activity during the later pair, related to success with both pairs, might contribute to distinctive encoding of one or both pairs, that is, however, unlikely to be like pattern separation.

If construction of distinctive representations is the main mechanism of resolution of interference, our findings during the earlier pair suggest that the distinctiveness process can begin even before both pairs are known. The anterior hippocampal and vmPFC activity during the earlier pair might already achieve some distinctiveness, enabling the participant to focus more on forming a distinctive representation of the later pair once it is presented.

This repertoire of possible mechanisms of resolution of interference suggests why our paradigm, in contrast to other associative interference paradigms, leaves some competition unresolved. Associative interference in other paradigms is typically in triad form, such as AB/AC. Constructing an integrated representation, ABC could result in AB and AC both being remembered (or both forgotten). Encoding the inferred, BC association, could result in good memory of both AB and AC. As already noted, assuming AC was not memorable, if the participant can retrieve B with A as a cue, the BC association offers a backup retrieval path to potentially produce C as well. In the three-item loops used by Horner et al. (2015), again, storing ABC or storing all component associations could both produce positive correlations in memory of AB, BC and CA. With our larger ring structure, those approaches may resolve competition in one part of the ring, but at the same time, increase competition in another part of the ring. Suppose the BCD is stored. That may positively correlate memory tests of BC and CD with one another, but it introduces an additional source of competition when testing the pairs AB and DE. Thus, both "integrative" solutions

may explain why our participants can resolve some competition between overlapping pairs, but this reasoning also shows why it may be quite challenging to resolve all interference after only a single exposure to a list.

Forming more distinctive representations is a process that might have a benefit without such a cost. Increasing the distinctiveness of BC from CD will also be likely to increase the distinctiveness of BC from AB. In fact, as just suggested, this might be the mechanism by which activity during the earlier-studied pair increases the chance of resolution of interference, even before the later-studied pair is known.

Convergent evidence of retrieval during study and the nature of retrieved memories

A complementary set of analyses of trial-to-trial variability produced more direct evidence for the presence of reactivation of the memory of the earlier-studied pair while studying the later pair. These analyses also suggested the relevant reactivated information was at a relatively high level of representation, different from more face-value visual processing of the stimuli. To understand the logic here, assume that a region (either a set of individual voxels or a legitimate voxel-pattern) reflects high-order features of memorial representations. Those features might be high in value or low in value, hence no difference is expected in average activity (and would be missed by the simple contrasts). What matters is whether the same value occurs both during the earlier pair and the later pair, when the earlier pair is brought back to mind. For example, suppose region X reflects the amount of vividness of an image constructed to bind two objects together. One stimulus-pair, AB, might be high in vividness; evidence of its reactivation would be high BOLD signal both during presentation of AB and during subsequent presentation of BC. A different pair, DE, might be remembered with verbal rather than imagery mediation. Consequently, BOLD signal in region X would be low during presentation of DE. If X reflects information that is reactivated, that low-value BOLD level would be expected to reiterate itself during study of a later pair, EF. Thus, the prediction is not that region X should (necessarily) exhibit greater activity when reactivation is successful versus not, but that its value should covary across trials (pairs) for which reactivation was likely to have been successful. This correlation should be greater than when computed across pairs for which reactivation was probably not successful. The results indeed supported similarity between the earlier-studied and later-studied pairs when reactivation would presumably have been more likely to have succeeded.

Moreover, the reactivation leading to subsequent memory of the earlier pair appeared at a high level of representation, further into the ventral visual pathway than online perceptual processing (Favila et al., 2020). Thus, participants do not, apparently, reactivate in the sense of re-imagining the two objects in the original pair with their detailed visual features, but rather, remember a highly processed, combined representation they had constructed of the two items. The control analyses confirmed that those were pair-specific distributed activity patterns (Koen & Rugg, 2016). Given the involvement of vmPFC, in particular, trial-to-trial variability in this region may reflect variability in producing the high-order representation of the association that is conducive to further elaboration. Such elaboration might, for example, support formation of an integrated representation or storage of the inferred, indirect association as just discussed.

Alternatively, if retrieval of the earlier-studied pair is decoupled from the low-level visual information in the stimulus, but rather, at a high level of representation, the more abstract representation might be more conducive to being transformed into a representation with more distinctiveness from other representations. Or, the high-level nature of the retrieval might indicate that the encoded representation of the earlier-studied pair may have often already been modified to be more distinctive.

Limitations

In order to stick closely to the previous paradigm that produce unambiguous evidence of pair-specific competition (Caplan et al., 2014), we had to use verbal stimuli that would be conducive to recall. Our findings might be restricted to the verbal domain. To expand into non-verbal memory domains, it will first be necessary to adapt and validate the paradigm for forced-choice responses.

Conclusion

Our behavioural paradigm, with brain activity analyzed during the entire study phase, revealed that associative interference is not produced passively due to strength-based competition between overlapping memories, but rather, due to proactive interference when the earlier-studied pair diverts encoding resources away from the later-studied pair, reflected in activity in the precuneus, among other regions. However, if the retrieval-related precuneus activity is not too strong, numerous additional regions, possibly coordinating with the precuneus, including angular gyrus and mid-frontal gyrus (but perhaps not hippocampus), can resolve interference. Finally, resolution of interference is enabled when the earlier-studied pair is studied in a particular way, involving activity in vmPFC and anterior hippocampus.

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