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The neural correlates of competition during memory retrieval are modulated by attention to the cues

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ABSTRACT

As people learn more facts about a concept, those facts become more difficult to remember. This is called the fan effect, where fan refers to the number of facts known about a concept. Increasing fan has been shown to decrease accuracy and increase response time and left ventrolateral prefrontal cortex (VLPFC) activity during retrieval. In this study, participants learned 36 arbitrary person–location pairings and made recognition decisions while we recorded brain activity using fMRI. We separately manipulated the fan of each person and location, as well as the training procedure with which each pair was studied. In the *person focus* condition, participants studied pairs with a picture of the person's face and used the person as a retrieval cue during training. In the *location focus* condition, participants studied pairs with a picture of the location and used the location as a retrieval cue during training. In the *location focus* condition, participants with a of the focused cue had a greater effect on response time, accuracy, and left VLPFC activity during retrieval than the fan of the unfocused cue. We also found that the parahippocampal place area (PPA) was more active during the recognition of pairs studied in the location focus condition, but not when the fan of the location was high. Overall, we found opposite effects of fan on VLPFC and PPA that were modulated by cue focus.

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1. Introduction

1.1. Associations compete during retrieval

We as human beings have stored a vast amount of information. It is a marvel, then, that we are often capable of singling out and accessing a specific piece of information from this expansive warehouse of knowledge with extreme ease. Whereas declarative memory can seem both infinitely large and extraordinarily efficient, it also has limited resources and is prone to interference. Interference in memory is often subtle but nonetheless reliable. Nowhere is this more apparent than in the case of the fan effect. The fan effect refers to the empirical finding that as people study more facts about a concept, those facts become more difficult to remember (Anderson, 1974). In the classic fan paradigm, people study associations between people and locations (e.g., "The hippie is in the park"). The number of associations, or fan, of the people and locations are manipulated such that some people and locations appear in only one association (low fan) and some appear in multiple associations (high fan). Anderson (1974) found that both studied associations and rearranged foils containing high fan concepts are identified more slowly and less accurately during recognition compared to those containing low fan concepts.

Anderson and Reder (1999) attribute the fan effect to competition during retrieval. This competition is described mathematically in Anderson's (2007) ACT-R theory, according to which the availability of a fact in memory is represented by its activation value. The activation value of a fact consists of two components: (1) base-level activation, which is determined by how recently and frequently the fact has been encountered, and (2) spreading activation, which is determined by the number of retrieval cues and their respective fan. This relationship is formally expressed in the *activation equation*,

$$A_i = B_i + \sum_j W_j S_{ji},$$

where A_i is the activation of fact *i*, B_i is the base-level activation and will reflect both the recency and frequency of fact *i*, and the summation is the amount of spreading activation to fact *i* from the retrieval cues *j*. The amount of spreading activation from a cue *j* is determined by the associative strength S_{ji} between cue *j* and fact *i* weighted according to the amount of attention devoted to that cue during retrieval, W_i . The associative strength between cue *j*

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and fact *i* is determined by the fan of *j*, such that as more facts are associated with *j*, the associative strength between *j* and any particular fact is weakened by competition. This can be thought of either as decreasing the associative strength between the cue and the target fact or increasing the amount of competition from the cue's other associates. Given a study sentence like 'The hippie is in the park', the retrieval cues are the person (i.e., hippie) and the location (i.e., park) and increasing the fan of either cue will reduce the amount of spreading activation to the associated fact ('The hippie is in the park'), thus making the fact more difficult to retrieve.

In ACT-R, W_j scales the effect of associative strength according to the amount of attentional resources devoted to a retrieval cue, such that the effect of fan is greater for cues with higher values of W_j . When equal attentional resources are allocated to each retrieval cue *j* during retrieval, W_j can be set to W/n, where *n* is the number of retrieval cues and *W* is the limit on attentional resources. In this case, the fan of all retrieval cues has the same impact on activation. However, in cases where different cues receive different amounts of attentional resources during retrieval, W_j can be larger for one cue and smaller for others. In this case, the fan of retrieval cues that receive more attention has a larger impact on spreading activation than the fan of cues that receive less attention.

Sohn, Anderson, Reder, and Goode (2004) investigated the effect of attention on the fan effect by having participants learn associations between people and locations using one of two learning procedures. In the person focus condition, participants were initially presented person-location associations (e.g., 'The hippie is in the park') with pictures of the person's face. After reading each sentence with a picture, participants went through a two-tiered question-answering phase in which they were given the name of the person and had to correctly identify that person's face (e.g., "Click on the hippie") as well as all associated locations (e.g., 'Where is the hippie?'). The training procedure ended when the participants answered each set of questions correctly twice. In the location focus condition, participants were initially presented person-location associations with a cell on a 5×5 grid associated with each location. After reading each sentence with the cell, participants went through a two-tiered question-answering phase in which they were given the name of the location and had to correctly identify that location's cell (e.g., "Click on the park") as well as all associated people (e.g., 'Who is in the park?'). The major difference between the focus conditions was that in the person focus condition the person was used as a retrieval cue during training and in the location focus condition the location was used as a retrieval cue during training. Sohn et al. (2004) hypothesized that this difference caused participants to group the material differently, with participants in the person focus condition grouping the material according to the person and participants in the location focus condition grouping the material according to the location. Sohn et al. (2004) found that effect of person fan was greater in the person focus condition and the effect of location fan was greater in the location focus condition, which they interpreted as inconsistent with competing models of the fan effect (Radvansky & Zacks, 1991). In their model of the task, the different training procedures caused participants to weigh the person and location cues differently during retrieval, with more weight (W_i) devoted to the person cue in the person focus condition, and more weight devoted to the location cue in the location focus condition. That is, during retrieval, more attention was paid to the cue that was also used as a cue during training. Overall, Sohn et al. (2004) found that different training procedures cause participants to attend to retrieval cues differently, resulting in modulation of the fan effect. The competing associations of the focused cue caused more interference than the associations of the non-focused cue. This suggests that the amount of interference caused by the competing associations of a cue is

proportional to the amount of attention devoted to that cue during retrieval.

1.2. Competition increases left ventrolateral prefrontal cortex activity during retrieval

Competition influences the extent to which control processes must be exerted during retrieval. Any brain region involved in guiding retrieval would be expected to increase activity as the amount of competition increases. Activity in the left ventrolateral prefrontal cortex (VLPFC) has been shown to increase as the amount of competition during retrieval increases (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999). Along the same lines, activity in this region during retrieval has been shown to increase as the fan of the retrieval cues increases (Danker, Gunn, & Anderson, 2008; Sohn, Goode, Stenger, Carter, & Anderson, 2003, 2005). Furthermore, activity in this region decreases when the retrieved association has been studied more often (Danker et al., 2008; Wheeler & Buckner, 2003), or when competing associations are forgotten (Kuhl, Dudukovic, Kahn, & Wagner, 2007). Whether the left VLPFC is involved in resolving competition specifically or guiding retrieval more generally has been a topic of substantial debate among researchers (Badre & Wagner, 2002; Thompson-Schill et al., 1997, 1998, 1999; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001), and some researchers have argued that distinguishing between these accounts is impossible (Danker et al., 2008; Martin & Byrne, 2006; Martin & Cheng, 2006; Thompson-Schill & Botvinick, 2006). Despite substantial debate about what specific function this region performs during retrieval, it is generally accepted that left VLPFC activity during retrieval is directly proportional to retrieval difficulty in general and the amount of competition specifically.

1.3. Brain regions engaged during encoding reactivate during subsequent retrieval

The process of remembering can sometimes involve vividly reexperiencing the remembered episode. There is growing evidence that the brain regions involved in encoding an episode are partially reactivated when that episode is later remembered (for review, see Danker & Anderson, 2010). That is, the process of remembering an episode involves partially recapitulating the brain state that was present during that episode. Neuroimaging studies have relied on an associative memory paradigm to provide evidence for reactivation (Nyberg, Habib, McIntosh, & Tulving, 2000; Wheeler, Petersen, & Buckner, 2000). This design relies crucially on the association of neutral retrieval cues with different categories of stimuli (e.g., sounds vs. pictures) that preferentially engage distinct brain regions during encoding. Because the neutral cue is presented alone at retrieval, preferential engagement of category-specific encoding regions during retrieval can be attributed to memory reactivation. In the typical experiment, during the study session, participants study neutral stimuli (e.g., words) that are randomly associated with different stimuli (e.g., a picture or a sound). During the test session, participants are presented with the neutral stimuli as retrieval cues and asked to make decisions about their memory of the cue and/or its associates. Any regions that are more active during both the encoding and the retrieval of one kind of stimuli (e.g., pictures) compared to other (e.g., sounds) are taken as evidence of reactivation. Using variations on this paradigm, evidence has been found that the fusiform gyrus is reactivated during the retrieval of pictures and the superior temporal gyrus is reactivated during the retrieval of sounds (Nyberg et al., 2000; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler and Buckner, 2003, 2004; Wheeler et al., 2000, 2006). Additionally, the parahippocampal place area (PPA), which selectively responds to images of places (Epstein, Harris, Stanley, & Kanwisher, 1999), has been found to reactivate when places are imagined (O'Craven & Kanwisher, 2000) or remembered (Polyn, Natu, Cohen, & Norman, 2005; Ranganath, Cohen, Dam, & D'Esposito, 2004). Likewise, the fusiform face area (FFA), which selectively responds to images of faces (Kanwisher, McDermott, & Chun, 1997), reactivates when faces are imagined (O'Craven & Kanwisher, 2000) or remembered (Polyn et al., 2005; Ranganath et al., 2004). It has been found that the amount of reactivation during retrieval is influenced by a number of factors. For example, reactivation is greater when participants report recollecting details of the study experience (Johnson & Rugg, 2007; Wheeler and Buckner, 2004; Woodruff, Johnson, Uncapher, & Rugg, 2005), or report vividly reliving a past experience (Daselaar et al., 2008). Reactivation has also been found to scale with the amount of retrieved information (Heil, Rosler, & Hennighausen, 1996, 1997; Khader, Burke, Bien, Ranganath, & Rosler, 2005; Khader, Heil, & Rosler, 2005; Khader et al., 2007; Rosler, Heil, & Hennighausen, 1995). However, it is unknown whether the amount of competition specifically or the difficulty of the retrieval generally affects the amount of reactivation that occurs during retrieval, and if so, whether these factors increase or decrease the amount of reactivation (Danker & Anderson, 2010).

1.4. Study and predictions

In the following study, we use Sohn et al.'s (2004) training procedure to manipulate the attentional weight of person and location cues during the recognition of person-location associations while simultaneously recording brain activity using fMRI. Our procedure diverges from that of Sohn et al. (2004) in several critical ways. Participants study associations between *famous* people and *famous* locations, and focus condition is manipulated *within* subject rather than *between* subjects. In the person focus condition, person-location pairs are associated with a picture of the famous person, and in the location focus condition, pairs are associated with a picture of the famous location (rather than a cell on a grid). We hope to replicate Sohn et al.'s (2004) finding that the fan effect is modulated by focus condition. We have several predictions that we believe follow directly from the known findings:

- (1) Based on evidence that the magnitude of left VLPFC activity during retrieval is proportional to the amount of competition (e.g., Thompson-Schill et al., 1997), we predict that fan effects in left VLPFC will be modulated by focus condition, with the effect of person fan being greater in the person focus condition and the effect of location fan being greater in the location focus condition.
- (2) Based on evidence that PPA and FFA reactivate during the retrieval of faces and places, respectively (e.g., Ranganath et al., 2004), we predict that, using text-only stimuli, FFA will be more active during the recognition of pairs studied in the person focus condition, and PPA will be more active during recognition of pairs studied in the location focus condition.
- (3) Most tentatively, we predict that the amount of reactivation in FFA and PPA will be greater when fan is low compared to when fan is high. We theorize that reactivation decreases rather than increases with fan because interference would reduce the amount of activation spreading to the target memory.

In addition to the recognition task, participants in our study also performed a mental imagery task between the study task and the recognition task in which they were asked to think about each individual famous person and location while we record brain activity. Based on the previous research, we might expect FFA to be more active during imagery for people and items studied in the person focus condition and the PPA to be more active during imagery for locations and items studied in the location focus condition.

2. Method

2.1. Participants

Twenty-two right-handed participants (8 female, 14 male, ages 18–27, mean age 20.95) who were eligible to participate in fMRI research were recruited locally and completed two sessions each. All participants gave informed consent to the experimenter in accordance with Carnegie Mellon University and University of Pittsburgh guidelines. Two participants were excluded from further analysis due to excessive movement in the scanner (>10 mm within session).

2.2. Stimuli and design

Stimuli for each participant were the 36 studied person-location pairs and 36 rearranged pairs. Each studied pair consisted of a famous person and a famous location, and studied pairs were randomly generated for each participant from a pool of 24 famous people and 24 famous locations. The design was $2 \times 2 \times 2 \times 2$ factorial with 16 conditions and four major factors: person fan (1 or 3), location fan (1 or 3), focus condition (person or location focus), and probe type (studied or rearranged). In half of the studied pairs, the person was unique to that pair (person fan 1), and in the remaining half the person appeared in two other studied pairs (person fan 3). Likewise, in half of the studied pairs, the location was unique to that pair (person fan 1), and in the other half the location appeared in two other studied pairs (location fan 3). Because some people and some locations appeared in multiple pairs, there were more unique person-location pairs (36) than there were either unique people (24) or unique locations (24), with 18 of the people and 18 of the locations appearing in only one pair each and 6 of the people and 6 of the locations appearing in three pairs each. Furthermore, half of the studied pairs (and the corresponding people and locations) were assigned to the person focus condition, and half were assigned to the location focus condition. Studied pairs in different focus conditions were learned by slightly different training procedures. Specifically, in the person focus condition, the pair was presented with a corresponding photograph of the person's face and the person was used as a retrieval cue during training. Likewise, in the location focus condition, the pair was presented with a corresponding photograph of the location and the location was used as a retrieval cue. The differences between the focus conditions are outlined in more detail in the procedure section, below. For each studied pair, a corresponding rearranged foil in the same person fan, location fan, and focus condition was created by reshuffling person-location pairs within that condition to produce a new person-location combination that had not been studied.

2.3. Procedure

Participants performed one training session and one test session. The training session consisted of a learning procedure in which participants learned the 36 pairs to criterion. The learning procedure consisted of two stages: (1) an initial presentation stage in which sentences describing the pairs were presented in random order along with accompanying pictures, and (2) a triple-pass question-answering procedure in which participants had to correctly answer two questions about each sentence three times in order to reach a learning criterion. During the initial presentation stage, participants were presented with each of the sentences and were instructed to study each sentence and the associated picture and indicate when they were ready for the next sentence by clicking

A. Person Focus



B. Location Focus



Fig. 1. Training procedure for the person and location focus conditions. (A) In the person focus condition, sentences describing associations between a person and one or three locations are presented with a photograph of the person. During the question-answering procedure, participants were required to identify the photograph of the person and the associated location(s) when given the name of the person as a retrieval cue. (B) In the location focus condition, sentences describing associations between a location and one or three people are presented with a photograph of the location. During the question-answering procedure, participants were required to identify the photograph of the location and the associated person(s) when given the name of the location as a retrieval cue.

a button. For pairs in the *person focus* condition, the initial presentation consisted of sentences in the format "(Person) went to (Location(s))" presented with a photograph of the person's face (see Fig. 1A). All locations associated with a given person were grouped into a single sentence (e.g., person fan 1: "Tom Cruise went to the Grand Canyon", person fan 3: "Tom Cruise went to the Grand Canyon, Big Ben, and the Colosseum"). For pairs in the *location focus* condition, the initial presentation consisted of sentences in the format "(Person(s)) is/are at (Location)" presented with a given location were grouped into a single sentence (e.g., location fan 1: "Brad Pitt is at the Eiffel Tower", location fan 3: "Brad Pitt, Angelina Jolie, and Oprah Winfrey are at the Eiffel Tower").

After participants studied each of the sentences, their memory of the sentences was perfected through a triple-pass questionanswering procedure. The procedure required participants to correctly answer two questions for each of the sentences. In the *person focus* condition, participants had to pick the photograph of the person's face out of an array of 12 faces (e.g., "Who is Tom Cruise?") and select the associated location(s) out of an array of location names when given the person as a retrieval cue (e.g., "Where did Tom Cruise go?" – see Fig. 1A). In the location focus condition, participants had to pick the photograph of the location out of an array of 12 photographs of locations (e.g., "Where is the Eiffel Tower?") and select the associated person(s) out of a random array of person names when given the location as a retrieval cue (e.g., "Who was at the Eiffel Tower?" – see Fig. 1B). Each pair of questions was drawn randomly from a pool of the questions that had not yet been correctly answered. When participants correctly answered both questions for a given sentence, those questions dropped out of the pool. In the case of an error, participants were presented the correct answer and the questions were left in the pool to be asked again later. The procedure ended when participants answered all of the questions in the pool correctly three times. No data was collected during training.

The test session was an fMRI scan that occurred between 0 and 48 h after the training session. Due to constraints in scheduling, participants were tested either immediately (n=4), after approximately 24 h (n=14), or after approximately 48 h (n=2). The following three tasks were performed during the functional scan: (1) a localizer for FFA and PPA, (2) a short imagery task in which participants were asked to think about each studied person and location, and (3) a recognition task in which participants had to distinguish studied pairs from rearranged pairs.

The localizer consisted of 5 blocks each of rapidly presented faces, locations, and flowers, ordered pseudorandomly such that 2 blocks of the same type did not occur in succession. During a block, images of a single type were presented every 500 ms for 16 s and participants had to click their index finger every time an image was presented twice in a row (i.e., a 1-back task). The only major factor was stimulus type. There was 10 s of fixation between blocks. The task lasted 6 min 40 s.

In the imagery task, participants were presented with the name of each person or location and asked to think about whatever comes to mind with respect to that person or location for 6 s. The major factors were whether the word referred to a person or a location (stimulus type), the fan of the word from training (1 or 3), and the focus condition of the word from training (person or location). There was 10 s between each item. Each item was presented once such that the task lasted 12 min 48 s.

In the recognition task, participants were presented with each of the 72 person-location pairs (36 studied pairs and 36 rearranged pairs) and asked to indicate whether that pair had been studied by clicking their index finger for yes and middle finger for no. The major factors were person fan (1 or 3), location fan (1 or 3), attentional focus (person or location focus), and studied/rearranged. Each stimulus was presented as text: no images were presented during the recognition task. Each pair was presented for 4s followed by 2s of feedback and 10s of fixation. Each item was presented three times¹ such that the experiment consisted of 216 trials presented in random order. Feedback indicated whether each response was correct or incorrect and allowed participants to recover memory for subsequent repetitions. The recognition task was divided into 9 blocks of 24 trials, lasting 6 min 24 s each. The entire recognition task lasted 57 min 36 s plus short breaks between blocks.

2.4. Imaging parameters

Event-related fMRI data were collected using a gradient echoplanar-image (EPI) acquisition on a Siemens 3T Allegra Scanner. Imaging parameters for all functional scans were TR = 2000-ms, TE = 30-ms, flip angle = 79° , FOV = 200-mm, matrix-size = 64×64 , slice thickness = 3.2-mm, slice gap 0-mm, and 34 axial slices per scan with AC-PC on the 11th slice from the bottom. There were a total of eleven functional runs consisting of the localizer (200 volumes), the imagery task (384 volumes), and nine blocks of recognition (192 volumes each). Anatomical scans were acquired prior to the functional data using a standard T2-weighted pulse sequence, with 34 slices and the AC-PC on the 11th slice from the bottom.

2.5. Data analysis

2.5.1. Behavioral

Response time and proportion correct (hits + correct rejections) were collected for each trial of the recognition task. Response times were analyzed for correct trials only (hits + correct rejections). Group statistics were performed on response time and error rate using repeated-measures analysis of variance (ANOVA). Factors included person fan (1 or 3), location fan (1 or 3), focus (person or location), and probe type (studied/rearranged).

2.5.2. Imaging

All preprocessing was done within the Neuro Imaging Software system (NIS, http://kraepelin.wpic.pitt.edy/nis/index.html). Preprocessing of the functional imaging data included sixparameter rigid-body motion correction using AIR (Woods, Cherry, & Mazziotta, 1992). Images were coregistered to a common reference anatomical MRI scan by means of the 12-parameter AIR algorithm (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998) and smoothed with a 6-mm full-width half-maximum threedimensional Gaussian filter.

Predefined analyses were performed using ROIs created in NIS. We used the same predefined left ventrolateral prefrontal region that has been the focus of several studies by our group (Danker et al., 2008; Sohn et al., 2003, 2005). This region consists of a box approximately 16 mm wide, 16 mm long, and 13 mm high $(5 \times 5 \times 4 \text{ voxels})$ centered at Talaraich coordinates x = -40, y = 21, z=21 (Fig. 3A). It contains parts of Brodmann areas 45 and 46 around the inferior frontal sulcus. Localized fusiform face area (FFA) and parahippocampal place area (PPA) ROIs were defined separately for each participant by contrasting faces > not faces and places > not places in the localizer task, respectively. The minimum threshold for defining these regions was p < .05 and was decreased until distinct regions were apparent in the appropriate anatomical locations. The range of thresholds used to isolate regions across participants varied between .05 and 5×10^{-7} for FFA (*M*=0.022, SD = 0.024) and .05 and 5×10^{-13} for PPA (M = 0.0026, SD = 0.011). Using this method, FFAs were localized on the right for 19 participants and on the left for 16 participants. Bilateral PPAs were localized for all 20 participants. Values from left and right PPA and FFA regions were averaged for each participant to produce a single value for each condition. Group statistics were performed on the predefined regions using repeated-measures analysis of variance (ANOVA), where the dependent measure was calculated as the average percent BOLD signal change across voxels in the region relative to baseline on the first scan. For each region, trials that included scan-to-scan fluctuations of greater than 5.0% BOLD or raw MR values below 200 were excluded from analyses. For the imagery task, factors included stimulus type (person or location), fan (1 or 3), focus (person or location), and scan (8 TRs). For the recognition task, factors included person fan (1 or 3), location fan (1 or 3), focus (person or location), studied/rearranged, and scan (8 TRs). When a region shows significant interactions between factors and scan, it indicates that the region shows an effect of that factor that changes over time, and this effect can oftentimes be characterized as a differential rise or fall in the percent BOLD change across conditions relative to baseline at the first scan. In order to ensure that significant effects were driven by differential rises or falls in the BOLD response across conditions, we followed up all significant interactions between factors and scan with corresponding t tests comparing mean activity around the peak (scans 3-6) across conditions.

Masked analyses were performed using mixed-effects ANOVA models (Braver et al., 1997; Snitz et al., 2005) within NIS with masks created in AFNI (Cox, 1996; Cox & Hyde, 1997). The localizer mask included all voxels that were differentially activated by faces and places in the localizer task (p < .005, 6019 voxels, approximately 12% of voxels in the brain). For the imagery task, voxel-wise 2stimulus type \times 2-fan \times 2 focus \times 8-scan ANOVAs were performed on all voxels in this mask with participant as a random factor. For the recognition task, voxel-wise 2-person fan \times 2-location $fan \times 2$ focus \times 2-studied/rearranged \times 8-scan ANOVAs were performed on all voxels in this mask with participant as a random factor. For the localizer mask, significant regions of interest were required to consist of at least 62 contiguous voxels at a voxelwise alpha of .05 or 18 contiguous voxels at a voxel-wise alpha of .01 such that the brain-wide alpha was estimated to be .05 by simulation. The smaller voxel-wise alpha of .01 is reported where it was necessary to reduce the alpha in order to separate distinct regions. The response mask included all voxels that showed a significant effect of scan during the recognition task (i.e., responded strongly to stimulus onset, $p < 5 \times 10^{-10}$, 15,731 voxels, approximately 31% of voxels in the brain). For the recognition task, voxel-wise 2-person fan \times 2-location fan \times 2focus × 2-studied/rearranged × 8-scan ANOVAs were performed on all voxels in this mask with participant as a random factor. For the response mask, significant regions of interest were required to consist of at least 73 contiguous voxels at a voxel-wise alpha of .05 such that the brain-wide alpha was estimated to be .05 by simulation.

All imaging analyses were performed only on correct trials (hits + correct rejections).

¹ The repetitions allowed us to increase our number of observations per condition without having an extremely long training procedure. None of the effects reported in this paper interacted with repetition.

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3. Results

3.1. Imagery task

3.1.1. Localized FFA

This region did not show the predicted preferences for people as a function of stimulus type and focus condition. The interaction between type and scan was not significant (F(7,126) = 1.32, p > .10), indicating that this region was not sensitive to whether participants thought about people or locations. The interaction between focus and scan was also not significant (F(7,126) = 0.84, p > .10).

3.1.2. Localized PPA

In accordance with our predictions, the PPA (Fig. 2A) was more active when participants were thinking about locations than people, and was more active in the location focus condition than the person focus condition (see Fig. 2B and D). In accordance with the observations, the interaction between type and scan was significant (F(7,133)=2.34, p < .05), and a follow-up t test comparing the average activation over scans 3–6 in the location and person conditions was significant (t(19)=3.36, p < .005), indicating that this region responded more strongly when participants thought about locations than people. The interaction between focus and scan was marginally significant (F(7,133)=2.03, p < .10), indicating that this region tended to respond more strongly in the location focus condition than the person focus condition, but a follow-up t test comparing the average activation over scans 3–6 in the location and person focus condition than the person focus condition, but a follow-up t test comparing the average activation over scans 3–6 in the location and person focus condition swas not significant (t(19)=1.32, p > .10).

3.1.3. Masked analysis

We looked for regions within the localizer mask that showed three kinds of effects in the imagery task: (1) stimulus type × scan interactions indicative of regions that responded differently when people and locations were thought about, (2) fan × scan interactions indicative of regions that respond differently depending on the number of associations of the person or location during training, and (3) focus × scan interactions indicative of regions that responded differentially depending on whether the person or location was part of a person focus or location focus pair during training. Because all regions were within the localizer mask, all of the regions responded more strongly to the visual presentation of either faces or places in the localizer task.

The regions within the localizer mask showing effects of stimulus type, fan, and focus are displayed in Table 1 along with their sizes, locations (Brodmann areas and Talaraich coordinates), activation for faces and places in the localizer, and activation according to imagery condition. The activation values represent the sums of the average % BOLD signal change in these regions summed over 13 scans in the localizer task and the sums over the eight scans in the imagery task. Of particular note, the parahippocampal gyrus, which preferred places in the localizer task, also responded more strongly when participants were instructed to think about locations or when they were thinking about people or locations studied in the location focus condition. This region also responded more strongly when fan was low. Several other visual processing regions responded more strongly both when places were presented visually in the localizer and when participants were instructed to think about locations in the imagery task, including superior occipital gyrus, precuneus, and lingual gyrus. However, no regions that responded more strongly to people's faces in the localizer also responded more strongly when participants were instructed to think about people in the imagery task. Interestingly, all the regions within this mask that showed effects of fan in the localizer task responded more strongly when fan was low. The opposite pattern is typically observed during recall and recognition tasks (Danker et al., 2008; Sohn et al., 2003, 2005).

3.2. Recognition task

3.2.1. Proportion correct

Proportion correct did not differ between participants tested at immediate (n=4, $M\pm SD=0.92\pm0.04$), 24 h (n=14, $M\pm SD=0.93\pm0.05$), and 48 h (n=2, $M\pm SD=0.89\pm0.01$) delays (all ps > .10), and there was no notable correlation across participants between retention interval and proportion correct (r=-.09). This observed lack of forgetting over substantial delays is not unusual in a paradigm where associations are learned to an extremely high criterion. For this reason, all further analyses include data from all three groups.

The mean proportion correct by condition is presented in Table 2. For both person fan and location fan, participants correctly responded to low fan pairs more than high fan pairs. Furthermore, person fan effects were greater in the person focus condition, and location fan effects were greater in the location focus condition. The magnitude of the person and location fan effects in proportion correct (fan 3–fan 1) are presented for the two focus conditions in Fig. 3A. In accordance with these observations, there were significant main effects of both person fan (F(1,19)=15.97, p < .001) and location fan (F(1,19)=25.36, p < .0001). Furthermore, there was a significant interaction between person fan and focus (F(1,19)=5.16, p < .05), confirming that the person fan effects were significantly greater in the person focus condition. The interaction between location fan and focus was not significant (F(1,19)=.13, p > .10), indicating the trend observed is not reliable.

3.2.2. Response time

The mean response time by condition is presented in Table 2. For both person fan and location fan, participants took longer to respond to high fan pairs than low fan pairs. Furthermore, person fan effects were greater in the person focus condition, and location fan effects were greater in the location focus condition. The magnitude of the person and location fan effects in response time (fan 3–fan 1) are presented for the two focus conditions in Fig. 3B. In accordance with these observations, there were significant main effects of both person fan (F(1,19)=50.97, p < .0001) and location fan (F(1,19)=73.93, p < .0001). Furthermore, there were significant interactions between person fan and focus (F(1,19)=20.73, p < .005) and between location fan and focus (F(1,19)=5.03, p < .05), confirming that the fan effects were significantly greater in the appropriate focus condition.

3.2.3. Predefined left VLPFC

In accordance with the predictions, person fan effects in left VLPFC were greater in the person focus condition, and location fan effects were greater in the location focus condition (Fig. 4B). In fact, person fan effects were actually reversed in the location focus condition, with low fan items producing more activity than high fan items (Fig. 4B and C). Likewise, location fan effects were greatly reduced in the person focus condition (Fig. 4B and D). The interaction between person fan and scan was not significant (F(7,133) = .97, p > .10), indicating that person fan effects were not present when focus condition was not taken into account. The interaction between location fan and scan was marginal (F(7,133) = 1.88, p < .10). However, the interaction between person fan, focus, and scan was marginally significant (F(7,133) = 1.78, p < .10) and the interaction between location fan, focus, and scan was significant (F(7,133)=2.16, p < .05), confirming that the fan effects were significantly greater in the appropriate focus condition. In order to determine whether left VLPFC generally showed greater fan effects on the focused dimension, we performed a follow-up t test on the fan effects averaged over scans 3-6. We compared the average of the location fan effect in the location focus condition and the person fan effect in the person focus condition with the average of the



Fig. 2. PPA activation during imagery and recognition. (A) Example of bilateral PPA localized in one participant. (B) Magnitude of PPA activity averaged over scans 3–6 by stimulus type and focus condition during imagery. (C) Magnitude of PPA activity averaged over scans 3–6 by location fan and focus condition during recognition. (D) Average BOLD response in PPA by stimulus type and focus condition during imagery. (E) Average BOLD response in PPA by location fan and focus condition during recognition. Confidence intervals are calculated using the method of Loftus and Masson (1994).

Table 1

Regions showing effects in the imagery task (masked with localizer).

Region of interest	Brodmann area(s)	Voxel count	Coordinates (x, y, z)	% BOLD faces	% BOLD places	Summed % B condition	OLD by imagery
Stimulus type \times scan (p < .01)						Person	Location
R. superior occipital gyrus	19	23	34, -82, 29	1.43	3.96	-0.64	0.30
L. superior occipital gyrus	19	24	-38, -82, 32	-4.28	-0.71	-0.42	1.17
R. precuneus	29, 31	122	14, -60, 22	-2.57	1.61	-0.10	0.95
L. precuneus	31	40	-18, -63, 23	-3.58	0.25	-0.07	0.89
L. lingual gyrus	18, 19	27	-12, -52, 2	-5.04	0.72	0.12	1.21
L. parahippocampal gyrus	19, 37	56	-29, -46, -5	0.06	6.51	0.13	1.09
Focus \times scan (p < .01)						Person focus	Location focus
R. middle occipital gyrus	37	25	44, -69, 4	11.40	4.67	-0.16	0.27
R. parahippocampal gyrus	19	42	23, -54, -4	3.45	9.05	-0.04	0.53
L. parahippocampal gyrus	19	44	-25, -57, -4	2.38	6.14	0.13	0.51
Fan x scan (p < .01)						Fan 1	Fan 3
L. precuneus	7	19	-11, -81, 51	-1.07	2.87	0.66	-0.27
R. precuneus	7	24	5, -82, 51	-0.61	2.98	0.08	-1.12
L. cuneus	18, 19	52	-14, -86, 26	-3.81	-1.16	0.20	0.07
R. cuneus	18, 19	26	21, -82, 25	7.76	9.24	0.47	-0.17
R. middle temporal gyrus	19	19	52, -68, 10	6.46	1.71	0.05	-0.69
L. middle temporal gyrus	19	56	-52, -73, 8	13.48	5.65	0.71	0.39
L. middle occipital gyrus	18	31	-31, -94, 11	15.44	15.19	1.59	0.74
R. middle occipital gyrus	18, 19	40	40, -80, -1	17.10	9.06	1.39	0.77
L. parahippocampal gyrus	19	42	-23, -58, -6	4.61	8.99	0.37	0.35
R. parahippocampal gyrus	19	47	24, -66, -8	10.38	13.75	0.62	0.23

l'able	2				
Mean	response	time and	proportion	correct	by condition.

		Response time (ms) Person fan/location fan			Proportion correct Person fan/location fan				
		1/1	1/3	3/1	3/3	1/1	1/3	3/1	3/3
Studied	Person focus	1458	1693	1732	1895	0.98	0.93	0.93	0.82
	Location focus	1527	1786	1621	1921	0.97	0.94	0.94	0.85
Rearranged	Person focus	1595	1881	2058	2169	0.98	0.91	0.86	0.85
	Location focus	1638	1949	1706	2063	0.99	0.89	0.97	0.92

location fan effect in the person focus condition and the person fan effect in location focus condition (comparing the outer bars to the inner bars in Fig. 4B). The difference was significant (t(19)=1.91, p < .05, one tailed).

3.2.4. Localized FFA

Our predictions were not borne out for this region, as it did not show the predicted effect of focus or the significant interaction between person fan, focus, and scan. Against our predictions, the interaction between focus and scan (F(7,126)=0.73, p > .10) and between person fan, focus, and scan (F(7,126)=1.27, p > .10) were not significant. Likewise, the interaction between location fan, focus, and scan was not significant (F(7,126)=1.70, p > .10).

3.2.5. Localized PPA

In accordance with the predictions, PPA was more active in the location focus condition than the person focus condition, suggesting that the pictorial information about locations is being accessed during retrieval. Furthermore, this effect of focus seems to be largely driven by the low location fan condition, such that activity is greatest in the location fan 1/location focus condition (see Fig. 2C and E). In accordance with our observations, there was a significant interaction between focus and scan (F(7,133) = 4.83), p < .0001), and a follow-up t test comparing the average activation over scans 3-6 in the location and person focus conditions was significant (t(19) = 2.21, p < .05), indicating that the PPA responded more strongly in the location-focus condition. There was also a significant interaction between location fan, focus, and scan (F(7,133) = 2.17, p < .05), and a follow-up *t* test comparing activation in the location fan 3/location focus condition with that in the other three conditions was significant (t(19) = 2.59, p < .05), indicating activation was greatest in the location fan 1/location focus condition. The interaction between person fan, focus, and scan was not significant (F(7,133) = 1.06, p > .10).

In order to highlight the differences in the effects shown between this region and our predefined VLPFC region, we performed a 2-region (PPA vs. VLPFC) \times 2-person fan \times 2-location fan \times 2-focus \times 2-studied/rearranged repeated-measured ANOVA with average activation over scans 3–6 as the dependent measure. As might be expected based on the results of the separate tests for each region, the interaction between region, location fan, and focus was significant (F(1,19) = 6.59, p < .05). In the location focus condition, left VLPFC responded more strongly to higher location fan, while PPA responded more strongly to lower location fan. A followup *t* test directly comparing the magnitude of location fan effects in PPA and VLPFC in the location focus condition was significant (t(19)=2.81, p<.05). Lastly, the interaction between region, person fan, and focus was marginally significant (F(1,19) = 3.36, p < .10), indicating the differences in the responses of these regions to person fan. Left VLPFC responded more strongly when person fan was high in the person focus condition, while PPA was insensitive to both person fan and its interaction with focus. A follow-up t test directly comparing the magnitude of person fan effects in PPA and VLPFC in the person focus condition was significant (t(19) = 2.37), p < .05). In the person focus condition, left VLPFC responded more strongly to higher person fan, while PPA was insensitive to person fan.

3.3. Masked analyses

3.3.1. Localizer mask

We looked for regions within the localizer mask that showed three kinds of effects in the recognition task: (1) focus \times scan interactions indicative of regions that responded differently depending on whether the recognized pair was studied in the person or



Fig. 3. Fan effects in proportion correct and response time. Fan effects are calculated as the difference between fan 3 and fan 1 conditions. (A) Magnitude of person and location fan effects in proportion correct by focus condition. (B) Magnitude of person and location fan effects in response time by focus condition. Confidence intervals are calculated using the method of Loftus and Masson (1994).



Fig. 4. Effect of fan and focus on left VLPFC activity during recognition. (A) The predefined left ventrolateral prefrontal region. (B) The magnitude of person and location fan effects by focus condition. Fan effects are calculated as the average difference in activity over scans 3-6 between fan 3 and fan 1 conditions. (C) Average BOLD response in left VLPFC by person fan and focus condition. (D) Average BOLD response in left VLPFC by location fan and focus condition. Confidence intervals are calculated using the method of Loftus and Masson (1994).

location focus condition, (2) person fan \times focus \times scan interactions indicative of regions that show person fan effects that depend on the focus condition, and (3) location fan \times focus \times scan interactions indicative of regions that show location fan effects that depend on the focus condition. Because all regions were within the localizer mask, all of the regions responded more strongly to the visual presentation of either faces or places in the localizer task.

The regions within the localizer mask showing effects of focus or interactions between location fan and focus are displayed in Table 3 along with their sizes, locations (Brodmann areas and Talaraich coordinates), activation for faces and places in the localizer, and activation according to fan and focus condition. The activation values represent the sums of the average % BOLD signal change in these regions summed over 13 scans in the localizer and the sums for the eight scans in the recognition task. Several regions that responded more positively to places in the localizer also responded more strongly in the location focus condition during recognition, including the left parahippocampal gyrus. As in the imagery task, no regions in the mask that preferred people's faces in the localizer responded more strongly in the person focus condition. No regions within the mask showed significant interactions between person fan, focus, and scan. However, several regions showed an interaction between location fan, focus, and scan, including the right parahippocampus, which, as in the localized PPA analysis,

responded most strongly in the location fan 1/location focus condition.

3.3.2. Response mask

We looked for regions within the response mask that showed two kinds of effects: (1) person $fan \times focus \times scan$ interactions indicative of regions that show person fan effects that depend on the focus condition, and (2) location fan \times focus \times scan interactions indicative of regions that show location fan effects that depend on the focus condition. Because all regions were within the response mask, all of the regions responded strongly to the recognition task.

The regions within the response mask showing interactions between fan and focus are displayed in Table 4 along with their sizes, locations (Brodmann areas and Talaraich coordinates), and activation according to fan and focus condition. For regions showing interactions with person fan, the fan conditions reported refer to person fan, and for regions showing interactions with location fan, the fan conditions reported refer to location fan. The activation values represent the sum of the average % BOLD signal change in these regions summed across eight scans in the recognition task. Several regions showed larger person fan effects in the person focus condition, including part of the left middle frontal gyrus near our predefined left VLPFC region. Only three of the regions showing location fan \times focus \times scan interactions showed greater fan effects

localizer).

Tuble 5				
Regions showing focus effects in	the recognition	task	(masked	with

Region of interest	Brodmann ar	ea(s)	S) Voxel count Coordinates (x, y, z)		x, y, z)	% BOLD faces	% BOLD places	Summed % BOI recognition co	LD by ndition
Focus × scan (p < .01)								Person focus	Location focus
R. superior occipital gyrus	19		31	38, -82, 28		1.03	3.62	-0.23	0.10
L. superior occipital gyrus	19		23	-36, -90, 30		-1.94	3.49	-0.35	-0.15
R. posterior cingulate	23, 31	1	80	11, -57, 12		-2.73	1.87	0.57	0.94
L. posterior cingulate	31		29	-17, -61, 16		-3.67	0.19	0.47	0.73
L. parahippocampal gyrus	37		27	-30, -39, -9		-1.46	5.48	0.15	0.52
Location fan × focus × scan (p <	:.05)					Fan 1/person	Fan 1/location	Fan 3/person	Fan 3/location
R. precuneus	7, 19	99	10, -78, 44	0.07	1.92	1.21	1.19	1.02	1.31
L. middle occipital gyrus	18, 19	62	-27, -96, 24	10.72	13.24	1.35	1.67	1.53	1.47
Medial cuneus	18	102	1, -92, 14	5.89	8.57	1.25	1.85	1.85	1.68
R. parahippocampal gyrus	19, 37	85	17, -42, -3	0.59	5.62	0.48	0.78	0.51	0.65

in the location focus condition. One of these regions responded positively (right precuneus), and two responded negatively (superior/medial frontal gyrus and angular gyrus).

4. Discussion

4.1. Fan effects in left VLPFC are modulated by attention to the retrieval cues

Activity in left VLPFC has been shown to correlate inversely with the accessibility of retrieved information during memory retrieval, such that activity in this region is greater when information is more difficult to retrieve. Many factors that influence the accessibility of information have been shown to influence activity in this region during retrieval, such as competition and the number of study presentations (Danker et al., 2008; Thompson-Schill et al., 1997; Wagner et al., 2001; Wheeler & Buckner, 2003). During associative memory retrieval, it has been repeatedly shown that increasing the fan, or number of associations, of the retrieval cues increases response time, error rate, and left VLPFC activity during retrieval (Danker et al., 2008; Sohn et al., 2003, 2005). According to Anderson and Reder (1999), when the fan of a retrieval cue is increased, the cue becomes less strongly associated with the retrieved association and more strongly associated with its other associates. Danker et al. (2008) argued that this could be thought of either as decreasing the associative strength between the cue and the target association or increasing the competition from the cue's other associations.

Sohn et al. (2004) found that when participants were trained to focus more on one cue than the other during recognition, the fan of the focused cue had a larger effect on response time and accuracy than the fan of the unfocused cue. In this study, we replicated the Sohn et al.'s (2004) findings with response time and accuracy. Given findings that the left VLPFC activity increases with fan (Danker et al., 2008; Sohn et al., 2003, 2005), and decreases when

competing associations are forgotten (Kuhl et al., 2007), we predicted that fan effects in left VLPFC activity would be modulated by Sohn et al.'s (2004) focus manipulation. Consistent with this prediction, we found that person fan increased left VLPFC activity more in the person focus condition, and location fan increased left VLPFC activity more in the location focus condition (Fig. 4B). From these findings, we conclude that: (1) preferentially using one cue over another during training leads participants to weigh that cue more heavily during retrieval, (2) the interference caused by the fan of a cue during retrieval is proportional to the amount of attention directed at that cue, (3) this interference is reflected in left VLPFC activity during retrieval. This is consistent with theories that propose the left VLPFC is involved guiding retrieval generally (e.g., Danker et al., 2008; Wagner et al., 2001), and resolving competition specifically (e.g., Badre & Wagner, 2007; Thompson-Schill et al., 1997). What most strongly differentiates these theories is that competition theories propose separate retrieval and selection processes (Badre & Wagner, 2007; Thompson-Schill et al., 1997), in which case left VLPFC could be said to be involved in selection among competitors but not retrieval generally, and controlled retrieval theories propose that retrieval is a selection process (Danker et al., 2008; Martin & Byrne, 2006; Martin & Cheng, 2006), in which case the distinction between retrieval and selection is immaterial. Our findings can be explained using either theory. According to competition theories, our focus manipulation might impact which retrieval cue is used, which in turn impacts how many competing associations are retrieved and, in turn, must be selected among. When a high fan, focused cue is used (e.g., location fan 3/location focus), many competitors would be retrieved and must be selected among, leading to interference, but when a high fan, unfocused cue is used (e.g., location fan 3/person focus), those competitors may not be retrieved at all, abolishing the fan effect. Likewise, according to retrieval theories, our focus manipulation might impact which retrieval cue is used, which in turn impacts how many competing items must be selected among during retrieval. Future empirical work

Table 4

Regions showing fan × focus interactions in the recognition task (masked with main effect of scan).

Region of interest	Brodmann area(s)	Voxel count	Coordinates (x, y, z)	Summed % BOLD by recognition condition			
				Fan 1/person	Fan 1/location	Fan 3/person	Fan 3/location
Person fan \times focus \times scan (p < .05)							
Superior frontal gyrus	6	76	3, 13, 50	0.88	1.03	1.27	0.85
L. superior parietal/precuneus	7, 29, 39	160	-28, -55, 41	1.34	1.54	1.86	1.35
L. middle frontal gyrus	9, 46	73	-49, 13, 34	1.03	1.50	1.70	1.10
Location fan \times focus \times scan (p < .05	i)						
Superior/medial frontal gyrus	8, 9	219	0, 60, 27	-0.73	-0.58	-0.67	-1.05
R. precuneus	7	220	6, -75, 44	1.50	1.31	1.50	1.62
L. angular gyrus	39	82	-53, -65, 33	-0.72	-0.51	-0.61	-0.87
L. thalamus/lentiform nucleus	-	77	-27, -25, 7	0.36	0.50	0.51	0.57
L. putamen	-	109	-20, 2, 16	0.48	0.47	0.72	0.69
L. posterior cingulate	30	82	-9, -49, 21	0.87	0.87	1.08	1.01

is required to provide evidence for one of these accounts over the other, as our current data does not favor one interpretation over the other.

However, one data point in particular seems inconsistent with the theory that left VLPFC is tracking retrieval difficulty and/or competition. The person fan 1/location focus condition shows more activation than the person fan 3/location focus condition (see Fig. 4C), despite the fact that theoretically the person fan 3 condition should induce similar or slightly more competition (because person is not the focused cue), and behaviorally it does induce more competition (see Fig. 3). We attribute this reversed fan effect in the left VLPFC to noise in our data. Consistent with this interpretation, this reversed person fan effect in the location focus condition is not statistically reliable (t(19) = 1.39, p > .10).

4.2. PPA is reactivated during both semantic and episodic retrieval

The fusiform face area is a region on the fusiform gyrus that is selectively activated during the perception of faces (Kanwisher et al., 1997). The parahippocampal place area (PPA) is a region on the parahippocampal gyrus that is selectively activated during the perception of locations, such as landmarks and buildings (Epstein et al., 1999). O'Craven and Kanwisher (2000) found that FFA activity was greater when participants were asked to imagine famous faces and PPA activity was greater when participants were asked to imagine familiar buildings. Furthermore, Ranganath et al. (2004) and Polyn et al. (2005) have found that FFA is more active during the retrieval of associated faces and PPA is more active during the retrieval of associated places. In our imagery task, we instructed participants to think about whatever comes to mind when cued with a famous person or famous location that they learned about during the training procedure. Consistent with the findings of O'Craven and Kanwisher, we found that PPA was more active when participants thought about locations compared to people (Fig. 2B). Consistent with the findings of Ranganath et al. (2004) and Polyn et al. (2005), activity in PPA was more active when participants thought about people or locations studied in the location focus condition compared to the person focus condition (Fig. 2B and D). Furthermore, during the recognition task, PPA was more active during the recognition of pairs studied in the location focus condition compared to the person focus condition (Fig. 2C and E). This suggests that during the imagery and recognition tasks, participants may be remembering the pictures of the associated places. Consistent with previous work, PPA was active during both the semantic retrieval of locations (location > person) and the episodic retrieval of images from training (location focus > person focus). However, in contrast to previous findings, we found that activity in the FFA was not affected by these manipulations. It is worth noting that participants were not required or directly instructed to retrieve images faces or faces during either the imagery task or the recognition task. Participants could think about whatever they wanted during the imagery task, and the recognition decision could be made without accessing images from memory. This makes our findings in PPA all the more impressive. For whatever reason, participants may have been more prone to retrieve images of places than images of faces. This could be because famous places are more strongly tied to their associated images than famous people, who are also strongly associated with a number of things (events, movies, songs, etc.) besides their faces. Furthermore, the failure to find reactivation in FFA may be theoretically important, especially considering we are not the only researchers to report reactivation in PPA but not FFA in the same experiment (Tubridy & Davachi, SFN posters, 2010, also using a long-term memory paradigm). That is, FFA and PPA may behave differently during memory retrieval.

4.3. Why is reactivation in PPA reduced by fan?

The magnitude of reactivation during retrieval has been found to be sensitive to a number of factors (Daselaar et al., 2008; Heil et al., 1996, 1997; Johnson & Rugg, 2007; Khader, Burke, et al., 2005; Khader, Heil et al., 2005; Khader et al., 2007; Rosler et al., 1995; Wheeler and Buckner, 2004; Woodruff et al., 2005). However, the effect of retrieval difficulty generally and competition specifically on the reactivation of encoding regions during retrieval is unknown (Danker & Anderson, 2010). Because we expected competition to interfere with reactivation, we predicted that increasing fan would reduce reactivation in PPA and FFA. Whereas FFA did not reactivate at all and demonstrated no sensitivity to fan, PPA was more active during the recognition of pairs studied with pictures of places compared to faces, and this reactivation was reduced when location fan was high (Fig. 2C). There are two primary explanations for the finding that increasing fan decreased reactivation. The first explanation is that competition reduces reactivation. That is, increasing location fan reduces reactivation because the competing associations would reduce reactivation associated with the target association. Essentially, less activation is spread from the location cue to the associated image, causing less activity in the part of cortex representing that image. However, because in this paradigm high fan items oftentimes require twice as many presentations during training to reach criterion, it is also possible that PPA activity is reduced during retrieval by repetition suppression because high fan items and images are presented more often during training and testing than low fan items and images. These repetitions might make high location fan images easier to process, which in turn might make them require less PPA reactivation to retrieve during recognition. This would be consistent with findings that parahippocampal cortex decreases activity with repetition suppression (Gonsalves, Kahn, Curran, Norman, & Wagner, 2005). However, this would be the first evidence to our knowledge of repetition suppression on reactivation during memory retrieval. That is, it has never been shown before to our knowledge that repeating a particular type of item reduces the reactivation associated with that item during memory retrieval. It is worth noting that previous studies that directly manipulated the number of encoding presentations of word-picture and word-sound associations found no detectable effect of repetition on the amount of reactivation during retrieval (Nyberg et al., 2000; Wheeler & Buckner, 2003).

Based on our findings, we can see that VLPFC and PPA respond very differently to our manipulations of competition. While VLPFC increases activity with fan, PPA decreases activity with fan. This raises the question: What is the relationship between activity in VLPFC and activity in PPA in our task? It is possible that competition has direct, independent effects on VLPFC and PPA such that competition increases cognitive control but decreases reactivation of the target memory. Alternatively, it is possible that reactivation represents the amount of bottom-up information evoked by the retrieval cue, and the amount of cognitive control required to resolve competition is inversely proportional to the amount of bottom-up information. That is, left VLPFC comes online as a result of a paucity of bottom-up information from the cue. In this case, competition may act directly on the amount of reactivation, which in turn influences the amount of left VLPFC activity. These results should motivate future research exploring the relationship between cognitive control and reactivation during memory retrieval.

5. Conclusions

In this study, we found that interference as reflected in response time, accuracy, and left VLPFC activity during retrieval can be modulated by the attentional weight given to the retrieval cues, such the fan of focused cues has a larger effect than the fan of unfocused cues. Furthermore, we found more activation in PPA during the recognition of pairs that were associated with a picture of a place during training. This reactivation was reduced when the fan of the location cue was high. We also found that PPA was more active when people thought about famous locations, or thought about famous people or locations associated with a picture of a location during training. Overall, our results (1) support the assertion that left VLPFC is involved in resolving competition during retrieval and (2) suggest that competition may reduce the amount of sensory reactivation that occurs during retrieval.

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References

- Anderson, J. R. (1974). Retrieval of propositional information from long-term memory. Cognitive Psychology, 5, 451–474.
- Anderson, J. R. (2007). How can the human mind occur in the physical universe? New York: Oxford University Press.
- Anderson, J. R., & Reder, L. M. (1999). The fan effect: New results and new theories. Journal of Experimental Psychology, 128, 186-197.
- Badre, D., & Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. Behavioral and Cognitive Neuroscience Review, 1, 206–218.
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45, 2883–2901.
- Braver, T. S., Cohen, J. D., Nystrom, L. É., Jonides, J., Smith, E., & Noll, D. C. (1997). A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage*, 5, 49–62.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. Computers and Biomedical Research, 29, 162–173.
- Cox, R. W., & Hyde, J. S. (1997). Software tools for analysis and visualization of FMRI data. NMR in Biomedicine. 10. 171–178.
- Danker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the brain regions engaged during encoding. *Psychological Bulletin*, 136, 87–102.
- Danker, J. F., Gunn, P., & Anderson, J. R. (2008). A rational account of memory predicts left prefrontal activation during controlled retrieval. *Cerebral Cortex*, 18, 2674–2685.
- Daselaar, S. M., Rice, H. J., Greenberg, D. L., Cabeza, R., LaBar, K. S., & Rubin, D. C. (2008). The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex*, 18, 217–229.
- Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: Recognition, navigation, or encoding? *Neuron*, 23, 115–125.
- Gonsalves, B. D., Kahn, I., Curran, T., Norman, K. A., & Wagner, A. D. (2005). Memory strength and repetition suppression: Multimodal imagina of medial temporal cortical contributions to recognition. *Neuron*, 47, 751–761.
- Heil, M., Rosler, F., & Hennighausen, E. (1996). Topographically distinct cortical activation in episodic long-term memory: The retrieval of spatial versus verbal information. *Memory & Cognition*, 24, 777–795.
- Heil, M., Rosler, F., & Hennighausen, E. (1997). Topography of brain electrical activity dissociates spatial versus verbal information from episodic long-term memory in humans. *Neuroscience Letters*, 222, 45–48.
- Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encodingrelated cortical activity. Cerebral Cortex, 17, 2507–2515.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuro*science, 17, 4302–4311.
- Khader, P., Burke, M., Bien, S., Ranganath, C., & Rosler, F. (2005). Content-specific activation during associative long-term memory retrieval. *NeuroImage*, 27, 805–816.
- Khader, P., Heil, M., & Rosler, F. (2005). Material-specific long-term memory representations of faces and spatial positions: Evidence from slow event-related potentials. *Neuropsychologia*, 43, 2109–2124.
- Khader, P., Knoth, K., Burke, M., Ranganath, C., Bien, S., & Rosler, F. (2007). Topography and dynamics of associative long-term memory retrieval in humans. *Journal of Cognitive Neuroscience*, 19, 493–512.

- Kuhl, B. A., Dudukovic, N. M., Kahn, I., & Wagner, A. D. (2007). Decreased demands on cognitive control reveal the neural processing benefits of forgetting. *Nature Neuroscience*, 10, 908–914.
- Loftus, G. R., & Masson, M. R. (1994). Using confidence intervals in within-subject designs. Psychonomic Bulletin & Review, 1, 476–490.
- Martin, R. C., & Byrne, M. D. (2006). Why opening a door is as easy as eating an apple: A reply to Thompson-Schill and Botvinick. *Psychonomic Bulletin & Review*, 13, 409–411.
- Martin, R. C., & Cheng, Y. (2006). Selection demands versus association strength in the verb generation task. *Psychonomic Bulletin & Review*, 13, 396–401.
- Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encodingrelated brain activity during memory retrieval. Proceedings of the National Academy of Sciences of the United States of America, 97, 11120–11124.
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, 12, 1013–1023.
- Polyn, S. M., Natu, V. S., Cohen, J. D., & Norman, K. A. (2005). Category-specific cortical activity precedes retrieval during memory search. *Science*, 310, 1963–1966.
- Radvansky, G. A., & Zacks, R. T. (1991). Mental models and the fan effect. Journal of Experimental Psychology: Learning, Memory & Cognition, 23, 1233–1246.
- Ranganath, C., Cohen, M. X., Dam, C., & D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *Journal of Neuroscience*, 24, 3917–3925.
- Rosler, F, Heil, M., & Hennighausen, E. (1995). Distinct cortical activation patterns during long-term memory retrieval of verbal, spatial, and color information. *Journal of Cognitive Neuroscience*, 7, 51–65.
- Snitz, B. E., MacDonald, A., Cohen, J. D., Cho, R. Y., Becker, T., & Carter, C. S. (2005). Lateral and medial hypofrontality in first-episode schizophrenia: Functional activity in medication-naïve state and effects of short-term atypical antipsychotic treatment. *American Journal of Psychiatry*, 162, 2322–2329.
- Sohn, M.-H., Goode, A., Stenger, V. A., Carter, C. S., & Anderson, J. R. (2003). Competition and representation during memory retrieval: Roles of prefrontal cortex and posterior parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 7412–7417.
- Sohn, M.-H., Anderson, J. R., Reder, L. M., & Goode, A. (2004). Differential fan effect and attentional focus. *Psychonomic Bulletin & Review*, 11, 729–734.
- Sohn, M.-H., Goode, A., Stenger, V. A., Carter, C. S., & Anderson, J. R. (2005). An information-processing model of three cortical regions: Evidence in episodic memory retrieval. *NeuroImage*, 25, 21–33.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 14792–14797.
- Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Science*, 95, 15855–15860.
- Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, 23, 513–522.
- Thompson-Schill, S. L., & Botvinick, M. M. (2006). Resolving conflict: A response to Martin and Cheng (2006). Psychonomic Bulletin & Review, 13, 402–408.
- Vaidya, C. J., Zhao, M., Desmond, J. E., & Gabrieli, J. D. E. (2002). Evidence for cortical specificity in episodic memory: Memory-induced re-activation of picture processing areas. *Neuropsychologia*, 40, 2136–2143.
- Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, 31, 329–338.
- Wheeler, M. E., & Buckner, R. L. (2003). Functional dissociations among components of remembering: Control, perceived oldness, and content. *Journal of Neuroscience*, 23, 3869–3880.
- Wheeler, M. E, & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *NeuroImage*, 21, 1337–1349.
- Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. Proceedings of the National Academy of Sciences of the United States of America, 97, 11125–11129.
- Wheeler, M. E., Shulman, G. L., Bucckner, R. L., Miezin, F. M., Velanova, K., & Petersen, S. E. (2006). Evidence for separate perceptual reactivation and search processes during remembering. *Cerebral Cortex*, 6, 949–959.
- Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Contentspecificity of the neural correlates of recollection. *Neuropsychologia*, 43, 1022–1032.
- Woods, R. P., Cherry, S. R., & Mazziotta, J. C. (1992). Rapid automated algorithm for aligning and reslicing PET images. *Journal of Computer Assisted Tomography*, 16, 620–633.
- Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R., & Mazziotta, J. C. (1998). Automated image registration. I. General methods of intrasubject, intramodality variation. *Journal of Computer Assisted Tomography*, 22, 139–152.