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Neural Signatures of Controlled and Automatic Retrieval Processes in Memory-based Decision-making

Patrick H. Khader¹, Thorsten Pachur², Lilian A. E. Weber³, and Kerstin Jost⁴

Abstract

■ Decision-making often requires retrieval from memory. Drawing on the neural ACT-R theory [Anderson, J. R., Fincham, J. M., Qin, Y., & Stocco, A. A central circuit of the mind. *Trends in Cognitive Sciences*, 12, 136–143, 2008] and other neural models of memory, we delineated the neural signatures of two fundamental retrieval aspects during decision-making: automatic and controlled activation of memory representations. To disentangle these processes, we combined a paradigm developed to examine neural correlates of selective and sequential memory retrieval in decision-making with a manipulation of associative fan (i.e., the decision options were associated with one, two, or three attributes). The results show that both the automatic activation of all

attributes associated with a decision option and the controlled sequential retrieval of specific attributes can be traced in material-specific brain areas. Moreover, the two facets of memory retrieval were associated with distinct activation patterns within the frontoparietal network: The dorsolateral prefrontal cortex was found to reflect increasing retrieval effort during both automatic and controlled activation of attributes. In contrast, the superior parietal cortex only responded to controlled retrieval, arguably reflecting the sequential updating of attribute information in working memory. This dissociation in activation pattern is consistent with ACT-R and constitutes an important step toward a neural model of the retrieval dynamics involved in memory-based decision-making. ■

INTRODUCTION

Memory processes are an explicit part of many models of decision-making (Thomas, Dougherty, Sprenger, & Harbison, 2008; Schooler & Hertwig, 2005; Juslin & Persson, 2002). However, the neural underpinnings of the memory dynamics involved are only poorly understood. On the basis of theories of information processing such as ACT-R (e.g., Anderson et al., 2004) and search of associative memory (Raaijmakers & Shiffrin, 1981) as well as on previous empirical findings (e.g., Kuhl, Johnson, & Chun, 2013; Nyberg, 2006), we assume that two separate retrieval processes contribute to the decision process: (1) incidental activation of all memory representations associated with a decision option, resulting from automatic activation spread, and (2) intentional activation due to a controlled focusing on task-relevant information. In a previous behavioral study (Khader, Pachur, & Jost, 2013), we had obtained evidence for a contribution of both automatic and controlled retrieval during decision-making. Our goal in this article is to delineate the neural systems that underlie automatic and controlled retrieval during the decision process, thus embedding memory-based decision-making within a broader neurocognitive framework.

The retrieval of knowledge—whether automatic or controlled—activates memory representations stored in

(material-specific) posterior brain areas (for a review, see Danker & Anderson, 2010). Executive processes operating on these representations have been found to be mediated by a frontoparietal network (e.g., Badre & Wagner, 2002, 2007; Buckner & Wheeler, 2001), with different sub-components making distinct contributions to automatic and controlled memory activation (Borst & Anderson, 2013; Anderson, Fincham, Qin, & Stocco, 2008). Specifically, the lateral pFC (BA 9, 44, 45, and 46) has been found to respond to increased effort involved in retrieving information from memory (Anderson et al., 2008; see also Badre & Wagner, 2002; Buckner & Wheeler, 2001) and should thus be sensitive to both the controlled and automatic activation of memory representations during decision-making. Activity in the posterior parietal cortex (BA 7, 39, and 40), by contrast, has been found to reflect the updating of currently relevant information in working memory (WM; e.g., Borst & Anderson, 2013; Anderson et al., 2008) and should thus be involved in controlled retrieval only.

In an fMRI study, we tested whether evidence for a neural dissociation of these retrieval mechanisms can be found during memory-based decision-making. Participants were instructed to use the “take-the-best” heuristic (TTB; Gigerenzer & Goldstein, 1996), a strategy typically employed for decisions from memory (Pachur & Aebi-Forrer, 2013; Bröder & Schiffer, 2003, 2006). TTB requires the sequential retrieval of attributes in the order of their importance and stops information search as soon as a given attribute allows for making a decision. This sequential

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processing requires controlled retrieval from long-term memory (LTM) and, consequently, a repeated updating of WM content. We manipulated controlled retrieval by varying the number of attributes required by TTB. To manipulate automatic memory activation, we additionally varied the fan level (Anderson, 1974), that is, the number of associations with a retrieval cue, by varying the number of attributes to which a decision option is associated. Increased fan levels have been found to prolong RTs—a finding that has been explained by increased interference due to automatic activation spread (e.g., Anderson & Reder, 1999). Importantly, a similar fan effect has also been observed in decision-making (see Khader et al., 2013).

We predicted that both manipulations—number of required attributes and fan level—modulate the activation of attribute-specific memory representations. Regarding the frontoparietal network, we expected that the lateral pFC, being generally related to retrieval activity, reflects both controlled and automatic retrieval. In contrast, we expected the posterior parietal cortex, which reflects updating processes in WM, to be sensitive only to the number of required attributes, but not to fan level.

METHODS

Participants were instructed to use the TTB heuristic for decisions based on memory (see Bröder & Schiffer, 2003, 2006). They had to decide which of two fictitious companies would be more successful in the future, relying on previously memorized attribute information. In TTB, attributes are processed sequentially according to their importance. Accordingly, participants had to first compare the decision options on the attribute that was most predictive of the company's success, namely, its location (in northern or southern Germany). If the companies differed on this attribute, no further attribute was to be inspected and the company with a positive value (i.e., the one indicating success) on that attribute was to be selected. If the most predictive attribute did not discriminate between the companies (e.g., if both companies were located in the south), then the attribute with the next-highest rank in importance was to be inspected. This was the manager of the company (Manager A or B). If the managers did not differ either, the third attribute was to be inspected, which was the product manufactured by the company (cups or plates). Application of TTB thus required the retrieval of one, two, or three attributes from LTM to make a decision, depending on which companies were compared (see Figure 1). Because of TTB's stopping rule, memory search should extend only to those attributes that are relevant for the decision—a selective and therefore controlled retrieval process.

To simultaneously study automatic activation of memory representations, we incorporated the fan paradigm (Anderson, 1974, 1983) into the design; that is, we also manipulated the number of attributes associated with

the companies (see Figure 1). Retrieval is typically found to take longer the more memory representations are associated with a retrieval cue. This fan effect is assumed to result from activation that automatically spreads from the retrieval cue to all associated memory representations. The relevant association is then more difficult to discriminate from the coactivated interfering representations ("network interference"; Anderson & Reder, 1999).

Participants learned the associations between company names and attributes in an initial learning phase. Attributes were chosen such that dissociable and material-specific representation areas became activated during retrieval allowing to track the activation of specific attributes: the geographical location of the company (spatial information), the face of the manager of the company (face information), and the product manufactured by the company (object information). These brain areas were defined by means of an fMRI localizer task.

Participants

Thirty-nine male, right-handed students at the University of Marburg, Germany, with normal or corrected-to-normal vision participated (mean age = 23.9 years, $SD = 2.4$ years). They gave informed consent and were reimbursed for their participation. All participants were naive with respect to the objective of the study and had no history of neurological or psychiatric illness. Three participants had to be excluded, because their responses in the decision task deviated from the decisions predicted by TTB in more than 15% of the trials. The final sample thus consisted of 36 students (mean age = 23.7 years, $SD = 2.4$ years). Because of technical problems during the functional localizer scan of one participant, the analysis of the localizer data is based on 35 participants.

Material

Twenty-four pronounceable nonwords with a length of five to six letters were taken from the ARC Nonword Database (www.psy.uwa.edu.au/MRCDataBase/uwa_mrc.htm; Rastle, Harrington, & Coltheart, 2002; see Figure 1 for examples) and used as fictitious company names. The attributes were represented by the same visual stimuli as in Khader et al. (2011, 2013; see Figure 1; for details, see Khader et al., 2011). As mentioned above, the selection of the stimuli was based on findings indicating that they are represented in dissociable posterior cortical areas. Specifically, we used faces assumed to be represented in the fusiform gyrus (Ishai, Ungerleider, Martin, & Haxby, 2000; O'Craven & Kanwisher, 2000) to code the company manager, spatial locations assumed to be represented in the inferior parietal and parahippocampal cortex (Khader et al., 2007; O'Craven & Kanwisher, 2000; Moscovitch, Kapur, Köhler, & Houle, 1995) to code where the company is located, and visual objects assumed to be represented in

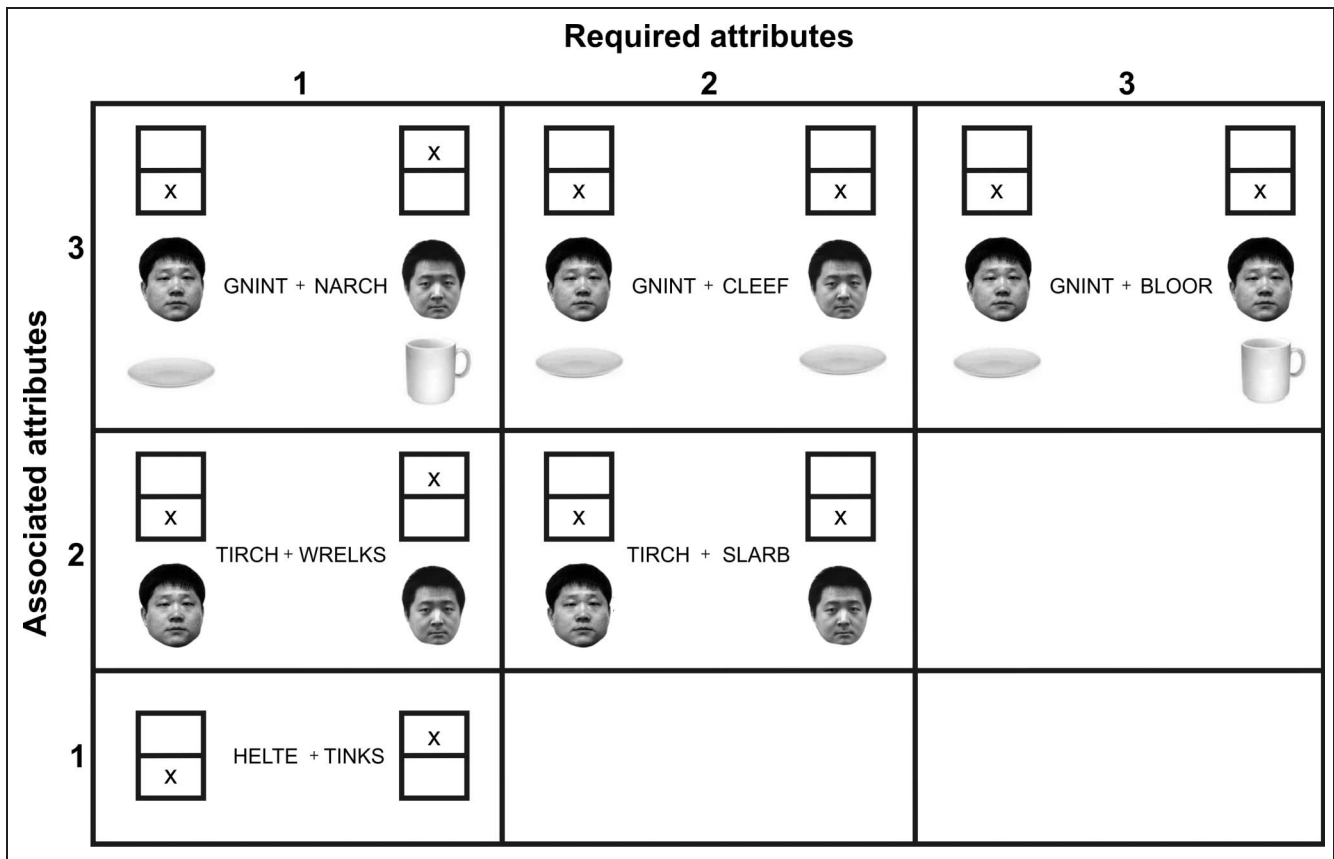


Figure 1. Overview of the experimental conditions, with examples of the pseudowords that were used as company names and the visual stimuli that were used as attributes. Companies were associated with either one, two, or three attributes (see rows). The attributes were the location of the company (north or south Germany; represented by a spatial position), the manager of the company (manager A or B; represented by a face), or the product made by the company (cups or plates; represented by an object). In each trial, the TTB decision heuristic requires the sequential retrieval of one, two, or three attributes in the order of their relative importance (see columns). The most important attribute was “location”; the second most important, “face”; and the least important, “object.”

visual association areas (Khader et al., 2007; Grill-Spector, Kourtzi, & Kanwisher, 2001; Ishai et al., 2000; Moscovitch et al., 1995) to code the product manufactured by the company.

To create different levels of associative fan, we associated the company names with one, two, or three attributes (depicted in the rows of Figure 1). Specifically, eight companies were associated with information on only the most important attribute (i.e., locations), eight companies were associated with information on the most and the second-most important attributes (i.e., locations and faces), and another eight companies were associated with all three attributes (i.e., locations, faces, and objects). To be able to compute group averages from the fMRI data (see below), we had to keep the attribute hierarchy constant across participants. Note, however, that the basic findings regarding selective retrieval in TTB seem to be independent of the specific attribute hierarchy (Khader et al., 2011, 2013). The mapping of the companies to the attribute patterns was random for each participant. The assignment of attribute values (e.g., cups or plates for the objects attribute) to companies was pseudorandom, with the restriction that every attribute

value and combination of attribute values had to occur equally frequently at each fan level.

The trials in the decision task were constructed such that only companies with the same number of attributes were compared with each other and that TTB always led to an unambiguous decision. Specifically, 16 pairs of companies with one associated attribute could be constructed by pairing the four companies with one attribute value with the four companies with the other attribute value. For these pairs, TTB required comparison of only one attribute. For companies with two associated attributes, there were 16 pairs for which TTB required comparison of only one attribute (i.e., the companies could be discriminated on the most important attribute) and 8 pairs for which comparison of two attributes was required (as only the second-most important attribute discriminated between the companies). For companies with three associated attributes, 16, 8, and 4 pairs could be constructed in which comparisons of one, two, or three attributes were required, respectively. To keep the number of trials and hence the signal-to-noise ratio comparable across the different levels of the factor “number of required attributes,” we presented company pairs

with two required attributes twice ($8 \times 2 = 16$ trials) and company pairs with three required attributes three times ($4 \times 3 = 12$ trials).¹ In summary, there were 16 trials each for company pairs with one required attribute and either one, two, or three associated attributes; 16 trials each for company pairs with two required attributes and either two or three associated attributes; and 12 trials for company pairs with three required attributes and three associated attributes, resulting in a total of 92 experimental trials.

Procedure

Learning Tasks prior to the Decision Task

The experiment started with several learning tasks in which participants were taught (1) the associations between company names and attributes, (2) how to use TTB, (3) the attribute hierarchy (i.e., how important the various attributes were for predicting a company's success), and (4) the attribute direction (i.e., which of the two locations, managers, or objects, respectively, indicated success of a company and which not). All learning tasks are described in detail in Khader et al. (2011, 2013).

In the first learning task, participants learned to associate each of the 24 company names with one, two, or three attribute stimuli (depending on the fan level) by trial and error in a self-paced way. For each attribute, they learned the attribute value by selecting one of the two picture stimuli (e.g., one face or the other), followed by feedback. The correct stimulus was then presented until participants started the next trial. Participants were instructed not to verbalize the stimuli but to encode them visually. After all attributes of a company had been learned (with the learning criterion that correct responses had been given twice in a row for all attributes), the next company was presented. After all companies had been presented, the whole learning cycle was repeated (with the companies and their attributes presented in a new random order) until perfect performance was achieved in two successive learning cycles. This task took on average 1 hr 42 min (range: 1 hr 00 min to 3 hr 45 min). Participants returned to the lab on the following day. They freshened up their attribute knowledge until again reaching the learning criterion. This took between 6 and 60 min.

In the subsequent strategy-learning task, participants were trained to make decisions using TTB in a fictitious applicant selection scenario. Specifically, they were asked to use TTB to indicate (based on three attributes such as programming experience, presented along with their importance for the decision) which of two candidates would be more suitable for the job. Only pairs of applicants were used in which TTB led to a different decision than a strategy that integrates across all attributes (e.g., an equal-weight strategy). This enabled us to ensure that the participants indeed used TTB. This task took between 3 and 20 min.

In a final learning task, participants learned (by trial and error) the attribute hierarchy, that is, how important each attribute was for the decision, and which of the two values of each attribute indicated success. Each attribute was presented separately, and participants had to indicate its importance (10, 9, or 8, respectively, with higher numbers indicating higher importance) by pressing the F10, F9, or F8 keys, respectively. This task was repeated until correct responses were given for all attributes three times in a row. Participants were then presented with the two stimuli of each attribute (e.g., cup and plate for the product attribute) and asked to select which stimulus indicates success until correct responses were given for all attributes twice in a row. To ensure that participants were able to apply the attribute hierarchy and direction quickly during the subsequent decision task, we had them repeat this task under time pressure (only 2 sec to respond). Participants needed 5–20 min to complete this task.

Decision Task

In the main task, the decision task with fMRI recorded, participants were shown pairs of company names, with one presented on the left and the other one on the right side of a fixation cross (until a response was given) and asked to decide, using TTB, which company would be more successful in the future. The interval between a decision and the next trial was randomly set to 2, 4, or 6 sec. Stimuli were projected on a canvas visible via mirrors mounted on the MRI head coil. Responses were given via two MRI-compatible response boxes attached to the participants' thighs. The company on the right side was selected by pressing (with the index finger) a button on the right response box; the company on the left side, by pressing a button on the left response box. Participants were instructed to decide as quickly and as accurately as possible. No feedback was provided during the fMRI session.

In addition to the six experimental conditions (see Figure 1), the decision task included a baseline condition with 16 trials (randomly interspersed among the others) in which no decision was required and thus no attributes had to be retrieved. Here, the same company name was shown on the left and the right side of the fixation cross, and participants were instructed to press both response buttons simultaneously. Thus, in the baseline condition, participants were exposed to the same visual stimulation as in the experimental conditions and were also required to respond, but, importantly, they did not need to retrieve any information from memory.

The 92 experimental + 16 baseline trials were equally distributed across two runs. Each run lasted about 10–12 min, depending on participants' RTs. Before the first run, several practice trials were administered to familiarize the participant with the testing procedure. Between the two runs, an anatomical reference volume was recorded, which took about 10 min.

Finally, a functional localizer task was administered to identify attribute-specific processing areas. Here, participants were presented with pictures of locations, faces, and objects that were either part of the learned attribute set or new (for each type two old and two new pictures). The task was to discriminate between old and new items, that is, to make an old–new decision by pressing the left or right button (counterbalanced across participants). Each stimulus was presented centrally for 2 sec, followed by a fixation cross for 4–7.5 sec (varied randomly in steps of 500 msec). Trial order was random. Each stimulus was presented six times, resulting in 72 trials with a total duration of 9 min and 30 sec. The rationale for the localizer task was based on the theory of cortical reactivation (e.g., Squire & Alvarez, 1995; Damasio, 1989; for reviews, see Danker & Anderson, 2010; Khader & Rösler, 2009), which states that information is stored in a material-specific way in those brain areas that are also active during the sensory processing of the information.

fMRI Data Acquisition, Preprocessing, and Statistical Analysis

Data Acquisition and Preprocessing

Participants lay in the MRI scanner in supine position with their head immobilized by a soft foam pillow to minimize involuntary head movements. Headphones were used to dampen scanner noise. Anatomical and functional imaging was performed with a 1.5T MR scanner (Signa, GE Medical Systems, Fairfield, CT). Functional BOLD images with 19 oblique slices covering the whole brain were acquired with a T2*-weighted EPI sequence (repetition time [TR] = 2 sec, echo time [TE] = 60 msec, flip angle = 80°, field of view [FOV] = 240/240 mm, matrix = 64 × 64, ascending slice acquisition, slice thickness = 5 mm, interslice gap = 1 mm, in-plane resolution = 3.75 × 3.75 mm) using a standard quadrature head coil. Anatomical whole-head images were acquired from

124 axial slices (1.4 mm thick) using a spoiled gradient recalled acquisition sequence (FOV = 240 × 180 mm, TE/TR = 6.0 msec/33.0 msec, flip angle = 40°, 256 × 192 acquisition matrix, in-plane resolution = 0.9375 × 0.9375 mm).

All analyses were performed with the BrainVoyagerQX software package (www.brainvoyager.com). The first four volumes of each run were discarded to allow for signal equilibration. After motion and slice scan time correction, temporal filtering (0.01 Hz high-pass), and linear trend removal, the functional data were aligned with the individual anatomical reference from the same session, transformed into Talairach space (Talairach & Tournoux, 1988), spatially smoothed with a Gaussian kernel (FWHM = 8 mm) and z standardized for each run. The experimental conditions were modeled with separate predictors in a random-effects general linear model. This model also included six motion parameter vectors from the realignment procedure to account for signal variance induced by head motion.

Definition of ROIs

The functional localizer was used to identify the brain areas involved in the representation of the different attributes. Responses to each were modeled with boxcar functions of 1 TR (2 sec) length, that is, the time that the stimuli were shown, convolved with the model HRF. Each attribute category was contrasted with the two other categories (with contrast coefficients 2, -1, -1), yielding attribute-specific ROIs.

With respect to the face attribute, numerous studies have shown the fusiform gyrus to play a central role in face processing (e.g., O’Craven & Kanwisher, 2000). Therefore, an ROI was defined by masking the activation pattern found by the functional localizer ($p < .01$ uncorrected), with an anatomical template of the fusiform gyrus as provided by the BrainVoyager software (see Figure 2A and the upper part of Table 1).

Figure 2. Face- and location-specific areas (ROIs) in the posterior cortex as determined by the functional localizer. (A) The face ROI was defined by an overlap of the activation with an anatomical template of the fusiform gyrus (shown in pink). The overlap is shown in brown. (B) For locations, the area that included the voxels with the highest t values was selected, located in the left supramarginal gyrus (see Methods for details). Activations are projected on the anatomical volume or partially inflated cortex reconstruction of one participant.

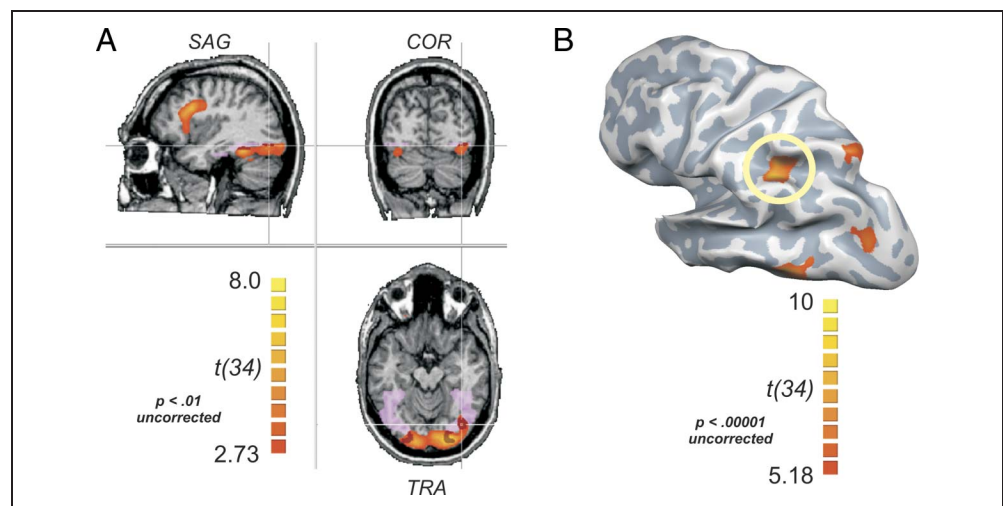


Table 1. Material-specific Posterior Representation Areas (Face and Location ROIs) as Determined by the Functional Localizer

<i>Region</i>	<i>BA</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t(34)</i>	<i>No. of Voxels</i>
<i>Faces</i>						
<i>p</i> < .01 uncorr.						
Lingual/fusiform gyrus	18/37	10	−85	−15	9.23	25633
<i>Anatomical template</i>						
Fusiform gyrus		−1	−48	−16		21819
<i>Overlap of activation and anatomical template</i>						
Fusiform gyrus	18/37	15	−80	−14	9.23	2092
<i>Locations</i>						
<i>p</i> < .00001 uncorr. ^a						
Left supramarginal gyrus	40	−38	−44	32	9.05	2231

BA = Brodmann's area; xyz = Talairach coordinates; *t* = peak *t* value.

^aThe significance threshold was adjusted such that the number of voxels was comparable to that of the face ROI.

For the location attribute, the respective contrast yielded more than one posterior brain area when it was thresholded at the same significance level as used for the face ROI. We therefore chose the area that included the voxels with the highest *t* values, which was located in the left supramarginal gyrus (see Figure 2B and the lower part of Table 1). To define the ROI, we adjusted the significance threshold to $p < .00001$ uncorrected, such that the number of voxels in this area was roughly comparable to that of the face ROI (see Table 1).

In contrast to our previous study (Khader et al., 2011), in which the same stimulus material was used, we did not find a reliable ROI for the object attribute. However, as will be explained below (see Results), the face and location attributes are sufficient to delineate specific effects of controlled and automatic retrieval processes.

Statistical Analysis

First, we investigated the effects of controlled and automatic activation in the material-specific posterior representation areas. To this end, BOLD signals were aggregated across all voxels of an ROI.² Conditions were then contrasted by means of *t* tests of average beta weights. We assumed that the activation within an ROI would increase both when the respective attribute was required for the decision (controlled retrieval) and when it was merely associated with the decision option (automatic activation).

Second, we attempted to locate the different retrieval processes within the frontoparietal network. For that purpose, we delineated, by means of a whole-brain analysis, the brain areas that were generally related to the

increasing cognitive effort associated with retrieving an increasing number of required and associated attributes, respectively. To account for the fact that RTs varied substantially across trials (depending on the number of required and associated attributes, but also due to substantial inter- and intraindividual variations in RT within an experimental condition), we adjusted the regressor functions by convolving the model HRF with a boxcar function with length = RT.

Neural correlates of automatic memory activation were captured by contrasting conditions with different numbers of associated attributes (i.e., fan levels), while keeping the number of required attributes constant (see Figure 1)—that is, contrasts of $1 < 2$ and $2 < 3$ associated attributes for trials in which one attribute was required and of $2 < 3$ associated attributes for trials in which two attributes were required.

Neural correlates of controlled retrieval, that is, the selective retrieval of attribute information as required by TTB, were captured by isolating voxels that showed systematic signal increases with an increasing number of required attributes, while keeping the number of associated attributes constant. Trials in which one, two, or three attributes were required (using companies that are associated with three attributes; see the first “column” of the experimental design as depicted in Figure 1) were combined with the baseline condition in a parametric contrast ($0 < 1 < 2 < 3$ required attributes). This contrast was computed by means of a conjunction analysis of two contrasts (with coefficients $-3, -1, 1, 3$ for the first and $1, 1, 1, 1$ for the second contrast). Note that such a parametric contrast could, in principle, also be conducted for

the analysis of automatic activation, by combining the baseline condition with the three conditions with different numbers of associated attributes. However, as the baseline condition included companies varying in the number of associated attributes, we refrained from conducting this analysis.

For the parametric contrast of controlled retrieval, we chose a significance threshold of $p < .001$ uncorrected, similar to our previous fMRI study. For the contrast of automatic retrieval, we chose a slightly lower significance level of $p < .005$, because behavioral effects of fan level are substantially smaller than the effects of required attributes (see below and Khader et al., 2013).

RESULTS

Behavioral Data

For the RT analysis, incorrect decisions (i.e., responses inconsistent with TTB) and outliers ($>3 SD$, computed separately for each participant and condition) were excluded. As can be seen in Figure 3, both RTs and error rates in the decision task increased with both the number of attributes required by TTB and the number of attributes associated with the companies, replicating previous findings (Khader et al., 2011, 2013; Bröder & Gaissmaier, 2007). An independent assessment of these effects is possible only when one factor is varied while the other is kept constant. Therefore, we will assess the effect of the number of required attributes only between conditions with the same number of associated attributes

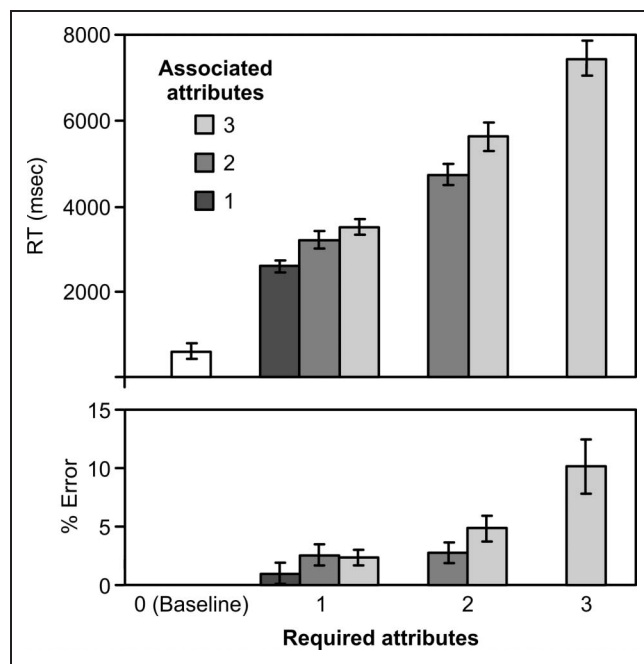


Figure 3. RTs and error rates in the decision task (the error bars represent standard errors of the mean), showing that both measures increased not only with the number of attributes required for a decision but also with the number of attributes associated with a company.

and the effect of the number of associated attributes only between conditions with the same number of required attributes.

For companies with three associated attributes, there was a main effect of the number of required attributes (1, 2, 3), $F(2, 70) = 94.62, p < .001$. t tests revealed significant differences between trials with one versus two and two versus three required attributes, $t(35) = 7.87, p < .001$, and $t(35) = 8.25, p < .001$, respectively. For companies with two associated attributes, the difference between trials with one versus two required attributes was also significant, $t(35) = 6.90, p < .001$ (as we had directional hypotheses, all p values are one-tailed and Bonferroni-corrected for three tests).

For companies with one required attribute, automatic activation was reflected by a main effect of the number of associated attributes (1, 2, 3), $F(2, 70) = 17.67, p < .001$. t tests revealed a significant difference between companies with one versus two associated attributes, $t(35) = 3.59, p = .002$. For companies with two required attributes, the differences between trials with two versus three associated attributes was also significant, $t(35) = 3.82, p < .001$. All in all, these results show that the RTs were modulated by both controlled retrieval and automatic activation.

Because of the intensive training of attribute knowledge and the decision strategy, error rates were very low. As Figure 3 (bottom) shows, the pattern of error rates across conditions was very similar to the pattern of RTs, showing increases with the number of required and associated attributes. For companies with three associated attributes, the statistical analysis revealed a significant main effect of the number of required attributes (1, 2, 3), $F(2, 70) = 7.86, p < .01$. t tests showed that the differences between one and two, as well as between two and three, required attributes were significant, $t(35) = 2.22, p < .05$, and $t(35) = 2.41, p < .05$, respectively. Effects of the number of associated attributes did not reach significance.

fMRI Data

Controlled and Automatic Activation of Attribute Knowledge in Material-specific Posterior Brain Areas

As outlined in the Methods, for faces and locations, we identified material-specific areas (ROIs) in which the respective attributes are assumed to be represented. The location attribute was the most important one for the decision. It was associated with every company and had to be inspected in every trial. The face attribute was second-most important, was not associated with every company, and had to be retrieved only in a subset of trials. The face ROI was therefore crucial in capturing effects of controlled and automatic memory activation, with activation being expected to increase when faces were required or only associated. The location ROI, by

contrast, served as a control and was not expected to show such effects, as locations were associated and required in every trial.

We expected that controlled activation would be reflected in activation modulated by the retrieval demands of TTB, that is, whether one, two, or three attributes were required for the decision (see the “columns” of the experimental design in Figure 1). Generally, to the extent that an ROI is sensitive to the controlled activation of the attribute it represents, it should show higher activation when the attribute is required for the decision than when it is not required. Accordingly, the face ROI should show increased activation when two versus one attribute(s) are required (locations + faces vs. locations only). Such a contrast can be computed for companies with two associated attributes (locations and faces) as well as for companies with three associated attributes (locations, faces, and objects). As can be seen in the first two rows of Table 2, both of these contrasts were significant in the face ROI, suggesting a boost of activation in the attribute-specific area when the respective attribute was required for a decision. This shows that the face ROI is sensitive to the requirement to retrieve face information during decision-making.

However, further analyses are necessary to show that this boosting in the face area is specific to the controlled retrieval of faces. First, an additional requirement to retrieve attributes other than faces—that is, objects—should not lead to comparable boost in the face ROI. Accordingly, we contrasted activation in the face ROI for trials differing in the requirement to retrieve objects. As shown in the third row of Table 2, this contrast yielded a smaller effect (as indicated by smaller beta weights and *t* values). Second, when faces are required, there should be no boost in the ROIs representing other attributes, that is, locations. A contrast of trials in which faces were required versus not required showed smaller effects in the location ROI than in the face ROI (Rows 4 and 5 vs.

Rows 1 and 2 in Table 2). Finally, a contrast of trials differing in the requirement to additionally retrieve objects in the location ROI also yielded a rather small effect (shown in Row 6 of Table 2). Overall, these results suggest that the increased activation in the face ROI when faces are required for a decision does not reflect a general effect of the requirement to retrieve an additional attribute, but a controlled and specific boosting. This is in accordance with previous findings (Khader et al., 2011).

Automatic activation of attributes should be reflected in neural activation that is modulated by fan level, that is, whether one, two, or three attributes are associated with the companies (see the different “rows” of the experimental design in Figure 1). If the fan effects apparent in the behavioral data are due to the activation of associated but currently not required attributes, then the attribute-specific areas should show higher activation when the respective attribute is associated with the companies than when not. Accordingly, the face ROI should show higher activation when two versus one attributes are associated (locations + faces vs. locations only), but only one (locations) is required. As can be seen in the first row of Table 3, this contrast was significant (depicted as the left-most bar in Figure 4A), indicating an increase in activation of the face ROI when faces were associated with the companies. This provides evidence that the face ROI is sensitive to the available, although irrelevant, knowledge of the face attribute. The specificity of this effect is substantiated by the finding that the additional association of objects did not lead to a significant activation increase in the face ROI (see the two other possible comparisons between fan levels in Rows 2 and 3 of Table 3, depicted as the second and third bars in Figure 4A). Moreover, when faces are associated with the companies, there should be no increased activation in ROIs representing attributes other than faces, that is, locations. Consistent with this prediction, the contrast of

Table 2. Controlled Activation in Material-specific Posterior Representation Areas: Effects of the Number of Required Attributes

<i>Contrast Name</i>	<i>Beta</i>	<i>SE</i>	<i>t</i> (35)	<i>p</i>
<i>Face ROI</i>				
2 vs. 1 required (Loc + Face vs. Loc), 2 associated	0.615	0.143	4.291	<.001
2 vs. 1 required (Loc + Face vs. Loc), 3 associated	0.571	0.139	4.114	<.001
3 vs. 2 required (Loc + Face + Obj vs. Loc + Face), 3 associated	0.416	0.150	2.772	<.01
<i>Location ROI</i>				
2 vs. 1 required (Loc + Face vs. Loc), 2 associated	0.430	0.138	3.178	<.01
2 vs. 1 required (Loc + Face vs. Loc), 3 associated	0.140	0.128	1.091	<i>ns</i>
3 vs. 2 required (Loc + Face + Obj vs. Loc + Face), 3 associated	0.384	0.146	2.629	<.05

Beta = average beta value difference; Loc = location; Obj = object.

Table 3. Automatic Activation in Material-specific Posterior Representation Areas: Effects of the Number of Associated Attributes

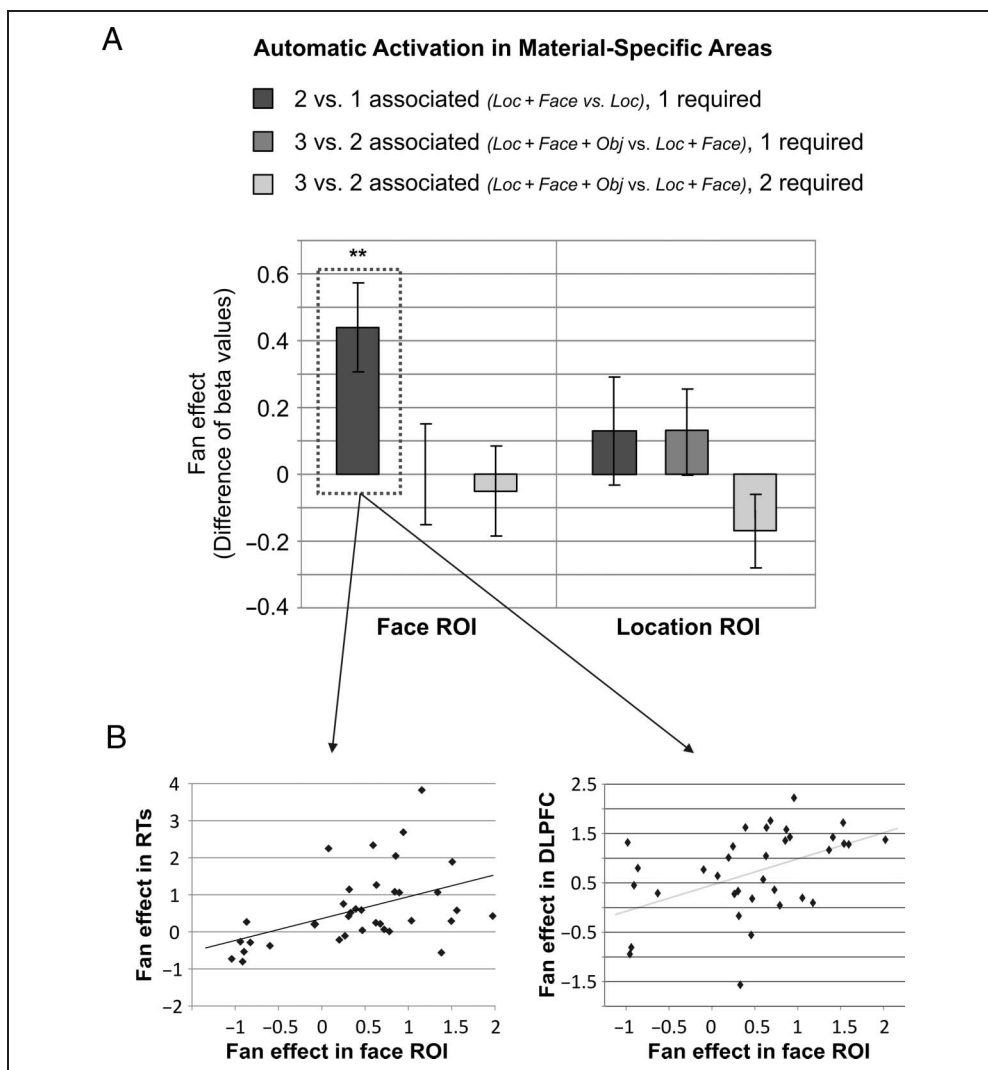
Contrast Name	Beta	SE	t(35)	p
<i>Face ROI</i>				
2 vs. 1 associated (Loc + Face vs. Loc), 1 required	0.444	0.133	3.336	<.01
3 vs. 2 associated (Loc + Face + Obj vs. Loc + Face), 1 required	-0.000	0.151	-0.001	ns
3 vs. 2 associated (Loc + Face + Obj vs. Loc + Face), 2 required	-0.044	0.134	-0.325	ns
<i>Location ROI</i>				
2 vs. 1 associated (Loc + Face vs. Loc), 1 required	0.133	0.161	0.827	ns
3 vs. 2 associated (Loc + Face + Obj vs. Loc + Face), 1 required	0.132	0.125	1.053	ns
3 vs. 2 associated (Loc + Face + Obj vs. Loc + Face), 2 required	-0.166	0.110	-1.519	ns

Beta = average beta value difference; Loc = location; Obj = object.

faces being associated versus not associated was not significant in the location ROI (Row 4 of Table 3). Also, the additional association of objects was not accompanied by an increase in activation of the location ROI (Rows 5

and 6 of Table 3, depicted as the two bars on the right of Figure 4A). These results support the specificity of the fan-related activation. Last but not least, the increased activation in the face ROI when faces were associated

Figure 4. (A) Automatic activation in posterior material-specific representation areas. Shown are the different fan effects (contrasts of different numbers of associated attributes) for the face and location ROIs. Activation in the face ROI significantly increased when faces were additionally associated, but irrelevant. An additional association of objects did not lead to a significant activation increase in the face ROI. Moreover, in the location ROI the additional associations of neither faces nor objects led to a significant activation increase (see Table 3 for statistical values). (B) Correlations of the face-specific fan effect in the face ROI with the behavioral data (left graph) and with the corresponding effect in the left DLPFC (right graph). Both correlations were significant with $p < .05$, suggesting that the fan-related activation in the posterior representation area is behaviorally relevant and linked to prefrontal retrieval processes.



(i.e., the difference in average beta values in the face ROI for two vs. one associated attribute(s) when only one attribute was required) was found to be correlated with the amount of behavioral slowing in the RTs (the RT difference between the two conditions), with $r = .46$, $p < .01$ (Figure 4B, left graph).

Activation in the Frontoparietal Retrieval Network

Having investigated controlled and automatic memory activation in the attribute-specific representation areas, we examined how the frontoparietal network responded to the manipulation of controlled and automatic retrieval. We therefore ran whole-brain analyses with factors number of required and number of associated attributes.

As outlined in the Methods, we tested for controlled retrieval by means of a parametric contrast representing the conditions with the different numbers of required attributes. The results of this analysis are shown in Figure 5A and the upper part of Table 4. The left dorsolateral pFC (DLPFC; middle frontal gyrus, BA 9/46) and the left superior parietal lobe (BA 19/39) responded maximally to the increasing number of required attributes (accompanied by a smaller activation in the left precuneus). These areas correspond closely to those found in two previous experiments on controlled retrieval in TTB (see Figure 3 in Khader et al., 2011). To further verify this overlap, we used the activation clusters in the left middle frontal and left inferior parietal lobe of the previous study (Experiments 1 and 2) as ROIs. These analyses revealed that effects of controlled retrieval were also highly significant in these regions ($p < .001$). This correspondence is important, as we used different attribute hierarchies across studies. Accordingly, the increased activations in the frontoparietal network are not material-specific, suggesting that they reflect general mechanisms of controlled and sequential memory retrieval as required by the TTB strategy.

In the next step, we examined effects of the number of associated attributes in the frontoparietal network, which can be assumed to reflect retrieval processes related to automatic activation of attributes that are not required for the decision. As will be shown, automatic retrieval showed similar but also distinct activations as compared to controlled retrieval.

As can be seen in Figure 5B and the lower part of Table 4, a higher number of associated attributes (i.e., fan level) was accompanied by increased activation in the left DLPFC, the right frontopolar cortex (BA 10), and the left precuneus. More specifically, these areas showed higher activation for two than for one associated attribute(s), that is, for locations + faces versus locations only, when only locations were required. Two further contrasts between fan levels can be used to examine effects of automatic activation (see Figure 1), namely, comparisons of trials with three versus two associated

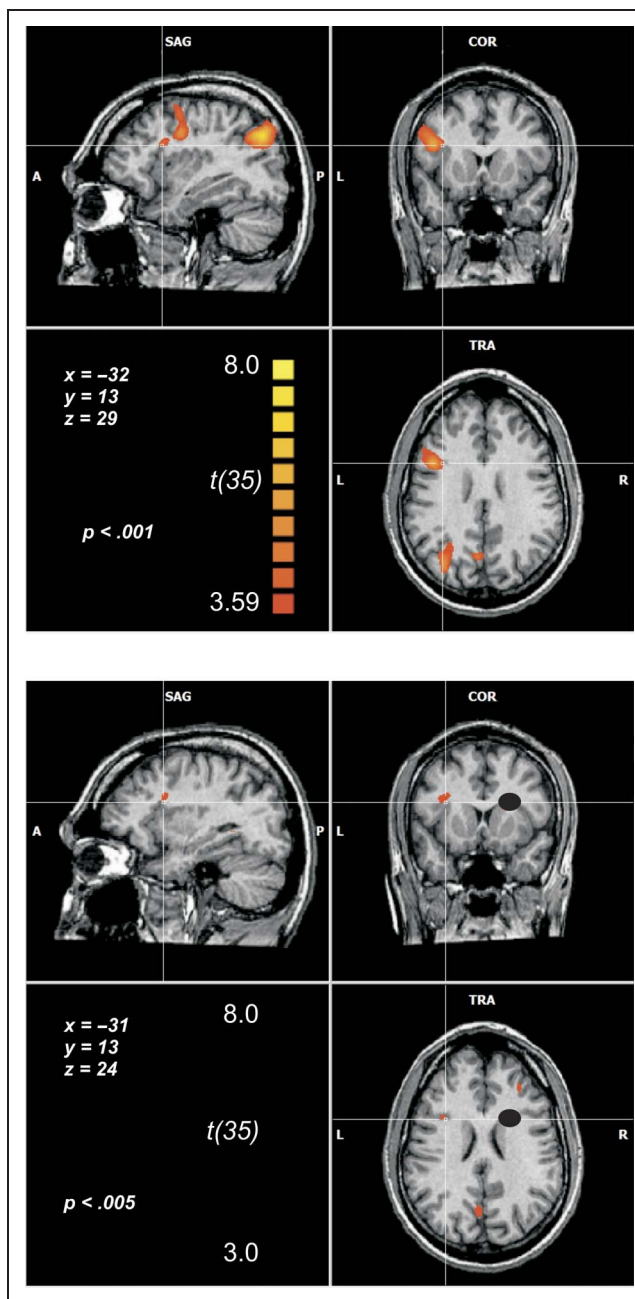


Figure 5. Common and distinct activations in the frontoparietal network for controlled and automatic retrieval. (A) Controlled retrieval was captured by means of a parametric contrast of conditions with an increasing number of required attributes, revealing activations in the left DLPFC and left superior parietal lobe, accompanied by a smaller activation in the left precuneus (see also Table 4, upper part). (B) Automatic retrieval was captured by means of contrasting two versus one associated attribute(s), that is, locations + faces versus locations only, when only locations were required. This contrast also revealed activation in the left DLPFC (accompanied by activations in the left precuneus and right frontopolar cortex; see Table 4, lower part), but, importantly, no significant activation of the left superior parietal lobe. Activations are projected on the anatomical volume of one participant.

attributes (locations + faces + objects vs. locations + faces) when either one or two attributes are required. These contrasts showed no significant effects. Note that the contrast that did reveal significant activations might be considered as the “purest” one to capture effects of automatic memory activation. Here, two conditions are compared with minimal numbers of additionally associated, but irrelevant, attributes (zero vs. one). The data for the other contrasts might be considerably noisier because of the higher numbers of associated and required attributes.

To further substantiate the functional role of the left DLPFC in automatic memory activation, we correlated the fan-related increase in activation in this area with the respective effect in the relevant representation area (i.e., in the face ROI). These analyses revealed a significant positive correlation of $r = .36$ ($p < .05$; see Figure 4B, right graph). This finding corroborates the link between the coactivation of attribute knowledge that is irrelevant for the decision and prefrontal retrieval processes.

The results so far show that the left DLPFC and the left superior parietal cortex responded to controlled activation and that the left DLPFC along with the right frontopolar cortex responded to automatic activation. Thus, as expected, the left pFC was sensitive to both types of retrieval processes. To further substantiate that controlled and automatic retrieval processes share a common neural substrate, we conducted an ROI analysis to test whether the fan effect was also significant in the voxels in the middle frontal/precentral gyrus (BA 6/9/46) that were found to be sensitive to the number of required attributes (see Table 4). In this ROI, activation was significantly affected by fan level (i.e., 2 vs. 1 associated attributes with one attribute required), $t(35) = 1.778$, $p < .05$ (one-tailed). Note that

this ROI is much larger (7909 voxels) than the set of voxels that proved to be significant in the direct test of automatic retrieval (285 voxels; see Table 4). This finding speaks for the robustness of the fan effect—that is, the fan-related activation is not restricted to the voxels that showed up in the direct analysis. Taken together, the common activation for automatic and controlled activation in the DLPFC suggests that this brain area responds to general retrieval effort.

In addition to the common activation in the left DLPFC, controlled and automatic retrieval also showed distinct activation patterns, namely, the right frontopolar cortex for automatic retrieval and the left superior parietal cortex for controlled retrieval. Whereas we had no a priori expectations for the right frontopolar cortex, the result pattern for controlled retrieval in the left superior parietal cortex (BA 19/39) replicates previous findings with the same paradigm (Khader et al., 2011) and is consistent with the notion that it mediates WM updating processes (Borst & Anderson, 2013; Anderson et al., 2008; Sohn, Goode, Stenger, Carter, & Anderson, 2003). In this line of reasoning, the sequential comparison mandated by TTB specifically activates the parietal cortex because of the necessity to update the contents of WM with each additionally required attribute. As additionally associated but irrelevant attributes are not part of TTB’s sequential retrieval process (and thus do not need to be updated), a fan effect should not appear in this area. Consistent with this hypothesis, the left superior parietal lobe did not show an effect of fan level, even when further lowering the significance threshold from $p < .005$ (as in Figure 5B) to $p < .05$. Note that the contrast for automatic retrieval also yielded activation in the left precuneus that roughly corresponded in terms of location and size to the respective activation found for the contrast for controlled retrieval

Table 4. Brain Areas in the Frontoparietal Network that Reflect Controlled Retrieval (the Number of Required Attributes) and Automatic Retrieval (the Number of Associated Attributes), as Obtained from Whole-brain Analyses

<i>Region</i>	<i>BA</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t(35)</i>	<i>No. of Voxels</i>
<i>Controlled Retrieval</i>						
$p < .001$ uncorrected						
L middle frontal/precentral gyrus	6/9/46	−40	7	38	6.11	7909
L superior parietal lobe	19/39	−32	−68	33	7.70	5560
L precuneus	31	−5	−64	25	5.11	754
<i>Automatic Retrieval</i>						
$p < .005$ uncorrected						
L middle frontal gyrus	6/9/46	−32	12	29	3.74	285
R middle frontal gyrus	10	28	36	18	3.57	573
L precuneus	31	−4	−66	21	3.77	414

BA = Brodmann’s area; xyz = Talairach coordinates; t = peak t value; L = left; R = right.

(see Table 4). Therefore, the lack of parietal activation for the fan effect cannot be due to global differences between the contrasts, such as a generally weaker signal-to-noise ratio.

Additional Analyses

As shown above, our analyses clearly speak for a role of the DLPFC in the controlled and automatic activation of memory representations during memory-based decision-making. This result is consistent with our previous fMRI study (Khader et al., 2011) and other studies that have found a link between the DLPFC and retrieval control (see, e.g., Penolazzi, Stramaccia, Braga, Mondini, & Galfano, 2014; Jaeger, Selmezy, O'Connor, Diaz, & Dobbins, 2012; Wheeler & Buckner, 2003). However, it should be noted that numerous studies have also highlighted a possible role of the ventrolateral pFC (VLPFC; encompassing BA 45/47) for this function (see, e.g., Barredo, Öztekin, & Badre, 2013; Badre & Wagner, 2007). Therefore, we directly tested for VLPFC activation in our study by computing ROI analyses of BA 45 and 47. These tests, however, did not show any significant effects, neither for controlled [$t(35) = .91$; $p = .371$] nor for automatic retrieval [$t(35) = 1.18$; $p = .246$]. One possible explanation of the lack of an activation in the VLPFC in our studies is that we used visual information, whereas the studies reviewed by Badre and Wagner (2007) mainly employed verbal material. In addition to the type of material, also the specific cognitive operation involved in the task might determine the site of activation within the lateral pFC. As has been delineated in reviews by Ranganath (2006) and Ranganath and D'Esposito (2005), the DLPFC is more strongly involved in the relational processing of maintained items, whereas the VLPFC is more strongly involved in maintaining task-relevant items. Our task consists of comparing retrieved attributes and thus requires relational processing, and this could thus be the reason for the more dorsal activation we consistently find in our studies.

Finally, given that several studies have found support for a contribution of the hippocampus in memory processes (see, e.g., Derdikman & Knierim, 2014, for a recent review), one might have suspected hippocampal involvement in this study as well. Our results, however, did not provide evidence for a contribution of the hippocampus. But note that this does not rule out that the hippocampus contributes to memory-based decision-making in general; it only suggests that it does not respond to an increasing number of associated or required attributes. However, it is also possible that the retrieval of highly overlearned associations, as realized in our study, might indeed be accomplished with only minimal hippocampal support.

DISCUSSION

What are the retrieval dynamics in memory-based decision-making and how are they reflected neurally? On the basis

of previous findings (Khader et al., 2011, 2013), we distinguished between two fundamental and distinct processes that contribute to memory-based decision-making—automatic activation and controlled retrieval of memory representations—and investigated their neural underpinnings by drawing on the neural model of ACT-R theory (e.g., Anderson et al., 2008). To disentangle these processes during memory-based decision-making, we combined an experimental paradigm developed to examine the neural correlates of selective and sequential memory retrieval in people's decisions (Khader et al., 2011) with the fan manipulation (Anderson, 1974, 1983). The results show that both the automatic activation of all attributes associated with the decision options and the controlled sequential retrieval of attributes can be traced in material-specific brain areas. Moreover, the two facets of memory retrieval were associated with distinct activation patterns within the frontoparietal network.

To investigate the activation of memory representations, we defined, by means of a functional localizer, areas that are specific for a decision attribute and that, according to the theory of neocortical reactivation (e.g., Squire & Alvarez, 1995; Damasio, 1989; for reviews, see Danker & Anderson, 2010; Khader & Rösler, 2009), are assumed to store the respective memory representations. Crucial for this study and the specific attribute hierarchy was the face-specific area located in the fusiform gyrus (see Figure 2A). It showed increased activation when the face attribute was required for the decision, but also when it was merely associated with a decision option. This indicates the existence of both controlled and automatic activation of memory representations during decision-making, with both processes affecting decision times.

We further expected that automatic and controlled retrieval would be mediated by distinct subcomponents within the frontoparietal network. Specifically, based on the current neural implementation of the ACT-R cognitive architecture (Borst & Anderson, 2013; Anderson et al., 2008), we assumed that the retrieval of stored information is managed by the lateral pFC (termed the “declarative module”), a notion that is also supported by other neural models of memory (e.g., Badre & Wagner, 2002; Buckner & Wheeler, 2001). Furthermore, we assumed, based on ACT-R, the updating of the current task representation in WM to be mediated by the superior parietal cortex (termed the “imaginal module,” also referred to as the “problem-state module”).

Our study indeed showed an activation pattern consistent with these predictions: The left lateral pFC responded systematically to the number of attributes required for a decision (replicating our previous findings; Khader et al., 2011). In addition, we found that the activation of the lateral pFC also increased with the number of associated attributes (i.e., fan level). The apparent sensitivity of this area to both controlled and automatic retrieval suggests that it is related to general retrieval effort. According to ACT-R, the declarative module, located in

the lateral pFC (BA 9, 44, 45, and 46) serves the role of maintaining the retrieval cue (Anderson et al., 2008). Therefore, its activation depends on the duration of the retrieval process. Our data are consistent with this notion: Increasing the number of required attributes made retrieval more effortful, prolonged decision times, and increased the activation in the lateral pFC. This also held for the number of associated attributes: With retrieval interference arising from task-irrelevant associations, the retrieval of the task-relevant attribute becomes more effortful and thus takes longer (see Danker, Fincham, & Anderson, 2011; Sohn et al., 2003, 2005, for similar findings that the lateral pFC also responds to manipulations of fan level or associative interference).

Besides the declarative module, ACT-R assumes an imaginal module being located in the posterior parietal cortex (BA 7, 39, and 40) and reflecting the updating of task-relevant representations in WM (Borst & Anderson, 2013; Anderson et al., 2008). It is thus similar to the “focus of attention” concept in current WM theories (e.g., Oberauer, 2002; Cowan, 1999, 2001). These theories claim that “there is some part of the LTM system that is not presently in the focus of attention, but...can easily be retrieved into that focus if it is needed for successful recall” (Cowan, 2001, p. 92). Consistent with these notions, in both our previous and present studies, activation in the superior parietal cortex increased as a function of the number of attributes to be retrieved. TTB requires the sequential retrieval of attributes in the order of their importance, starting with the most important attribute. If this attribute is not differing between the companies, the next-important attribute has to be retrieved. This means that the task-relevant representation has to be updated, which requires a shift of the attentional focus to a new attribute. Importantly, the parietal cortex did not show an effect of associative fan, suggesting that it is not sensitive to retrieval interferences triggered by additional activations. This is also in line with the assumptions of ACT-R theory: As the irrelevant attributes producing the fan effect are not part of TTB’s sequential retrieval process, they do not require an updating of the task-relevant representation.

We also obtained an additional activation in the right frontopolar cortex that exclusively responded to the number of associated attributes (i.e., fan level). Together with the superior parietal cortex being exclusively related to the number of required attributes, this activation pattern constitutes a double dissociation between automatic and controlled retrieval during memory-based decision-making. The functional role of the right frontopolar cortex for automatic retrieval, however, is yet to be determined. The right pFC has repeatedly been linked to inhibitory control in different cognitive domains (Aron, 2007; Aron, Robbins, & Poldrack, 2004). With respect to memory retrieval, it has been suggested that this area might be involved in the inhibition of competing memories during the attempt to retrieve a target memory.

Whether the activation we observed here indeed reflects this kind of regulatory process to counteract fan-related interference has to be investigated in future studies.

Overall, we regard this study as an important step toward a neural model of the retrieval dynamics involved in memory-based decision-making. These dynamics can be outlined as follows: First, upon presentation of a decision option, all memory representations associated with it are automatically activated in the material-specific posterior brain areas (state of automatic activation). This leads to retrieval interference between the activated attributes, prolonging decision times and activating the left DLPFC to maintain the retrieval cue until the retrieval of task-relevant information is completed successfully. Second, the attribute that is relevant for a decision is moved into the focus of attention, leading to a boost of activation in the attribute-specific representation area (state of controlled activation). Whereas the increased retrieval effort (associated with both states of activation) is reflected by activation in the left DLPFC, the updating of WM is specifically mediated by the left superior parietal cortex.

Our findings also have implications for current theories of decision-making. The evidence for automatic activation during the decision process suggests that memory processes involved in decision-making may not operate in a purely controlled and sequential fashion, as implied by the commonly accepted process description of TTB (Gigerenzer & Goldstein, 1996). A more complete and neuronally plausible account of memory-based decision-making also needs to accommodate the automatic activation of attribute knowledge. Current cognitive models of decision-making, by contrast, typically focus either on controlled retrieval (e.g., Pachur, Hertwig, & Rieskamp, 2013; Brandstätter, Gigerenzer, & Hertwig, 2006; Gigerenzer & Goldstein, 1996; Payne, Bettman, & Johnson, 1993) or on automatic activation spread (Thomas et al., 2008; Schooler & Hertwig, 2005; Juslin & Persson, 2002; Dougherty, Gettys, & Ogden, 1999; Fiedler, 1996).

Furthermore, our work complements the “neuroeconomics” literature, which has been mainly concerned with the neural mechanisms of risk and reward processing (Rangel, Camerer, & Montague, 2008; Glimcher & Rustichini, 2004), by elaborating the mnemonic and attentional processes involved in decision-making. Given that economic decisions often involve information stored in memory (e.g., risk information, reinforcement history), a next step is to combine the insights regarding memory and reward-related mechanisms within a common framework.

The findings from this study might also contribute to a better understanding of variations in decision-making due to situational conditions, changes across the life span, and individual differences in general. For instance, the distinction between automatic and controlled retrieval bears resemblance to the distinctions between familiarity and recollection (Yonelinas, 2002), associative and strategic aspects of memory (Shing, Werkle-Bergner, Li,

& Lindenberger, 2008), and incidental and intentional/goal-directed reactivation (e.g., Kuhl et al., 2013; Nyberg, 2006). An understanding of the contribution of memory processes to decision-making may thus make it possible to explain differences in decision-making on a functional level. To illustrate, in cases where the ability to selectively retrieve specific attributes is compromised (e.g., due to a reduction of frontoparietal control functions), automatically activated attributes would have a stronger impact on decision-making, rendering decisions less consistent with decision heuristics that require controlled selective retrieval.

To conclude, this study shows for the first time that different retrieval processes contributing to memory-based decision-making are associated with distinguishable neural structures. It demonstrates the usefulness of combining memory and decision-making research with neural measures to investigate the mechanisms of decision-making on the basis of information stored in memory and to embed decision-making within a broader neurocognitive framework.

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Notes

1. Note that repeating company pairs might introduce priming effects. On a behavioral level, these would supposedly facilitate the comparison processes, leading to faster decisions. On a neural level, it has been found that repetition priming typically leads to decreased BOLD signals (for a review, see, e.g., Martin, 2007). Because the repeated pairs are those in which a higher number of attributes needs to be retrieved, the effect of the repetitions is likely, if anything, to counteract our hypothesis of prolonged RTs and higher BOLD signals when a larger number of attributes has to be retrieved.

2. Material-specific memory activation could, in principle, be also assessed by means of multivoxel pattern analysis (see Rissman & Wagner, 2012, for a review). However, the complexity of our design and, in particular, the large RT differences between some of the conditions represent a major challenge for any decoding analysis (Woolgar, Golland, & Bode, 2014; Todd, Nystrom, & Cohen, 2013). Therefore, the applicability of multivoxel pattern analysis to our data seems limited.

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