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Framing memories: How the retrieval query format shapes the neural bases of remembering

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ABSTRACT

The way memory questions are framed influences the information that is searched, retrieved, and monitored during remembering. This fMRI study aimed at clarifying how the format of the retrieval query shapes the neural basis of source recollection. During encoding, participants made semantic (pleasantness) or perceptual (number of letters) judgments about words. Subsequently, in a source memory test, the retrieval query was manipulated such that for half of the items from each encoding task, the retrieval query emphasized the semantic source (i.e., semantic query format: "Is this word from the pleasantness task?"), whereas for the other half the retrieval query emphasized the alternate, perceptual source (i.e., perceptual query format: "Is this word from the letter task?"). The results showed that the semantic query format was associated with higher source recognition than the perceptual query format. This behavioral advantage was accompanied by increased activation in several regions associated to controlled semantic elaboration and monitoring of internally-generated features about the past event. In particular, for items semantically encoded, the semantic query, relative to the perceptual query, induced activation in medial prefrontal cortex (PFC), hippocampal, parahippocampal and middle temporal cortex. Conversely, for items perceptually encoded, the semantic query recruited the lateral PFC and occipital-fusiform areas. Interestingly, the semantic format also influenced the processing of new items, eliciting greater L lateral and medial PFC activation. In contrast, the perceptual query format (versus the semantic format) only prompted greater activation in R orbitofrontal cortex and the R inferior parietal lobe, for items encoded in a perceptual manner and for new items, respectively. The results highlight the role of the retrieval query format in source remembering, showing that the retrieval query that emphasizes the semantic source promotes the use of semantic strategies via medial and L lateral PFC activations. These frontal activations are accompanied by differential recruitment of more posterior regions, depending on the type of information that had been encoded.

1. Introduction

The question asked to evaluate memory can influence the information that is retrieved and the subsequent response. Several studies have shown that the way the retrieval question is framed (i.e., the wording of a question) influences eyewitness testimony (Lindsay and Johnson, 1989; Loftus, 1996) and the likelihood of endorsing false memories (Johnson et al., 1997; Mather et al., 1997). Research on source memory has also increasingly focused on the strong influence that the retrieval question exerts on the ability to recollect a past event along with its contextual details. These studies have promoted the formalization of important theoretical approaches, notably the *source monitoring framework* (Johnson et al., 1993), and the development of key concepts in the cognitive and neuroimaging literature, such as *source-constrained retrieval* (Jacoby et al., 2005), *retrieval-orientation* (Rugg and Wilding, 2000), and *domain-sensitive biasing* (Dobbins and Wagner, 2005).

Studies have explored the impact of the retrieval question on source remembering by contrasting two distinct source retrieval tasks, one involving the retrieval of perceptual features of the items (e.g., the size of the objects) and the other entailing retrieval of semantic information about the prior encounter (e.g., the conceptual task performed at encoding). For instance, Dobbins and Wagner (2005) reported that when perceptual information about previously seen items had to be retrieved, activation was found in right (R) ventrolateral prefrontal cortex (PFC) and bilateral occipito-temporal cortices associated with visuo-perceptual processing. Conversely, when participants were prompted to retrieve semantic information about the same items significant activation was seen in left (L) ventrolateral PFC and L middle temporal region, linked to controlled semantic elaboration and monitoring of

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semantic features. Thus, when different features are required at retrieval (i.e., remembering the size of the object or the prior task performed), distinct activations are observed depending on the tasks' goals and agendas (Dobbins and Wagner, 2005; Dobbins and Han, 2006; Johnson et al., 1993; Mitchell et al., 2008; Rugg and Wilding, 2000; Speer et al., 2003).

Another factor that is known to influence source memory judgments is the number of sources mentioned in the query (Dodson and Johnson, 1993; Henkel et al., 2000; McDuff et al., 2009). When questioned about the source of a given item, participants are more likely to falsely attribute items to a source when that source is the only one mentioned at retrieval (e.g., is the item from source A?) compared to when multiple sources are mentioned (e.g., is the item from source A or source B?). More strikingly, when the query mentions a single source, performance is affected by the nature of the information that is emphasized by that query. In a study by Marsh and Hicks (1998) participants had to retrieve the task previously performed with the item which was either reading an intact word or generating a word from an anagram. Critically, the way the retrieval query was framed differed, emphasizing either one task or the other. Half of the items from each source were associated with the specific query as to whether or not the item had been generated from anagram (i.e., "generated" query format), while the remaining items from each source were associated with the query as to whether or not the item had been seen intact during encoding (i.e., "seen" query format). There was a main effect of query format, as participants were more accurate when the test question asked if the item had been generated as compared to having been seen, regardless of the actual source of the item. This query framing effect suggests that when participants were specifically queried about generating the items, the cognitive operations performed enabled them to accurately retrieve the source. Conversely, when asked whether the items had been seen, the cognitive processes carried out were not as effective. The authors propose that the "generated" query format highlights semantic operations, which are more diagnostic of the origin of the item than perceptual operations induced by the "seen" query format, independently of the encoding task. Dobbins and McCarthy (2008) extended these findings, by showing that when the query format does not promote successful strategies (as in the case of the "seen" query), subjects tend to use item memory in a heuristic fashion during source attributions, which increases false attributions of source. Moreover, Jacoby et al. (2005) and Shimizu and Jacoby (2005) have shown that specifying different sources at retrieval influenced memory not only for old items but also for new items (foils). In particular, memory for foils was superior when the retrieval query emphasized a semantic rather than a perceptual source on an earlier test. Together, these studies converge on the idea that the format of the question leads participants to inspect memory traces in qualitatively different ways.

Building on these studies, we investigated if and how the format of the retrieval query affects source memory judgments, by examining the neural activity when participants were asked to consider one source versus another source. We adapted the design proposed by Marsh and Hicks (1998) and Dobbins and McCarthy (2008) for our fMRI study. In a source recognition task, during the encoding phase, participants were asked to judge the pleasantness of words or decide about the number of letters the words contained. Subsequently, the retrieval phase required participants to remember the source of the items. For half of the items from each source, participants were prompted with the retrieval query as to whether the item came from the pleasantness task (i.e., semantic query format). For the other half of the items from each source, participants were presented with the retrieval query as to whether the item came from the letter task (i.e., perceptual query format). Importantly, both conditions entail the retrieval of the specific task performed at encoding, and therefore, one could expect that the two query formats induce similar behavioral and neural patterns. In this case, results should be equivalent regardless of how the question is framed. Alternatively, if as proposed by the *source monitoring framework* (Johnson et al., 1993), the information emphasized by the retrieval question modulates source remembering, by inducing the activation and monitoring of different features, then we expect different behavioral and neural results, depending on whether the retrieval query emphasizes one encoding task or the other.

According to this view, and in line with previous behavioral studies (Dobbins and McCarthy, 2008; Marsh and Hicks, 1998), we anticipate greater accuracy when source memory is prompted by the semantic query format compared to the perceptual query format, regardless of the actual source of the item. We predict that the behavioral advantage for the semantic format will be accompanied by increased activation in L lateral PFC, associated with semantic elaboration processes (Dobbins and Wagner, 2005; Dobbins and Han, 2006; Raposo et al., 2009), and medial PFC, which mediates retrieval of internally-generated details about the items, such as the thoughts and associations produced during the semantic (pleasantness) encoding task (Mitchell et al., 2008; Mitchell and Johnson, 2009; Simons et al., 2005; Simons et al., 2008). The semantic elaboration and retrieval of internally-generated information may increase the overlap between the semantic information being considered during retrieval and that which would have been central had the item been encountered during encoding. This increases the odds of source recollection for items encoded in the semantic task and, moreover, it reduces the likelihood of false endorsement of new items or items encoded in the perceptual task (Han et al., 2012; Raposo et al., 2009). Thus, these prefrontal operations should occur for all semantic query conditions, independently of the actual origin of the item (i.e., semantically encoded, perceptually encoded or new items). These activations are not expected in the perceptual (letter) format, which should prompt the processing of more perceptual, external details, and therefore L lateral and medial PFC activation should be attenuated. We expect regions involved in visuo-perceptual retrieval processing, notably bilateral occipito-temporal cortices, to yield greater activation when retrieval is prompted by the perceptual query format than the semantic query format.

While some regions may show differential activation depending on the item's origin (e.g., the prior encoding task), as shown by many previous studies (e.g., Johnson and Rugg, 2007; Nyberg, 2002), our main hypothesis is that if the way the source retrieval query is framed modulates recollection, then we should find differences in brain activity when the query emphasizes one source vs. the other, independently of the actual origin of the item. Such differential activations will elucidate how remembering an event's origin is modulated by the query format.

2. Method

2.1. Participants

Eighteen healthy participants (18–22 years old, 15 females) took part in the study. All participants were right-handed, native speakers of Portuguese, and had no history of neurological impairment or head injury. They all gave informed written consent to the experimental procedure, which was approved by the local ethics committee.

2.2. Materials and procedure

The stimuli consisted in 180 words, 120 were used in the

encoding and retrieval phases and the remaining 60 words were used as new words in the retrieval phase. The words had, in average (and standard deviation), 6.53 (1.66) letters, 2.13 (0.67) score in familiarity (Marques, 2004) and 2.19 (0.97) logarithmic frequency (Nascimento, 2006). The words' scores in each of these variables were matched across conditions ($p > .05$ in all cases). The same words were used for all participants.

Each participant underwent two encoding-retrieval cycles, in which both the encoding and the immediately following retrieval periods were scanned. The two cycles were counterbalanced across participants. During each encoding phase, participants were presented with written words. For half of the words participants performed a semantic task, while for the other half they performed a perceptual task. The semantic task consisted in a pleasant/unpleasant judgment on each word (i.e., pleasantness decision). It was stressed that there were no correct or incorrect responses and that they should indicate their personal preference. The perceptual task consisted in evaluating whether or not each word had six or more letters (i.e., letter decision). The semantic and the perceptual tasks were randomly presented item by item. The encoding prompt and word remained on the screen for 2500 ms, during which participants had to respond via button box using the left hand. This was followed by a blank screen of a variable duration (500, 1000 and 1500 ms) in order to optimize statistical efficiency (Dale, 1999). Each encoding phase consisted of 30 words encoded in the semantic task, 30 words in the perceptual task and 20 fixation baseline trials intermixed. During the fixation trials, a series of crosses ("+++++++") were presented and participants had to press a button with their left index finger. In total, each participant studied 120 words.

Immediately following each encoding phase, a source memory test was administered. Participants were presented with single words that were either taken from the previous encoding list or were new words. The word appeared in the center of the computer screen and below a source retrieval query was presented. The format of the retrieval query was manipulated. In particular, half of the items that had been previously encoded in the semantic task and half of the items encoded in the perceptual task were associated with the specific query as whether or not the participant had performed the pleasantness judgment. For brevity, we refer to this query as the semantic query format. The remaining items from each source were associated with the specific query as whether or not the participant had performed the letter decision. We refer to this query as the perceptual query format. Half of the new items were also prompted with the semantic query format and the other half with the perceptual query format. Thus, in the semantic query format, words that had been previously encoded in the semantic (pleasantness) task should be endorsed with a "yes" response, while words encoded in the perceptual (letter) task and new words should be endorsed with a "no" response. Similarly, in the perceptual query format, words previously studied in the perceptual (letter) task should be associated with a "yes" response, whereas words studied in the semantic (pleasantness) task and new words should have a "no" response. The semantic and perceptual retrieval formats were intermixed, being randomly presented item by item. The retrieval query and word remained on the screen for 3500 ms, during which participants had to respond via button box using the left hand. This was followed by a blank screen of a variable duration (1000, 1500 and 2000 ms). Each retrieval phase consisted of 45 words prompted with the semantic query format (15 encoded in the semantic task, 15 encoded in the perceptual task and 15 new words), and 45 words presented with the perceptual query format (15 encoded in the semantic task, 15 encoded in the perceptual task and 15 new words). There were also 30 fixation baseline trials intermixed, which consisted in a series of crosses ("+++++++") and participants had to press a button with their left index finger. Thus, the total number of words for source memory was 180.

Before performing the tasks, participants read the instructions and completed a brief training session. Presentation and timing of stimuli were controlled using EPrime software (www.psnet.com).

2.3. MRI acquisition and imaging analysis

Scanning was conducted at Sociedade Portuguesa de Ressonância Magnética on a 3-Tesla Philips MR system (Philips Medical Systems, Best, NL) using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR = 2000 ms, 34 bottom-up interleaved slices parallel to the AC-PC line, 3 mm thick, interslice gap of 0.5 mm, 2 mm × 2 mm × 3 mm in-plane resolution, FOV = 23 cm × 23 cm, matrix size = 116 × 115). Acquisition covered the entire brain. Before functional data collection, three dummy volumes were discarded to allow for T1 equilibrium. High-resolution T1-weighted anatomical images were acquired for visualization.

Preprocessing and statistical analysis of the data were performed using Statistical Parametric Mapping software (SPM8, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn MA, USA). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice collected, followed by rigid body motion correction. Functional data were spatially normalized to a canonical echo-planar imaging template using a 12-parameter affine and nonlinear transformation, and then spatially smoothed with an 8 mm Gaussian kernel.

For the encoding blocks, three conditions of interest were modeled separately: perceptual encoding task, semantic encoding task and baseline. Each condition included all trials, independently of the actual response. As for the retrieval blocks, there were seven conditions of interest modeled separately: two retrieval query format conditions (semantic query format and perceptual query format) by the three source conditions (semantic encoding, perceptual encoding and new words) and the baseline. Each condition included trials with correct and incorrect responses, as we were interested in the neural mechanisms prompted by the query format, independently of retrieval success (for a similar procedure, see Mitchell et al., 2004).[1]

Participants were treated as random effects. Data for each subject were modeled with the general linear model using the canonical hemodynamic response function (HRF). The least squares parameter estimates of the best-fitting canonical HRF for each condition of interest were used in pairwise contrasts and stored as a separate image for each subject. These images were then tested against the null hypothesis using one-tailed t tests. The analysis was performed for each participant and results were combined into a group random effects analysis. Results were thresholded at $p < .001$ uncorrected at voxel level and only clusters that survived $p < .05$ FWE corrected for multiple comparisons across the entire brain volume were considered significant.

To examine whether brain regions activated during encoding were reactivated at retrieval, as evidenced by prior studies (Danker and Anderson, 2010; Nyberg et al., 2000; Vaidya et al., 2002), two regions of interest (ROI) were defined based on the contrasts of semantic encoding task versus perceptual encoding task and vice-versa. The resulting images were used as a mask for the contrasts between the two retrieval query formats, during retrieval of

[1] We conducted the same analysis including only the trials associated with correct responses. The findings were qualitatively similar with the same neural patterns emerging. However, in this unreported analysis, some clusters did not reach statistical significance, presumably due to the lower statistical power associated with the reduction in the number of trials.

semantically encoded items and retrieval of perceptually encoded items, respectively. In this way, analysis of retrieval activity was restricted to those regions that were differentially activated for each encoding task. Given *a priori* expectations that encoding-related activity could be reactivated at retrieval and following numerous episodic memory studies (Dobbins and Wagner, 2005; Johnson and Rugg, 2007; Wagner et al., 2001), activations within the ROI were considered reliable if they consisted of five or more contiguous voxels exceeding an uncorrected threshold of $p < .001$.

3. Results

3.1. Behavioral data

Separate repeated measures ANOVAs were carried out on the proportion of correct responses and response time (RT) data. Table 1 shows the proportion of correct responses for source recognition. A repeated measures ANOVA was conducted, examining the factors of item origin (semantic encoding task vs. perceptual encoding task vs. new items) and retrieval query format (semantic query format vs. perceptual query format). Results yielded a main effect of item origin ($F(2,34)=43.04$, $p < .001$, $\eta^2=.72$) associated with higher proportion of correct responses for new items (mean=.89) compared to both semantically (mean=.82) and perceptually encoded items (mean=.60), as well as higher proportion of correct responses for semantically encoded items relative to perceptually encoded items ($p < .01$ in all cases). There was also a main effect of retrieval query format ($F(1,17)=62.97$, $p < .001$, $\eta^2=.79$), such that the semantic format (mean=.86) produced superior source recognition than the perceptual format (mean=.68). We also found a significant interaction between item origin and retrieval query format ($F(2,34)=6.35$, $p < .01$, $\eta^2=.27$). As seen in Table 1, the difference in correct responses for the semantic query format relative to the perceptual query format was larger for items encoded in the perceptual task ($t(17)=-5.10$, $p < .001$) than for items encoded in the semantic task ($t(17)=-4.38$, $p < .001$) and larger in this condition compared to new items ($t(17)=-2.23$, $p < .05$).

As our design tested source memory but not item memory, we should note that when source recognition fails, participants may remember having seen the item but fail to identify the source or they may fail to remember the item assuming it was not presented before. This is especially important in the case of items encoded in a perceptual manner where the memory trace is overall poorer. To ensure that, despite the lower source recognition scores for perceptually encoded items, participants were able to discriminate between these items and new items, we compared the correct recognition rate of perceptually encoded items to new items' intrusion rates (i.e., incorrect source recognition for new items). The proportion of correct responses for perceptually encoded items was significantly higher than the proportion of new items' intrusions following both the semantic query (mean recognition=.75; mean intrusion rate=.07; $t(17)=19.9$, $p < .001$) and the perceptual query (mean recognition=.44; mean intrusion rate=.15; $t(17)=6.1$, $p < .001$). This indicates that despite the lower scores for perceptually encoded words, participants are able to discriminate these words from new ones, through either source or item memory.

Table 1
Mean (and standard deviation) of the proportion of correct responses in the source recognition task. "Relative accuracy" denotes the difference in correct responses for the semantic query format relative to the perceptual query format.

	Retrieval query format		
Item origin	*Perceptual query format*	*Semantic query format*	*Relative accuracy*
Perceptual encoding task	.44 (.23)	.75 (.12)	.31
Semantic encoding task	.75 (.13)	.89 (.09)	.14
New items	.85 (.14)	.93 (.06)	.08

Table 2
Mean (and standard deviation) of the response times (in ms) for correct trials in the source recognition task. "Relative difference" denotes the difference in response times for the perceptual query format relative to the semantic query format.

	Retrieval query format		
Item origin	*Perceptual query format*	*Semantic query format*	*Relative difference*
Perceptual encoding task	1798 (217)	1720 (198)	78
Semantic encoding task	1778 (215)	1500 (186)	278
New items	1583 (232)	1559 (215)	25

To complement the accuracy data, we analyzed the RT for correct responses (Table 2). ANOVAs performed on mean RT for correct trials yielded a main effect of item origin ($F(2,34)=21.18$, $p < .001$, $\eta^2=.56$). Participants were faster to correctly respond to new items (mean=1571 ms) and to items previously encoded under the semantic condition (mean=1639 ms) relative to the perceptual encoding condition (mean=1759 ms; $p < .001$ in both cases). There were no differences in RTs between semantically encoded items and new items ($p > .05$). There was also a main effect of retrieval query format ($F(1,17)=42.30$, $p < .001$, $\eta^2=.71$), with faster RTs for the semantic format (mean=1593 ms) than the perceptual format (mean=1720 ms). We also found a significant interaction between item origin and retrieval query format ($F(2,34)=14.66$, $p < .001$, $\eta^2=.46$). The difference in RTs for the perceptual query format relative to the semantic query format was only significant for semantically encoded items ($t(17)=9.27$, $p < .001$), not reaching statistical significance for items encoded in the perceptual task ($t(17)=1.68$, $p > .05$) and new items ($t(17)=1.10$, $p > .05$).

3.2. Functional imaging data: encoding scans

The primary purpose of the encoding analysis was to verify if any effects obtained in the retrieval phase were related to the neural network activated during the encoding tasks. We contrasted activation during the processing of items in the semantic encoding task relative to the perceptual encoding task, and found a very large cluster in L lateral PFC (BA 47, 45), which extended to L orbitofrontal cortex (BA 47) and L middle temporal gyrus (BA 21), and another large cluster covering the L medial PFC (BA 9/10). On the R hemisphere, there was significant activation in R lateral PFC (BA 47) and R middle temporal pole (BA 38). In more posterior regions, significant activations included the precuneus bilaterally (BA 31), R cuneus (BA 17), L calcarine (BA 17) and L angular gyrus (BA 39; Table 3 & Fig. 1A). The reverse contrast, comparing the perceptual encoding task with the semantic encoding task, showed three large clusters of activation. One cluster was located in L inferior parietal lobule (BA 40), extending to L superior parietal (BA 7), R inferior parietal (BA 40), R precuneus (BA 7) and R angular gyrus (BA 39). Another cluster had the peak of activation in R lateral PFC cortex (BA 45, 44), and extended to R orbitofrontal (BA 11) and superior frontal cortex (BA 6, 8). The third cluster included posterior regions of the R temporal gyri, notably R

Table 3
Encoding task effects. Regions demonstrating significant activations during the processing of items in the semantic encoding task relative to the perceptual encoding task and vice-versa. The highest peak from each cluster is shown.

Region	BA	No voxels	Z score	MNI coordinate		
				x	y	z
Semantic encoding > Perceptual encoding						
L precuneus	31	853	6.31	-4	-54	16
L lateral PFC	47	3668	5.62	-50	28	-10
L medial PFC	9/10	3296	5.45	-8	52	36
L calcarine cortex	17	314	5.05	-8	-84	-6
R cuneus	17	595	4.75	14	-96	16
L angular gyrus	39	287	4.54	-46	-68	26
R lateral PFC	47	129	4.13	32	34	-12
R middle temporal pole	38	97	4.04	50	16	-28
Perceptual encoding > Semantic encoding						
L inferior parietal lobule	40	7032	5.47	-40	-52	50
R lateral PFC	45	1378	5.22	40	48	18
R superior frontal gyrus	8	877	5.11	24	4	54
Cerebellum/R fusiform gyrus	20	1014	4.74	36	-74	-24
L lateral PFC	47	169	4.68	-20	26	-2
L superior frontal gyrus	6	259	4.30	-28	6	48
L lateral PFC	45	196	4.28	-36	30	28
R lateral PFC	44	221	4.25	46	6	22
R putamen	–	82	4.18	22	18	-8
L lateral PFC	46	102	4.03	-28	50	20
L occipital gyrus	19	107	4.00	-42	-68	-4

fusiform (BA 20), R inferior temporal (BA 20, 37) and R middle temporal (BA 21), as well as the cerebellum. There was also significant activation in L lateral PFC in both ventral (BA 47) and dorsal areas (BA 44, 45, 46), as well as in L inferior occipital cortex (BA 19) and putamen bilaterally (Table 3 & Fig. 1B).

3.3. Functional imaging data: retrieval scans

Our main goal was to explore the effect of retrieval query format upon the neural mechanisms of source remembering, independently of the source of the items. To this end, we compared the semantic query format with the perceptual query format, collapsed across all items' origins (semantically encoded, perceptually encoded and new items). Source recognition prompted by the semantic query format recruited an extensive network of regions. There were two significant clusters of activation in the L medial PFC (BA 10), while another cluster involved the L ventrolateral PFC (BA 47), extending to the L orbitofrontal (BA 47). There was also significant activation in L temporal pole (BA 38), extending to more posterior portions of the middle (BA 21) and superior temporal gyri (BA 22). Similarly, on the R hemisphere, activation involved the middle (BA 21) and superior temporal gyri (BA 22). Finally, there were two significant clusters in L calcarine (BA 17), one of them extending to the L inferior occipital cortex (BA 18) and L lingual gyrus (BA 18), another cluster in L angular gyrus (BA 39), and another in L supramarginal gyrus (BA 40; Table 4 & Fig. 2). We note that the same contrast of semantic query format vs. perceptual query format, but including only items that had been previously studied (i.e., excluding new items), produced a very similar pattern of activation. The opposite contrasts comparing the perceptual query format relative to the semantic query format (across all items' origins and for studied items only) showed no activations above threshold.

To further inspect the query format effect and assess how it relates to the prior encoding task, we conducted two separate analyses: one contrasting the semantic and perceptual query

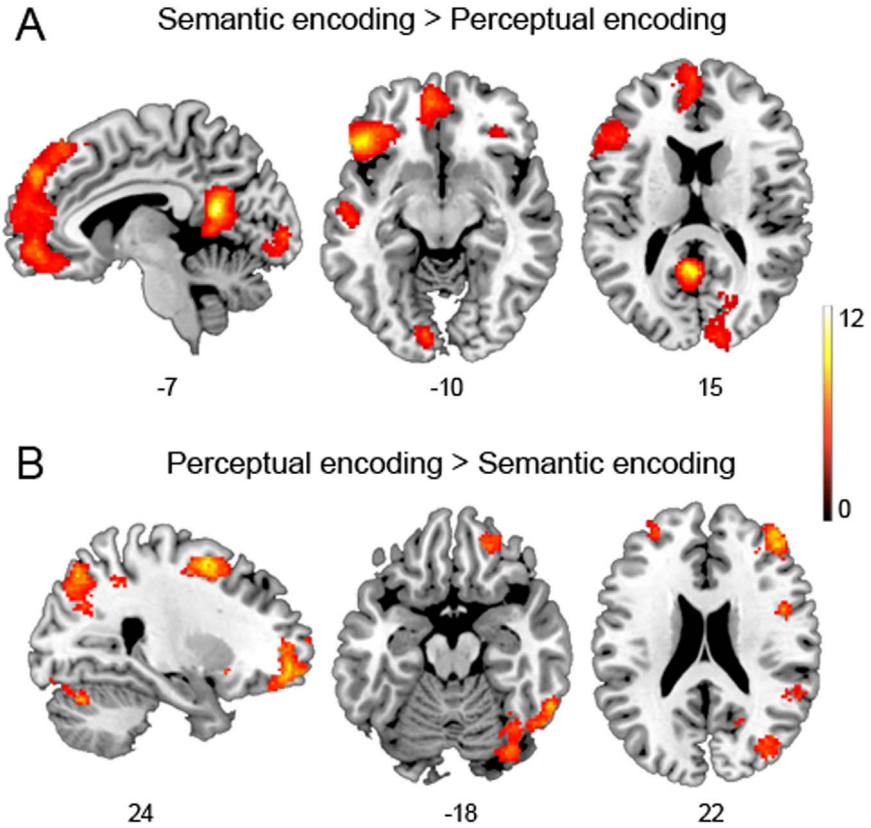

Fig. 1. Encoding task effects. Regions demonstrating significant activations for the processing of items during the semantic encoding task relative to the perceptual encoding task and vice-versa.

Table 4
Source memory effects of the retrieval query format. Regions demonstrating significant activations during source memory for the semantic query format relative to the perceptual query format. The highest peak from each cluster is shown.

Region	BA	No voxels	Z score	MNI coordinate		
				x	y	z
Semantic query > Perceptual query						
L middle temporal pole	38	310	6.49	-50	14	-24
L calcarine	17	1192	5.82	-6	-96	-6
L medial PFC	10	863	4.99	-8	60	28
L lateral prefrontal cortex	47	560	4.90	-44	28	-14
L calcarine	17	112	4.82	-24	-56	12
R middle temporal gyrus	21	180	4.51	50	-48	20
L precuneus	7	284	4.49	-6	-46	48
L medial PFC	10	231	4.20	-12	46	-4
L angular gyrus	39	173	4.20	-44	-66	26
L supramarginal gyrus	40	126	3.99	-60	-40	36

Table 5
Source memory effects of the retrieval query format for items encoded in the semantic task. Regions demonstrating significant activations for semantically encoded words prompted by the semantic query format relative to the perceptual query format. The highest peak from each cluster is shown.

Region	BA	No voxels	Z score	MNI coordinate		
				x	y	z
Semantically encoded words: Semantic query > Perceptual query						
L calcarine	17	264	5.52	-8	-94	-6
L medial PFC	10	2302	5.04	-4	60	24
L middle temporal gyrus	21	84	4.91	-52	12	-26
L parahippocampus	20	206	4.84	-26	-28	-14
R lingual gyrus	17	121	4.45	12	-88	-2
Posterior cingulate gyrus	23	576	4.42	4	-36	44
R parahippocampus	20	180	4.33	28	-22	-14
L calcarine	17	75	4.33	-24	-58	12
R lingual gyrus	19	255	4.27	20	-44	2
Posterior cingulate gyrus	23	172	4.25	2	-14	36

formats for items encoded in the semantic task; the other comparing both query formats for items encoded in the perceptual task. For items encoded in the pleasantness task, the semantic query format (relative to the perceptual query format) induced activation in medial PFC (BA 10), bilateral parahippocampal gyrus (BA 20), extending to the hippocampus, and L middle temporal gyrus (BA 21). Significant activation was also seen in occipital areas, notably, L calcarine (BA 17), R lingual gyrus (BA 17, 19) spreading to the L lingual gyrus, and posterior cingulate cortex (BA 23; Table 5 & Fig. 3). The reverse contrast of source retrieval for semantically encoded words triggered by the perceptual (vs. semantic) query format did not show any above threshold activations.

To specifically assess reactivation of encoding-related activity during retrieval of semantically encoded items, we conducted an ROI analysis in which the activation found during the semantic encoding task (relative to the perceptual encoding task) was used as a mask. Within these regions, retrieval of semantically encoded items when triggered by the semantic query (versus the perceptual query) revealed significant activation in medial PFC (BA 10), L lateral PFC (BA 47), L middle temporal gyrus (BA 21), R middle temporal pole (BA 38) and L calcarine (BA 17). In contrast, when prompted by the perceptual query (relative to the semantic query), the retrieval of semantically encoded items did not display any significant activation, showing no evidence of overlap with encoding.

For items encoded in the letter task, the whole brain analysis showed that the semantic query format (relative to the perceptual query format) engaged the L lateral PFC (BA 47 extending to BA 45), L middle temporal gyrus (BA 21) and posterior regions of the bilateral occipital cortex namely the L calcarine (BA 17) and lingual gyrus (BA 18; Table 6 & Fig. 4A). The opposite contrast comparing source recollection for items encoded in the perceptual task prompted by the perceptual query format (vs. semantic query format) showed a significant cluster in the R orbitofrontal cortex (BA 11), extending to the R gyrus rectus and anterior cingulate (BA 32; Table 6 & Fig. 4B).

An ROI analysis was conducted to examine reactivation of encoding-related activity during retrieval of perceptually encoded items. The activation observed during perceptual encoding (versus semantic encoding) was used as a mask. Within these regions, the retrieval of perceptually encoded items, prompted by either the semantic or the perceptual query format, did not show any significant activation. In other words, there was no overlap between the activation found at encoding and at retrieval of perceptually encoded items.

Finally, we compared both query formats in the identification of new items in a whole brain analysis. The question with the semantic format (compared to the perceptual format) recruited L ventrolateral PFC (BA 47), L medial PFC (BA 10), bilateral superior frontal (BA 9) and bilateral calcarine (BA 17). The reverse contrast showed that the perceptual format relative to the semantic format elicited significant activation in R inferior parietal lobe (BA 40; Table 7 & Fig. 5).

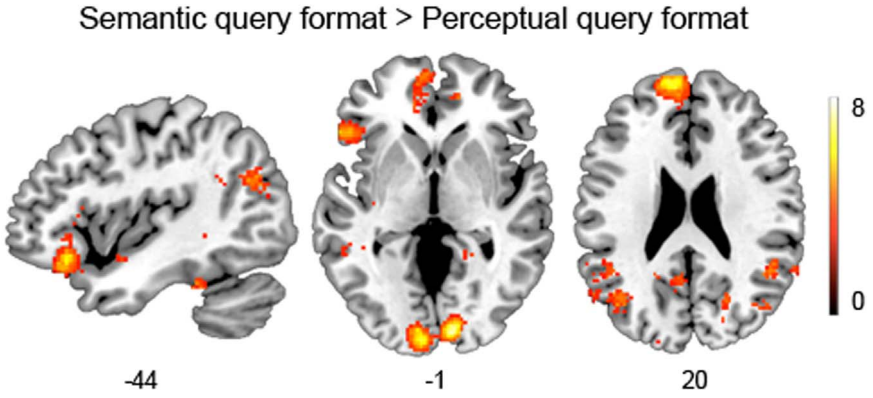

Fig. 2. Source memory effects of the retrieval query format. Regions demonstrating significant activations during source retrieval for the semantic query format relative to the perceptual query format.

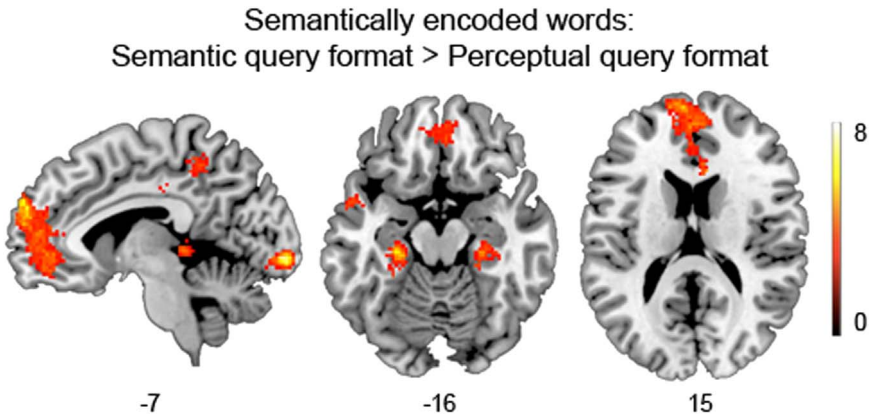

Fig. 3. Source memory effects of the retrieval query format for items encoded in the semantic task. Regions demonstrating significant activations for semantically encoded words prompted by the semantic query format relative to the perceptual query format

Table 6
Source memory effects of the retrieval query format for items encoded in the perceptual task. Regions demonstrating significant activations for perceptually encoded words prompted by the semantic query format relative to the perceptual query format and vice-versa. The highest peak from each cluster is shown.

Region	BA	No voxels	Z score	MNI coordinate		
				x	y	z
Perceptually encoded words: Semantic query > Perceptual query						
R superior occipital gyrus	18	483	5.33	20	-96	8
L calcarine	17	275	4.61	-8	-92	-6
L lateral PFC	47	351	4.49	-46	24	0
L middle temporal gyrus	21	96	4.27	-52	-38	-8
L middle occipital gyrus	18	141	3.91	-20	-92	10
Perceptually encoded words: Perceptual query > Semantic query						
R orbitofrontal gyrus	11	232	4.19	10	52	-20

4. Discussion

This study investigated how the retrieval query format affects the neurocognitive mechanisms of source remembering. We built on previous research that demonstrated that source memory depends on the way the retrieval question is framed (Dodson and Johnson, 1993; Johnson, et al., 1993; Mitchell et al., 2008). We asked participants about the prior encoding task, selectively emphasizing one source in the retrieval query (i.e., "Is this item from the pleasantness task?") or emphasizing the alternate source (i.e., "Is this item from the letter task?"). In line with earlier behavioral studies, we found that the retrieval query that emphasizes the semantic task was associated with higher source recognition than the retrieval query that mentions the perceptual task (Dobbins and McCarthy, 2008; Jacoby et al., 2005; Marsh and Hicks, 1998; Shimizu and Jacoby, 2005). That is, when prompted by the query with the semantic format participants are more likely to correctly accept items from that source and correctly reject items from the alternate source or new items, than when prompted by the query with the perceptual format. This increase of correct responses following the semantic query was accompanied by faster response times. This shows that the two query frames encourage different retrieval strategies, with the semantic format inducing cognitive operations that are more effective for source recognition (Jacoby et al., 2005; Marsh and Hicks, 1998; Mitchell and Johnson, 2009; Shimizu and Jacoby, 2005). The observed interaction between item's origin and retrieval query format demonstrates that the semantic query format boost is greater for items encoded in a perceptual manner for which the encoding trace is poorer. It should be noted that a limitation of the current design is that only source memory was tested. Thus, as discussed above, when source recognition fails, it may be that participants remember having seen the item but fail to identify the source or, alternatively, they may fail to remember the item assuming it is new. This is particularly relevant for items encoded in a perceptual manner, as the memory trace in this condition is overall poorer. Importantly, the proportion of correct responses to perceptually encoded items was significantly higher than the proportion of new items' intrusions following both the semantic query and the perceptual query. This suggests that participants are able to discriminate between studied words and new words, and therefore one may assume that perceptually encoded words are not being treated as new words. Overall, the data contribute to a growing body of studies showing that the format of the query changes how participants inspect and monitor memory (Dobbins and McCarthy, 2008; Hicks and Marsh, 1999; Finn, 2008; Jacoby et al., 2005; McDuff et al., 2009; Marsh and Hicks, 1998; Mill and O'Connor, 2014; Mitchell et al., 2008; Woodruff et al., 2006).

At a neural level, source recollection prompted by the question with the semantic format (relative to the perceptual format) recruited a network of regions that included the L lateral and medial PFC. These regions have been implicated in controlled retrieval of source information. In particular, L lateral PFC activation has been reported in a variety of source memory tasks, in which participants attempt to retrieve specific details about the prior encounter with the item. In contrast, when memory judgments are based on item familiarity or detection of novelty minimal lateral PFC activation is observed (Dobbins et al., 2002; Henson et al., 1999; Ranganath et al., 2000; Rugg et al., 2003; Yonelinas, 2002). Recent evidence suggests that increased recruitment of L lateral PFC during source memory reflects controlled semantic operations that facilitate recollection. Notably, this region is more active during source monitoring of semantic than perceptual information and when participants are able to use distinctive semantic attributes of the items to make the source memory judgment (Badre et al., 2005; Badre and Wagner, 2007; Dobbins and Han, 2006; Dobbins and Wagner, 2005; Han et al., 2012; Raposo et al., 2009; Wagner et al., 2001). Regarding the medial PFC, several studies have shown the involvement of this region, particularly the anterior frontopolar portion, in memory for internally-generated and self-referential information (Mitchell et al., 2008; Mitchell and Johnson, 2009; Simons et al., 2005, 2008). Recent studies further propose that there is considerable functional specialization within this region according to the types of self-relevant features associated with source monitoring (Simons et al., 2008). Earlier studies have

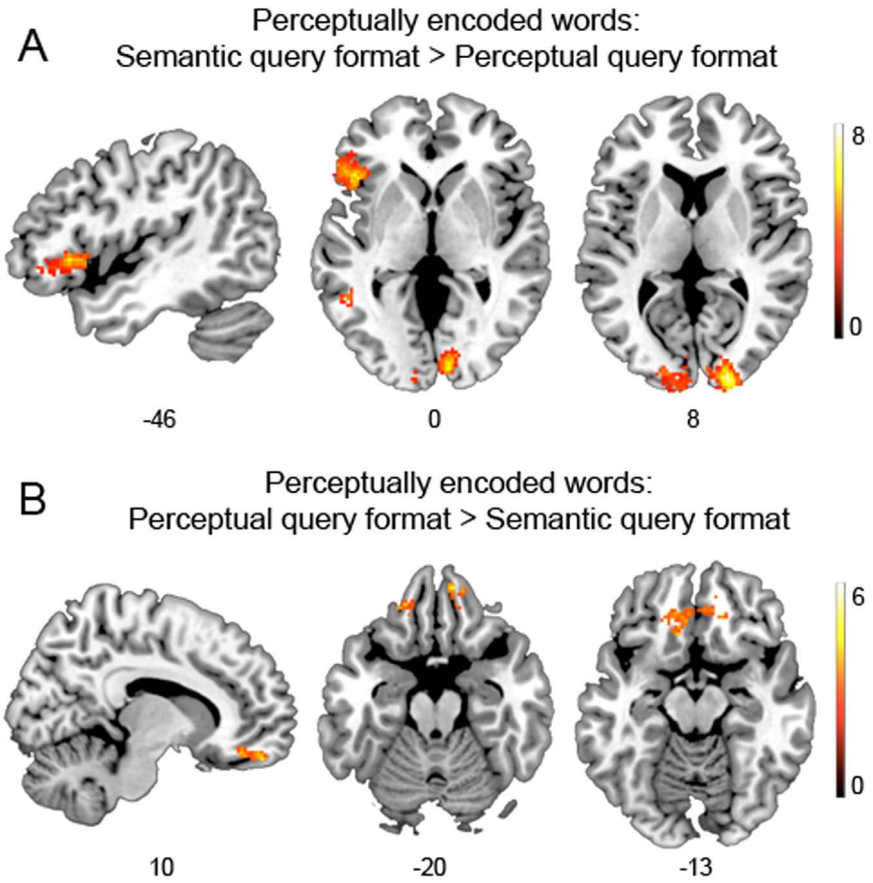

Fig. 4. Source memory effects of the retrieval query format for items encoded in the perceptual task. Regions demonstrating significant activations for perceptually encoded words prompted by the semantic query format relative to the perceptual query format (A); and regions demonstrating significant activations for perceptually encoded words prompted by the perceptual query format relative to the semantic query format (B).

Table 7
Effects of retrieval query for new words. Regions demonstrating significant activations for new words prompted by the semantic query format relative to the perceptual query format and vice-versa. The highest peak from each cluster is shown.

Region	BA	No voxels	Z score	MNI coordinate		
				x	y	z
New words: Semantic query > Perceptual query						
L calcarine	17	336	5.27	-10	-92	-4
L lateral PFC	47	343	4.62	-48	20	-2
R superior frontal	9	99	4.31	14	48	42
L superior frontal	9	196	4.18	-6	56	42
R calcarine	17	75	4.05	12	-94	6
L medial PFC	10	125	3.99	-6	52	20
New words: Perceptual query > Semantic query						
R inferior parietal	40	125	4.61	44	-40	48

demonstrated that such controlled operations are engaged during the retrieval of semantic information about the past event. Critically, here we show that such operations are modulated by the way the retrieval query is framed. Across conditions, participants always had to perform a source memory decision that concerned the prior encoding task. However, only when the format of the question emphasized the semantic task, independently of the actual encoding, were such controlled semantic operations engaged in. Thus, the framing of the source retrieval question encouraged participants towards a more controlled semantic processing, which resulted in higher source recognition rates.

Although the hypothesis that the semantic query format (relative to the perceptual format) would lead to greater semantic elaboration and monitoring via L lateral and medial PFC activation was supported, it is important to note that this effect was partially modulated by the encoding task. For items encoded in the semantic task, the semantic query format specifically activated the medial anterior PFC, while for items previously encoded in the perceptual task, the semantic query format elicited activation in L lateral PFC. The results highlight the differential contribution of the medial and lateral PFC to source recollection. Solid evidence suggests that medial PFC activity is linked to internally-generated information associated with reality monitoring (Brandt et al., 2014; Simons et al., 2005, 2008; Raposo et al., 2011; Vinogradov et al., 2006). We argue that the semantic query format promotes the self-referential processes carried out during the pleasantness decision, which in turn supports source retrieval and monitoring. In contrast, L lateral PFC was found when source recollection was also prompted by the semantic query format, but for items encoded in the perceptual task. The results are consistent with the view that this region plays a key role in source monitoring, notably in the specification of semantic retrieval cues (Badre and Wagner, 2007; Dobbins and Wagner, 2005; Simons et al., 2005). Following this view, we suggest that the semantic query aided source recollection, even when items were studied in a perceptual fashion, as it elicited the semantic elaboration processes necessary for source retrieval. Despite the functional differences between L lateral and medial PFC regions, these results converge in strengthening the hypothesis that the semantic format, but not the

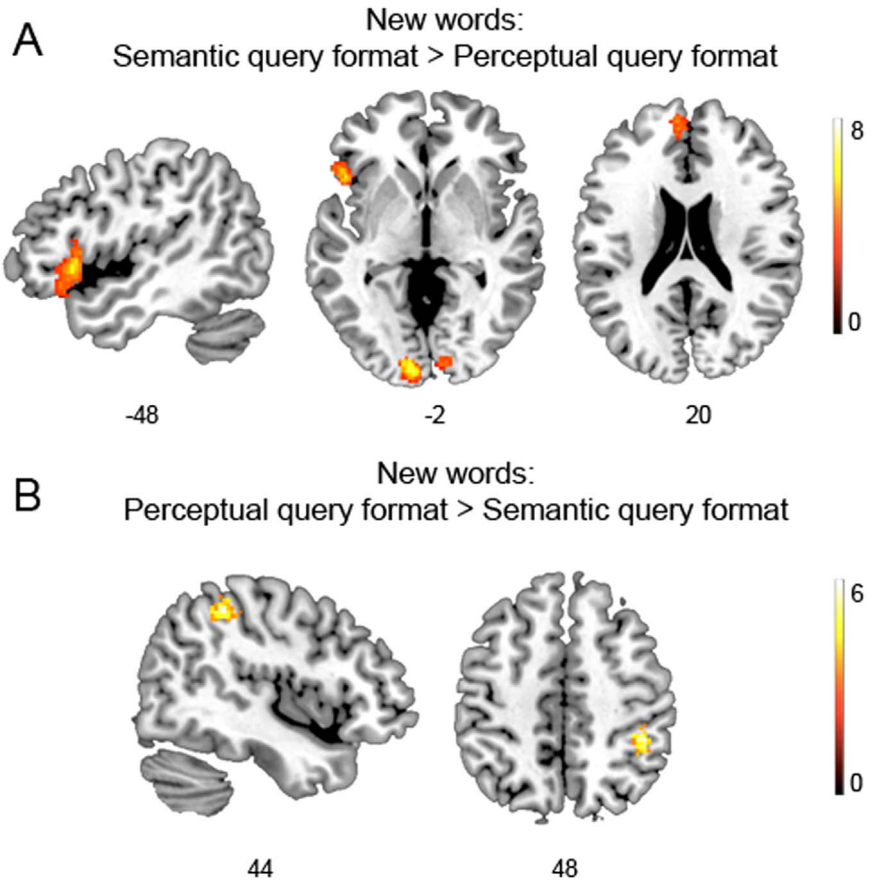

Fig. 5. Source memory effects of the retrieval query format for new items. Regions demonstrating significant activations for new words prompted by the semantic query format relative to the perceptual query format (A); and regions demonstrating significant activations for new words prompted by the perceptual query format relative to the semantic query format (B).

perceptual format of the retrieval query, promotes the use of semantic strategies.

Other regions also showed differential sensitivity to the semantic query format depending on the previous encoding task. For items encoded in the semantic task, the semantic query triggered, along the medial PFC, activation in middle temporal gyrus, associated with semantic processing (Binder and Desai, 2011; Binder et al., 2009; Dobbins and Wagner, 2005; Rose et al., 2015), and hippocampus and parahippocampus, linked to relational encoding (e.g., Davachi et al., 2003) and recovery of relational and contextual information (Duncan et al., 2014; Eichenbaum et al., 2007). Interestingly, the ROI analysis demonstrated that some of the regions that were activated during retrieval of semantically encoded items overlapped with those that were differentially recruited during semantic encoding, notably, medial PFC (BA 10), L lateral PFC (BA 47) and L middle temporal gyrus (BA 21). Critically, such reactivation was observed only when retrieval was triggered by the semantic query format, but not by the perceptual query format. These results suggest that, during source recognition, there is reinstatement of some of the processes engaged during encoding (Danker and Anderson, 2010; Nyberg et al., 2000; Vaidya et al., 2002). Such recapitulation processes were presumably potentiated by the match between the task performed at encoding (pleasantness decision) and the query used at retrieval ("Is this item from the pleasantness task?"). The findings show that recollection depends on the extent to which the information provided during retrieval overlaps with that which was central during the encoding of the events (Humphreys et al., 2003; Tulving and Thompson, 1973). Conversely, source retrieval of items encoded in the perceptual task prompted by the semantic query format was associated with greater activation in posterior occipito-temporal areas. However, in this case there was no overlap between the regions activated at retrieval and those observed during perceptual encoding, as shown by our ROI analysis. The absence of a match between the task performed at encoding (letter decision) and the query used at retrieval ("Is this item from the pleasantness task?"), may be one of the reasons for the lack of overlapping regions. Nevertheless, in both encoding and retrieval, occipito-temporal clusters were found, though in distinct regions. Thus, source retrieval of perceptually encoded items, when triggered by the semantic retrieval query (but not the perceptual retrieval query) promoted activation in occipito-temporal cortices linked to the processing and recollection of visuo-perceptual features (Dobbins and Wagner, 2005; Johnson and Rugg, 2007). Together, the present results suggest that the semantic (as opposed to the perceptual) retrieval query encourages specific and differential source retrieval processes, depending on the type of information that had been encoded. PFC regions, likely associated with controlled processing of semantic features, exhibited different co-activation patterns in more posterior areas, reflecting the processing of the previously encoded features (i.e., middle temporal activations for the retrieval of semantically encoded items and occipito-temporal areas during retrieval of perceptually encoded items). This suggests that the semantic query elicits processes that are compatible with the type of information that had been encoded. An important goal for future research includes finer-grained analyses of how the retrieval query format modulates PFC and more posterior regions, as different types of features are processed and monitored. It will also be relevant to evaluate the conditions under which the semantic query format fosters recapitulation of the encoding-related

activity.

The differences found between the semantic and perceptual query formats in the processing of new items provide strong and direct evidence that the way the retrieval query is framed modulates the processes that take place at retrieval. These findings demonstrate that the semantic format, but not the perceptual format, elicits activation in L ventrolateral and medial PFC, associated with greater semantic elaboration and monitoring in the processing of new words. This provides neural support to the view that the semantic format prompts cognitive operations that aid discriminating the source and complement previous results on the impact of the retrieval query upon new foils (Hornberger et al., 2006; Jacoby et al., 2005; Shimizu et al., 2005; Woodruff et al., 2006).

Finally, our prediction that a query that emphasizes perceptual information would likely not engage a semantic elaboration strategy, even for items encoded in a semantic manner, and instead would recruit visuo-perceptual processing regions, was only partially supported. As expected, ventrolateral and medial PFC activations were not observed under the perceptual query condition. However, in contrast to our hypothesis, we did not find activation in visuo-perceptual areas. As reported above, the recruitment of these areas was specific to items encoded in the perceptual task, when prompted by the semantic query. Instead, the R orbitofrontal cortex and the R inferior parietal lobe displayed significant activation for the perceptual query format (versus the semantic format), for items encoded in a perceptual manner and for new items, respectively. These regions have been implicated in source memory decisions that are based in the perceptual context of the past event. For instance, Han et al. (2012) observed greater response in a similar region of the R inferior parietal cortex when the source retrieval task involved the recovery of the perceptual context of the item. Activation of the R orbitofrontal cortex has been reported in tasks that require the encoding of visual stimuli that provide minimal opportunities for controlled processing, such as semantic monitoring and organizational strategies (e.g., Frey and Petrides, 2000, 2002). Interestingly, in our perceptual encoding task, there was also significant activation in R orbitofrontal cortex, which extended to the R inferior and superior PFC. Our results suggest that the R orbitofrontal cortex is relevant, not only during encoding but also when retrieval provides minimal support for controlled semantic processing.

In summary, our behavioral and neuroimaging data converge in showing that the way the retrieval query is framed, stressing either one source or the other, has implications to source remembering. When the format of the retrieval query emphasizes semantic information (regardless of the actual encoding task, and even for new items) there is a boost in source recollection accompanied by increased activation in L lateral and medial PFC associated with the controlled retrieval and monitoring of semantic features. In contrast, when the framing of the retrieval query stresses the perceptual source, such semantic controlled operations are attenuated, even when the items had been studied in a semantic manner. Our results provide clear evidence for the source monitoring perspective (Johnson et al., 1993; Mitchell et al., 2008), highlighting that the way questions are framed can influence the information that comes to mind and how it is used during remembering.

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