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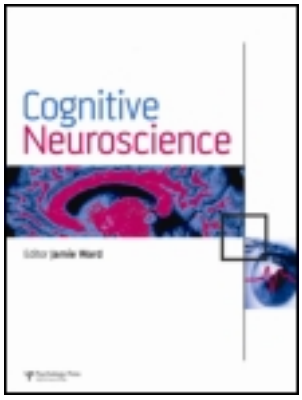

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Visual memory and visual mental imagery recruit common control and sensory regions of the brain

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Visual memory and visual mental imagery recruit common control and sensory regions of the brain

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Separate lines of research have shown that visual memory and visual mental imagery are mediated by frontal-parietal control regions and can rely on occipital-temporal sensory regions of the brain. We used fMRI to assess the degree to which visual memory and visual mental imagery rely on the same neural substrates. During the familiarization/study phase, participants studied drawings of objects. During the test phase, words corresponding to old and new objects were presented. In the memory test, participants responded "remember," "know," or "new." In the imagery test, participants responded "high vividness," "moderate vividness," or "low vividness." Visual memory (old-remember) and visual imagery (old-high vividness) were commonly associated with activity in frontal-parietal control regions and occipital-temporal sensory regions. In addition, visual memory produced greater activity than visual imagery in parietal and occipital-temporal regions. The present results suggest that visual memory and visual imagery rely on highly similar—but not identical—cognitive processes.

Keywords: fMRI; Long-term memory; Visual imagery.

Visual memory requires accessing stored visual information whereas visual mental imagery requires constructing a representation in short-term memory that is often accompanied by the experience of "seeing with the mind's eye." Separate lines of research have shown that visual memory and visual mental imagery rely, in part, on frontal-parietal control regions (Kosslyn, Ganis, & Thompson, 2001; Slotnick, Moo, Segal, & Hart, 2003; Thompson, Slotnick, Burrage, & Kosslyn, 2009; Wheeler & Buckner, 2004). Furthermore, visual memory and visual mental imagery can rely on occipital-temporal sensory regions associated with processing specific visual features. Specifically, when participants engage in tasks that require memory or imagery of spatial location, the contralateral extrastriate cortex typically is activated (Fabiani, Stadler, & Wessels, 2000; Klein et al., 2004; Slotnick, 2009a; Slotnick, Thompson, & Kosslyn, 2005); when they rely on memory or imagery of color, the color-processing cortex typically is activated (Howard et al., 1998; Kosslyn, Thompson, Costantini-Ferrando, Alpert, & Spiegel, 2000; Simmons et al., 2007; Slotnick, 2009b); and when they rely on memory or imagery of motion, the motion-processing cortex typically is activated (Kaas, Weigelt, Roebroeck, Kohler, & Muckli, 2010; Slotnick & Thakral, 2011).

Such findings suggest that visual memory and visual mental imagery may rely on the same or similar frontal-parietal control regions and occipital-temporal sensory regions. Cognitive analysis is consistent with this view, given that visual memory can involve imagery of remembered items, and visual mental imagery usually involves accessing representations of previously learned stimuli. However, such analysis is inherently speculative. At present, there is little empirical or theoretical basis for arguing, a priori, that visual

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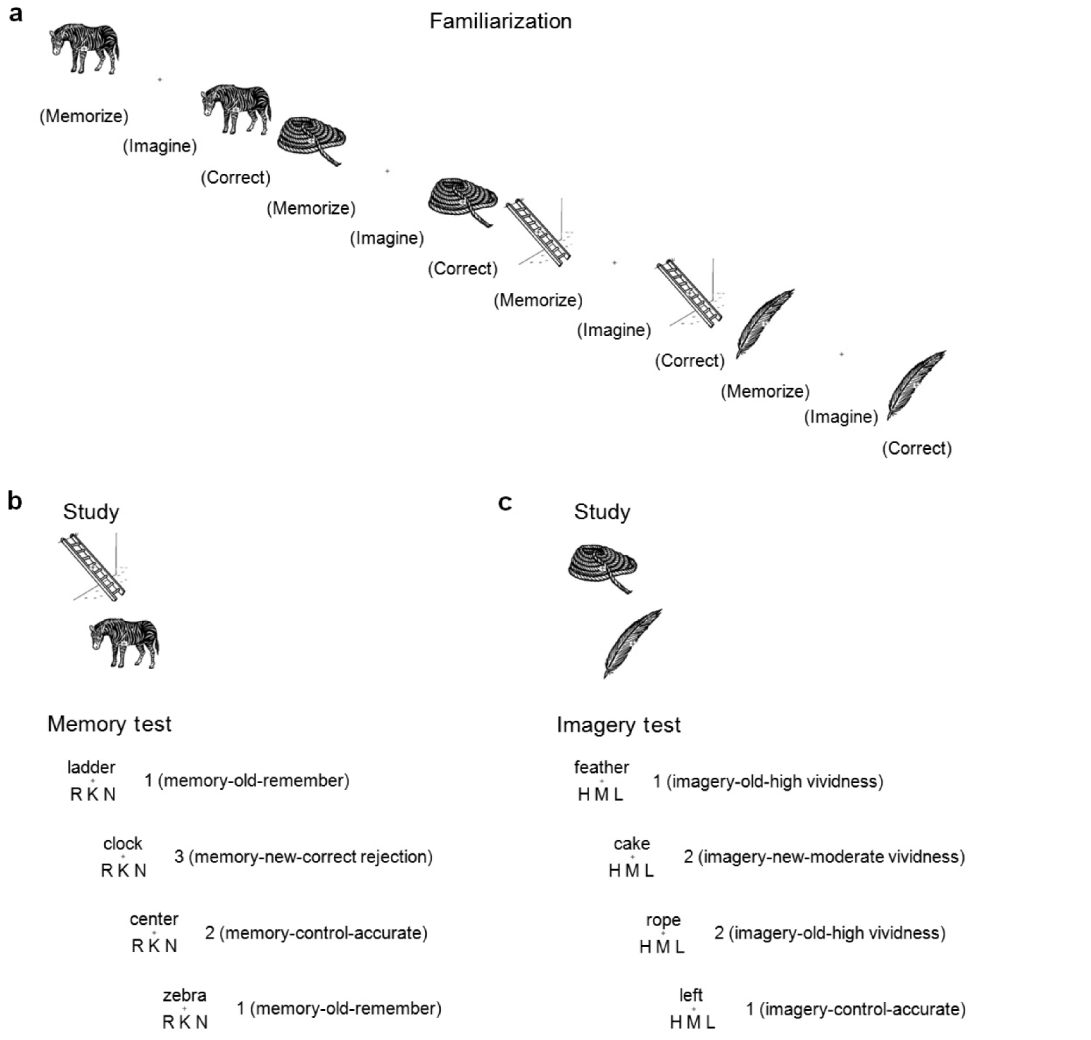

Figure 1. (a) During familiarization, pictures of objects were memorized, imagined, and then the mental image was compared to the picture of the object and corrected (words in parentheses were not shown during the experiment). (b) During both memory and imagery study phases, pictures of objects from familiarization were presented. During the memory-test phase, words corresponding to old (studied) objects, new words, and control words were presented at fixation. Participants responded "remember" (R, 1 key), "know" (K, 2 key), or "new" (N, 3 key) to old-item words and new-item words, and responded with the corresponding response key to control words ("left," "center," or "right"). Example responses and the corresponding event types are shown to the right of each word. (c) During the imagery-test phase, the same word types were presented and participants responded "high vividness" (H, 1 key), "moderate vividness" (M, 2 key), or "low vividness" (L, 3 key) to old-item words and new-item words in addition to the same control responses. Example responses and the corresponding event types are shown to the right of each word.

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memory and visual mental imagery are mediated by the same or different neural substrates. We conducted the present study to obtain empirical evidence that will allow us to begin to gain traction on this issue.

To compare imagery and memory processes in the same participants, we used fMRI to identify the neural substrates associated with each function. We developed a novel task consisting of an object-familiarization phase (Figure 1a), which is common in imagery studies; an object-study phase (Figures 1b and 1c, top), which is common in memory studies; and a memory-test phase (Figure 1b, bottom) and imagery-test phase (Figure 1c, bottom). We used a conjunction analysis to identify the brain regions commonly associated with visual memory and visual mental imagery, and used contrasts to identify the brain regions that were separately associated with these two cognitive activities.

METHOD

Participants

Twelve right-handed Boston College undergraduates with normal or corrected-to-normal visual acuity volunteered to take part in the study (eight women, four men,

age range 18.6–22.2 years). The protocol was covered by approvals obtained from appropriate Institutional Review Boards at Boston College, Massachusetts General Hospital and Harvard University.

Stimuli and tasks

Stimuli were drawn from the pool of the International Picture Naming Project at the UCSD Center for Research in Language, and primarily consisted of pictures of objects from the Snodgrass and Vanderwart (1980) set. All selected objects had a 96% valid response rate and 90% or greater name agreement, one or two syllables, and the pictures subtended 0.9–5.7° of visual angle. To gain familiarity with the tasks, participants first completed a one-fourth length practice session.

During the full-length familiarization set of trials, 40 pictures of objects were presented at fixation. Each object was presented twice, separated by a fixation period. Participants were instructed to memorize each picture during the first presentation, create a mental image of the picture as vividly as possible during the subsequent fixation period, and then compare their mental image to the second presentation of the picture and correct any deviations between their image and that rendition of the object (Figure 1a). The participants controlled the presentation rate by pressing the space bar. After all of the pictures were presented once, we randomized their order and presented them two more times. Following a delay of 1–7 days, the fMRI scans were completed.

Memory and imagery blocks had identical study phases (Figures 1b and 1c). The study-phase instructions did not inform participants about the type of test phase (memory or imagery) that would follow, to encourage common encoding strategies. Each study phase consisted of 20 pictures of objects from the familiarization session, which were each presented for 2.5 s, followed by a 0.5-s fixation period. Participants were instructed to remember each object. Half the participants completed the memory block first and the other half of the participants completed the imagery block first. It is important to note that we conducted a random effect fMRI analysis (see below), which identifies brain activity that is consistent across all participants regardless of test order.

In both the memory-test phase and the imagery-test phase, 20 words corresponding to old (studied) objects (that were used in either the memory- or imagery-study phase), 20 new words, and nine control words ("left," "center," and "right" presented equally often) were randomized and presented at fixation. We presented each word for 3.5 s, followed by a 0.5–6.5 s fixation period (words subtended 0.7–2.1° of visual angle horizontally).

During the memory-test phase (Figure 1b), participants responded "remember" (memory with specific detail; key 1), "know" (memory without specific detail; key 2), or "new" (key 3) for each word (adapted from Eldridge, Sarfatti, & Knowlton, 2002).

During the imagery-test phase (Figure 1c), participants were instructed to visualize the picture of the object from the familiarization/study phase for old-item words or to generate a new image for new-item words, and to indicate the image's vividness. Specifically, they indicated whether the mental image had "high vividness" (i.e., their image ranged from clear and reasonably vivid to perfectly clear and almost as vivid as normal vision; key 1), "moderate vividness" (moderately clear and vivid; key 2), or "low vividness" (ranged from vague and dim to no image at all; key 3). The imagery-vividness scale was adapted from Marks (1973).

When control words ("left," "center," or "right") were presented, participants pressed the corresponding response button (keys 1, 2, and 3, respectively), which required both word/language processing and a motor response without memory or imagery components. During all trials, we asked the participants to maintain fixation and respond with the ring (key 1), middle (key 2), or index (key 3) finger of their left hand.

We intentionally designed the memory and imagery protocols to be as similar as possible, only differing in the cognitive operations of interest. By making the tasks minimally different, we could observe the consequences of just the operations that distinguished them. However, in so doing, we may have introduced a problem: One might claim that the protocols were so similar that the identical cognitive strategies were employed. For instance, participants probably used mental imagery during both memory-old-remember trials and imagery-high-vividness trials, and may have also made old-new judgments during both memory and imagery trials. It is worth keeping in mind, however, that if participants used the identical cognitive strategies during memory and imagery tasks, this would produce the identical pattern of behavioral and neural findings. It follows that different results in the two conditions would rule out the possibility that participants used the identical cognitive strategies during the tasks.

We selected stimuli for the different types of conditions (memory-old, memory-new, imagery-old, imagery-new) so that they had comparable object naming times (mean values 909, 873, 875, and 884 ms), visual complexity (mean values 16,886, 16,586, 16,608, and 16,782), and log of frequency (mean values 2.98, 2.99, 3.12, and 2.97). We counterbalanced objects across participants by using a Latin square design.

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fMRI acquisition and analysis

MRI data were acquired on Siemens 3 Tesla Trio scanners. Half of the participants were tested at the Athinoula A. Martinos Center for Biomedical Imaging at Massachusetts General Hospital and the other half of the participants were tested at the Center for Brain Science at Harvard University. We conducted the analysis with BrainVoyager QX (Brain Innovation B.V., Maastricht, The Netherlands), and acquired the functional images using an echo planar imaging sequence (2000-ms TR, 30-ms TE, 90° flip angle, 256-mm field-of-view^2, 64 × 64 acquisition matrix, 32–33 slices, 4-mm slice thickness with no gap; 4-mm isotropic resolution). We also acquired anatomic images using a magnetization prepared rapid gradient echo sequence (30-ms TR, 3.3-ms TE, 40° flip angle, 256 × 256-mm^2 field-of-view, 256 × 256 acquisition matrix, 128 slices, 1.33-mm slice thickness with no gap; 1.33 × 1 × 1-mm resolution). Functional data preprocessing included slice-time correction, motion correction, and temporal filtering by removal of linear trends and components at or below 2 cycles per run length. We transformed all images into Talairach space.

We conducted a random-effect general linear model analysis (hemodynamic response models were generated from each event onset and the subsequent behavioral response). Event types included items at study, old and new items during memory classified by response type, old and new items during imagery classified by response type, memory control items classified by accuracy, imagery control items classified by accuracy, failures to respond, and a constant. Encoding trials and trials without a response had durations of 2.5 and 3.5 s, respectively. Only memory-old-remember, memory-new-correct rejection, memory-control-accurate, imagery-old-high vividness, and imagery-control-accurate responses had a sufficient number of responses across participants to conduct a meaningful analysis of the fMRI data (this was expected given that old objects had been studied four times, which typically translated into detailed memories and highly vivid images).

We used two-tailed, paired *t*-tests for behavioral comparisons. For all fMRI contrasts, we used one-tailed, paired *t*-tests and enforced an individual voxel threshold of $p < .001$, cluster extent corrected for multiple comparisons to $p < .05$ (a 4-voxel extent was required, based on contrast image spatial autocorrelations of 3–3.3 mm that were entered into 10,000-iteration Monte Carlo simulations; Thompson et al., 2009). The threshold for each contrast entered into a conjunction was $p < .01$, which yielded a joint p value of $p < .001$ (computed by Fisher's technique, 1973). Activations were projected onto a cortical surface representation of one participant (see Slotnick, 2005).

RESULTS

Behavioral results

Participants generally had detailed memories and highly vivid visual mental images when presented with old item cues and otherwise responded accurately. During memory trials, participants responded "remember" to 83.5 ± 6.6% of old item words and responded "new" to 95.2 ± 2.2% of new words. During imagery trials, participants responded "high vividness" to 77.2 ± 7.6% of old item words. Across both memory and imagery trials, participants accurately responded to 99.5 ± 0.5% of control words. Additionally, there was a behavioral marker that the memory and imagery tasks were performed by different cognitive operations—the percentage of new words that received a "high vividness" rating during imagery (27.9 ± 9.0%) was significantly greater than the percentage of new words that received a "remember" response (0.9 ± 0.6%; $t(11) = 3.02$, $p < .05$).

Common brain activation

We identified regions of the brain associated with both visual memory and visual mental imagery by using the conjunction (memory-old-remember > memory-control-accurate) ∩ (imagery-old-high vividness > imagery-control-accurate). Common activity during visual memory and visual mental imagery occurred in frontal-parietal control regions, including the anterior frontal cortex, dorsolateral prefrontal cortex, and intraparietal sulcus (Figure 2, top). We also observed common activity in occipital-temporal visual sensory regions, including the fusiform gyrus and striate cortex (Figure 2, bottom; see Table 1 for a full list of activations). It is important to highlight that each contrast entered into the conjunction produced bilateral activity in frontal-parietal control regions and occipital-temporal sensory regions, but only left lateralized activity survived the threshold employed (at a relaxed threshold of $p < .01$, the conjunction also produced bilateral activity). We also conducted a conjunction analysis, using the same imagery contrast along with the memory contrast memory-old-remember > new-correct rejection (a classic memory baseline), and observed the identical pattern of results.

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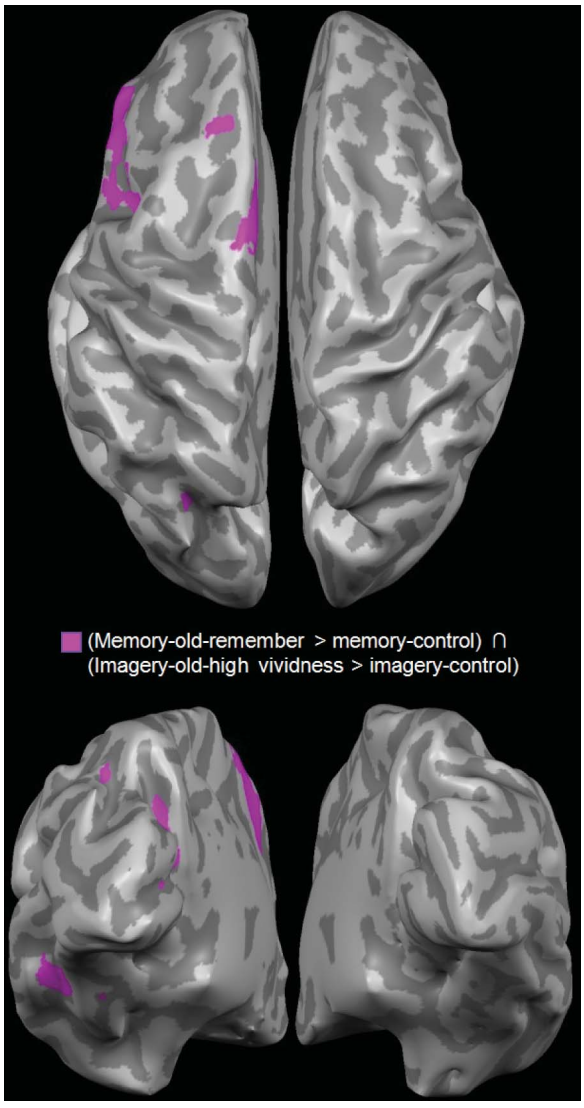

Figure 2. Common activity associated with memory-old-remember and imagery-old-high vividness projected onto an inflated cortical surface representation (gyri and sulci are shown in light and dark gray, respectively; top, superior view; bottom, posterior-inferior view; key at center).

Different brain activation

We next identified activation that was not shared by the two functions, but rather was present more strongly (or only) during memory or imagery by directly contrasting memory-old-remember and imagery-old-high vividness. The imagery-old high vividness > memory-old-remember contrast did not reveal any areas that were activated more strongly during imagery than during memory. Although this null finding could have reflected greater difficulty for memory-old-remember than imagery-old-high-vividness trials, the memory-old-remember response time (1539 ± 102) was significantly faster than the imagery-old-high vividness response time (1731 ± 76 ms; $t(11) = 2.57$, $p < .05$), a finding that is inconsistent with a difficulty explanation.

TABLE 1
Neural regions commonly associated with memory-old-remember and imagery-old-high vividness

Region	*BA*	*x*	*y*	*z*
Anterior frontal cortex	10/46	–45	36	9
Inferior frontal sulcus	46	–41	25	17
Inferior frontal gyrus	44	–48	14	23
Inferior frontal sulcus	9/44	–37	6	29
Middle frontal gyrus	9	–49	16	29
Superior frontal gyrus	8	–16	29	44
Superior frontal gyrus	6	–10	2	63
Medial frontal cortex	6/8/32	–6	8	45
Orbital frontal cortex	11	–30	30	–9
Intraparietal sulcus	7/19/39/40	–28	–68	32
Precuneus	31	–13	–62	27
Precuneus	23	–11	–60	18
Fusiform gyrus	20	–33	–39	–14
Fusiform gyrus	37	–42	–46	–10
Striate cortex	17	–19	–74	6

Notes: BA refers to Brodmann area and the Talairach coordinate (x, y, z) refers to the center of activation within each region.

The memory-old-remember > imagery-old-high vividness contrast, by comparison, revealed activity in parietal control regions, including the superior parietal lobule, the inferior parietal lobule, and the precuneus (Figure 3, top). This contrast also revealed activity in occipital-temporal visual sensory regions, including the fusiform gyrus, extrastriate cortex, and striate cortex (Figure 3, bottom; see Table 2 for a full list of activations). Additional activations in the retrosplenial cortex and middle temporal gyrus may reflect associative memory (Bar, Aminoff, & Schacter, 2008) and verbal memory (Garoff-Eaton, Slotnick, & Schacter, 2006), respectively. We underscore that this contrast did not reveal any more activity in the frontal cortex during memory than during imagery (even at a relaxed threshold of $p < .01$).

GENERAL DISCUSSION

The present results indicate that visual memory and visual mental imagery rely on the same frontal-parietal control regions and occipital-temporal sensory regions (Figure 2, Table 1). However, the two types of cognitive activity are not identical: We found greater activity during memory than during imagery in parietal control regions and occipital-temporal sensory regions (Figure 3, Table 2), and the number of different regions

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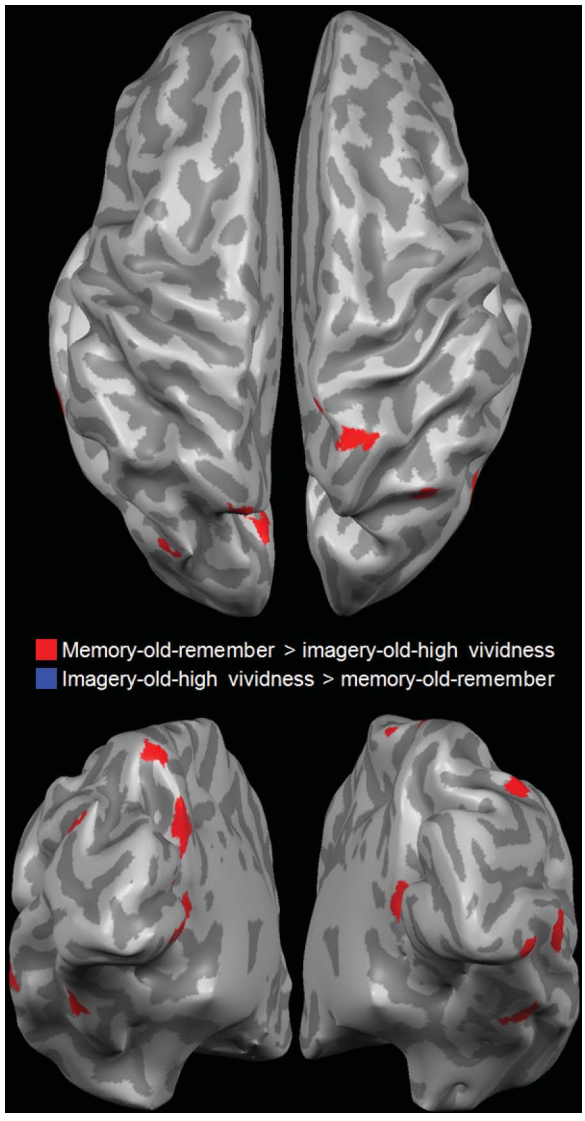

Figure 3. Differential activity associated with memory-old-remember and imagery-old-high vividness projected onto an inflated cortical surface representation (key at center).

TABLE 2
Neural regions differentially associated with memory-old-remember and imagery-old-high vividness

Region	*BA*	*x*	*y*	*z*
Memory-old-remember > Imagery-old-high vividness				
Superior parietal lobule	7	–17	–81	40
Superior parietal lobule	7	17	–52	63
Inferior parietal lobule	39	35	–68	40
Precuneus	7	–9	–78	42
Precuneus	7	2	–48	58
Retrosplenial cortex	26/29	–9	–52	6
Retrosplenial cortex	26/29	8	–49	9
Middle temporal gyrus	21	–54	–41	–3
Fusiform gyrus	20/37	38	–45	–15
Fusiform gyrus	37	–44	–49	–15
Superior occipital gyrus	19	–37	–76	38
Cuneus	18/19	–4	–76	30
Inferior occipital gyrus	18/19	42	–77	–4
Extrastriate cortex	18	–4	–68	1
Striate cortex	17	–8	–66	8
Cerebellum	–	–15	–77	–30
Cerebellum	–	42	–56	–33
Cerebellum	–	22	–71	–29
Imagery-old-high vividness > Memory-old-remember				
No activations				

Notes: BA refers to Brodmann area and the Talairach coordinate (x, y, z) refers to the center of activation within each region.

was greater than the number of common regions. Moreover, we also found significant behavioral differences in the performance of the memory and imagery tasks. These different neural and behavioral results rule out the possibility that participants used *identical* cognitive strategies during visual memory and visual mental imagery (as could have been predicted from the common practice/object familiarization protocols). At a minimum, the findings implicate differences in the specific degree to which particular processes contributed to each task. As such, these disparate findings document important differences in how participants performed the memory and imagery tasks.

Although visual memory engendered greater activity than did visual mental imagery in the parietal cortex and occipital-temporal cortex, we stress that both cognitive processes produced activity in these regions. Visual memory and visual mental imagery produced quantitatively—not qualitatively—different patterns of activity in these regions. The different effects in these regions may reflect a greater degree of attentional processing during visual memory (Wagner, Shannon, Kahn, & Buckner, 2005). In support of this possibility, we observed significantly faster memory-old-remember responses than imagery-old-high-vividness responses (such speeded reaction times are a marker of attention). Moreover, the memory-old-remember versus imagery-old-high-vividness contrast produced activity in the bilateral superior parietal lobule, a region that has been associated with shifts in attention (Thakral & Slotnick, 2009). This suggests that visual memory may involve a relatively greater number of shifts in attention during retrieval of object information—perhaps between retrieved object features during visual memory construction—and this in turn may have amplified activity in occipital-temporal regions.

A recent line of research has investigated the neural basis of remembering the past versus imagining the future (Addis, Wong, & Schacter, 2007; Szpunar, Watson, & McDermott, 2007). Although such studies have compared memory and imagery, the imagination

tasks in these studies are autobiographical and thus involved an explicit memory component. As such, these past-future studies have not isolated the cognitive processes associated with visual memory and visual mental imagery. In contrast, the present paradigm was designed to tap into visual memory or visual mental imagery per se.

The current findings indicate that visual memory and visual mental imagery are mediated by largely overlapping neural substrates in both frontal-parietal control regions and occipital-temporal sensory regions. These neural findings suggest that visual memory and visual mental imagery are mediated by many of the same cognitive processes. In spite of the observed differences, we also found some similar patterns of neural results in the two tasks. However, these commonalities may overestimate the similarity in processing memory versus imagery in general. The fact that we designed the tasks to be so similar may have contributed to the relatively high degree of common neural findings, and subsequent studies may benefit from employing more disparate tasks. In any case, the different results for the two functions that we report here indicate that the two functions are not identical; mental imagery is not simply visual memory.

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