

Visual imagery and memory: Do retrieval strategies affect what the mind's eye sees?

Todd C. Handy

Department of Psychology, University of British Columbia, Vancouver, BC, Canada

Michael B. Miller

Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH, and Department of Psychology, University of California, Santa Barbara, CA, USA

Bjoern Schott

Department of Neurology II, University of Magdeburg, Germany

Neha M. Shroff and Petr Janata

Center for Cognitive Neuroscience, and Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

John D. Van Horn, Souheil Inati, and Scott T. Grafton

Center for Cognitive Neuroscience, Department of Psychological and Brain Sciences, and Dartmouth Brain Imaging Center, Dartmouth College, Hanover, NH, USA

Michael S. Gazzaniga

Center for Cognitive Neuroscience, and Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

A variety of visual mental imagery tasks have been shown to activate regions of visual cortex that subserve the perception of visual events. Here fMRI was used to examine whether imagery-related visuocortical activity is modulated if imagery content is held constant but there is a change in the memory retrieval strategy used to invoke imagery. Participants were scanned while visualising common objects in two different conditions: (a) recalling recently encoded pictures and (b) based on

Correspondence should be addressed to Todd C. Handy, Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC, V6T 1Z4, Canada. Email: tchandy@psych.ubc.ca

This research was funded by NIH grant NS17778-21 awarded to MSG, and the Dartmouth Brain Imaging Center. We thank Bill Kelley, Andy Yonelinas, and Emrah Düzel for helpful comments, and Tammy Laroche for her assistance with data collection.

their knowledge of concrete nouns. Results showed that retrieval-related activations in frontal cortex were bilateral when pictures were visualised but left-lateralised when nouns were visualised. In posterior brain regions, both imagery conditions led to activation in the same set of circumscribed areas in left temporal-parietal cortex, including a region of the left fusiform gyrus that has previously been implicated in visual imagery. These findings suggest that the posterior network activated during imagery did not vary with strategic task-related changes in the frontal network used to retrieve imagery content from memory.

Retrieving information from memory allows us to visualise places and things not currently available in our perceptual milieu. Over the last decade it has become increasingly clear that the neural basis of visual mental imagery is tied to the endogenous activation of cortical areas subserving visual perception (e.g., Behrmann, 2000; Denis, Goncalves, & Memmi, 1995; Farah, 1995; Kosslyn, Ganis, & Thompson, 2001; Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998a; Roland & Gulyás, 1994; Sakai & Miyashita, 1993). The emerging consensus is that the retrieval of visual representations from memory leads to the reactivation of cortical areas that were initially activated during the perceptual encoding of those representations (e.g., Ishai & Sagi, 1997; Ishai, Ungerleider, & Haxby, 2000; Kosslyn, Thompson, & Alpert, 1997; Krelman, Koch, & Fried, 2000). In support of this “reactivation” hypothesis, visual imagery generation has been shown to increase activity in both primary visual cortex (e.g., Kosslyn et al., 1993, 1999; Kosslyn, Thompson, Kim, & Alpert, 1995b; Le Bihan, Turner, Zeffiro, Cuénod, Jezzard, & Bonnerot, 1993; Thompson, Kosslyn, Sukel, & Alpert, 2001) and object recognition areas of ventral temporal cortex (e.g., D’Esposito et al., 1997; Fletcher, Frith, Grasby, Shallice, Frackowiak, & Dolan, 1995; Ishai et al., 2000; Mellet, Tzourio, Denis, & Mazoyer, 1998b; O’Craven & Kanwisher, 2000; Wheeler, Petersen, & Buckner, 2000). Integral to this cortical reactivation is the retrieval of imagery content from memory. Nevertheless, the question of how—or even if—strategic memory retrieval processes influence reactivation during imagery has received comparatively little attention.

The issue centres on appreciating the different ways in which the content of visual imagery can be generated from memory, and how this may alter the strategic retrieval processes invoked. In one commonly used paradigm, participants are first presented with a set of objects to encode as memoranda, and then cued to visually recall the items that have been encoded (e.g., Kosslyn et al., 1995b, 1999; Le Bihan et al., 1993; Thompson et al., 2001; Wheeler et al., 2000). A second common paradigm has relied on more general or semantic-based knowledge for imagery generation, where participants are simply given the names of common visual objects as the cues for imagery (e.g., D’Esposito et al., 1997; Mellet et al., 1998b). Although both paradigms may give rise to vivid imagery in the mind’s eye, the paradigms may also lead to nontrivial differences

in the strategic processes engaged during the retrieval of imagery content from memory.

In particular, studies of memory retrieval have shown that activation of right frontal cortex (RFC) appears to vary in a systematic fashion with the parameters of the retrieval task involved (for a review, see Buckner & Wheeler, 2001). In this regard, the collective evidence predicts that recalling the visual appearance of objects encoded as temporally unique (or episodic) events should engage strategic processes in RFC, but that RFC activation should be reduced or absent when visualising the appearance of common objects in more semantic-type retrieval tasks that place no emphasis on when or where imagery content has been acquired (e.g., Buckner, Raichle, Miezin, & Petersen, 1996; Cabeza, Kapur, Craik, McIntosh, Houle, & Tulving, 1997; Düzel et al., 1999; Fletcher et al., 1995; Gabrieli et al., 1996; Haxby, Ungerleider, Horwitz, Maisog, Rapoport, & Grady, 1996; Nyberg, Habib, McIntosh, & Tulving, 2000; Schacter, Alpert, Savage, Rauch, & Albert, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; Wagner, Poldrack, Eldridge, Desmond, Glover, & Gabrieli, 1998). Although debate exists over how to functionally interpret task-related differences in RFC activation during retrieval (e.g., Buckner & Wheeler, 2001; Kelley, Buckner, & Petersen, 1998; Nyberg, Cabeza, & Tulving, 1998), the issue is tangential to the goal here. Stated simply, if the aforementioned predictions are correct, does the engagement of retrieval processes in RFC influence the extent to which visual imagery reactivates visual cortex, relative to imagery conditions showing less reliance on strategic processing in RFC?

The question sits at a key juncture in the links between imagery and memory. A recent meta-analysis of neuroimaging studies has suggested that medial occipital cortex (MOC) and bilateral occipitotemporal cortex are all regions labile to activation during imagery, but that there is unexplained variance in how these regions have responded to task conditions across studies (Thompson & Kosslyn, 2000). The growing belief is that the content of imagery plays a critical role in determining visuocortical activation during imagery, with MOC involvement more likely when high resolution images are necessary for optimal task performance (e.g., Kosslyn et al., 2001; Mellet et al., 1998a). Indeed, behavioural reports have suggested that imagery predicated on semantic memories may be less vivid or detailed than imagery generated from event-specific, episodic memories (e.g., Brewer & Pani, 1996). Such evidence suggests that the source of a visual mental image in memory may be sufficient to influence the content or resolution of imagery, altering in turn the pattern of imagery-related activity in visual cortex. Consistent with this possibility, recent neuroimaging evidence has indicated that image resolution alone may not determine whether MOC activity will be invoked during imagery (Thompson et al., 2001).

Taking a key first step in understanding how strategic memory processes may influence imagery-related cortical reactivation, Mellet et al. (2000) recently

examined how the strategy used at the time of encoding affects the pattern of imagery-related activation in posterior cortical areas. The same participant cohort was scanned using positron emission tomography (PET) while a set of objects was imaged that (1) had been viewed during encoding, or (2) that had been verbally described at encoding with no accompanying visual object representation. Results showed that the form of encoding—visual or verbal based—did not affect the network of areas in posterior cortex activated during imagery. Methodologically, the study is notable in that the content of imagery was held constant between conditions while memory processing associated with imagery content was varied. Switching the focus from encoding to retrieval, our aim was to examine the effect of different retrieval strategies on cortical reactivation during imagery.

Specifically, we manipulated within-subjects the retrieval conditions under which visual imagery was generated while participants were scanned in a blocked fMRI design. There were three experimental conditions, as summarised in Figure 1. In the first condition participants were auditorially cued to visualise objects that were encoded just prior to the scanning run (pictures imagery condition). In the second condition participants were auditorially cued to visualise the appearance of concrete nouns that were common visual objects (nouns imagery condition). As a third condition participants were also scanned while encoding the object memoranda for the pictures condition (visual encoding condition). The paradigm thus held constant the participant cohort and the qualitative content of imagery while varying the nature of the task used to retrieve imagery content. Data analysis then centred on determining whether (1) there were differences in anterior cortical regions activated between the two imagery tasks, and (2) whether imagery-related reactivation of visual cortex co-varied with the imagery condition.

METHODS

Participants

Fifteen healthy, right-handed adults participated in the experiment (10 female, 18–29 years of age). All had normal or corrected-to-normal vision and gave their informed written consent prior to scanning. All methods and procedures were approved by the Dartmouth College Committee for the Protection of Human Subjects.

Procedure and apparatus

Each participant was scanned under two different imagery conditions. In the pictures condition, participants were cued to recall visual images of pictures they had just encoded (see below). In the nouns condition, participants were cued to recall the appearance of various common objects—explicit instructions were

| EPOCHS | | |
|------------------|---|---|
| CONDITION | TASK | REST |
| ENCODING: | Eyes open. Viewing objects. Hearing object name. | Eyes open. Viewing blank screen. Hearing abstract word. |
| PICTURES: | Eyes closed. Imaging encoded object. Hearing object name. | Eyes closed. No imagery. Hearing abstract word. |
| NOUNS: | Eyes closed. Imaging object noun. Hearing object name. | Eyes closed. No imagery. Hearing abstract word. |

Figure 1. Task conditions. In the encoding condition participants were presented with the objects used as memoranda for imagery generation in the pictures condition. In the nouns condition imagery was based on hearing concrete nouns that named common visual objects. Participants listened to abstract words during all rest epochs, and the two imagery conditions (pictures and nouns) were performed with eyes closed for the duration of the functional run.

given that images should be based on a general understanding of how the named object appears rather than in reference to a specific event associated with the named object. Both imagery conditions were performed with eyes closed in a darkened scanning room, and single words naming each object were presented over headphones as the cues for imagery. Auditory stimulation was controlled using VAPP stimulus presentation software (<http://nilab.psychiatry.ubc.ca/vapp/>) running on a Dell Pentium PC and amplified via stereo receiver (Technics S4-EX10). The stimulus signal was passed through an electric-acoustic audio signal transducer (Etymotic Research, ER-30 transducer) and presented to the participant via rubber tubing mounted into the headphones and equipped with 3 mm foam eartips (Etymotic Research) for insertion into the ear canal.

Participants performed two functional runs in each of the two imagery conditions. Each run consisted of 38 s epochs of “imagery” that were interleaved with 30 s epochs of “rest”. In order to keep auditory stimulation operationally equivalent across all epoch types, during rest epochs participants passively listened to abstract words (e.g., “unity” and “belief”) presented over the headphones at the same temporal rate as in the imagery epochs. Within each imagery epoch 10 imagery cues were given, one every 3.5 s, with an additional 3 s blank interval at the end of the epoch; within each rest epoch eight abstract words were given, one every 3.5 s, with an additional 2 s blank interval at the end of the epoch. Each functional run began with a rest epoch followed by a task epoch, a pattern that repeated three more times for a total of four epochs of each type within each functional run. In order to minimise confusion as to whether a to-be-imagined object had been encoded or not, the pictures and nouns conditions were presented in separate functional runs, with the order of runs counterbalanced between subjects. In all four functional runs the difference between rest and imagery epochs was emphasised by using a female voice during imagery epochs and a male voice during rest epochs.

In order to provide the memoranda for the pictures condition, each run in this condition was preceded by a functional run during which the to-be-encoded pictures were presented (encoding condition). In each encoding run colour pictures of common objects (e.g., a flower, a helicopter, a shovel) were rear-projected (Epson ELP-7000 LCD projector) onto a screen at the participant’s feet using the stimulus presentation software described above. Participants viewed the screen using a headcoil-mounted mirror. Each picture was presented for 2 s, against a white background, followed by a 1.5 s blank interval when only a fixation point was present. In conjunction with each picture, the participants heard the name of the object over headphones, the word that would then serve as the imagery cue during the subsequent pictures run. During rest epochs participants maintained fixation on a grey screen while listening to abstract words. In order to facilitate comparison between visual areas active during visual perception and visual imagery, the timing and auditory aspects of the task and rest epochs were identical to those used in the two imagery conditions described above. At the beginning of each encoding run participants were informed that they would be asked to later recall images of the pictures presented. The order of recall in the pictures condition that followed was randomised relative to the order of visual presentation during the encoding condition.

A total of 80 different colour images were used for the encoding condition, 40 in each of the two functional runs. As a result, in the pictures condition each of these encoded pictures was imaged exactly once. Likewise, there were 80 different nouns used in the nouns condition (40 in each functional run), with no overlap between this set of items and the set of 80 items used in the pictures and encoding conditions. Because each of the two functional runs in the pictures condition was immediately preceded by the paired encoding functional run (see

above), the delay between the encoding and subsequent imagery of each picture was approximately 6–8 min, on average. The items used for imagery in both imagery conditions were common objects that one might typically encounter in everyday life (e.g., ladder, airplane, doughnut, spoon). As such, items imaged in the pictures and nouns conditions came from a variety of different object categories (e.g., food, tools).

Participants did not manually signal item-by-item success in generating imagery. Instead, they were instructed to closely monitor their rate of imagery failure during each imagery run. The first 10 participants in the study were asked to report at the end of each imagery run whether they had had more than five failed imagery attempts on that run. Nine participants reported a negative response to this question on every run; one participant reported no imagery on any run and was excluded from subsequent analysis. To more precisely quantify imagery failure, the final five participants reported at the end of each run their best estimate of how many failed imagery attempts had occurred on that run.

fMRI acquisition and analysis

Data were collected using a 1.5T SIGNA scanner (GE Medical Systems) with a fast gradient system for echo-planar imaging (EPI). Foam padding was used for head stabilisation. EPI images sensitive to the blood oxygen-level-dependent (BOLD) signal were acquired using a gradient-echo pulse sequence (TR = 2000 ms, TE = 35 ms, flip angle = 90°, 27 contiguous slices at 5 mm thick, and an in-plane resolution of 64 × 64 pixels in a FOV of 24 cm, producing voxels of 3.75 mm × 3.75 mm × 5 mm). Each scan began with four 2 s “dummy” shots to allow for steady-state tissue magnetisation. High-resolution, T1-weighted axial images were also taken of each subject (TR = 25 ms, TE = 6 ms, bandwidth = 15.6 kHz, voxel size = 0.9375 mm × 1.25 mm × 1.2 mm). Image reconstruction was performed on-line. Off-line data were processed and analysed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). For each subject the EPI images were corrected for motion (Friston, Williams, Howard, Frackowiak, & Turner, 1996), the EPI and anatomical images were co-registered and then spatially normalised into stereotaxic coordinates approximating the atlas of Talairach and Tournoux (1988) (Friston, Holmes, Worsley, Poline, Frith, & Frackowiak, 1995b). Finally, the normalised EPI images were spatially smoothed using an isotropic 8 mm Gaussian kernel.

Single-subject statistical analysis was based on a multiple regression using the general linear model (Friston, Ashburner, Frith, Poline, Heather, & Frackowiak, 1995a). Prior to parameter estimation the time series data for each subject were proportionally scaled in order to remove global changes in the BOLD signal intensity (but see Aguirre, Zarahn, & D’Esposito, 1998; Desjardins, Kiehl, & Liddle, 2001). Imagery and encoding epochs were modelled using a box-car reference waveform that was convolved with the haemodynamic

response function (HRF). Voxel-wise mean parameter estimates (β s) were then calculated within each run in order to quantify the degree to which the BOLD signal approximated the convolved HRF reference waveform; linear, quadratic, and cubic regressors were included in the regression model as effects of non-interest. Subsequent group-level analyses were based on a random-effects model using one-sample t -tests.

RESULTS

Behavioural performance

Participants were required to monitor and report their rate of imagery failure during each functional run (see Methods). For participants reporting the specific number of imagery failures per run, the mean in the pictures condition was 3.4 failed attempts per run (range: 0–8) and the mean in the nouns condition was 2.6 failed attempts per run (range: 0–5). Upon debriefing at the conclusion of the experiment, all 14 participants included in the data set reported vivid mental imagery during the imagery epochs.

fMRI data

Region of interest criteria. Analysis of fMRI data focused on two primary questions. First, was there evidence that different retrieval processes were engaged in right prefrontal cortex during the two imagery conditions? Second, did visuocortical activation differ between imagery conditions? In order to address these questions, five contrasts of interest were performed: (1) comparing task to rest epochs in the pictures imagery condition, (2) comparing task to rest epochs in the nouns imagery condition, (3) comparing task to rest epochs in the visual encoding condition, (4) a direct comparison between the pictures and nouns conditions showing areas more active during the pictures condition, and (5) a direct comparison between the pictures and nouns conditions showing areas more active during the nouns condition. In the group analyses all five contrasts were thresholded at a t probability value of $p < .0001$ (uncorrected) with a minimum cluster size of 10 contiguous voxels. At this criterion level no significant voxel clusters were found in the nouns $>$ pictures contrast. The significant clusters in the four remaining contrasts of interest are shown in Figure 2. Talairach coordinates (Talairach & Tournoux, 1988) and statistics for all clusters in anterior and posterior cortical regions are reported in Tables 1 and 2, respectively.

The data in Figure 2 established the initial regions of interest (ROIs). Further analyses were restricted to ROIs that showed a consistent statistical response across the three imagery contrasts of interest. In particular, for a region to be considered more active in the pictures condition relative to the nouns condition there had to be a significant voxel cluster in that region in the pictures and the

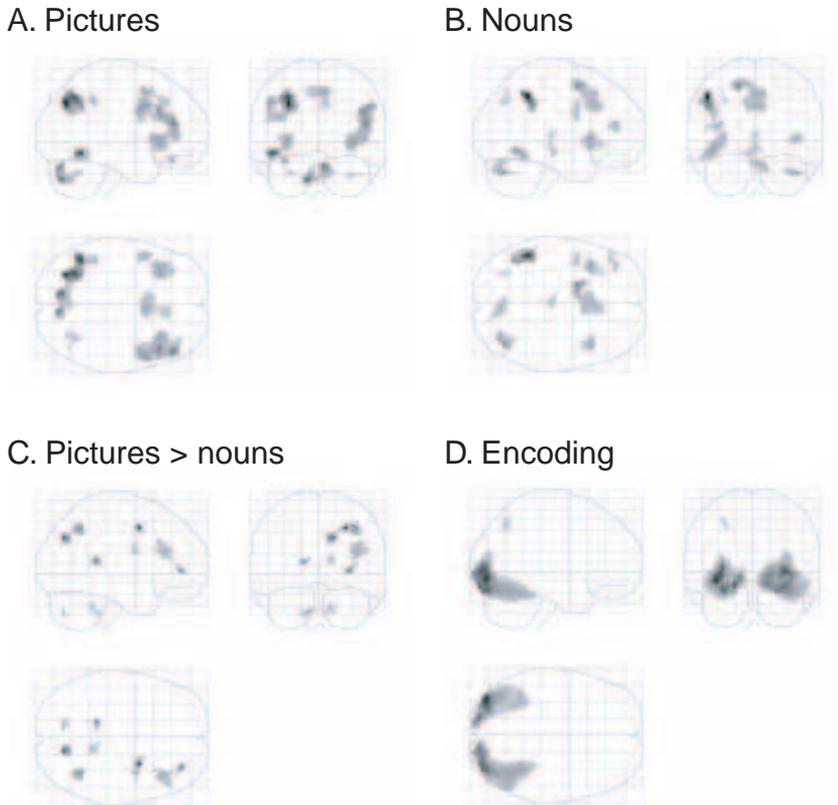


Figure 2. BOLD response in each contrast of interest. The data shown were thresholded at $p < .0001$ (uncorrected) with a minimum cluster size of 10 contiguous voxels. These data suggest that the primary differences in the pattern of cortical activation between the pictures (A) and nouns (B) imagery conditions were in the right frontal and right parietal regions (C). During the visual encoding condition (D), large activations were found in the lateral occipital and ventral temporal regions. At this threshold criterion there were no significant voxel clusters in the nouns > pictures contrast.

pictures > nouns contrast, and no significant voxel cluster in that region in the nouns contrast. For a region to be considered comparably active during both the pictures and nouns conditions there had to be a significant voxel cluster in the region in both the pictures and nouns contrasts, and an absence of a significant voxel cluster in that region in the pictures > nouns contrast. The analyses reported below are restricted to the relevant brain regions meeting these between-contrast criteria. Because the question of memory retrieval processes concerns activations in anterior brain regions and the question of visuocortical activation during imagery concerns responses in posterior brain regions, results are presented in separate subsections based on this anatomical division.

TABLE 1
Significant voxel clusters in anterior cortex as a function of contrast

| Contrast | Coordinates | | | | | Location | |
|---------------------|-------------|----------|----------|----------|----------|----------|--------------------------|
| | <i>x</i> | <i>y</i> | <i>z</i> | <i>k</i> | <i>t</i> | BA | Anatomical label |
| P_task > P_rest | 48 | 36 | 18 | 419 | 8.42 | 46/9 | R middle frontal gyrus |
| | -33 | 36 | -21 | 12 | 7.73 | 11 | L inferior frontal gyrus |
| | -48 | 9 | 39 | 84 | 7.03 | 47 | L middle frontal gyrus |
| | 6 | 9 | 48 | 144 | 7.02 | 6 | R superior frontal gyrus |
| | -30 | 24 | 0 | 93 | 7.19 | 13 | L insula |
| | -36 | 27 | 24 | 55 | 6.88 | 46 | L middle frontal gyrus |
| N_task > N_rest | -18 | 6 | 54 | 271 | 7.75 | 6 | L medial frontal gyrus |
| | 42 | 18 | 3 | 40 | 6.91 | 45 | R inferior frontal gyrus |
| | -36 | 42 | 15 | 26 | 6.83 | 46 | L middle frontal gyrus |
| | -39 | 15 | -6 | 79 | 6.74 | 47 | L inferior frontal gyrus |
| | -39 | 3 | 27 | 40 | 6.05 | 6 | L precentral gyrus |
| (P_task > P_rest) > | 27 | 3 | 45 | 18 | 8.95 | 8 | R medial frontal gyrus |
| (N_task > N_rest) | 30 | 45 | 3 | 15 | 8.21 | 10 | R middle frontal gyrus |
| | 36 | 27 | 21 | 59 | 6.50 | 45 | R inferior frontal gyrus |
| | 36 | 0 | 21 | 16 | 6.32 | 13 | R insula |

Coordinates are in Talairach space, *t* values are for the statistical maxima within each cluster, the minimum cluster size *k* was 10 voxels, and all contrasts are reported at $p < .0001$ (uncorrected). P = pictures, N = nouns, BA = Brodmann's area, L = left, R = right.

There were no significant voxel clusters in anterior cortex in the encoding condition.

Anterior activations. The data shown in Figures 2A and 2B indicate that RFC activation was more pronounced in the pictures condition relative to the nouns condition. The data shown in Figure 2C suggest that all frontal regions significantly more active in the pictures imagery condition relative to the nouns imagery condition were restricted to the right cerebral hemisphere. This conclusion is supported by the data reported in Figure 3, which shows the response of regions in dorsolateral frontal cortex in the three imagery-related contrasts of interest. Significant voxel clusters were found in the right midfrontal gyrus and right insula regions in both the pictures and pictures > nouns contrasts, but not in the nouns contrast. This suggests that activation in these two regions of RFC was restricted to the pictures imagery condition. In comparison, there was a significant voxel cluster in the left precentral gyrus in both the pictures and nouns contrasts, but not the pictures > nouns contrast, suggesting that this region of left prefrontal cortex was comparably active during both imagery conditions.

To quantify the magnitude of response in the ROIs highlighted in Figure 3, for each ROI identified in the group data the mean β value across all voxels in the cluster was computed within each subject for each of the four contrasts of interest. That is, a single group-level contrast was used to identify an ROI, and

TABLE 2
Significant voxel clusters in posterior cortex as a function of contrast

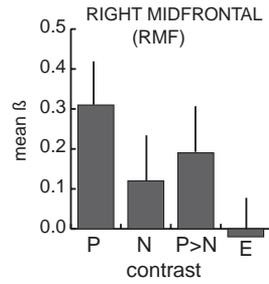
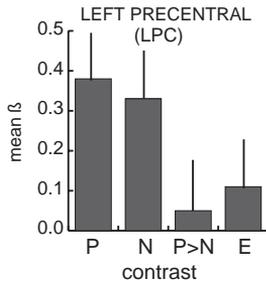
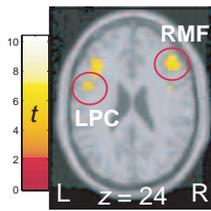
| <i>Contrast</i> | <i>Coordinates</i> | | | <i>k</i> | <i>t</i> | <i>Location</i> | |
|--|--------------------|----------|----------|----------|----------|-----------------|----------------------------|
| | <i>x</i> | <i>y</i> | <i>z</i> | | | <i>BA</i> | <i>Anatomical label</i> |
| P_task > P_rest | -30 | -69 | 39 | 206 | 10.35 | 19 | L intraparietal sulcus |
| | -45 | -54 | -12 | 66 | 9.83 | 37 | L fusiform gyrus |
| | -45 | -42 | 42 | 24 | 6.57 | 40 | L inferior parietal lobule |
| N_task > N_rest | -48 | -45 | 42 | 78 | 9.91 | 40 | L inferior parietal lobule |
| | -42 | -54 | -12 | 57 | 7.19 | 37 | L fusiform gyrus |
| | -30 | -69 | 39 | 15 | 6.07 | 19 | L intraparietal sulcus |
| (P_task > P_rest) > (N_task > N_rest) | 15 | -72 | 36 | 34 | 8.25 | 7 | R precuneus |
| | 36 | -57 | 45 | 39 | 7.24 | 40 | R inferior parietal lobule |
| E_task > E_rest | -36 | -84 | -9 | 702 | 16.24 | 18 | L inferior occipital gyrus |
| | 33 | -87 | 0 | 857 | 14.58 | 18 | R middle occipital gyrus |
| | -30 | -63 | 51 | 17 | 6.50 | 7 | L superior parietal lobule |

Coordinates are in Talairach space, *t* values are for the statistical maxima within each cluster, the minimum cluster size *k* was 10 voxels, and all contrasts are reported at $p < .0001$ (uncorrected). P = pictures, N = nouns, BA = Brodmann's area, L = left, R = right.

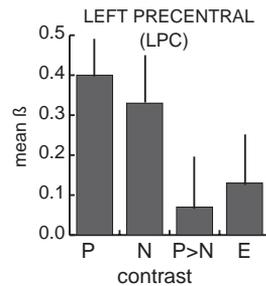
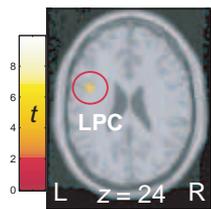
then the magnitude of response (β) in that ROI was computed for each contrast of interest, as shown in the graphs to the right of each brain slice in Figure 3. As a result, the response of an ROI defined in one contrast could be examined in turn in all contrasts of interest. While the clusters reported in the right midfrontal gyrus and right insula region showed evidence of a larger magnitude of response in the pictures imagery condition (Figures 3A and 3C), the clusters reported in the left precentral gyrus manifest a comparable magnitude of response between the two imagery conditions (Figures 3A and 3B). In sum, the data are suggestive of significantly greater activation in RFC during the pictures relative to nouns imagery conditions.

Posterior activations. The only region of visual cortex that was activated during imagery was in the left ventral cortex in the fusiform gyrus. As shown in Figure 4, the same region of the left fusiform gyrus was activated in both the pictures (Figure 4A) and nouns (Figure 4B) imagery conditions. This interpretation was supported by two lines of evidence. First, of the 66 voxels in the pictures cluster and the 57 voxels in the nouns cluster (see Table 2), 42 voxels were common to both voxel clusters. Second, as shown in the graphs in Figure 4A and 4B, each of the two clusters showed a comparable magnitude of response in the two imagery conditions when the mean β value was computed for each cluster across all contrasts of interests. Importantly, these graphs also indicate that there was a large response in each fusiform ROI during the visual

A. Pictures



B. Nouns



C. Pictures > nouns

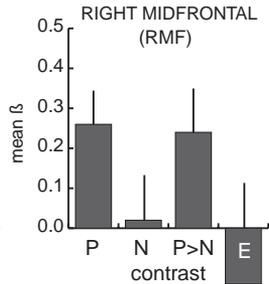
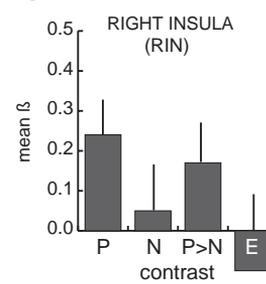
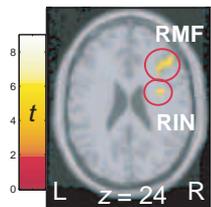
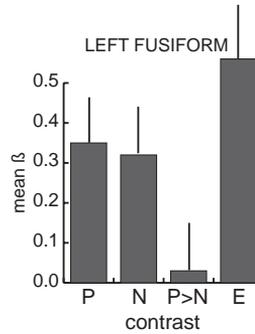
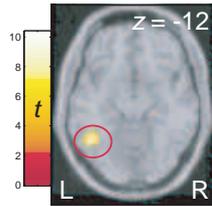
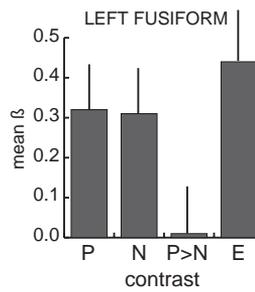
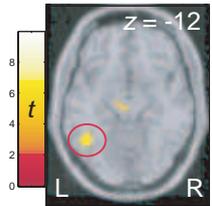


Figure 3. BOLD response in prefrontal cortex as a function of contrast. The data were thresholded at a value of $p < .0001$ (uncorrected), the minimum cluster size was 10 contiguous voxels, and the images shown are at $z = 24$. The graphs to the right of each image plot the mean β value for the highlighted cluster across the four contrasts of interest: P = pictures imagery condition, N = nouns imagery condition, P > N = the direct comparison between the two imagery conditions, and E = visual encoding condition. These data suggest that the left precentral region (LPC) was significantly active in both the pictures (A) and nouns (B) conditions, but that the right midfrontal region (RMF) and right insula (RIN) were only active in the pictures condition (C). The statistical results are overlaid on the single-subject T1 anatomical image provided in SPM99. Error bars show 1 standard deviation.

A. Pictures



B. Nouns



C. Encoding

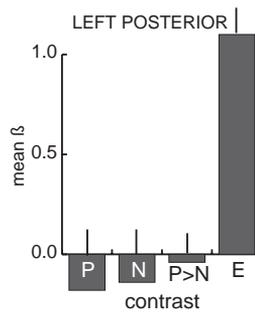
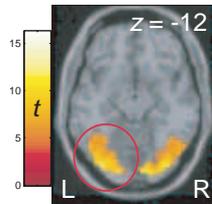


Figure 4. BOLD response in ventral temporal cortex as a function of contrast. The data were thresholded at a value of $p < .0001$ (uncorrected), the minimum cluster size was 10 contiguous voxels, and the images shown are at $z = -12$. The graphs to the right of each image plot the mean β value for the highlighted cluster across the four contrasts of interest: P = pictures imagery condition, N = nouns imagery condition, P > N = the direct comparison between the two imagery conditions, and E = visual encoding condition. These data indicate that a common region of the left fusiform gyrus was significantly active in both the pictures (A) and nouns (B) conditions. The visual encoding condition produced much more widespread activation in visual cortex (C). The statistical results are overlaid on the single-subject T1 anatomical image provided in SPM99. Error bars show 1 standard deviation.

encoding condition. Consistent with this interpretation, of the 42 voxels in the left fusiform gyrus activated during both imagery conditions, 23 of these voxels were also activated during the encoding condition. However, that imagery led to activation only in a small portion of visual cortex and is highlighted in Figure 4c, which shows both the anatomic extent of activation in visual cortex during visual stimulation, and the mean magnitude of response in visually activated cortex across all contrasts of interest.

Notably, there was no imagery-related activation in the region of MOC at the ROI criteria threshold of $p < .0001$ (uncorrected). Given the wide interest in understanding the behaviour of this region during imagery, we re-examined voxels in MOC at less conservative statistical thresholds. Even at a t probability value of $p < .01$ (uncorrected) there were no significant voxels in MOC in the pictures, nouns, or encoding contrasts. To better understand this null result in the group data, we then looked at the single-subject BOLD responses in this region

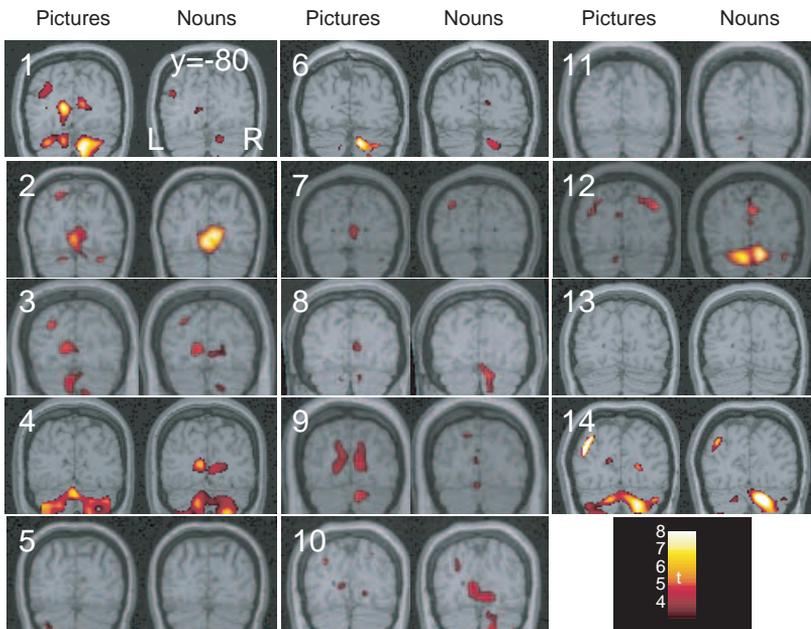


Figure 5. Single-subject BOLD responses in MOC. The data were thresholded at a value of $p < .001$ (uncorrected), there was no minimum cluster size, and all images are shown at $y = -80$. For each subject, the BOLD response in this slice plane is shown as a function of contrast (pictures and nouns), with the individual participants identified via the number in the upper left-hand corner of each pair of images. These single-subject images reveal the wide individual variability in the BOLD response in MOC during the two imagery conditions. The data shown are spatially normalised and statistical overlaid on each subjects' normalised anatomical image. Cluster statistics are reported in Table 3.

by contrast (pictures and nouns). As shown in Figure 5, there was wide variance across participants in terms of whether there were significant voxel clusters in the MOC region in either one or both contrasts at a threshold of $p < .001$ (uncorrected). Talairach coordinates and statistics for these single-subject clusters are reported in Table 3. Importantly, not only does the variance across participants in the MOC BOLD response explain the lack of a significant effect in the group data, it is consistent with the growing belief that there is a high degree of individual variability in MOC activation during imagery.

TABLE 3
Significant voxel clusters in the medial occipital (MOC) region, by subject and contrast

| Subject | $P_{task} > P_{rest}$ | | | | | $N_{task} > N_{rest}$ | | | | |
|---------|-----------------------|----------|-------------|----------|----------|-----------------------|----------|-------------|----------|----------|
| | <i>x</i> | <i>y</i> | <i>z</i> | <i>k</i> | <i>t</i> | <i>x</i> | <i>y</i> | <i>z</i> | <i>k</i> | <i>t</i> |
| 1 | -9 | -75 | 6 | 4397 | 7.60 | -9 | -84 | 3 | 32 | 3.87 |
| | 12 | -75 | 6 | 220 | 7.60 | | | | | |
| 2 | 6 | -87 | -3 | 461 | 6.80 | 6 | -84 | 3 | 1137 | 6.60 |
| 3 | -12 | -84 | 3 | 226 | 5.41 | -12 | -81 | 3 | 219 | 4.90 |
| | | | | | | 18 | -81 | -3 | | 3.65 |
| 4 | | | no clusters | | | 0 | -99 | 0 | 812 | 6.19 |
| 5 | | | no clusters | | | | | no clusters | | |
| 6 | | | no clusters | | | 12 | -78 | 12 | 107 | 3.90 |
| 7 | 6 | -84 | -3 | 198 | 4.49 | 6 | -90 | 6 | 10 | 3.23* |
| 8 | 9 | -90 | 12 | 108 | 4.53 | 6 | -90 | 12 | 13 | 3.77 |
| 9 | -12 | -81 | 9 | 1681 | 4.17 | 0 | -96 | 0 | 121 | 4.89 |
| | 9 | -84 | 6 | | 5.17 | | | | | |
| 10 | -12 | -84 | 0 | 23 | 3.88 | 0 | -84 | -9 | 202 | 5.26 |
| | 18 | -81 | -6 | 23 | 3.68 | | | | | |
| 11 | | | no clusters | | | | | no clusters | | |
| 12 | -9 | -78 | 6 | 18 | 3.04* | -12 | -72 | 6 | 2039 | 4.60 |
| | 12 | -81 | 12 | 1301 | 3.15* | | | | | |
| 13 | | | no clusters | | | | | no clusters | | |
| 14 | -15 | -78 | 12 | 30315 | 6.94 | | | no clusters | | |
| | 21 | -78 | 9 | | 5.29 | | | | | |

Coordinates are in Talairach space, *t* values are for the local maxima in the MOC region within each cluster, and the minimum cluster size *k* was 10 voxels. Voxel clusters are reported at $p < .001$ (uncorrected), except those designated with an asterisk (*), which were clusters that were found to be significant only at a more permissive threshold ($p < .005$; uncorrected). If only one *k* value is reported for a pair of maxima, those maxima were in a contiguous voxel cluster at the reported threshold. P = pictures, N = nouns.

DISCUSSION

The data shown in Figure 3 suggest that the two imagery tasks invoked different retrieval processes in frontal cortex. While activations were comparable between conditions in the region of the left precentral gyrus, there were activations in both the right midfrontal and right insula regions during the pictures condition that were absent in the nouns condition. Importantly, this finding parallels a large corpus of evidence from the memory literature indicating that retrieval of temporally unique (or episodic) events engages processes in RFC that are typically not engaged during retrieval of more semantic-based information (e.g., Buckner et al., 1996; Cabeza et al., 1997; Düzel et al., 1999; Fletcher et al., 1995; Gabrieli et al., 1996; Haxby et al., 1996; Nyberg et al., 2000; Schacter et al., 1996; Tulving et al., 1994; Wagner et al., 1998). Although it remains an open question how to best characterise the functional nature of retrieval-related processing in RFC (e.g., Buckner & Wheeler, 2001; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999), the key point here is that processing in this region was differentially engaged in the two imagery conditions.¹

Given the effect of imagery condition on retrieval processing, was there a corresponding difference between conditions in the pattern of visuocortical reactivation? The short answer is no. In both imagery conditions the same region of the left fusiform gyrus showed increased activation during imagery epochs relative to rest epochs (Figure 4). Indeed, there was substantial overlap in the two fusiform clusters, as quantified by the number of voxels showing above threshold activation in both conditions (see Results). That left ventral temporal cortex was engaged during imagery parallels the results of prior studies that have also shown activation in this region during imagery-related tasks (e.g., D'Esposito et al., 1997; Mellet et al., 1998b; Wheeler et al., 2000). The common fusiform response between conditions supports the argument that, despite the lack of an overt behavioural measure of task performance on each imagery attempt, both tasks did in fact lead to mental imagery. The data are thus relatively unambiguous in suggesting that despite apparent differences in the strategic retrieval mechanisms engaged during imagery generation, a common

¹ Given the lack of a direct behavioural measure of imagery performance in each condition, we cannot eliminate the possibility that there were common retrieval strategies used between conditions, at least for some items. However, the differential pattern of the bold response in frontal cortex indicates that, on average, there was in fact a difference in the retrieval strategies used between the two imagery conditions. Nevertheless, although we attribute these frontal differences between the pictures and nouns conditions to strategic processes associated with "episodic" and "semantic" retrieval, respectively, there may be additional contributing factors to consider as well. For example, the items imaged in the pictures condition may have been more like specific exemplars, while the items imaged in the nouns condition may have been more "prototypic" in nature. If so, there would be greater likelihood of individual variability in terms of imagery content generated in the nouns condition, in that there may be variance across participants in what passes as a prototypic image for a given object.

region of visual cortex was reactivated by the information retrieved from memory.

The data thus support the conclusion that a common visuocortical network was activated when the content of imagery was being held constant but the retrieval demands were varied. However, we stress that other factors are quite capable of influencing the pattern of cortical reactivation during imagery. For instance, imagery of spatial information is more likely to engage processing in parietal rather than ventral temporal cortex (e.g., Cohen et al., 1996; Mellet, Tzourio, Crivello, Joliot, Denis, & Mazoyer, 1996; Moscovitch, Kapur, Köhler, & Houle, 1995; see Mellet et al., 1998a). Likewise, visualising different categories of objects (e.g., faces vs. houses) has been shown to activate corresponding category-specific regions of ventral temporal cortex (e.g., Ishai et al., 2000; O'Craven & Kanwisher, 2000), and comparisons between visual and auditory imagery demonstrate that sensory-specific imagery content reactivates sensory-specific cortex (e.g., Wheeler et al., 2000). Common across these studies have been paradigms that vary the qualitative content of imagery between conditions in order to examine how it influences cortical reactivation.

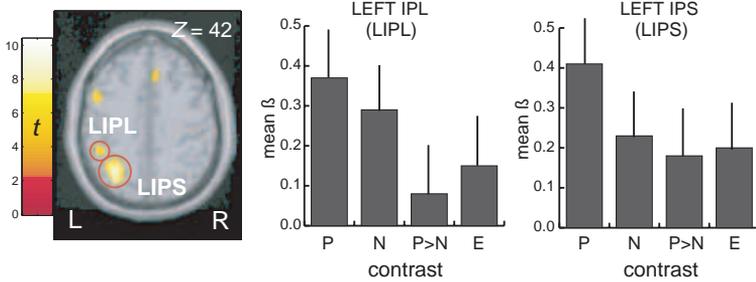
In contrast, the experiment here demonstrates that if the content of imagery is held constant, reactivation of ventral temporal cortex appears to remain unaffected despite strategic changes in the memory retrieval processes used to generate that content. The finding closely parallels the results of Mellet et al. (2000), who showed that differences in encoding strategies also appear to have little influence on the network of posterior cortical regions activated during imagery. Our data are also consistent with the proposal that imagery content is perhaps the most decisive factor in determining the pattern of imagery-related activation in posterior cortex (e.g., Behrmann, 2000; Kosslyn & Thompson, 2000; Mellet et al., 1998a; Thompson & Kosslyn, 2000). As such, it remains an open question whether imagery-related activity in MOC may be labile to modulation by retrieval processes under conditions more suitable for observing task-related imagery effects in that region.

Although the focus of our study has been on determining the extent to which memory retrieval modulates visual cortical activity during imagery, the region of left fusiform gyrus found to be active in both imagery conditions is consistent with a wider network of posterior cortical areas that have been implicated in the interplay between memory and imagery (see Thompson & Kosslyn, 2000). In particular, both imagery tasks led to activation in the same pair of regions in left parietal cortex, namely the left inferior parietal lobule and left intraparietal sulcus (Figure 6). This finding is consistent with reports that left parietal regions are an integral component of the network of cortical areas involved in memory retrieval (e.g., Buckner & Wheeler, 2001; Habib & Lepage, 1999; Rugg & Wilding, 2000; see also Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999) as well as visual imagery (e.g., Ishai et al., 2000; Mellet et al., 1998a). The common thread running through these discussions is that parietal regions

are engaged during the retrieval attempt itself, and during the “top-down” reactivation of sensory cortex (if retrieval is successful).

Taken in this light, perhaps the least contentious conclusion to draw from the data in Figure 6 is that both the left inferior parietal lobule and left intraparietal sulcus were comparably involved in the two imagery tasks (see also Figure 2C). However, the data also provide partial evidence in support of the proposal of Mellet et al. (1998a) that this region is differentially more involved in imagery tied to episodic retrieval. The magnitude (β) and anatomical extent of the response in the left intraparietal sulcus appeared to be larger in the pictures task relative to the nouns task (see Table 2). There was also evidence in the pictures > nouns contrast that the right inferior parietal lobule and precuneus were more active in the pictures condition as well. We offer these data as potential points of

A. Pictures



B. Nouns

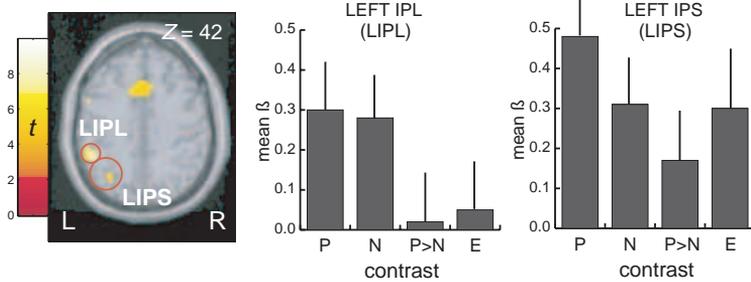


Figure 6. BOLD response in parietal cortex as a function of contrast. The data were thresholded at a value of $p < .0001$ (uncorrected), the minimum cluster size was 10 contiguous voxels, and all images shown are at $z = 42$. The graphs to the right of each image plot the mean β value for the highlighted cluster across the four contrasts of interest: P = pictures imagery condition, N = nouns imagery condition, P > N = the direct comparison between the two imagery conditions, and E = visual encoding condition. These data suggest that common regions of the left inferior parietal lobule (LIPL) and the left intraparietal sulcus (LIPS) were significantly active in both the pictures (A) and nouns (B) conditions. The statistical results are overlaid on the single-subject T1 anatomical image provided in SPM99. Error bars show 1 standard deviation.

interest for future investigations focusing on the role of parietal cortex in memory retrieval and visual imagery.

At a more global level, one of the long-standing issues in the imagery literature has been whether there is cerebral hemisphere specialisation in the processes mediating visual imagery (e.g., Behrmann, 2000; Farah, 1995; Kosslyn, 1988; Kosslyn, Maljkovic, Hamilton, Horwitz, & Thompson, 1995a; Mellet et al., 1998a). The data in Figures 2C and 3C suggest that, in general, what was common between imagery conditions was processing in the left hemisphere and what was different between imagery conditions was processing in the right hemisphere. As such, our results are consistent with the proposition that a common network of areas in the left hemisphere were engaged during the two imagery conditions, including prefrontal, lateral parietal, and ventral temporal regions. If so, it raises the question of whether task manipulations that influence retrieval processing in left frontal cortex (e.g., repetition priming) would lead to corresponding changes in processing in the left hemisphere network implicated in the current study.

In conclusion, there are clear and important links between the neural systems we use to retrieve stored information and the systems we use to visualise an item that has been retrieved (e.g., Gonsalves & Paller, 2000; Ishai & Sagi, 1997; Mellet et al., 1998a; Wheeler et al., 2000). The data reported here speak directly to these links. From the memory perspective our results suggest that the segregation of strategic retrieval processes in frontal cortex does not extend to the visual areas activated during visual imagery. Rather, dissociable retrieval processes in frontal cortex appear to engage a common network of temporal and parietal areas when the intention of retrieval is to generate a visual mental image. In this sense, what the mind's eye sees during imagery appears to be unaffected by changes in the strategic processes in frontal cortex used to retrieve imagery content from memory.

PrEview proof published online May 2004

REFERENCES

- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). The inferential impact of global signal covariates in functional neuroimaging analyses. *NeuroImage*, 8, 302–306.
- Behrmann, M. (2000). The mind's eye mapped onto the brain's matter. *Current Directions in Psychological Science*, 9, 50–54.
- Brewer, W. F., & Pani, J. R. (1996). Reports of mental imagery retrieval from long-term memory. *Consciousness and Cognition*, 5, 265–287.
- Buckner, R. L., Raichle, M. E., Miezin, F. M., & Petersen, S. E. (1996). Functional anatomic studies of memory retrieval for auditory words and visual pictures. *Journal of Neuroscience*, 16, 6219–6235.
- Buckner, R. L., & Wheeler, M. E. (2001). The cognitive neuroscience of remembering. *Nature Reviews Neuroscience*, 2, 624–634.

- Cabeza, R., Kapur, S., Craik, F. I. M., McIntosh, A. R., Houle, S., & Tulving, E. (1997). Functional neuroanatomy of recall and recognition: A PET study of episodic memory. *Journal of Cognitive Neuroscience*, *9*, 254–265.
- Cohen, M. S., Kosslyn, S. M., Breiter, H. C., DiGirolamo, G. J., Thompson, W. L., Anderson, A. K., Bookheimer, S. Y., Rosen, B. R., & Belliveau, J. W. (1996). Changes in cortical activity during mental rotation: A mapping study using functional magnetic resonance imaging. *Brain*, *119*, 89–100.
- Denis, M., Goncalves, M. R., & Memmi, D. (1995). Mental scanning of visual images generated from verbal descriptions: Toward a model of image accuracy. *Neuropsychologia*, *33*, 1511–1530.
- Desjardins, A. E., Kiehl, K. A., & Liddle, P. F. (2001). Removal of confounding effects of global signal in functional MRI analyses. *NeuroImage*, *13*, 751–758.
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., Farah, M. J. (1997). A functional MRI study of mental image generation. *Neuropsychologia*, *35*, 725–730.
- Düzel, E., Cabeza, R., Picton, T. W., Yonelinas, A. P., Scheich, H., Heinze, H. J., & Tulving, E. (1999). Task-related and item-related brain processes of memory retrieval. *Proceedings of the National Academy of Sciences, USA*, *96*, 1794–1799.
- Farah, M. J. (1995). Current issues in the neuropsychology of image generation. *Neuropsychologia*, *33*, 1455–1471.
- Fletcher, P. C., Frith, C. D., Grasby, P. M., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). Brain systems for encoding and retrieval of auditory-verbal memory. *Brain*, *118*, 401–416.
- Friston, K. J., Ashburner, J., Frith, C. D., Poline, J.-P., Heather, J. D., & Frackowiak, R. S. J. (1995a). Spatial registration and normalization of images. *Human Brain Mapping*, *2*, 165–189.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995b). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Friston, K. J., Williams, S., Howard, R., Frackowiak, R. S., & Turner, R. (1996). Movement-related effects in fMRI time-series. *Magnetic Resonance in Medicine*, *35*, 346–355.
- Gabrieli, J. D. E., Desmond, J. E., Demb, J. B., Wagner, A. D., Stone, M. V., Vaidya, C. J., & Glover, G. H. (1996). Functional magnetic resonance imaging of semantic memory processes in the frontal lobes. *Psychological Science*, *7*, 278–283.
- Gonsalves, B., & Paller, K. A. (2000). Neural events that underlie remembering something that never happened. *Nature Neuroscience*, *3*, 1316–1321.
- Habib, R., & Lepage, M. (1999). Novelty assessment in the brain. In E. Tulving (Ed.), *Memory, consciousness, and the brain*. Philadelphia: Psychology Press.
- Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences, USA*, *93*, 922–927.
- Ishai, A., & Sagi, D. (1997). Visual imagery: Effects of short- and long-term memory. *Journal of Cognitive Neuroscience*, *9*, 734–742.
- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.
- Kelley, W. M., Buckner, R. L., & Petersen, S. E. (1998). Response from Kelley, Buckner, & Petersen. *Trends in Cognitive Science*, *2*, 421.
- Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature*, *399*, 148–151.
- Kosslyn, S. M. (1988). Aspects of a cognitive neuroscience of mental imagery. *Science*, *240*, 1621–1626.
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., Hamilton, S. E., Rauch, S. L., & Buonanno, F. S. (1993). Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience*, *5*, 263–287.
- Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, *2*, 635–642.

- Kosslyn, S. M., Maljkovic, V., Hamilton, S. E., Horwitz, G., & Thompson, W. L. (1995a). Two types of image generation: Evidence for left and right hemisphere processes. *Neuropsychologia*, *33*, 1485–1510.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., Ganis, G., Sukel, K. E., & Alpert, N. M. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*, *284*, 167–170.
- Kosslyn, S. M., & Thompson, W. L. (2000). Shared mechanisms in visual imagery and visual perception: Insights from cognitive neuroscience. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed.). Cambridge, MA: MIT Press.
- Kosslyn, S. M., Thompson, W. L., & Alpert, N. M. (1997). Neural systems shared by visual imagery and visual perception: A positron emission tomography study. *NeuroImage*, *6*, 320–334.
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995b). Topographical representations of mental images in primary visual cortex. *Nature*, *378*, 496–498.
- Krelman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, *408*, 357–361.
- Le Bihan, D., Turner, R., Zeffiro, T. A., Cuénod, C. A., Jezard, P., & Bonnerot, V. (1993). Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study. *Proceedings of the National Academy of Sciences, USA*, *90*, 11802–11805.
- Mellet, E., Petit, L., Mazoyer, B., Denis, M., & Tzourio, N. (1998a). Reopening the mental imagery debate: Lessons from functional anatomy. *NeuroImage*, *8*, 129–139.
- Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., & Mazoyer, B. (1996). Functional anatomy of spatial mental imagery generated from verbal instructions. *Journal of Neuroscience*, *16*, 6504–6512.
- Mellet, E., Tzourio, N., Denis, M., & Mazoyer, B. (1998b). Cortical anatomy of mental imagery of concrete nouns based on their dictionary definition. *Neuroreport*, *9*, 803–808.
- Mellet, E., Tzourio-Mazoyer, N., Bricogne, S., Mazoyer, B., Kosslyn, S. M., & Denis, M. (2000). Functional anatomy of high-resolution visual mental imagery. *Journal of Cognitive Neuroscience*, *12*, 98–109.
- Moscovitch, M., Kapur, S., Köhler, S., & Houle, S. (1995). Distinct neural correlates of visual long-term memory for spatial location and object identity: A positron emission tomography study in humans. *Proceedings of the National Academy of Sciences, USA*, *92*, 3721–3725.
- Nyberg, L., Cabeza, R., & Tulving, E. (1998). Asymmetric frontal activation during episodic memory: What kind of specificity? *Trends in Cognitive Science*, *2*, 419–420.
- Nyberg, L., Habib, R., McIntosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences, USA*, *97*, 11120–11124.
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*, 1013–1023.
- Roland, P. E., & Gulyás, B. (1994). Visual imagery and visual representation. *Trends in Neuroscience*, *17*, 281–289.
- Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Science*, *4*, 108–115.
- Sakai, K., & Miyashita, Y. (1993). Memory and imagery in the temporal lobe. *Current Opinion in Neurobiology*, *3*, 166–170.
- Schacter, D. L., Alpert, N. M., Savage, C. R., Rauch, S. L., & Albert, M. S. (1996). Conscious recollection and the human hippocampal formation: Evidence from positron emission tomography. *Proceedings of the National Academy of Sciences, USA*, *93*, 321–325.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme Medical Publishers.
- Thompson, W. L., & Kosslyn, S. M. (2000). Neural systems activated during visual mental imagery: A review and meta-analysis. In W. Toga & J. C. Mazziotta (Eds.), *Brain mapping: The systems*. San Diego: Academic Press.

- Thompson, W. L., Kosslyn, S. M., Suckel, K. E., & Alpert, N. M. (2001). Mental imagery of high- and low-resolution gratings activates area 17. *NeuroImage*, *14*, 454–464.
- Tomita, H., Ohbayashi, M., Nakahara, K., Hasegawa, I., & Miyashita, Y. (1999). Top-down signal from prefrontal cortex in executive control of memory retrieval. *Nature*, *401*, 699–703.
- Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences, USA*, *91*, 2016–2020.
- Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport*, *9*, 3711–3717.
- Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences, USA*, *97*, 11125–11129.