Mental Imagery of Faces and Places Activates Corresponding Stimulus-Specific Brain Regions

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Abstract

■ What happens in the brain when you conjure up a mental image in your mind's eye? We tested whether the particular regions of extrastriate cortex activated during mental imagery depend on the content of the image. Using functional magnetic resonance imaging (fMRI), we demonstrated selective activation within a region of cortex specialized for face perception during mental imagery of faces, and selective activation within a place-selective cortical region during imagery of places. In a further study, we compared the activation for imagery and perception in these regions, and found greater response magnitudes for perception than for imagery of the same items. Finally, we found that it is possible to determine the content of single cognitive events from an inspection of the fMRI data from individual imagery trials. These findings strengthen evidence that imagery and perception share common processing mechanisms, and demonstrate that the specific brain regions activated during mental imagery depend on the content of the visual image. ■

INTRODUCTION

A number of studies have suggested that mental imagery, or ''seeing with the mind's eye,'' engages many of the same cognitive (Kosslyn, Sukel, & Bly, 1999; Gilden, Blake, & Hurst, 1995; Ishai & Sagi, 1995; Finke, 1985; Segal & Fusella, 1970; Perky, 1910) and neural (Kosslyn, Thompson, Kim, & Alpert, 1995; Kosslyn, Pascual-Leone, et al., 1999; Roland & Gulyas, 1995; Farah, Soso, & Dasheiff, 1992) mechanisms that are involved in visual perception. Much of this debate has focused on the question of whether retinotopic visual areas are engaged during visual imagery (Chen et al., 1998; Kosslyn et al., 1993; Le Bihan et al., 1993) or not (Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998; Mellet, Tzourio, Denis, & Mazoyer, 1998; D'Esposito et al., 1997; Roland & Gulyas, 1994, 1995). A key problem in resolving this question is the choice of a nonimagery control condition. ''Resting'' baselines can be problematic (Binder et al., 1999; Kosslyn & Ochsner, 1994) because they may inadvertently engage mental imagery processes, thereby causing imagery activations to be subtracted away. On the other hand, auditory and other control tasks can also be problematic, because they may produce cross-modal inhibition of visual cortex (Woodruff et al., 1996; Kawashima, O'Sullivan, & Roland, 1995), thereby creating spurious imagery activations in these regions.

The present study avoids these problems by asking a different set of questions about the neural basis of mental imagery. First, do the particular regions of cortex that are active during visual imagery depend on the content of the visual image? Second, how does the magnitude of the functional magnetic resonance imaging (fMRI) response during mental imagery compare to that of the response evoked during perception? Third, are fMRI signals during mental imagery clear and selective enough that the content of single mental imagery events can be categorized (as a face or a place) based on the fMRI data alone?

Our study exploited the perceptual selectivity of two recently described extrastriate areas, and asked whether these areas exhibit a parallel selectivity during mental imagery. A region of ventral occipito-temporal cortex called the fusiform face area, or FFA (Kanwisher, McDermott, & Chun, 1997), responds strongly when subjects view photographs of faces, but only weakly when they view other classes of stimuli such as familiar objects or complex scenes (McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Haxby et al., 1991, 1999). Conversely, a ventromedial cortical region called the parahippocampal place area (PPA) responds strongly to images of indoor and outdoor scenes depicting the layout of local space, but not at

all to faces (Epstein & Kanwisher, 1998). These two regions provide an ideal arena for testing the selectivity of cortical activations during mental imagery because they exhibit opposite response properties: the optimal stimulus for the FFA is a very weak stimulus for the PPA and vice versa. Thus, we were able to look for a double dissociation of brain activity in response to imagery of two different classes of stimuli, instead of comparing imagery to nonimagery tasks as most previous studies have done.

Our first experiment sought to determine whether any extrastriate brain areas were differentially active during imagery of faces versus imagery of places, and if so, whether those areas fell within the FFA and PPA, respectively. Subjects were scanned with fMRI in two closely matched paradigms, one involving the perception of faces and scenes (presented visually), and the other involving mental imagery of the same faces and scenes (with eyes closed).

In order to directly compare the magnitude of the stimulus-specific activation during imagery to the activation during perception, our second experiment included both imagery and perceptual conditions within each scan. One might predict that fMRI responses during imagery would be of greater magnitude, since it may require more processing to generate an internal mental image than to merely process a stimulus that is visually present; this relationship has been reported in retinotopic cortex (Kosslyn et al., 1993). Alternatively, one might expect the more vivid experience of actually seeing a visual stimulus to produce a stronger fMRI response than the weaker and more ephemeral experience of mental imagery (Chen et al., 1998; Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998).

Our final experiment used true single-trial fMRI (not multitrial event-related fMRI) to determine whether the observed imagery activations were sufficiently strong and reliable that the category of stimulus imaged—face or place—could be determined on each individual trial from a simple inspection of the fMRI time courses in the FFA and PPA.

RESULTS

Experiment 1

For the perception paradigm in the first experiment, each of eight subjects was run on two scans in which they viewed alternating epochs of photographs of famous faces and familiar places (scenes from the MIT campus). For the imagery paradigm, the same subjects were run on four scans in which they closed their eyes and heard the names of the same people and places they had viewed during the perception runs, and were instructed to form a vivid mental image of each one. The perception and imagery scans used the same nominal stimuli, presentation rate, and temporal sequence; the only difference was that actual photographs were vi-sually presented on the screen for the perception scans, whereas the visual stimuli were only imagined in the imagery scans.

For each subject, the two perception scans were averaged together, and the four imagery scans were averaged together. We then carried out both a group analysis, and individual analyses of each subject.

For the group analysis, the data from each subject were transformed into a common space (Talairach & Tournoux, 1988) before averaging across subjects. Activation maps were then constructed by calculating (separately for the perception and imagery data) whether the MR signal intensity at each voxel was significantly different during face processing and during place processing.

The resulting statistical maps (see Figure 1) reveal a striking similarity between regions activated during imagery and those activated during perception of the corresponding stimulus class. Specifically, regions that were consistently more active across subjects during face perception than place perception are shown at the top (Figure 1a). These data show bilateral midfusiform activations (peaks at 37, −36, −18, and −37, −39, −15), consistent with prior reports of face selectivity in this region (Haxby et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997). The comparison of face imagery to place imagery (Figure 1b) reveals a highly specific activation of the right mid-FFA only (peak at 34, −39, −15).

The reverse comparisons (places vs. faces) on the same data set are shown for the perception data (Figure 1c) and the imagery data (Figure 1d). Here again, the activations during place imagery are very similar to those during place perception, and consist of two nearby but distinct activated regions. First, as predicted, activation was found for both perception and imagery of places in the PPA. The anatomical locus of this activation (31, −39, −6; −28, −39, −3), straddling the collateral sulcus, matches that of the PPA described in earlier studies (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998).

Second, overlapping activation was seen in anterior calcarine cortex (9, −48, 6; −21, −60, 18). While we did not predict that this region would be activated for place imagery, it has been reported in prior studies of scene perception (Epstein & Kanwisher, 1998). This finding could reflect activation of peripheral retinotopic cortex in both perception and imagery by larger images (Kosslyn et al., 1993), since the scenes in these experiments were slightly larger than the faces. However, we think it is more likely to constitute a distinct functional region that merits investigation with retinotopically balanced stimuli in the future. Consistent with this suggestion, activity in the anterior calcarine region has also been observed with a task of imagining walking around one's hometown (Chen et al., 1998).
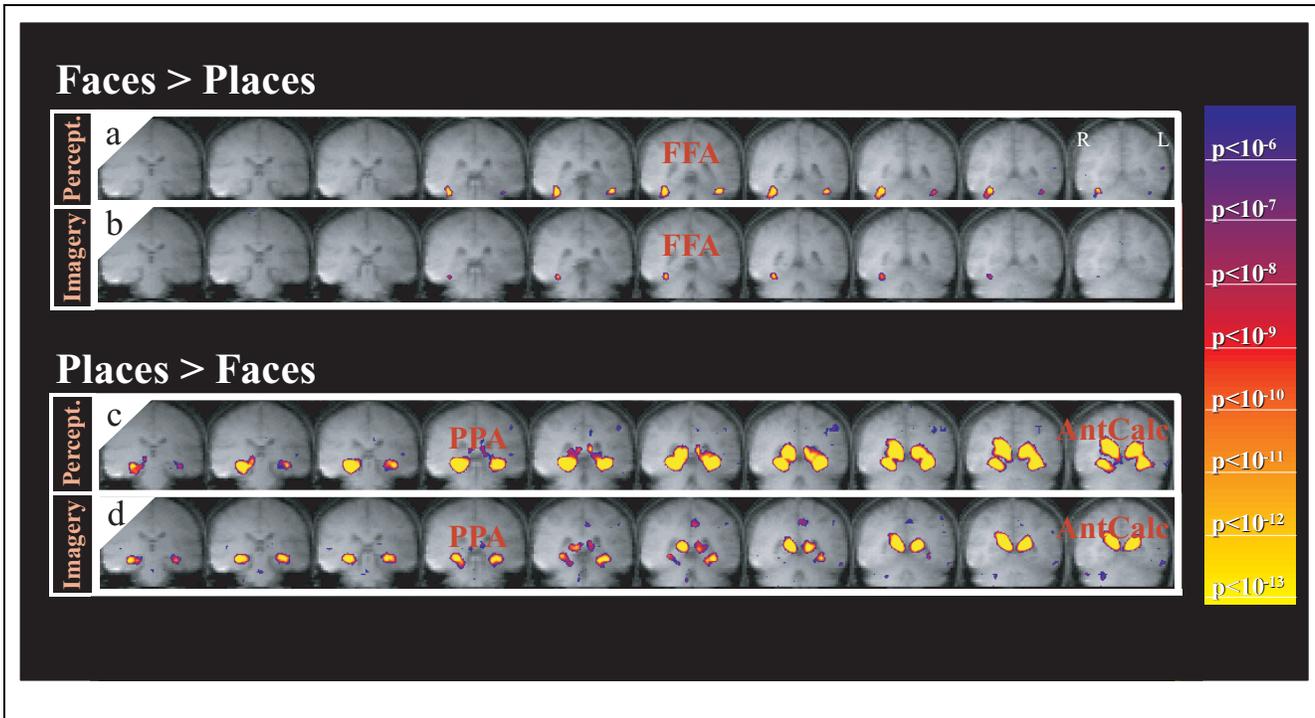
Figure 1. Posterior coronal brain slices showing the group average, in Talairach space, of the results from Experiment 1. Note the striking similarity between corresponding activations for (a) perception of faces and (b) imagery of faces and between those for (c) perception of places and (d) imagery of places. Statistical maps are overlaid on the corresponding gray-scale anatomical image (averaged over six subjects).
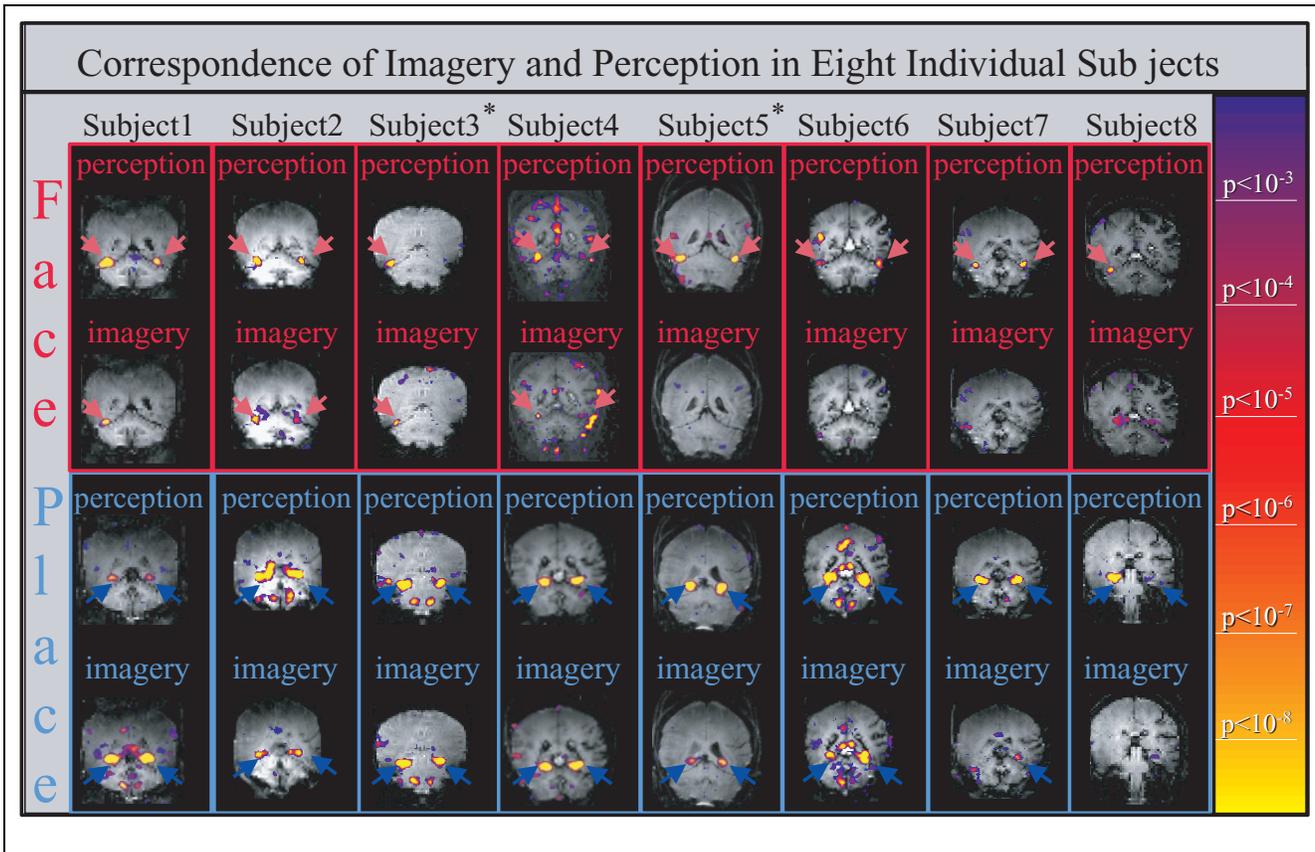

Figure 2. The brain slice from each subject that most clearly shows the overlap in activation between analogous perception and imagery conditions in the first experiment. Each image is a T1-weighted structural image overlaid with a color-coded representation of the significance of the statistical KS test comparing MR signal intensity between the conditions shown. Red arrows indicate the location of the FFA (top two rows) and blue arrows indicate the PPA (bottom two rows). Asterisks designate the two subjects not included in the group analysis.

The correspondence between the imagery and perception activations observed in the group data can even be seen in the data of many of the individual subjects (Figure 2). For seven out of eight subjects, imagery of places (vs. imagery of faces) activated a portion of the PPA region that was active during perception of places (vs. perception of faces) in the same subject. Similarly, mental imagery of faces activated a subset of the FFA region that was activated by perception of faces for four of the eight subjects.

A quantification of the amount of overlap in the perception and imagery activations for each stimulus type is provided in Table 1. Table 1 shows the number of voxels in the vicinity of the PPA and FFA for each subject that reach significance in (i) the perception comparisons, (ii) the imagery comparisons, and (iii) both. Table 1 also shows the percentage of the voxels significant in the imagery comparison that fall within the region activated by the corresponding perceptual comparison. Most of the voxels in the ventral pathway that were activated during imagery for a particular stimulus type fell within the region activated during perception of the same stimulus class (on average, 92% for places and 84% for faces). The regions that were active during both imagery and perception of the two stimulus classes were defined for each subject, designated as FFAo and PPAo, for use as regions of interest (ROIs) in Experiments 2 and 3.

Thus, regions of extrastriate cortex that respond selectively during perception of specific stimulus classes also respond selectively during imagery of those same stimulus classes. It should be noted that this effect is not seen in every subject's individual data, and imagery for a particular stimulus class activates only a subset of the region that is activated during perception of that stimulus class. Both effects were observed even when lower statistical thresholds were used, and both have been reported previously for imagery activations in earlier visual areas such as V1 and LGN (Chen et al., 1998). The variability in imagery activations across subjects may reflect the well-known individual differences in imagery ability (e.g., Galton, 1883), as suggested by previously reported correlations between imagery activations and behavioral measures of imagery ability (Kosslyn, Thompson, Kim, Rauch, & Alpert, 1996; Charlot, Tzourio, Zilbovicius, Mazoyer, & Denis, 1992). It would be of interest in the future to test for similar correlations between imagery ability and imagery activations for faces and places. However, this will require the development and validation of new behavioral tests of these specific abilities, because there is only a weak relationship between behavioral performance on different imagery tasks within an individual (Kosslyn, Brunn, Cave, & Wallach, 1984; Poltrock & Brown, 1984).

Experiment 2

Having established that imagery of specific categories can activate the same extrastriate cortical regions that process those items when visually presented, we sought to directly compare the magnitude of the responses to imagery with those to perception, within the subset of

Table 1. The Number of Voxels in the FFA and PPA Regions for Each Subject That Reach Significance (i) in the Perception Comparisons, (ii) in the Imagery Comparisons, and (iii) in Both the Perception and Imagery Comparisons and (iv) the Percent of All of the Voxels Reaching Significance in the Imagery Comparison That Fall Within the Region That Reached Significance in the Perceptual Comparison

Subjects	FFA: Faces > places				PPA: Places > faces			
	Perception	Imagery	Both	% Imagery within perception	Perception	Imagery	Both	% Imagery within perception
1	36	11	10	90.9	90	81	69	85.2
2	37	12	11	91.7	138	18	18	100.0
3	27	5	5	100.0	89	56	53	94.6
4	72	15	8	53.3	73	87	59	67.8
5	44	0	–	–	123	11	11	100.0
6	9	0	–	–	133	54	53	98.1
7	16	0	–	–	95	5	5	100.0
8	13	0	–	–	71	0	–	–
AVG	63	11	9	84.0	116	45	38	92.2
AVGx	32	6	4	–	102	39	34	–

A criterion of $p < 10^{-6}$ (uncorrected) was used for all comparisons. The average (AVG) is across only those subjects showing at least some voxels significant for both imagery and perception. AVGx is across all subjects.

the FFA and PPA that showed responses for both of these tasks. Six of the eight subjects who participated in Experiment 1 were also run in Experiment 2, in which both imagery and perception tasks were performed within each scan. Data from one subject (S2) were omitted due to technical problems with the stimulus presentation. The results of the remaining five subjects are described in Table 2. Figure 3 shows the responses of the two critical areas for the subjects run in Experiment 2 who had overlapping imagery and perception activations for both faces and places in Experiment 1, and reveals a strong qualitative similarity of the responses during perception and imagery.

For the PPAo (the region that showed significantly greater activation for places than faces both perceptual and imagery comparisons in the independent data from Experiment 1, defined for each subject), the percent signal change (from a fixation baseline) was 0.91% higher for place perception than face perception, and 0.69% higher for place imagery than face imagery (averaged over the four subjects run on Experiment 2 who had a PPAo in Experiment 1). For the FFAo (the region that showed significantly greater activation for faces than places in both perceptual and imagery comparisons in Experiment 1), the percent signal change averaged 1.94% higher for face perception than place perception, and 0.72% higher for face imagery than place imagery (averaged over the two subjects run on Experiment 2 who had an FFAo in Experiment 1).

For the two subjects who had both an FFAo and a PPAo, we performed a paired sign test to determine whether the magnitude of activation during perception was reliably greater than the magnitude of activation during imagery. Of the 16 comparisons involving the preferred stimulus for each region (2 subjects × 4 runs × 2 regions/stimuli), the percent signal change for perception was higher than for imagery in 16/16 cases ($p < .00001$). A similar paired sign test showed that the imagery activations were stimulus specific. That is, of 16 comparisons (2 subjects × 4 runs × 2 regions), in every case the response for a given brain region was higher for the imagery runs when the subject imagined the preferred stimulus for that region, compared to when they imagined the nonpreferred stimulus ($p < .00001$).

Experiment 3

Experiment 3 was run on only the three subjects who had shown the strongest imagery effects in the first experiment. Subjects closed their eyes and heard the name of a different famous person or MIT building once every 12 sec in a random order. Subjects were asked to form a vivid mental image of each named face or place, maintain the image for a few seconds, and then to relax and wait for the next item.

Figure 4 shows the data from a single representative run, demonstrating that for most of the individual mental imagery events, the response is higher in the region selective for the cued item. A data coder blind to the order of the items was able to correctly identify the category of stimulus the subject was instructed to imagine (by inspecting the PPA and FFA responses) on 85% of the trials; 30/32 for S1, 15/16 for S4, and 54/68 for S3, which is significantly above the chance level of 50% correct ($p < .001$ for each subject individually on a binomial sign test).

DISCUSSION

Our first major finding is that cortical regions that are selectively involved in visually processing a specific type of object when the stimulus is physically present show similar selectivity during imagery. Thus, a portion of the FFA, which is more active during viewing of faces than viewing of scenes, is also more active during imagining faces than imagining scenes. Conversely, a portion of the PPA, which is more active during viewing of scenes than viewing of faces, is also more active during imagining scenes than imagining faces. The striking similarity of corresponding perception and imagery activations is apparent from an inspection of Figure 1.

Previous work has demonstrated that common mechanisms are involved in visual perception and visual imagery (Ishai & Sagi, 1995; Finke, 1985; Segal & Fusella, 1970; Perky, 1910; but see Cabeza, Burton, Kelly, & Akamatsu, 1997), and that imagery may

Table 2. Differences in Percent Signal Change (from fixation baseline) for the Second Experiment for Face Versus Place Perception and Face Versus Place Imagery in the FFAo and PPAo

| Subject | FFAo (%) | | PPAo (%) | |
	Perception Face > place	Imagery Face > place	Perception Place > face	Imagery Place > face
1	1.87	0.71	0.96	0.89
3	2.01	0.73	1.12	0.92
5	–	–	0.98	0.62
7	–	–	0.57	0.33
8	–	–	–	–
AVG	1.94	0.72	0.91	0.69
AVGx	0.78	0.29	0.73	0.55

Dashes indicate that no voxels met the threshold for the ROI. AVG is across only those subjects showing at least some voxels significant for both imagery and perception ($n = 2$ for FFAo, $n = 4$ for PPAo). AVGx is across all five subjects.

Figure 3. Time course of percent signal change (averaged over subjects 1 and 3; four runs each) for the FFAo (top) and PPAo (bottom) for the second experiment, which includes both imagery and perception epochs for faces and places.
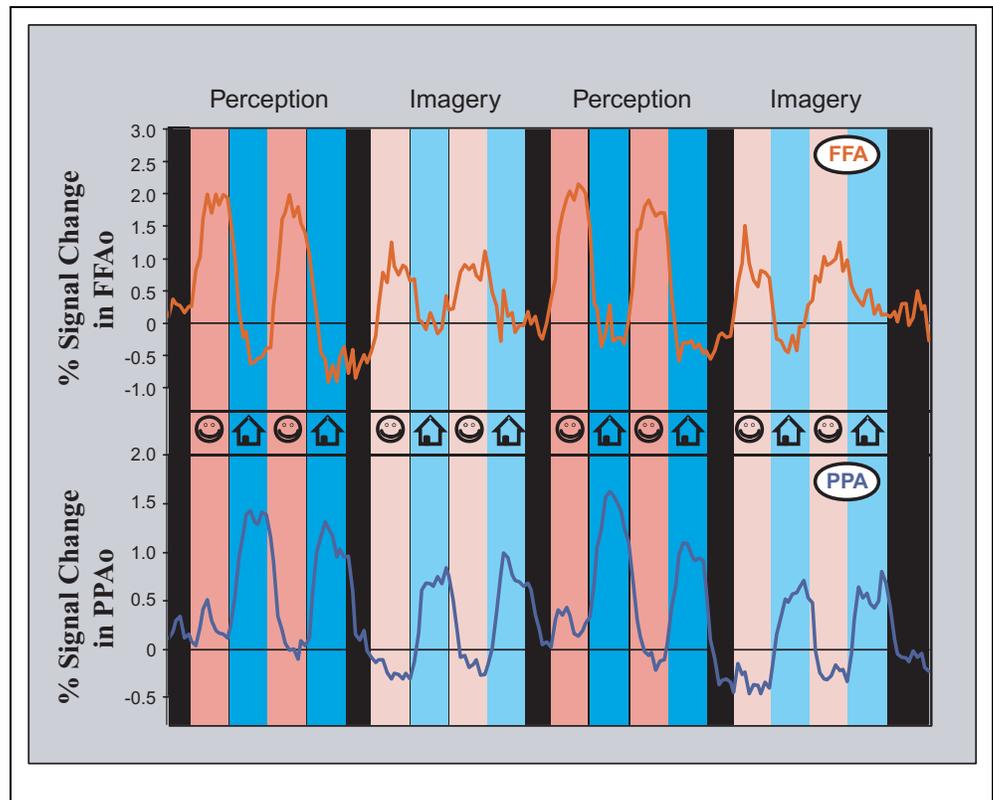
engage retinotopic regions of cortex (Kosslyn et al., 1995; Farah et al., 1992; but see D'Esposito et al., 1997; Roland & Gulyas, 1994, 1995). Further, some

studies have shown that retrieving visual information from memory (Maguire, Frackowiak, & Frith, 1997; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995),

Figure 4. Unaveraged time course of percent signal change for the FFAo (red) and PPAo (blue) from a single scan in the third experiment for subject 1. The arrows show the points in the sequence (one every 12 sec) at which imagery instructions were given (shifted by the estimated hemodynamic lag). From a visual inspection of the raw time course of MR signal intensity in these two regions, the content of most of the single imagery events can be categorized as a face or a place; the icon in the circle indicates what the subject was instructed to image.
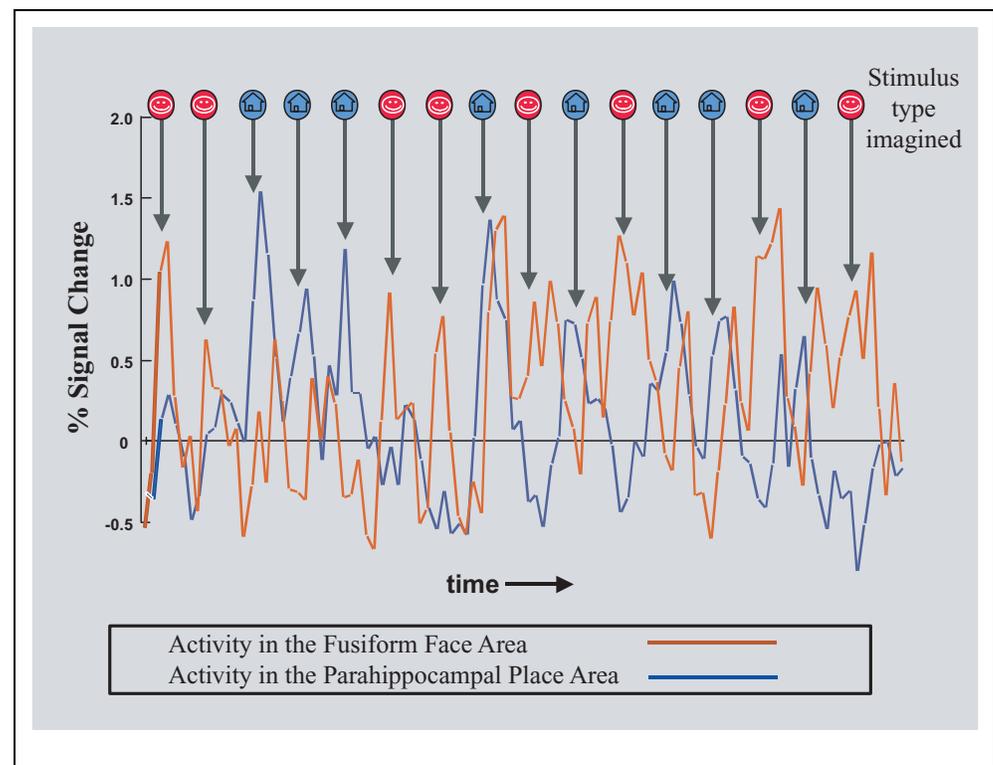
mentally imaging visual attributes such as color (Howard et al., 1998), or experiencing hallucinations of faces or colors (ffytche et al., 1998; Silbersweig et al., 1995) may activate cortical regions near those involved in perceptually processing the same information. Several other studies have shown that mental navigation in familiar environments (in the absence of a stimulus) activates a network that includes regions in or near the PPA (Ghaem et al., 1997; Mellet, Tzourio, Denis, & Mazoyer, 1995). However, our study presents a more striking correspondence between imagery and perception by demonstrating that many of the same regions that are selectively activated during perception of a particular class of stimuli are also activated during imagery of that same stimulus class. Consistent with our results, another recent study shows activation of visual motion area MT during imagery of moving compared to stationary stimuli (Goebel et al., 1998; see also O'Craven & Kanwisher, 1997). Thus, at a macroscopic level, the neural instantiation of a mental image resembles the neural instantiation of the corresponding perceptual image.

Our second major finding is that the magnitude of the activation is lower during imagery than during perception (see also Goebel et al., 1998). This result is entirely in line with the observations of David Hume over 250 years ago, who saw the relationship between percepts and images as follows: "The difference betwixt these consists in the degrees of force and liveliness, with which they strike upon the mind . . . [Perceptions] enter with most force and violence . . . By ideas I mean the faint images of these in thinking and reasoning" (Hume, 1739).

Third, the fMRI responses during imagery were robust enough that the content of a single mental event could be determined with high accuracy from an inspection of the raw fMRI data (see Figure 3). Note that this finding differs importantly from the results of the now widely used technique of event-related fMRI (D'Esposito, Zarahn, & Aguirre, 1999; Dale & Buckner, 1997), in which the analysis involves combining the data from many trials. No combining across trials was carried out in Experiment 3, and the effects we report reflect the neural correlates of single cognitive events. Several recent reports have shown fMRI responses in motor (Kim, Richter, & Ugurbil, 1997) and parietal cortex (Richter, Ugurbil, Georgopoulos, & Kim, 1997) from unaveraged single trials and one study has shown that different motor behaviors can be distinguished from fMRI responses on single trials (Dehaene, 1998). Our data are the first to show that the content of a single thought can be inferred from its fMRI signature alone. This finding demonstrates (at least for some subjects when scanned at 3T) the surprisingly clear correspondence between the fMRI signal on a particular trial and the internal mental event that occurred on that same trial. Just a few years ago, Grabowski & Damasio (1996)

commented that "the imaging of the neural correlates of single and discrete mental events, such as one image or one word, remains a most desirable dream." That dream is now reality.

What component of mental imagery do our activations reflect? The fact that the same region is selectively activated during both imagery and perception suggests that it reflects some process that occurs in both. Logical candidates would be the (i) representation and/or perceptual analysis of the visual information, (ii) the semantic analysis of the same information, or (iii) encoding information into or (iv) retrieving it from long-term memory. Semantic analysis seems unlikely given that Tempini et al. (1998) found fusiform activity for a matching task with both famous and nonfamous faces, but not with famous names. The fact that neither the FFA (Dubois et al., 1999; George et al., 1999) nor the PPA (Epstein et al., 1999) responds differently to familiar and unfamiliar stimuli also argues against memory encoding or memory retrieval. Thus, the most plausible account of the activations reported here is that they reflect the representation and/or perceptual analysis of the stimulus, whether it was physically present or simply imagined.

Further clues about the processes underlying our imagery activations come from studies of patients with severe agnosias who retain the ability to form detailed mental images of the very stimulus classes they are unable to recognize (Bartolomeo et al., 1998). Such cases have been explained in terms of deficits at relatively early stages of processing (Behrmann, Moscovitch, & Winocur, 1994) that may be critical for visual recognition but not imagery. It has been proposed that prosopagnosia (an impairment in face recognition) can result from a deficit at either a perceptual stage of processing (i.e., the knowledge-independent structural encoding of faces) or a "mnestic" stage (i.e., access to stored knowledge of particular faces), and that severe deficits in face imagery result from impairments of the latter rather than the former (Young, Humphreys, Riddoch, Hellawell, & de Haan, 1994; Ellis, 1989, cited in Young, 1994). To the extent that the FFA is involved in the memory-independent structural encoding of faces (Dubois et al., 1999; George et al., 1999), this account would predict that face imagery may be possible even after damage to the FFA. Consistent with this suggestion, one prosopagnosic whose damage appears to include much of the region where the FFA would have been likely to reside nonetheless shows normal face imagery (Bartolomeo et al., 1998). To determine whether the FFA is not only activated by but also necessary for face imagery, it will be useful in the future to scan prosopagnosic patients with preserved face imagery to see what neural structures are activated when they imagine faces.

In addition to providing new information about the neural specificity of mental imagery, the present find-

ings are also relevant to recent studies on the neural mechanisms underlying visual attention. According to one theory of visual attention (Desimone & Duncan, 1995), top-down signals serve to bias the competition between representations of different objects (O'Craven, Downing, & Kanwisher, 1999). Much research has been directed toward determining whether attention functions by modulating the gain of incoming signals (McAdams & Maunsell, 1999) or by injecting a pure top-down bias signal, or both. Recent evidence for a bias effect comes from studies showing a ''baseline shift'' in the neural response in retinotopic cortex when a person (Kastner, Pinsk, De Weerd, Desimone, & Ungfserleider, 1999) or monkey (Luck, Chelazzi, Hillyard, & Desimone, 1997) attends to the relevant region of space before the stimulus appears. Our imagery responses in the absence of a stimulus may reflect the corresponding phenomenon of a bias effect in the ventral ''what'' pathway (see also Chawla, Rees, & Friston, 1999; Shulman et al., 1999). This interpretation would suggest both that common neural mechanisms may be involved in mental imagery and attention (Kosslyn et al., 1993), and that baseline shifts may play a critical role in directing attention not only to spatial locations but also to specific object types.

Our findings can be seen as the latest step in a series of recent discoveries that demonstrate the power of extra-retinal signals in freeing visual processing from the control of the stimulus. Earlier work using single-unit recording (Maunsell & Ferrera, 1993; Moran & Desimone, 1985) and human imaging (Wojciulik, Kanwisher, & Driver, 1998; Clark et al., 1997; O'Craven et al., 1999; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Beauchamp & DeYoe, 1996; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991) has shown that neural activity in extrastriate cortex is not solely determined by the stimulus, but can be strongly modulated by visual attention. A recent study (Tong, Nakayama, Vaughn, & Kanwisher, 1998) has gone a step further by showing that when subjects view perceptually bistable displays (using binocular rivalry) with retinal input held constant, activity in the FFA and PPA is determined by the content of current awareness. The present study takes the final step in this progression by showing that content-specific neural activity in extrastriate visual cortex can be created by a pure act of will even when no visual stimulus is present at all.

METHODS

Subjects

Subjects (age 20–39; two males, six females) were chosen to participate in this study only if they reported having good visual imagery. All were MIT students or affiliates familiar with the campus buildings. All gave informed consent before participating.

Scanning Procedures

Scanning was done on a 3T General Electric Signa scanner (modified by ANMR to perform echo planar imaging) at the MGH-NMR Center, Charlestown, MA. A custom bilateral surface coil (built by Tommy Vaughn) provided a high signal-to-noise ratio in posterior brain regions. High-resolution anatomical and functional images were collected using 10 coronal slices, oriented parallel to each subject's brainstem and centered over the occipito-temporal junction to encompass the FFA and PPA. Standard fMRI procedures were used (gradient echo pulse sequence, TR = 1.5 sec, TE = 30 msec, flip angle = 90°). A bite bar minimized head motion. Functional data resolution was 3.125 mm in-plane, with 6–7 mm contiguous slices (no gap).

Experimental Design and Tasks

Experiment 1

Each scan lasted 4.5 min. The two perception scans contained three 30-sec epochs of photographs of famous faces alternating with three 30-sec epochs of photographs of familiar MIT campus buildings, with a 12-sec epoch of visual fixation interleaved between each stimulus epoch. Each stimulus set (faces and buildings) consisted of 14 black and white photographs, and the order of presentation within a block was random. Stimuli subtended approximately 10° of visual angle, though some faces did not cover the full extent. Pictures were presented at a rate of one every 2 sec. Subjects were instructed to identify each person or building by pronouncing the name silently to themselves. The four imagery scans were identical except that instead of seeing photographs, the subjects heard the names of the same famous people and familiar buildings, and were instructed to form vivid, detailed mental images of the corresponding photographs seen during the perception scans.

Experiment 2

Six of the subjects in the first experiment also participated in the four runs of the second experiment during the same scanning session. Scanning procedures were as in the first experiment, except that each scan lasted 5 min. Subjects kept their eyes open and fixated the central fixation point for the entire scan. Two 60-sec perception epochs alternated with two 60-sec imagery epochs, with 9 sec of fixation between each epoch. Each perception and imagery epoch was divided into four 15-sec subepochs, during which the face conditions alternated with the place conditions, with a new picture appearing every 2 sec.

For each subject, we used the independent data set from the first experiment to define ROIs to be used in analyzing the data from Experiment 2. The PPAo is the

set of all voxels that showed overlapping activation for both place imagery and place perception in Experiment 1. Similarly, the FFAo contains all voxels that showed overlapping activation for both face imagery and face perception in Experiment 1. Note that for some subjects this leaves no region of interest in the FFA and/or PPA; the analysis for Experiment 2 was carried out only when such an overlap region existed. These ROIs are unbiased with respect to the question of the relative magnitude of activations during perception and imagery in the second experiment because they were selected on the basis of having produced significant activations during both perception and imagery comparisons in the independent data set from the first experiment.

Experiment 3

Each scan lasted 3.5 min. Every 12 sec, the subject heard the name of a famous person or familiar place from the stimulus set described above. Order was random, with faces and places intermixed. Subjects were instructed to generate a vivid mental image of the designated item when they heard the cue, hold it for a few seconds, and then relax and await the next item.

Using the imagery-perception overlap analysis described above to define FFAo and PPAo ROIs individually for each subject, we then extracted the raw time course of MR signal intensity for each region. Scanning procedures were the same as in the previous experiments, except that TR was reduced to 1 sec. Seven slices, covering FFA and PPA, were imaged.

Data Analysis

All data were corrected for motion using a modified AIR algorithm. Each image underwent three-dimensional realignment to achieve registration with the first image of the first functional run. Data were analyzed separately for each subject. For each subject, all runs of a given type were combined by averaging the signal intensities at each timepoint for each voxel. Statistical tests were performed using a signed Kolmogorov–Smirnov (KS) test, correcting for linear drift and using a 1-2-1 Hanning kernel. While some investigators have criticized the KS test for fMRI data (Aguirre, Zarahn, & D'Esposito, 1998), others have argued that it is no more prone to error than other commonly used statistical approaches (Purdon & Weisskoff, 1998) and is indeed more conservative.

The three-dimensional PPAo and FFAo ROIs were determined for each subject by selecting all contiguous voxels in the vicinity of the appropriate anatomical area that met the threshold of $p < 10^{-6}$ for both perception and imagery tasks in Experiment 1. Time courses evaluated in Experiments 2 and 3 were generated by applying these ROIs to the independent data from those experiments.

To calculate percent signal change, we averaged all images during which subjects fixated (no faces or places), and separately averaged the final seven images during which each of the four tasks was performed. The first three images of each task epoch were omitted in order to allow the response to stabilize, which was particularly important in the imagery conditions. A 3-sec delay was employed to account for hemodynamic lag.

Because images were collected with a surface coil, transformation into Talairach space was challenging, and the data from two subjects (S3 and S5) were not included in the group analysis because anterior landmarks necessary for registration were not identifiable. Data from the other six subjects were coregistered to a standard brain and averaged. Statistical analysis for the group data was identical to that described for the individual data. Activations were defined by growing regions around peak activation (minimum p value), and including all contiguous voxels that exceeded the threshold of $p < 10^{-6}$. The Talairach coordinates are given relative to an origin at the anterior commisure, and represent the peak of activation for each region.

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