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Research report

Retinotopic organization of visual mental images as revealed by functional magnetic resonance imaging

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Abstract

In this study, we used event-related functional magnetic resonance imaging to investigate whether visual mental images retinotopically activate early visual cortex. Six participants were instructed to visualize or view horizontally or vertically oriented flashing bow-tie shaped stimuli. When compared to baseline, imagery globally activated Area V1. When the activation evoked by the stimuli at the different orientations was directly compared, distinct spatial activation patterns were obtained for each orientation in most participants. Not only was the topography of the activation patterns from imagery similar to the topography obtained with a corresponding visual perception task, but it closely matched the individual cortical representation of either the horizontal or the vertical visual field meridians. These findings strongly support that visual imagery and perception share low-level anatomical substrate and functional processes. Binding of spatial features is suggested as one possible mechanism.

Theme: Sensory Systems
Topic: Visual Cortex: striate

Keywords: Mental imagery; Retinotopy; Visual cortex; fMRI

1. Introduction

The role of the striate cortex (primary visual area, area V1) in visual mental imagery has long been debated. Many neuroimaging studies have revealed activation of early visual areas during visual mental imagery [1,13,16–19] (for a review, see Ref. [15]), but many other studies have not revealed such activation (e.g., Refs. [3,21]; for reviews, see also Refs. [11,14,20,22,24]). Nevertheless, the results from applying focal repetitive transcranial magnetic stimulation (rTMS) to the occipital cortex strongly suggest that the primary visual cortex is recruited at least in some forms of visual imagery. Specifically, performance was impaired in analogous imagery and perception tasks that required participants to compare gratings of different orientations and shapes after neural activity in visual occipital cortex was temporarily disrupted by focal TMS [18]. In addition, the existence of back-projections from high-order visual areas to low-level retinotopic areas provides neuroanatomical grounds for inferring that mental images may be produced via backward projections from visual memory areas down to V1 [8,30].

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If visual imagery and visual perception share anatomical substrates, they should be affected by the functional characteristics of those structures. In the striate cortex of primates, including humans, images from the external visual world are known to project onto the cortical ribbon along a retinotopic anatomical layout. Accordingly, the cortical ribbon along the visual cortex is functionally organized in a retinotopic manner [28,31]. Mental images 'projected' onto the early visual cortex should thus exhibit some degree of retinotopy. Indeed, based on a study using positron emission tomography, a previous report showed that the spatial extent of activation in visual areas varied with the size of the mental images, coarsely following the retinotopic eccentricity along V1 [17]. However, no study has yet obtained retinotopic maps during mental imagery and compared those maps with retinotopic maps obtained during perception. Such a direct comparison would provide strong evidence that visual imagery and visual perception do in fact share low-level neuronal mechanisms.

In the present study, we used event-related (ER) functional magnetic resonance imaging (fMRI) to investigate whether visual mental images *retinotopically* activate early visual cortex. With ER-fMRI, it is possible to obtain on an individual basis high-resolution retinotopic maps from specific visual perception paradigms [4,5,26,27,29] and to monitor activation patterns from single imagery events [13]. Individual mapping is particularly important to overcome the great anatomical and functional variability of the visual cortex. Participants were instructed to visualize horizontally or vertically oriented flashing bow-tie shaped stimuli. These orientations were chosen because visual perception of similar stimuli is known to activate well-defined and well-separated retinotopic loci on the visual cortical ribbon, namely the horizontal meridian (along the calcarine fissure) and the vertical meridian (along the lateral V1/V2 border).

2. Method

2.1. Participants

Six healthy participants (four male and two female, aged 20 to 25 years) participated in the study. All reported being in good health and free of any ophthalmologic disorders. All volunteers gave their informed written consent. The study was approved by the local Institutional Ethic Committee.

2.2. Materials and task design

The participants were scanned under three experimental conditions (visual perception, visual imagery, and visual retinotopic mapping).

In the perceptual condition (Fig. 1a), participants were supine and looked up into adjustable mirror glasses to view a back-projection screen positioned at the back of the scanner. Head movements were limited by a foam padding. Participants fixated on a central cross while they were presented a flickering black-and-white, bow-tie shaped stimulus at either a horizontal or vertical orientation, flickering at 8 Hz. The stimuli, which spared the central 1° of the visual field, stimulated horizontal and vertical areas in the visual field with a radius of 7°. Each visual stimulus was associated with an auditory tone, which differed for each orientation of the stimulus; the tones were counterbalanced between the horizontal and vertical bow-tie shaped stimuli across participants. Stimuli were randomly presented in runs of 24 trials, and the stimulation duration was randomly varied between 50 and 3000 ms. During this perceptual condition, the participants were instructed to stare continuously at the fixation point, knowing in advance that they later would need to visualize the stimuli. Furthermore, participants were asked to press a button with their right hand when they recognized orientation of the flashing stimulus.

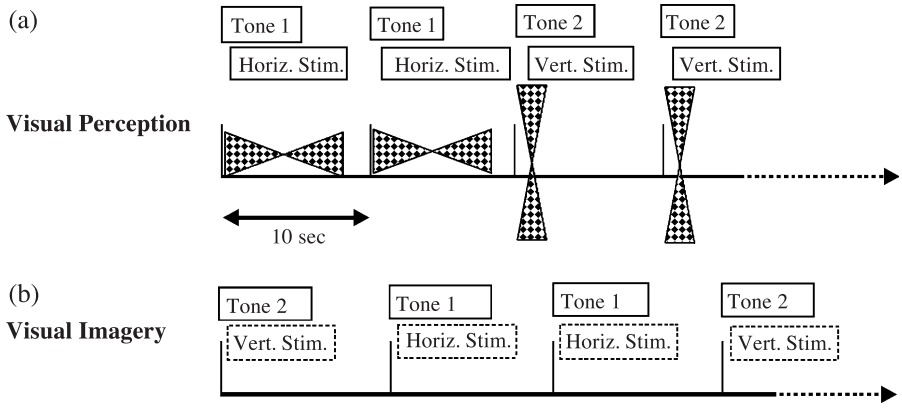

Fig. 1. Task design. (a) In the perceptual condition, the participants received simultaneously an auditory tone and a horizontal or vertical visual stimulus (a flickering black-and-white bow-tie shape). They were to press a button once they recognized the orientation of the stimulus. (b) In the imagery condition, only the auditory cues were delivered and participants were to visualize the corresponding horizontal or vertical flickering stimulus. Once they had clearly visualized the stimulus, they pressed a button.

In the visual imagery condition (Fig. 1b), only the tones were delivered. When the participants heard the auditory cue, with eyes closed and in complete darkness, they were to visualize the corresponding horizontal or vertical stimulus, as presented in the previous perceptual condition, while they imagined that they were keeping their gaze on a central fixation point. Once they had clearly visualized the stimulus, they pressed a button. Each run comprised 30 trials, which randomly intermixed an equal number of horizontal and vertical imagery stimuli. To avoid confounding effects with motor responses and visual mapping, the same right handed response was used in all cases. Before the actual experiment, participants received practice sessions (with feedback regarding instructions) comprising one perception run and one imagery run until the variance of reaction times stabilized to a value less than 5%. This level was generally reached after three sessions of training.

In the final condition, the participants viewed a phase-encoded visual stimulus that allowed us to obtain polar angle and eccentricity maps of the visual cortex, using the methodological procedure described in Ref. [6]. This procedure allowed us to determine for each participant the localization of the cortical representations of the vertical and horizontal meridians.

2.3. Data acquisition

We obtained echo-planar images on a 3 Tesla whole-body MRI system (Brucker, Karlsruhe, Germany) using a gradient echo sequence (TR [repetition time]=2000 ms, TE [echo time]=40 ms, flip angle=90°). A quadrature radio frequency head coil was used, and 20 contiguous axial 4-mm slices were acquired per scan covering the whole brain (voxel size: 3.75×3.75×4 mm). Twelve seconds of 'dummy' gradient and RF pulses preceded the actual data acquisition. We used a T1 weighted 3D Inversion-Recovery Fast Gradient Echo sequence for anatomical identification of activated foci (1.2×1×1 mm of resolution) following functional imaging. In addition, we employed a double-echo sequence to correct for EPI distortions. Each participant received three runs per condition (always following the same order of presentation, that is, perception then imagery), and a total of 120 and 150 BOLD contrasted images per slice were acquired for each perception and imagery run, respectively.

2.4. Data analysis

We analyzed the data with a multiple linear regression algorithm that incorporated a standard haemodynamic response model, SPM99 (Wellcome Department of Cognitive Neurology, London, UK), based on the theories presented in Refs. [9,10]; for details, see http://www.fil.ion.ucl.ac.uk/. We conducted an individual analysis. Images were first corrected for EPI distortions, then were corrected for temporal dephasing and motion. Spatial smoothing was applied (FWHM=7.5 mm), and data were high-pass filtered (at a frequency about twice the paradigm). The time series of activation (across the 120 images of each slice for each perception run and 150 images for each imagery run) was analyzed on a voxel-by-voxel basis. For each kind of stimulus (horizontal or vertical, perceived or imagined), the cortical response was modeled by convolving the time course of the stimulus events with the standard haemodynamic response. For the imagery trials, the time course of the event was determined by the interval between the tones and the button response. In order to test for activation in a voxel, the measured signal was fitted with this model and simple *t*-tests were performed. The height threshold for significance was fixed at 0.01 (uncorrected for multiple comparisons) for four contiguous voxels.

We overlaid significant activation clusters on hemispheric inflated cortical surfaces for easier comparison of spatial activation patterns obtained during the perceptual and imagery conditions. To create phase maps, a linear regression with sine and cosine regressors was performed at the stimulus frequency (0.03 Hz). The phase of the vascular response was also considered in the model and residual phase delays were canceled by subtracting the average of the phase angles obtained for opposite directions of stimulus motion (contraction versus expansion and clockwise versus counter-clockwise). Representations of the unfolded cortex were obtained after we segmented white–gray matter segmentations within each hemisphere. The unfolding procedure followed the approach described in Ref. [6]. Functional data sets were then interpolated onto the surface reconstruction, as well as the borders between visual areas (determined by the retinotopic mapping procedure).

Finally, in order to test for retinotopic effects within each condition, perception and imagery, we computed additional *t*-contrasts, such as between horizontal versus vertical within each condition. To provide a quantitative assessment of the retinotopic organization of visual mental images, we counted the number of voxels activated in common between the perception and imagery conditions. We also compared the locations of the activated clusters in the perceptual versus imagery conditions (contrasting horizontal versus vertical and vertical versus horizontal) relative to the cortical representations of the horizontal and vertical meridians at the borders of retinotopic areas.

3. Results

For each participant, reliable cortical representations of the horizontal and vertical meridians were obtained from the phase-encoded retinotopic paradigm. The spatial activation patterns associated with the actual (perceived) horizontal and vertical stimuli precisely matched the corresponding location of the horizontal and vertical meridians (Fig. 2). During visual imagery, we found significant activation in V1 in five out of the six participants (threshold *p*

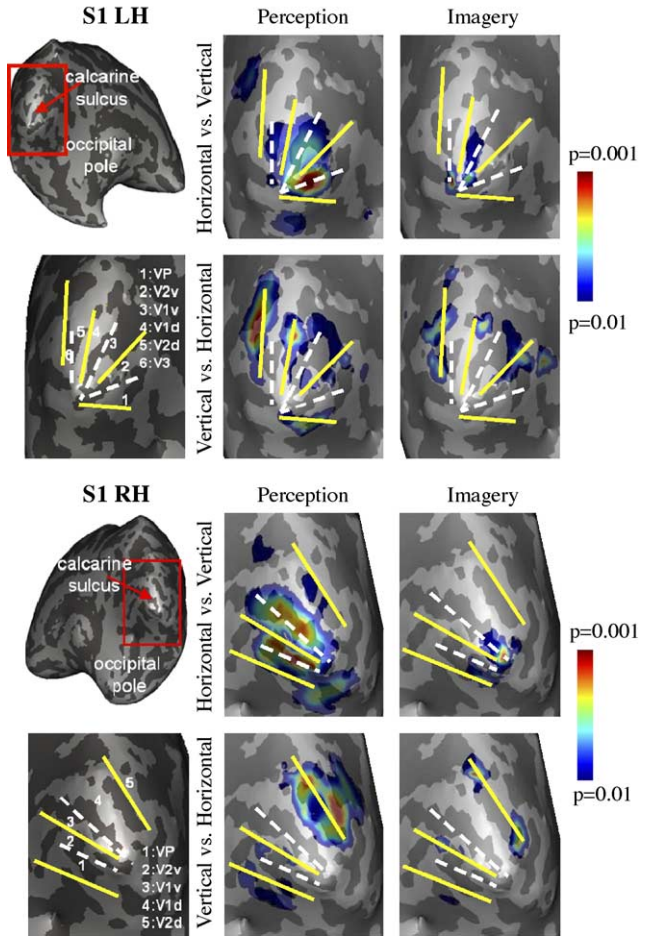

Fig. 2. Perception and imagery retinotopic maps of the occipital cortex. Statistical maps (p<0.01, non-corrected, at least four contiguous voxels) of the horizontal/vertical and vertical/horizontal contrasts, for visual perception and imagery, are presented for one participant (Participant #1; LH, left hemisphere; RH, right hemisphere). Maps are projected on individual inflated occipital cortex (red zoomed region defined on the whole hemisphere). The horizontal and vertical meridians were obtained from retinotopic phase-encoded acquisitions (horizontal: dotted white lines; vertical: yellow lines); they define the frontiers between visual areas.

value=10^{-2}, clusters of at least four contiguous voxels). When we compared activation to the mean signal level (baseline condition), the spatial activation pattern did not reflect a retinotopic organization. This finding was in contrast to the functional maps obtained in the perception task, where the horizontal and the vertical activation patterns clearly differed.

Table 2
Number of significant activated voxels (p<0.01) with retinotopic coordinates

	Horizontal versus vertical (p<0.01)	Vertical versus horizontal (p<0.01)
Participant 1	57	44
Participant 2	23	110
Participant 3	47	25
Participant 5	21	9

A further analysis based on a *direct* comparison between the images acquired for the horizontally and vertically oriented imagined stimuli unmasked different spatial activation patterns for the two orientations. In four out of six participants, the topography of the activated patterns from the imagery task was found in same cortical locations to those observed in the perception task. These activated voxels also matched the individual cortical representation of either the horizontal or the vertical visual field meridians. However, the strength of this retinotopic effect varied considerably across participants. In particular, when subtracting the activity associated with the imagined horizontal stimuli from that associated with the vertical stimuli, V1 activation along the anatomical representation of the horizontal meridian (i.e., coarsely along the calcarine fissure) was significant in four out of six participants in the right hemisphere (Participants #1, 2, 3, and 5) and three out of six in the left hemisphere (Participants #1, 2, and 3) (p=10^{-2}) (Table 1). As observed with the perceived horizontal bow-tie stimuli, the location of the horizontal meridian appeared for some participants more lateral within the visual occipital cortex, either at the borders between dorsal areas V2 and V3 or ventrally at the site of the V2v/VP frontier (Table 1).

In contrast, the activation of the vertical meridian during imagery was more robust across all participants, corresponding to the expected location at the V1/V2 dorsal and/or ventral frontiers, as defined from the individual retinotopic maps of each hemisphere. Moreover, in one participant (Participant #4), we found that the corresponding locus of the horizontal meridian within V1 was more strongly activated by the vertical than by the horizontal imagined

Table 1
Summary of topographical activation loci observed among the six participants along the horizontal and vertical meridian's representations at the borders of retinotopic areas during visual imagery (p<0.01)

	V1 medial (horizontal meridian)	V1v/V2v (vertical meridian)	V1d/V2d (vertical meridian)	V2v/VP (horizontal meridian)	V2d/V3d (horizontal meridian)	VP/V4v (vertical meridian)	V3d/V3a (vertical meridian)
Horizontal versus vertical	4/6 (R) 3/6 (L)	0/6	0/6	3/6 (R) 2/6 (L)	2/6 (R) 4/6 (L)	0/6	0/6
Vertical versus horizontal	1/6 (R) 1/6 (L)	2/6 (R) 4/6 (L)	4/6 (R) 4/6 (L)	0/6	0/6	0/6	3/6 (L) 0/6 (R)

L, left hemisphere; R, right hemisphere.

Table 3
Quantitative match between imagery and perception activated voxels across four participants who displayed a retinotopic effect during visual imagery ($p<0.01$)

Perception	Imagery	
	Horizontal versus vertical	Vertical versus horizontal
Horizontal versus vertical	69	5
Vertical versus horizontal	0	88

stimuli; however, this pattern of activation was not retinotopic, and did not match the expected size of the stimulus (7° radius) as found for other participants.

To quantify the degree of spatial correspondence in activated parts of topographically mapped areas in the imagery and perceptual conditions, we tabulated the number of common activated voxels in the two conditions. Table 2 indicates for each type of contrast (horizontal versus vertical and vice versa) the number of significant activated voxels ($p<0.01$) that showed expected retinotopic patterns of activation in the imagery condition in four out of six participants. In Table 3, we report the total number of voxels across participants that anatomically matched activated voxels in corresponding perceptual condition. We found a greater number of activated voxels along the horizontal visual field coordinates when participants visualized the horizontal flashing bow-tie stimuli than when they visualized the vertical flashing stimuli—and vice versa when they visualized the vertical flashing bow-tie stimuli.

4. Discussion

In this study, we clearly obtained V1 activation for all participants and all imagery events, although the degree and precise location of activation varied among participants. This finding in itself confirms previous research demonstrating that area V1 is involved in visual mental imagery. However, when we compared activation during imagery to the baseline, we did not find evidence that V1 activation was retinotopically organized. However, one has to keep in mind that with the current fMRI method, only images contrasting two (or more) neuronal states can be obtained. This subtraction approach may, in some cases, introduce a bias in the interpretation of the results. Here, V1 was so much more strongly activated during imagery than during the baseline that the more subtle retinotopic effect was masked. We did obtain evidence for retinotopic organization in the perception condition, but the baseline differed between the perception and the imagery tasks. In the perception condition, visual activity was present during the baseline because participants had to look at a fixation point. Subtracting the baseline thus removed much of the "general" activation engendered by visual input per se. In the imagery condition, in contrast, there was no visual activity during the baseline—and thus the activation produced during imagery was much more pronounced in the comparison to the baseline.

More interestingly, retinotopic characteristics were clearly revealed when we directly compare the horizontal and the vertical imagery conditions. This is the first report of retinotopic activation maps observed without a physical visual stimulus. Remarkably, not only did the patterns of activation clearly differ for the horizontal and the vertical imagined stimuli, but the activated loci closely matched those activated during visual perception of similar objects and colocalized with the horizontal and vertical visual field meridians, as determined for each individual using a retinotopic localizer task. The fact that the vertical meridian was more robustly activated than the horizontal one may be explained by a difference in the number of back projection fibers arriving at those meridians (e.g., Refs. [2,28]).

One may thus envision V1 activation during imagery as a two-level process: First, the visual cortex must be "turned on" before any processing may occur; and second, after V1 is "turned on," activation is "fine tuned" to represent a specific shape. The subtraction of the baseline condition from the imagery condition could reveal this global (non-retinotopic) switch effect during the first phase, which is not present in the perception comparison because visual cortex was already activated in the baseline condition. Non-human primate studies have reported backward connections between inferior temporal regions and V1 that do not preserve topography [23]. Attentional effects are also known to modulate V1 activity [12], and other effects might contribute to an overall, non-specific V1 activation, such as the acoustic tones used to trigger imagery events. However, a control test performed in three participants did not show V1 activation when the tones were not associated with imagery events. Only one participant (Participant #6) did not show V1 activation—and this participant explained he had difficulty generating visual images when he heard the auditory tones.

In light of these results, one may seriously argue that visual imagery and perception not only share anatomical substrates in the early visual areas, but also functional processes. One may speculate that a particular function for V1 (among others) would be 'spatial binding', i.e., linking together fine spatial features (here, horizontal or vertical points of a bow-tie shaped stimulus) of a mental object, so that these features are preserved as a whole to be further processed by other cortical regions. One possible output could then be temporal bound or synchronized neuronal firing associated with each spatially bound feature [7]. This idea is consistent with results showing V1 activation by haptic touch in early blind people reading Braille [25]. Here also, fine-scale spatial features must be bound for further processing and recognition.

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