

Research Report

Neural impact of the semantic content of visual mental images and visual percepts

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Abstract

The existence of hemispheric lateralization of visual mental imagery remains controversial. In light of the literature, we used fMRI to test whether processing of mental images of object drawings preferentially engages the left hemisphere to compared non-object drawings. An equivalent comparison was also made while participants actually perceived object and non-object drawings. Although these two conditions engaged both hemispheres, activation was significantly stronger in the left occipito-temporo-frontal network during mental inspection of object than of non-object drawings. This network was also activated when perception of object drawings was compared to that of non-object drawings. An interaction was nonetheless observed: this effect was stronger during imagery than during perception in the left inferior frontal and the left inferior temporal gyrus. Although the tasks subjects performed did not explicitly require semantic analysis, activation of this network probably reflected, at least in part, a semantic and possibly a verbal retrieval component when object drawings were processed. Mental imagery tasks elicited activation of early visual cortex at a lower level than perception tasks. In the context of the imagery debate, these findings indicate that, as previously suggested, figurative imagery could involve primary visual cortex and adjacent areas.

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1. Introduction

During the last decade, the issue of how visual mental imagery is implemented in the brain has been widely studied [27,35]. There is now a consensus regarding the involvement of associative visual areas during various mental imagery tasks. While the hemispheric specialization of figurative (object) mental imagery has not yet been clearly established, advances have recently been made in the study of the spatial mental imagery domain (i.e., processing of spatial relations between objects or processing of part of

objects such in mental navigation, mental rotation, etc.). It has been suggested that the right intraparietal sulcus is preferentially involved when spatial mental imagery tasks deal with metric spatial relations (“coordinates”), while the homologous region in the left hemisphere is preferentially involved in spatial tasks involving above/below or left/right (“categorical”) judgments [46]. An alternative interpretation has recently been offered that the left posterior parietal cortex (PPC) is preferentially engaged in processes of mental image generation (i.e., visualization of previously memorized patterns), while the right PPC plays a role in mental image transformation (i.e., mental rotation of patterns) [14]. Altogether, these studies argue for bilateral involvement of the parietal cortex in spatial mental imagery, with a specific role for each hemisphere.

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Whether this type of organization exists in the ventral temporal cortex for figurative imagery has been a matter of intense debate [45]. It has been suggested that although both hemispheres might be involved in image generation, they act in different fashions. Early single case reports suggest the hypothesis that the left temporo-occipital cortex might be specialized for the generation of multipart mental images [13]. However, we have reported unilateral right activation of the occipito-temporal cortex in tasks that bear strongly on multipart image generation [34,37]. Interestingly, in one of these studies, the mental images involved represented three-dimensional shapes with no semantic attributes or lexical entries [34]. This suggests the hypothesis that the object and non-object types of mental imagery affect the lateralization of activation. Mental images that include semantic content or refer to a lexical entry might preferentially elicit left-sided activation. As a matter of fact, regarding the ventral pathway, most of the studies that have reported activation predominantly in the left hemisphere have used mental images that included some lexico-semantic information [3,9,19,36]. Moreover, this effect might involve not only the ventral pathway but also the frontal region, in particular the left inferior frontal gyrus, which is known to play a key role in semantic processing of percepts. In the visual domain, it was found that this region was more activated by object than by non-object visual stimuli [29,51]. Accordingly, we postulated that figurative mental imagery with meaningful content (i.e., lexical and conceptual knowledge implicitly associated with the object drawn) would more strongly engage the left inferior frontal gyrus than meaningless images.

In summary, comparison of findings obtained with these two kinds of images suggests the existence of a left lateralized network including inferior temporal and fusiform gyrus belonging to the ventral pathway and the inferior frontal cortex, and indicates that processing of figurative mental imagery involves semantic processing networks. The purpose of the present study was to test this hypothesis using a mental imagery generation task involving drawings representing both usual objects and animals, and non-object drawings that do not represent an existing object or animal. It has been shown that visual perception and mental imagery share a common neural substrate ([26,35], for review). In order to compare the effect of type of drawing during imagery and actual perception, we also included a perceptive version of the task using the same object and non-object drawings. We paid particular attention to early visual cortex, considering the debate regarding its involvement in visual mental imagery. We have previously suggested that activation of early visual cortex could reflect the effort paid to maintain a clear and vivid mental image [30]. Assuming that this effort is more intense for imagery of non-object drawings than for that of object drawings, we expected that activation would be greater in the former than in the latter condition.

2. Materials and methods

2.1. Participants

Fifteen healthy volunteers (age: 18–27 years, 4 women) were included in this study. All were free of neurological disease and injury and had no abnormality on T1-weighted magnetic resonance imaging (MRI). The local Ethics Committee approved this study, and written informed consent was obtained from each subject after the procedures to be used in the study had been fully explained. All participants were right-handed as confirmed by the Edinburgh questionnaire (mean score: 77 ± 20). In order to ensure optimal homogeneity of subject sample with respect to imagery abilities, participants were selected as “high imagers” (having high spatial ability) on the basis of their scores on the Mental Rotations Test (mean MRT score: 17 ± 2.8) [49].

2.2. Materials

2.2.1. Stimuli

The first set of stimuli was composed of line drawings depicting objects belonging to various semantic categories (objects, tools, animals, etc.). These items were chosen from a French naming test [38]. The second set included non-object drawings and was created by pseudo-random spatial shuffling of the object items. We attempted to match visually as closely as possible the complexity of the two sets of drawings (number of lines, etc.). Despite this effort, however, it is possible that some differences remain. For example, objects may have appeared more symmetric than non-objects. The difficulty here is that non-object drawings may be too suggestive of existing objects or symbols when symmetry is preserved (see below). Object and non-object drawings are presented in Fig. 1. We tested the non-object drawings in a pre-experimental study with 15 participants (differing from the participants included in the fMRI study) who were forced to name the non-object pictures. It was included in the set of non-object pictures only when the participants required more than 5 s to identify and name an existing object as present in a non-object drawing. In addition, we excluded non-object drawings that evoked the same objects for two participants (and were thus likely to actually evoke an existing object).

2.2.2. Learning and training phases out of the scanner

Prior to fMRI scanning, the participants memorized 12 object and 12 non-object drawings. They were informed that, during the fMRI experiment, they would have to create an accurate mental image of each drawing in order to evaluate some figurative properties. Each object drawing was associated with a letter (from A to L) and each non-object drawing with a number (from 1 to 12). The participants were requested to memorize a drawing and its paired symbol as accurately as possible and were then tested

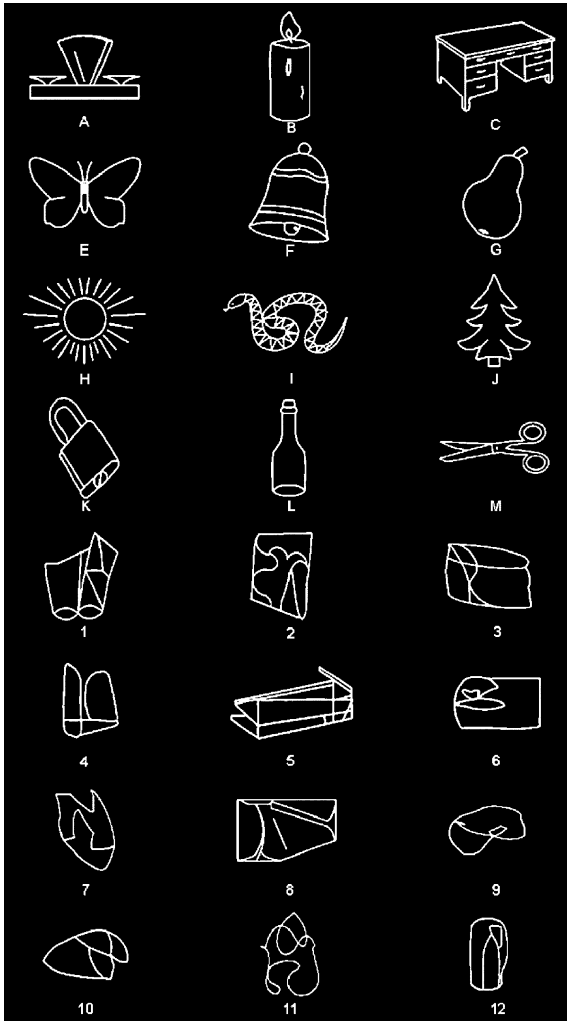


Fig. 1. Object drawings (top) and their derived non-object drawings (bottom).

with a cued recall task. The learning phase was considered complete only when the participants could associate all symbols with their corresponding drawings without mistake. They then participated in the training phase, during which they had to perform one session of imagery and one of perception (see details below).

2.2.3. Tasks

The study included five conditions: a Baseline condition, an Imagery of object drawing condition, an Imagery of non-object drawing condition, a Perception of object condition, and a Perception of non-object condition. Each imagery session included two blocks of Imagery of object drawings and two blocks of Imagery of non-object drawings interleaved with five Baseline blocks. Each perception session included two blocks of perception of object drawings and two blocks of perception of non-object drawings interleaved with five Baseline blocks. At the beginning of each block, a “bip” sounded to notify the participant of switching between task and baseline. For the

perception sessions, this bip was a signal to open (perception) or close (baseline) eyes. The object and non-object drawing blocks were alternatively presented within each session. After a baseline block, a session began alternately with an object or a non-object condition in order to control for effects of order of presentation. Each subject underwent a total of three imagery and three perception sessions. The same order of session presentation was used for each of the fifteen participants.

2.2.3.1. Baseline condition. Participants were instructed to listen to letters or numbers (symbols different from the pre-learned drawings), to evaluate whether the letter was a vowel or if the number was even, and then to press a “true” or a “false” key. This condition was chosen because it was unlikely to promote intense mental imagery activity. The Baseline condition was performed with eyes closed in total darkness (as during the Imagery conditions), with a black tent-like chamber covering the entire MRI scanner. The Baseline blocks lasted 30 s and included five items.

2.2.3.2. Imagery of object drawings and non-object drawings tasks (IO and INO). In the seconds prior to scanning, the participants saw on a screen a statement such as “includes more than 4 closed shapes”, “higher than wide”, or “wider than high”. The screen was then switched off, and the participants were then asked to close their eyes and to keep them closed during the entire scanning session. During the scanning, they heard a letter or a number and had to form an image of the corresponding drawing in order to evaluate the statement and then to press a “true” or a “false” key. A different statement was presented before each session. When a key was pressed, another letter or number was delivered. Each block of imagery conditions included six items. Responses and response times were recorded using STIM software (Neuroscan, El Paso TX, US).

2.2.3.3. Perception of object drawings and non-object drawing tasks (PO and PNO). The perception conditions were similar to those for imagery, except that the subject actually saw the drawings on a screen. The subject had to assess the veracity of a statement presented on the screen prior to the session. Each perception condition block included eight items. A different statement was presented before each session.

We performed a post-test debriefing: participants were asked to report by introspection what they did (or thought they did) during the different tasks. Notably, this introspective information provides only a rough indication of the activities the participants performed during scanning.

2.2.4. Data acquisition

Data were acquired on a General Electric 1.5-T Signa Horizon EchoSpeed scanner. The protocol included two anatomical MRI acquisitions and six functional sessions. The imagery conditions were given during the first three

sessions and the Perception conditions during the last three sessions. The first anatomical acquisition was a T1-weighted MRI (T1-MRI) of high resolution ($0.9375 \times 0.9375 \times 1.5 \text{ mm}^3$) acquired with an IR-SPGR 3D sequence. The second anatomical acquisition was a proton density/T2-weighted MRI (PD-MRI, T2-MRI) including 21 slices covering the same field of view (FOV) as the functional acquisition. The FOV encompassed all of the cerebrum and the upper part of the cerebellum. The functional MRI acquisitions were recorded using a gradient echo, one-shot echo planar imaging (EPI) sequence (TR = 3 s, TE = 60 ms, FA = 90°). In each session, the entire FOV (21 slices of 5 mm thickness with $3.75 \times 3.75 \text{ mm}^2$ in slice sampling) was scanned continuously every 3 s, over 6 min, and 30 s. The first three volumes of each session were discarded until the signal reached equilibrium. In the following paragraph, the first none-discarded volume of the first functional session is labeled fMRI₀.

2.2.5. Data preprocessing

Each subject datum was processed by two automatic procedures separated by manual verification of the data. These procedures utilized both in-house and public software packages (see below).

The first procedure was used for registration of functional data in the standard stereotactic space defined by the Montreal Neurological Institute (MNI) template [7]. This pipeline included (1) computation of the rigid registration matrix of DP-MRI onto T1-MRI (AIR, [52]), (2) extracerebral tissue stripping of T1-MRI (Atomia, [50]), (3) extracerebral tissue stripping of the T2-MRI (using the results of the two previous steps), (4) computation of the rigid registration matrix of fMRI₀ onto T2-MRI, (5) computation of the non-linear registration matrix of T1-MRI onto the MNI templates (SPM99, [1]), (6) combination of rigid (step 1 and 4) and non-linear (step 5) registration matrices for registration of fMRI₀ onto the MNI template, (7) visual verification of the registration of fMRI₀ and T1-MRI in the MNI template space (MPITool, Max-Planck-Institute, Germany).

The second procedure brought every functional image into the MNI template space while adjusting both spatial and temporal features. This pipeline included (1) for each session, shift of voxel time profiles as if they were sampled at the middle of each repetition time period (SPM99, Wellcome Department of Cognitive Neurology, London, UK), (2) registration of each fMRI volume to the fMRI₀ volume (SPM99), (3) resampling of each fMRI volume in the MNI template space using the matrix computed at step 6 of the first procedure, (4) global normalization of each fMRI volume to 4000 (One normalization value per session computed), (5) spatial smoothing of the fMRI volume using a Gaussian filter of 8-mm full width at half maximum (FWHM), yielding a final smoothness of 12-mm FWHM.

2.2.6. Data analyses

2.2.6.1. Group analyses. The data were analyzed with SPM99 using a model implemented with a two-level procedure [15,16]. We performed two analyses with this model. In both cases, the effects of interest were modeled by convolving the box car with a standard hemodynamic response function to create the regressors. The box car function was computed using individual behavioral data and a high-pass filter (470 s) was used to remove the low frequency drifts.

In the first analysis, we defined Imagery (pooling the object and non-object Imagery conditions) as the first regressor, perception (pooling the object and non-object perception conditions) as the second regressor, and Baseline as the third regressor. We concatenated the three sessions of imagery and the three sessions of perception into two files, simulating two imaging sessions. Session-specific parameter estimates pertaining to each type of effect of interest were calculated for each voxel in each subject, producing an image of parameter estimates. The specific contrasts of the parameter estimates were calculated in a voxel-wise manner to produce, for each subject, Imagery minus Baseline and Perception minus Baseline contrast images. At a second level of analysis, the 15 individual contrast images of each comparison were entered into two one-tailed *t* tests with 14 degrees of freedom.

In the second analysis, we also concatenated the six sessions into two files. We defined regressors for Object Imagery (IO), Non-object Imagery (INO), Object Perception (PO), and Non-object Perception (PNO) conditions. Two individual contrast images were realized: IO minus INO and PO minus PNO. Then, at a higher level of analysis, these contrasts were entered into a multiple regression without constant term model analysis. Within this analysis, we examined different reciprocal contrasts such as IO minus INO, INO minus IO, PO minus PNO, and PNO minus PO.

The SPMs for each modeled effect were transformed into SPM (*Z*)'s. The activations were thresholded at $P < 0.05$ (corrected for multiple comparisons). We also reported activations below a threshold corresponding to $P < 0.001$ (uncorrected for multiple comparisons) in regions for which we had an a priori hypothesis (inferior frontal gyrus and sulcus, occipito-temporal and fusiform cortex, and calcarine cortex). Anatomical localization of the maximum *Z* score relied on the automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single subject brain [48]. We also focused on these three regions of interest to compare the effect of type of drawing in perception and imagery (i.e., interactions). They were anatomically defined by the intersection between the clusters of activation (contrast IO minus INO for left inferior frontal and temporal gyrus and PO minus PNO for calcarine sulcus) and the anatomical region drawn on the

MNI standard brain [48]. The average of signal change within these regions was then compared for IO minus INO and PO minus PNO contrasts (paired *t* test).

2.2.6.2. Functional asymmetries. We performed a two-stage procedure analysis to measure the functional asymmetry for both the IO minus INO and PO minus PNO contrasts. The first stage consisted of flipping the 15 individual activation contrasts (IO minus INO for Imagery and PO minus PNO for Perception) to obtain a mirror image of each original contrast image (left hemisphere on the right side and right hemisphere on the left side). Then, each flipped image was subtracted from the corresponding original contrast image, resulting in 15 asymmetry contrast images for imagery and 15 asymmetry contrast images for perception. The two sets of asymmetry contrast images were entered in a regression analysis without constant term with 28 degrees of freedom for each. The SPMs were transformed into SPM (*Z*)'s. All the left–right differences reported in the asymmetry contrasts (IO minus INO) and (PO minus PNO) were detected above a threshold corresponding to $P < 0.001$ (uncorrected for multiple comparisons).

3. Results

3.1. Behavioral results

We found a correlation between response time and the number of correct responses in the Imagery conditions ($r_{(14)} = -0.37$, $P = 0.04$; Spearman): correct responses were associated with shorter response times, ruling out a speed–accuracy tradeoff effect. No correlation was found between response time and number of correct responses in the Perception conditions ($r_{(14)} = -0.15$, $P = 0.32$; Spearman). The small range of values for RT and a “ceiling effect” for number of correct responses (the rate of correct responses were close to 100% in this condition) could explain the absence of correlation in this case.

3.1.1. Imagery conditions

The number of correct responses was significantly higher during the Object Imagery condition ($88.7 \pm 8.9\%$) than during the Non-object Imagery condition ($84.3 \pm 9.4\%$; $P = 0.01$; Wilcoxon). Moreover, participants performed significantly faster during the Object Imagery condition (4.0 ± 1.1 s) than during the Non-object Imagery condition (4.6 ± 1.0 s; $P = 0.02$; Wilcoxon).

3.1.2. Perception conditions

The number of correct responses was higher during the Object Perception condition ($97.2 \pm 3.6\%$) than during the Non-object Perception condition ($91.5 \pm 5.1\%$; $P = 0.001$; Wilcoxon). The response times did not differ significantly between the Object Perception (1.7 ± 0.5 s) and the Non-

object Perception conditions (1.7 ± 0.4 s; $P = 0.82$; Wilcoxon).

3.2. Post-test debriefing

The participants reported that they refrained from forming images or performing the task during the Baseline conditions. All of the participants stated that they made no use of a verbal strategy with non-objects drawings (e. g., they made no use of substantives to name such drawings) during either the learning phase or the Non-object Imagery conditions.

Table 1
Brain areas activated during Imagery compared to Baseline ($P_{\text{corr}} < 0.05$, $*P_{\text{uncorr}} < 0.001$)

Imagery minus baseline				
Anatomical location of max. voxel	Coordinates			
	x	y	z	Z score
Occipito-temporal cortex				
L. inferior occipital/temporal gyms junction	–48	–58	–10	5.2
R. inferior occipital/temporal gyms junction	50	–58	–16	4.6*
L. calcarine cortex	–6	–84	2	5.1
L. calcarine cortex	–16	–76	10	5.0
Parietal cortex				
R. angular gyms	36	–50	38	5.7
R. inferior parietal gyms	36	–54	48	5.6
R. angular gyms	32	–68	46	5.1
L. inferior parietal gyms	–44	–46	42	5.7
L. intraparietal sulcus	–28	–74	28	5.8
L. superior occipital gyms	–24	–76	42	5.1
L. intraparietal sulcus	–30	–66	52	5.2
L. inferior parietal gyms	–32	–52	40	5.1
Frontal cortex				
R. superior frontal/precentral sulcus	32	0	52	5.6
L. superior frontal/precentral sulcus	–32	0	52	5.5
L. inferior frontal sulcus	–54	28	28	5.4
L. inferior frontal sulcus	–46	24	24	5.0
R. inferior frontal sulcus	46	32	20	4.5*
R. pre-SMA	8	14	50	5.5
Limbic cortex				
R. anterior cingulate cortex	14	30	26	5.5
L. middle cingulate cortex	–10	26	38	5.3
L. middle cingulate cortex	–6	14	48	5.0
Insular cortex				
R. anterior insular cortex	40	26	–4	6.0
L. anterior insular cortex	–36	20	–4	5.2
L. anterior insular cortex	–34	22	6	5.2
Vermis	0	–36	–14	5.0
Sub-cortical areas				
L. thalamus	–14	–10	2	6.0
L. thalamus	–14	–2	–4	5.4
L. thalamus	–8	–10	10	5.1
R. thalamus	16	–8	10	5.0
R. superior colliculus	6	–26	–4	5.6
L. pallidum	–18	2	14	5.1
R. pallidum	16	0	–4	5.2

The data are local maxima of activated region detected with SPM 99 software. The anatomical localization of the maximum *Z* scores of these regions is given on the basis of the averaged high resolution MRI of the 15 participants normalized into the MNI space using their stereotactic coordinates in mm (R.: right; L.: left).

3.3. Group analyses of activation

3.3.1. Imagery compared to Baseline

We detected bilateral activation of the occipito-temporal cortex during the Imagery task regardless of type of drawing, with right-lateralized activation just below the $P < 0.05$ corrected threshold. The calcarine cortex was also activated. We detected activation in the parietal lobe, including the depth of the left intraparietal sulcus, and in the right angular gyrus extending to the right inferior parietal gyrus. In addition, we detected several foci in the frontal lobe, including bilateral activation in the depth of the superior frontal sulcus at the junction with the precentral sulcus and bilateral banks of the inferior frontal sulcus. Bilateral insular cortex activation was detected during Imagery tasks (Table 1 and Fig. 2).

3.3.2. Perception compared to Baseline

The activations largely overlapped the pattern observed during Imagery and described above. During the Perception condition (Object and Non-object), we found activation in the bilateral occipito-temporal cortex extending to the calcarine cortex, the superior occipital cortex, the inferior temporal cortex, and into the hippocampal region. We detected activation in the bilateral parietal lobe, including the right intraparietal sulcus and extending to the left inferior parietal gyrus. In addition, we observed several foci in the frontal lobe, including bilateral activation in the precentral gyrus and bilateral inferior frontal gyrus (opercular cortex). The thalamus was also activated bilaterally (Table 2 and Fig. 2).

3.3.3. Imagery of Object drawings compared to that of Non-object drawings

We compared the two imagery conditions in order to determine which areas were more active when the images were generated from an object drawing. The IO Imagery condition elicited a left-lateralized pattern compared to the

INO condition. A large activation was observed in the depth of the left inferior frontal sulcus extending to the inferior frontal gyrus (in both its opercularis and triangularis portions) and in the left precentral sulcus. A cluster of activation was detected in the left inferior temporal gyrus extending to the left fusiform gyrus. A small focus in the right calcarine sulcus was also detected (Tables 3–5; Fig. 3).

Activation was also found in the left inferior parietal lobule, spreading to the left supramarginal gyrus.

Functional asymmetry analysis confirmed a significant difference between the left and right hemispheres in the inferior frontal gyrus (opercular and triangular), inferior occipito-temporal junction, and left intraparietal sulcus ($P < 0.001$, uncorrected for multiple comparisons). No lateralization difference was observed in the calcarine cortex.

3.3.4. Imagery of Non-object drawings compared to that of Object drawings

No cluster was found in regions for which we had an a priori hypothesis in this analysis at either $P_{\text{corr}} < 0.05$ or the $P_{\text{uncorr}} < 0.001$ statistical threshold. In particular, no activation was detected in the calcarine sulcus.

3.3.5. Perception of Object drawings compared to that of Non-object drawings

In the occipital lobe, the medial bilateral calcarine cortex and left fusiform gyrus were more activated in PO than in PNO condition ($P_{\text{uncorr}} < 0.001$). Another small focus was found in the right collateral sulcus. In the frontal lobe, we observed activation of the left inferior frontal sulcus and at the junction of the precentral sulcus with the pars opercularis of the inferior frontal gyrus (Tables 3–5; Fig. 3).

Comparison of signal between the left and right hemispheres revealed significant differences from the corresponding right hemisphere cortex in the left inferior frontal

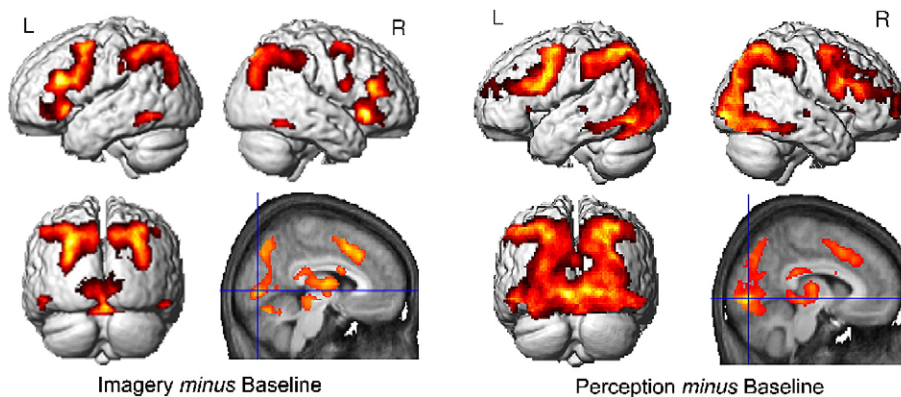


Fig. 2. (Left) Rendering of the areas activated when participants generated images as compared to baseline whichever the type of stimuli. (Right) Areas when participants saw drawings as compared to baseline whichever the type of the stimuli. The activated areas are projected onto the averaged high-resolution MRI of the 15 participants normalized into the MNI space (L: left; R: right) on a 3D view and on the sagittal slice passing through the maximum voxel in calcarine sulcus. Volumes were thresholded at $P_{\text{uncorr}} < 0.001$.

Table 2
Brain areas activated during Perception compared to Baseline ($P_{\text{corr}} < 0.05$)

Perception minus baseline				
Anatomical location of max. voxel	Coordinates			
	x	y	z	Z score
Occipito-temporal cortex				
R. inferior occipital gyrus	24	-96	-2	6.1
L. posterior calcarine cortex	-8	-86	-2	6.0
R. posterior calcarine cortex	10	-94	4	6.0
R. superior occipital gyrus	30	-74	40	6.1
R. middle occipital gyrus	34	-78	28	5.8
R. hippocampus	22	-30	-2	6.0
L. hippocampus	-20	-32	-4	5.7
L. inferior temporal gyrus	-56	-48	-14	5.7
R. inferior temporal gyrus	50	-56	-12	5.7
L. inferior occipital/temporal gyrus junction	-46	-72	-10	5.6
L. fusiform gyrus	-34	-74	-12	5.4
L. middle occipital gyrus	-18	-98	-2	5.6
L. middle occipital gyrus	-26	-82	20	5.4
R. fusiform gyrus	34	-58	-18	5.2
L. middle occipital gyrus	-24	-92	10	5.1
Parietal cortex				
R. intraparietal sulcus	34	-54	50	6.0
L. inferior parietal gyrus	-40	-48	42	5.7
L. superior parietal gyrus	-30	-68	56	5.6
Frontal cortex/Paralimbic cortex				
L. precentral gyrus/L. middle frontal gyrus	-32	0	54	6.7
R. middle cingulate cortex/R. SMA	6	18	44	6.2
L. SMA	-4	14	48	6.1
L. precentral gyrus	-50	4	36	5.7
R. inferior frontal gyrus pars opercularis	54	10	24	5.6
R. precentral gyrus	32	-6	46	5.3
R. middle frontal gyrus	34	2	54	5.3
L. inferior frontal gyrus pars opercularis	-56	14	22	5.0
Sub-cortical areas				
R. thalamus	10	-12	8	5.3
L. thalamus	-10	-18	10	5.1

See Table 1 for details.

gyrus, left inferior temporal and inferior occipital gyrus, and in the left intraparietal sulcus ($P < 0.001$, uncorrected for multiple comparisons). No lateralization difference was observed in the calcarine cortex.

3.3.6. Perception of Non-object drawings compared to that of Object drawings

A cluster of activation was detected in the right precuneus ($P_{\text{uncorr}} < 0.001$) (Table 4).

3.3.7. Effect of type of drawing in the imagery and perception conditions within regions of interest

We detected an interaction between the modality (imagery or perception) and the type of drawings (object or non-object) in a set of regions of interest (ROI) chosen in both contrasts “IO minus INO” and “PO minus PNO”. The ROI set included the left inferior frontal gyrus, left inferior temporal gyrus, and bilateral calcarine cortex ($P_{\text{uncorr}} <$

Table 3
Brain areas activated during Object Imagery compared to Non-object Imagery condition ($P_{\text{corr}} < 0.05$, $*P_{\text{uncorr}} < 0.001$)

Object Imagery minus Non-object Imagery				
Anatomical location of max. voxel	Coordinates			
	x	y	z	Z score
Frontal cortex				
L. inferior frontal gyrus pars opercularis	-52	8	16	4.5*
L. inferior frontal gyrus pars triangularis	-52	36	20	4.3*
L. precentral gyrus	-54	6	36	4.2*
R. precentral gyrus	64	4	36	3.9*
Parietal cortex				
L. postcentral gyrus	-60	-14	18	3.9*
L. inferior parietal gyrus	-60	-28	48	3.6*
L. supramarginal gyrus	-66	-28	30	3.6*
L. inferior parietal gyrus	-44	-38	36	3.6*
Occipito-temporal cortex				
L. inferior occipital/temporal gyrus junction	-50	-54	-14	5.9
R. calcarine cortex	6	-76	8	3.4*
Sub-cortical areas				
L. thalamus	-16	-30	6	3.2*

See Table 1 for details.

0.001). Fig. 4 shows the amplitude of the response evoked in each contrast, within the three regions of interest. In the left inferior frontal gyrus and the left inferior temporal gyrus, the activation evoked by the difference in fMRI signal between object and non-object imagery was higher than the difference elicited by the equivalent perceptive contrast for object drawings ($t_{(14)} = 2.1$, $P = 0.05$ and $t_{(14)} = 2.2$, $P = 0.04$, respectively; paired t test). A different pattern was observed in the calcarine cortex: the difference between

Table 4
Foci of activations during Object Perception minus Non-object Perception and Non-object Perception minus Object Perception ($P_{\text{uncorr}} < 0.001$)

Anatomical location of max. voxel	Coordinates			
	x	y	z	Z score
Object Perception minus Non-object Perception				
R. Calcarine cortex	6	-80	0	4.9
R. Calcarine cortex	14	-94	4	4.7
R. Calcarine cortex	4	-90	4	4.6
L. calcarine cortex	-12	-98	0	3.8
L. lingual/fusiform gyrus	-28	-72	-12	4.5
L. fusiform gyrus	-32	-58	-20	4.5
L. inferior temporal sulcus	-50	-54	-14	4.2
L. inferior temporal gyrus	-58	-60	-8	3.6
R. collateral sulcus	38	-68	-18	3.7
R. cuneus	18	-86	26	3.5
L. middle occipital gyrus	-44	-76	20	3.1
R. precuneus	8	-44	60	3.1
L. inferior frontal sulcus	-46	30	16	3.1
L. precentral sulcus/inferior frontal gyrus pars opercularis	-50	6	20	3.1
Non-object Perception minus Object Perception				
R. precuneus	22	-64	50	3.5

See Table 1 for details.

Table 5

Loci of maximum difference between the left and the right hemisphere activation for the Object Imagery minus non-object Imagery and for Object Perception minus non-object Perception ($P_{\text{uncorr}} < 0.001$)

Lateralization regions				
Anatomical location of max. voxel	Coordinates			
	x	y	z	Z score
Object Imagery minus Non-object Imagery				
Parietal cortex				
L. postcentral gyrus	-56	-22	30	3.8
L. inferior parietal gyrus	-46	-50	50	3.6
L. intraparietal sulcus	-38	-50	38	3.6
Frontal cortex				
L. inferior frontal gyrus pars opercularis	-52	8	24	4.4
L. precentral gyrus	-46	4	30	4.3
L. inferior frontal gyrus pars triangularis/L. inferior frontal sulcus	-48	36	22	4.1
L. superior frontal gyrus	-24	2	42	3.9
Occipito-temporal cortex				
L. inferior occipital/temporal gyrus junction	-48	-54	-14	4.1
L. inferior occipital gyrus	-46	-72	-8	3.5
L. inferior temporal gyrus	-42	-62	-10	3.2
L. middle temporal gyrus	-62	-56	2	3.6
Object Perception minus Non-object Perception				
Parietal cortex				
L. inferior parietal gyrus	-52	-46	48	4.4
L. intraparietal sulcus	-26	-64	48	4.2
Frontal cortex				
L. inferior frontal gyrus pars opercularis	-50	6	24	5.0
L. inferior frontal gyrus pars triangularis	-40	18	28	3.3
R. inferior frontal gyrus pars triangularis	30	30	26	4.7
L. inferior frontal gyrus pars opercularis	-62	12	8	3.8
Occipito-temporal cortex				
L./R. posterior calcarine cortex	2	-88	2	4.1
L. middle occipital gyrus	-34	-80	26	4.0
L. inferior occipital/temporal gyrus junction	-48	-54	-14	3.7
L. inferior occipital gyrus	-26	-88	-10	3.1

See Table 1 for details.

effects of object and non-object stimuli was stronger during perception than during imagery ($t_{(14)} = 2.6$, $P = 0.02$; paired t test) (Fig. 4).

3.4. Individual activations in calcarine cortex during imagery

All participants exhibited activation in the calcarine sulcus during the Imagery condition. However, individual analyses revealed variability of these activations across the participants in terms of both amplitude and spatial extent (Fig. 5).

4. Discussion

The main goal of the present fMRI study was to investigate the effects of object and non-object types of mental images on the functional lateralization of mental imagery. We further compared these effects to those of an equivalent perceptive task. In the imagery condition, we observed left lateralization when activation elicited by object stimuli was compared to that related to non-object stimuli. Note, however, that compared to baseline, most of the activation was in fact bilateral in both imagery and perception conditions. This was true in particular for the occipito-temporal cortex and inferior frontal cortex, on which we focus our discussion. The left lateralization observed was thus relative and does not imply that mental imagery is a left-lateralized process, as previously proposed [9]. Rather, it suggests that mental image content affects the lateralization of this cognitive function.

A critical finding was that the left hemisphere advantage for object drawings was also noted in the perception condition. However, it was more intense in the left inferior frontal gyrus and in the left inferior temporal gyrus for imagery than for perception conditions. On the other hand, the differences related to the type of drawings were stronger in early visual areas for perception than for imagery. This result indicates that while functional overlap exists between perception and imagery, as has already been reported [17,23,27,33], these two modalities were affected differently depending on the type of stimulus.

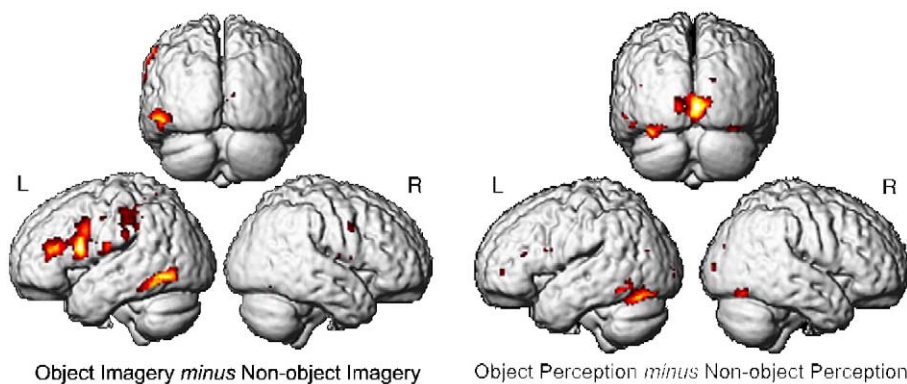


Fig. 3. (Left) Rendering of the areas activated when participants performed the Object Imagery tasks compared to Non-object Imagery tasks ($P_{\text{uncorr}} < 0.001$). (Right) Rendering of the areas activated when participants performed the Object Perception tasks compared to Non-object Perception tasks ($P_{\text{uncorr}} < 0.001$). The activated areas are projected onto the averaged high resolution MRI of the 15 participants normalized into the MNI space (L: left; R: right).

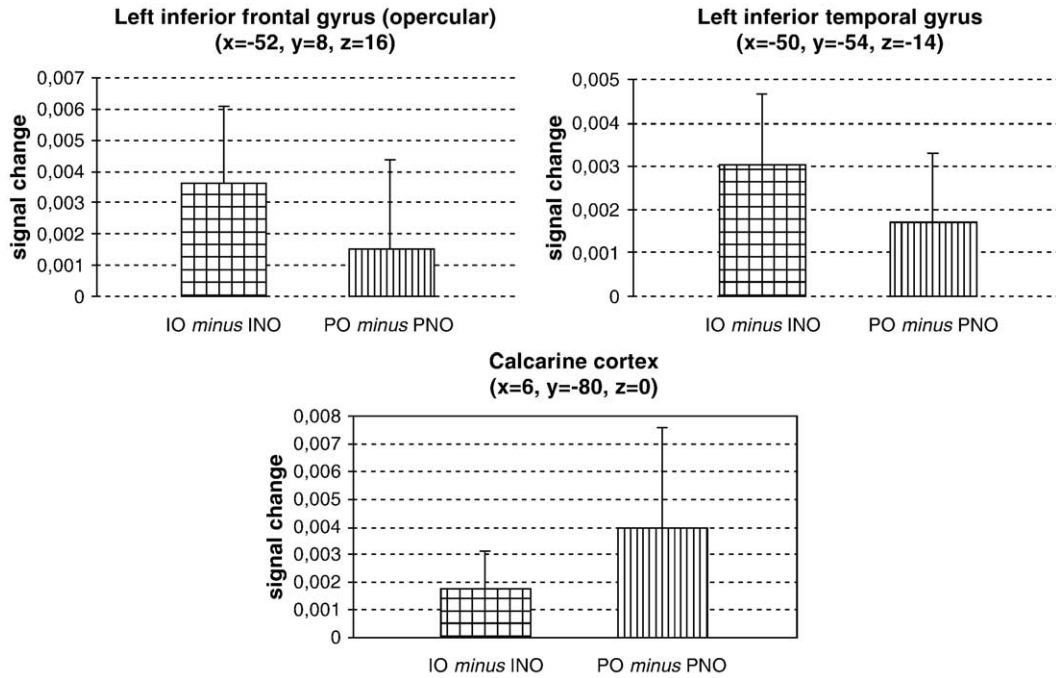


Fig. 4. Plots of the mean BOLD signal change during the both contrasts Object Imagery (IO) minus Non-object Imagery (INO) and Object Perception (PO) minus Non-object Perception (PNO). The percentage of signal change is observed in three clusters: left inferior frontal gyrus, left inferior temporal gyrus, and the bilateral calcarine cortex localized within the region of interest of the MNI template of the automated anatomical labeling software ($P_{\text{uncorr}} < 0.001$). See Materials and methods for details.

We will further discuss the parieto-frontal network involvement and then, within the context of the imagery debate, focus on the activation observed within the early visual cortex in both group and individual analyses.

4.1. Left hemisphere and meaningfulness

We hypothesized that mental imagery of object images relies more strongly on the left hemisphere than that of non-

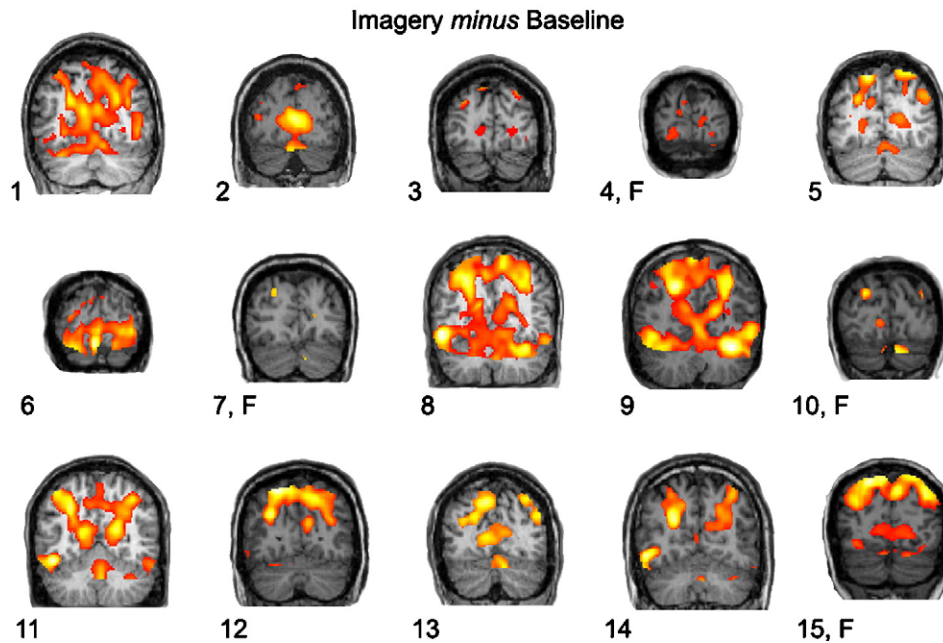


Fig. 5. Single-subject BOLD responses in the calcarine cortex. These single-subject images reveal the individual variability of the BOLD response in calcarine cortex during the Imagery condition. The individual participants are identified by the number in the upper left-hand corner of each pair of images and by gender (F: female). The data were thresholded at a value of $P_{\text{uncorr}} < 0.001$. The statistical data overlaid on each subject's anatomical image.

object images. More specifically, we assumed that the left ventral pathway would be more activated than its right homologue when mental images referred to object drawings. In fact, we found left activation of the inferior temporal cortex with object imagery compared to non-object imagery, with a significant difference in activation between left and right inferior temporal gyrus. This left region also responded more strongly during the perception of objects than of non-objects, as has already been suggested [40,51]. However, to our knowledge, the present study is the first to report a similar effect when stimuli are no longer perceived but only imagined. Overall, our results indicate that the left occipito-temporal cortex is more sensitive to verbal and/or semantic content than the right counterpart region for both percepts and mental images. This claim is consistent with a previous priming fMRI study that showed that the left occipito-temporal cortex is sensitive to the meaning of perceived pictures while its right counterpart processes specific visual form information [28].

Beside the ventral pathway, and in agreement with our hypothesis, we observed an effect of meaningfulness on activation of the inferior frontal cortex. It might be suggested that the left inferior frontal activation reflected covert naming of the object drawings. Although it is impossible to rule out this possibility, this seems unlikely for several reasons. In the debriefing session, the participants were explicitly asked whether they had used a verbal strategy, and none of them reported naming activity. Even if subjects had mentally named object drawings, this activity would have lasted a very short time in comparison to the mental imagery activity required by the task and thus could not have caused the activation observed. Moreover, it is worth noting that Broca's area is not involved in the naming of objects as such [12]. This region is not modality-specific (i.e., not dedicated to language) but is involved in executive aspects of semantic processing [2] although its specific function(s) is still unclear [43]. Interestingly, it has been suggested that the left inferior frontal gyrus plays a particular role in the retrieval of items that have been encoded with their semantic attributes (source memory) compared to item memory (with no semantic processing during encoding) [10]. In this context, it is possible that object and non-object drawings differed in the way they were encoded: implicit semantic and/or verbal processing could have accompanied the encoding of object drawings (name, category, function), but not the non-object drawings.

Our results suggest that imagining object drawings activates a left semantic network including the occipito-temporal cortex and inferior frontal cortex, although no semantic processing was explicitly required by the task assigned to subjects. It is worth noting that although imagery of non-object drawings appeared slightly more difficult (due in particular to lack of symmetry), no area was more activated during non-object imagery than during object drawing imagery. The regions activated during non-object imagery thus appeared to be a subset of those

involved in object imagery. It has already been suggested that cognitively less demanding tasks can lead to a more extensive pattern of activation [4]. In our experiment, the additional activation detected in the imagery of object condition reflected cooperation between visual and semantic and verbal regions. Notably, our interpretation bears on the most obvious differences between object and non-object drawings (i.e., lexical and semantic). A potential limitation of this study could involve differences in low-level physical aspects between the sets of drawings used (spatial frequency in some cases, differences in symmetry, etc.). However, the activations reported here mainly involved "high-level" processing areas. It is thus unlikely that differences in low-level features of stimuli alone could explain the left-lateralized activation we detected.

Interestingly, and in agreement with previous studies, this network was also more activated during the perception of objects than that of non-object drawings [28,51]. The difference between object and non-object stimuli in these regions (left occipito-temporal cortex and left inferior frontal cortex) was, however, greater for the imagery modality than for perception, supporting a role for these cortical areas in retrieval. It has recently been suggested that, during image generation, top-down processes arise in part from prefrontal areas, while during perception bottom-up processes arise from early visual areas [32]. Our results are in agreement with this outcome: the left inferior frontal gyrus during imagery was more affected because top-down processes originated from this region. On the other hand, meaningfulness effect was stronger in the early visual areas from which bottom-up processes arose during perception.

4.2. Visual mental imagery engaged both hemispheres

We consider now the pattern of activation elicited in the ventral pathway by the visual mental imagery task, regardless of object or non-object type of imagined drawing. Activation of the occipito-temporal cortex was detected bilaterally. A series of studies has demonstrated that this region responds more strongly to the perception of shapes than to that of scrambled objects or textures [22]. We have confirmed here that these areas are also involved during the evocation of previously learnt drawings in the absence of any visual input. Indeed, this result is consistent with previous findings of engagement of occipito-temporal cortex during various object mental imagery tasks and suggests that this region is one site for the storage of visual representations [6,23,30,35,41]. Activation of stored representations would then lead to the subjective experience of visual imagery.

When the Imagery conditions were compared to the Baseline task, we also detected bilateral activation of the inferior frontal cortex. This region corresponds to our region of interest, including the left inferior frontal gyrus and sulcus. In agreement with previous proposals and in line with the above discussion, the left and right frontal cortex

could have acted in different fashions during our task. The left inferior frontal cortex may be preferentially involved in the semantic aspects of retrieval, while the homologous right region may be more specifically in charge of drawing retrieval and of generation of complex imagery-based representations [18,20]. In fact, these regions are involved in the intentional retrieval of information from memory [5,42,47]. The activations of inferior frontal cortex must be understood in the context of the bilateral involvement of the anterior insular cortex, which also plays a role in memory retrieval [11].

4.3. *Parieto-frontal network and visual mental imagery*

Object and non-object imagery elicited activation of a parieto-frontal network including the bilateral intraparietal sulcus and a frontal region in the depth of the superior frontal sulcus at its junction with the precentral sulcus. This network has been widely shown to be involved in spatial working memory [8] and spatial mental imagery [30,34,37]. The imagery task we used involves figurative processing, to a large extent, but the participants were required to scan mental images and perform spatial judgments on the figurative display in order to answer questions such as “higher than wide?” Activation of a parieto-frontal network could thus be related to the spatial processing required by the Imagery tasks. Moreover, a recent study examined the interactions between cortical regions during imagery and perception tasks [32], and emphasized the role of parietal cortex in attentional top-down processes during mental imagery. Nonetheless, it should be noted that in our experiment similar parietal activation was detected in the perception condition. This is in agreement with a recent study that reported highly analogous activation of the parietal cortex during imagery and perception of drawings [17]. It is thus possible that the parietal activation we observed reflects both attentional and spatial processes.

4.4. *Early visual cortex*

We detected activation in the early visual cortex during the visual mental imagery tasks, regardless of whether object or non-object type drawings were imagined by the participants. In the framework of the imagery debate, this result provides additional evidence that figurative imagery is more likely to engage early visual cortex than spatial imagery [25,31,44]. Importantly, this activation was much weaker than that observed during perception, in agreement with the findings of a recent study that compared imagery and perception using an identical task in the two modalities [17]. The authors reported that the overlap between imagery and perception was lower in occipital regions than in frontal and parietal regions. In our study, the individual contrasts between imagery and baseline conditions showed that calcarine cortex activation was indeed present in all participants but was variable in both amplitude and spatial

extent. It is likely that this individual variability is a source of discrepancies across studies regarding the involvement of early visual areas in visual mental imagery. A second possible source of confusion is the content of the mental image. As a matter of fact, and contrary to our predictions, mental imagery of object drawings led to slightly more activation of the calcarine cortex than mental imagery of non-objects. As discussed above, this effect also appeared with much stronger intensity in the perceptive version of the task. Previous studies have argued that this type of activation could be attributable to differences in complexity and number of component parts [21,39]. However, this explanation appears unlikely to apply to the present study, since object and non-object drawings were matched in terms of complexity. During imagery, this activation is likely to reflect a top-down process; this is the only way to explain how activation in early visual cortex may occur in the absence of perceptual input. It remains unclear, however, why this process led to a more substantial activation in the early visual cortex when the image represented an object. In the perceptual domain, visual attention has been shown to enhance the BOLD signal in this portion of visual cortex (for review, see [24]). It could also have played a role in our study and contributed to the better performances displayed during imagery of object drawings.

5. Conclusion

Although both hemispheres appeared to be involved in the visual mental imagery tasks our subjects performed, the present study showed that mental image content affects hemispheric lateralization of mental imagery. We found that a left occipito-temporo-frontal network was more activated during mental imagery of object drawings than during that of non-object drawings. This network probably reflects cooperation between visual and verbal processes that facilitate the generation of mental images of objects. The same effect was found for perception, but to a lesser degree than for imagery. This suggests that although imagery and perception make use of a common neural network, this network could be differentially affected depending on the type of image or percept.

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