Visual mental imagery engages the left fusiform gyrus, but not the early visual cortex: a meta-analysis of neuroimaging evidence

Alfredo Spagna[1,2], Dounia Hajhajate[2], Jianghao Liu[2,3], Paolo Bartolomeo[2,*]

[1] Department of Psychology, Columbia University in the City of New York, NY, USA, 10027

[2] Inserm U 1127, CNRS UMR 7225, Sorbonne Université, Institut du Cerveau et de la Moelle épinière, ICM, Hôpital de la Pitié-Salpêtrière, 75013 Paris, France

[3] Dassault Systèmes, Vélizy-Villacoublay, France

* Corresponding author

Paolo Bartolomeo, M.D., Ph. D.

Inserm U 1127, CNRS UMR 7225, Sorbonne Université, Institut du Cerveau et de la Moelle épinière, ICM, Hôpital de la Pitié-Salpêtrière, 75013 Paris, France

paolo.bartolomeo@icm-institute.org

Abstract

The neural bases of visual mental imagery (VMI) are the object of intense debate. Their identification is central to define the brain substrates our conscious experience and can be clinically important to reveal consciousness in non-communicating patients or to alleviate post-traumatic stress disorder. The dominant model of VMI stipulates a functional and anatomical equivalence between visual mental imagery and visual perception. In patients with acquired brain damage, the model predicts a systematic co-occurrence of perceptual and imaginal deficits. However, patients with lesions restricted to the occipital cortex often experience vivid mental images, even in case of cortical blindness resulting from bilateral V1 damage. Instead, patients with extensive left temporal damage are more likely to have impaired VMI. On the other hand, some neuroimaging and neuromodulatory evidence does suggest an implication of striate cortex in VMI. To address this discrepancy, we conducted an activation-likelihood-estimation-based large-scale meta-analysis of 46 functional magnetic resonance imaging experiments to map the extent of cortical activation associated with three contrasts: (1) all studies combined; (2) VMI *versus* Control, (3) VMI *versus* Perception, and (4) Motor Mental Imagery *versus* Control. Results from the VMI *versus* Control contrast demonstrated an association between VMI and activation increase in the frontoparietal and cingulo-opercular networks, as well as in the left fusiform gyrus. Results from the VMI *versus* Perception contrast showed the association between VMI and activation increase of the anterior insular and supplementary motor area / anterior cingulate cortices, bilaterally. Conjunction analyses between the VMI *versus* Control and the VMI Mental Imagery *versus* Perception contrasts showed the activation of the left anterior insular cortex and in the bilateral supplementary motor area / anterior cingulate cortex. Results from the Motor Mental Imagery *versus* Control contrast showed that mental motor imagery increases the activation of the cerebellum and of the superior frontal gyri bilaterally, of the left supplementary motor area, of the anterior portion of the left calcarine sulcus, and of the

left fusiform / parahippocampal gyri. Conjunction analyses between the VMI *versus* Control and the Motor Mental Imagery *versus* Control contrasts showed the activation of the bilateral superior frontal gyrus as well as of the left supplementary motor area / anterior cingulate cortex. Thus, the results stress the importance for VMI of brain networks associated with attentional control and working memory functions, together with rostral portions of the cortical ventral visual stream. Bayesian analysis confirmed the lack of evidence for an activation of the early visual areas in VMI, consistent with the results from brain-damaged patients. Our evidence suggests a revision of the VMI model. A Fusiform Imagery Node (FIN) in the area FG3 of the left fusiform gyrus might act as a hub retrieving visual information from long-term semantic memory in the anterior temporal lobe. FIN connections with the medial temporal lobe provide vivid VMI episodic experiences. Fronto-parietal networks subserving attention and working memory initiate, modulate and maintain activity of the core VMI network in the left temporal lobe. The revised model of VMI reconciles findings from neuroimaging with the reports from patients with brain damage.

Keywords: mental imagery, attentional networks, fusiform gyrus, medial temporal lobe, fronto-parietal networks.

Introduction

Close your eyes and think of Leonardo da Vinci's *Monna Lisa*. Is she looking at you or not? Is her hair curled or straight? Visual Mental Imagery (VMI) is the set of abilities whereby we can "see" things that are elsewhere (or nowhere: now imagine *Monna Lisa* frowning at you). These capacities are important for predicting the outcome of everyday tasks [1], for example to decide whether our car fits in a narrow parking spot. The subjective vividness of visual mental images varies substantially across individuals [2-5]. Some individuals experience mental images as "quasi-visual" in nature, while others have less vivid images, down to the total absence of VMI experience in otherwise normal individuals, a condition dubbed as "aphantasia"[6-9]. The neural bases of this remarkable set of cognitive functions are the object of intense research efforts [3,10-15]. Identifying the brain circuits subserving VMI and motor imagery is also essential for clinical reasons, because detecting their activity in neuroimaging can reveal consciousness in non-communicating patients in apparent vegetative state [16]; uncontrolled VMI activity could also contribute to the unbidden recollections of traumatic memories resulting in post-traumatic stress disorder [17].

The dominant model of VMI [3,18] stipulates the existence of common neural substrates underlying VMI and visual perception, spanning across the ventral cortical visual stream. Neuroimaging studies in healthy volunteers supported a strong version of the model, by demonstrating the engagement of early, occipital visual areas in VMI [19,20]. Further, TMS interference on V1 was shown to impact VMI [21]. The model also provided a principled account of inter-individual differences in VMI, because the level of activation in low-level visual areas correlates with the subjective experience of "vividness" of VMI [5,22] (but see Ref. [7]). However, this neuroimaging evidence is correlational, and does not directly speak to the causal role of these structures in VMI. In fact, causal evidence from neurological patients is sharply discordant with the perception-VMI equivalence model [23-25]. Whereas the model would predict a systematic

co-occurrence of perceptual and imaginal deficits after brain damage [26], patients with brain damage restricted to the occipital cortex often have spared VMI abilities [27-30], with preserved subjective VMI vividness despite damaged early visual cortex [31], even in the case of bilateral cortical blindness [27,32,33]. Instead, deficits of VMI for object form, object color, faces or orthographic material typically arise as a consequence of more anterior damage [26,34-40], often extensively including the temporal lobes, especially in the left hemisphere [23,24,41]. Such a strong evidence of dissociation is at odds with models proposing a substantial overlap between perception and imagery, and suggests an engagement in VMI of higher-order associative areas, especially in the left temporal lobe, rather than early visual cortex. Also, accumulating evidence shows that the temporal dynamics of VMI and perception are different [12,42-44]. VMI and perception build on distinct brain connectivity patterns [13], characterized by a reversed cortical information flow [14], and supported by anatomical connectivity between striate, extrastriate, and parietal areas [45]. In addition, studies on VMI mainly focused on the ventral cortical visual stream, but evidence also indicates VMI-related increases in BOLD response in fronto-parietal networks [42,46,47]. Thus, what VMI shares with visual perception may not be the passive, low-level perceptual aspect, but the active, exploratory aspects of vision [24,25,48], such as those sustained by visual attention [49]. However, the precise identity of these mechanisms, and of the underlying brain networks, remains unknown.

To address these issues, we conducted a meta-analysis of functional magnetic resonance imaging studies that examined the neural correlates associated with visual and motor mental imagery. Our specific aims were to assess the role of low- and high-level visual cortex, as well as the role of the fronto-parietal networks in mental imagery, by identifying the brain regions with higher activation for mental imagery in healthy volunteers. To evaluate the relationships between modality-specific and more general processes in mental imagery, we also assessed the neuroimaging of *motor* mental imagery (MMI). The included studies reported the coordinates of

brain regions with a significant activation increase in the contrasts of: VMI *versus* Control; VMI *versus* Perception; and MMI *versus* Control. We predicted the involvement in VMI of fronto-parietal and cingulo-opercular network areas, together with high-level areas in the visual cortical ventral stream. Based on patient evidence, we did not expect to find an activation of the early visual areas associated with visual mental imagery. If confirmed, this prediction would challenge the current dominant model stating the substantial overlap between VMI and visual perception, and delineate a new, alternative model, based on a critical role in our VMI experience of high-level visual region and of fronto-parietal networks important for attention and visual working memory.

Method

Literature search

First, we searched for functional magnetic resonance imaging (fMRI) studies in the domain of mental imagery using the online database NeuroSynth (http://NeuroSynth.org - RRID: SCR_006798) [50]. At the time of access (October 15, 2018), the database contained 3,884 activation peaks from 84 studies. To achieve an exhaustive search of studies, we further expanded our literature search to other databases (i.e., PubMed, Google Scholar), using the following search terms: Visual mental imagery, Mental imagery, Vividness, Mental rotation, and carefully screened the reference list of previously conducted reviews and meta-analyses. This final step led to the discovery of 39 additional studies.

Inclusion and Exclusion criteria

We first applied the following inclusion criteria: (1) studies published in peer-review journals in English; (2) studies with normal healthy adults (age ≥ 18 years); (3) studies with table(s) reporting brain activation foci from whole-brain analysis; (4) studies with the coordinates of the activation reported either in the Montreal Neurological Institute (MNI) or in the Talairach space. We then applied the following exclusion criteria: (1) single-subject studies

(excluded n = 2); (2) studies not using fMRI (e.g., voxel based morphometry studies or DTI studies; n = 8); (3) non-first hand empirical studies such as review articles (excluded n = 7); (4) studies of special populations of adults (e.g., with a specific personality trait or neurological disorders), whose brain functions may deviate from neurotypical controls' (excluded n = 31); (5) studies not reporting coordinates for contrasts of interest in this study (n = 2). (6) studies that could not be clearly classified into one of our three subdomains, or reporting contrasts not of interest for this study (n = 19); (7) studies using analytic approaches not of interest for this study (e.g., ROI analyses, multivariate pattern analysis, functional or effective connectivity analysis)(n = 15). The resulting final number of studies included in the meta-analysis was 41.

Data extraction

Within the included studies, we identified the tables that reported positive activation from defined contrasts of (1) VMI greater than control or rest conditions; (2) VMI greater than visual perception condition; (3) MMI greater than control or rest condition. "Control" conditions included experimental conditions unrelated to the specific imagery task. "Visual perception" included all conditions in which participants viewed visual stimuli related to the items employed in the VMI conditions. In the present work, we will use the term "experiment" as the result of one statistical map, with a single study potentially reporting results from more than one map. In fact, five of the 41 studies reported multiple experiments or multiple contrasts of interest for this study (e.g., reporting coordinates for both VMI *versus* Control and VMI *versus* Perception), which brought the total number of included experiments to 46. Specifically, we found (1) 27 experiments (376 foci from a total of 380 subjects) reporting contrasts regarding the difference in activation between VMI and rest or control condition; (2) 4 experiments (62 foci from a total of 52 subjects) reporting contrasts regarding the difference in activation between visual mental imagery and perception, and (3) 15 experiments (340 foci from a total of 239 subjects) reporting

contrasts regarding differences in activation between motor mental imagery and rest. **Figure 1** illustrates the selection process based on inclusion and exclusion criteria.

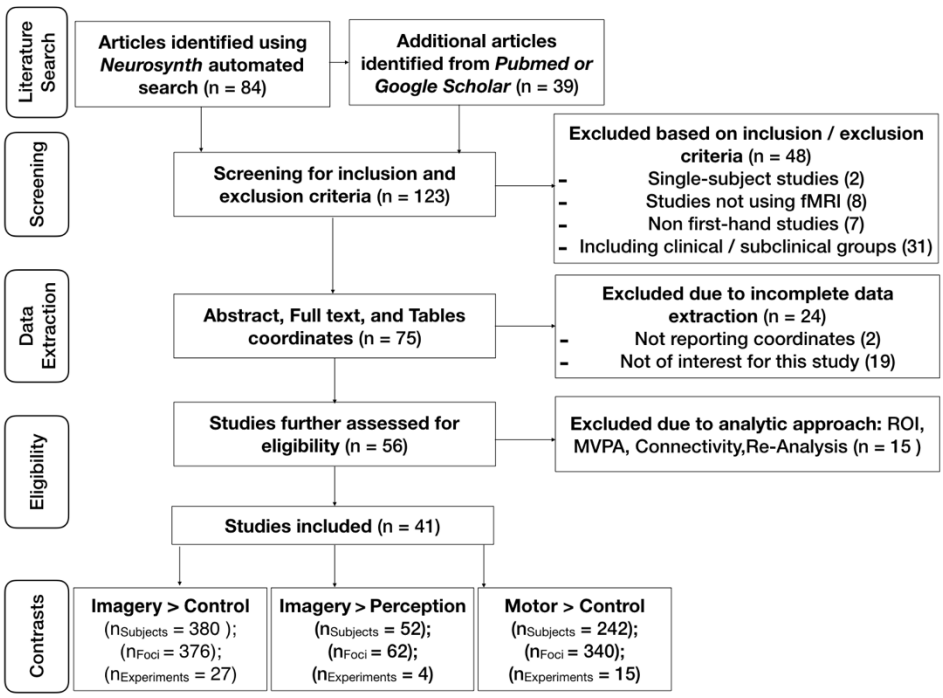

Figure 1. *Flow chart of the selection process conducted in the present meta-analysis showing the following steps: (1) identification of studies through literature searches (studies repeated in the two searches were included only once); (2) screening for inclusion and exclusion criteria; (3) assessment for appropriate data extraction; (4) evaluation of study eligibility based on analysis conducted (excluding studies that did not report results from whole-brain analyses either in the main text or in the supplementary material); (5) attribution of the included studies to one or more contrasts (some of the studies reported coordinates contrasts that could be included in more than one contrast).*

Figure 2 shows the published activation foci from the included studies projected onto an inflated cortical surface for the contrast of a) VMI > Control, b) VMI > Perception, c) MMI > Control. See the supplementary videos on Github for a dynamical representation of the foci included in the VMI > Control, VMI > Perception, MMI > Control analyses.

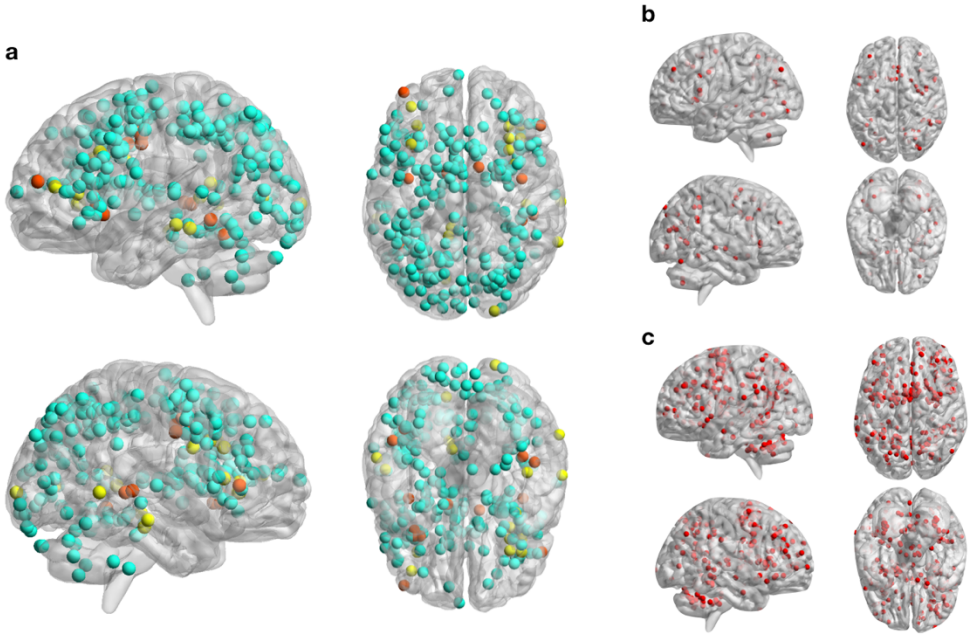

Figure 2. Activation foci reported in the studies included in the present meta-analysis for the contrasts a) VMI > Control, b) VMI > Perception, c) MMI > Control. For the VMI > Control panel, coordinates are color coded to represent the three categories of contrasts included: Object Form (cyan); Faces (yellow); Orthographic Material (orange).

Activation likelihood estimation

The three meta-analyses were conducted using GingerALE 3.0 (all platform version, http://brainmap.org/builds/; RRID: SCR_014921) with the activation likelihood estimation (ALE) algorithm [51-53]. ALE calculates the overlap of activation distributions across studies by modeling the foci as 3D Gaussian distributions centered at the reported coordinates with the full-width half-maximum (FWHM) weighted by the sample size of each study and combining the probabilities of activation for each voxel [51]. **Tables 1-3** report author names, publication year, type of stimuli used in the study, type of contrast, and number of subjects that were included in the contrasts VMI *versus* Control, VMI *versus* Perception, and MMI *versus* Control, respectively. Further, we conducted *conjunction* and *disjunction* analyses between (VMI *versus* Control) & (VMI *versus* Perception) as well as *conjunction* and *disjunction* analyses between (VMI *versus* Control) & (MMI *versus* Control).

Foci included in the dataset were either reported in MNI space or converted from Talairach space to MNI space by using the icbm2tal transform in GingerALE. The ALE map was assessed against a null-distribution of random spatial association across studies using a non-linear histogram integration algorithm [51,52]. All ALE maps were thresholded at a cluster-level corrected $p < .05$, with a cluster-forming $p < .001$ with 10,000 permutations for multiple comparison correction. Conjunction and disjunction analyses were then conducted at a $p < .05$ threshold and 10,000 permutations.

Spatial Bayesian Latent Factor Regression for Coordinate-Based Meta-Analysis

A specific aim of this study was to assess whether or not early visual activation occurred in the VMI vs Control condition, as a way to assess the potential contribution of early visual areas to VMI. Because the logic of our argument rests on testing the *absence* of activation in brain region, we conducted a spatial Bayesian latent factor regression model, where the probability that a voxel is reported as an activated focus, is modeled via a doubly stochastic Poisson process [54]. To test the activation degree of each voxel, the null hypothesis (H_0) stated that the voxel was specifically activated as a focus during VMI vs Control condition. We took the posterior probability $p(v)$ as the probability of null hypotheses for each voxel. The alternative hypothesis (H_1) was that the activation of the voxel belongs to the ongoing brain activity and was not specific. Thus, we took the mean activation probability of the whole brain voxels to get the H1 probability (see Ref. [54] for additional details about the method and a general discussion of the properties of this model). We defined Bayes Factors [55] for accepting and rejecting the null hypothesis. To compute the odds hypothesis conditionally on observed data $Bayes\ Factors\ =\ Pr(H0|data)/Pr(H1|data)$: BF (odds) > 3 were considered as the criteria to accept null hypothesis. Bayes Factors (BF) (odds) < 0.33 were considered as the criteria to reject the null hypothesis and thus to accept the alternative hypothesis. Spatial Bayesian latent factor regression analysis was conducted on the dataset consisting of 27 studies on VMI >

Control condition for a total of 376 foci (see **Table 1** for the list of studies included in this analysis). For each study, we also included three supplementary covariates: inference method (fixed / random effects), p-value correction (corrected / uncorrected), the number of participants scanned. We used a standard brain mask of 91 x 109 x 91 voxels of 2mm in size. Kernels falling outside the mask were discarded. We assigned a Gamma(1, 0.3) prior distribution with mean 1/3 to the diagonal elements of Σ^{-1}. The sampler was run for 10,000 iterations and the algorithm converged, with the first 5,000 samples discarded as a burn-in and collecting every 50th sample to thin the chain. We obtained the posterior intensity values of the full brain voxels, which we used to compute the BFs.

Results

The meta-analysis conducted on all the coordinates from the 46 experiments (*mental imagery vs all*) showed activation increases in areas within the fronto-parietal networks (including the bilateral superior frontal gyrus, and the bilateral inferior parietal lobe), and the bilateral anterior insular cortices. In addition, unilateral activation increases consistent across the studies were found in the right precuneus and in the anterior portion of the left calcarine sulcus, in the left fusiform and parahippocampal gyri. **Figure 3** shows the surface views of brain regions showing consistent activation increase across all domains, while **Table 4** reports the coordinates of common activation across all domains.

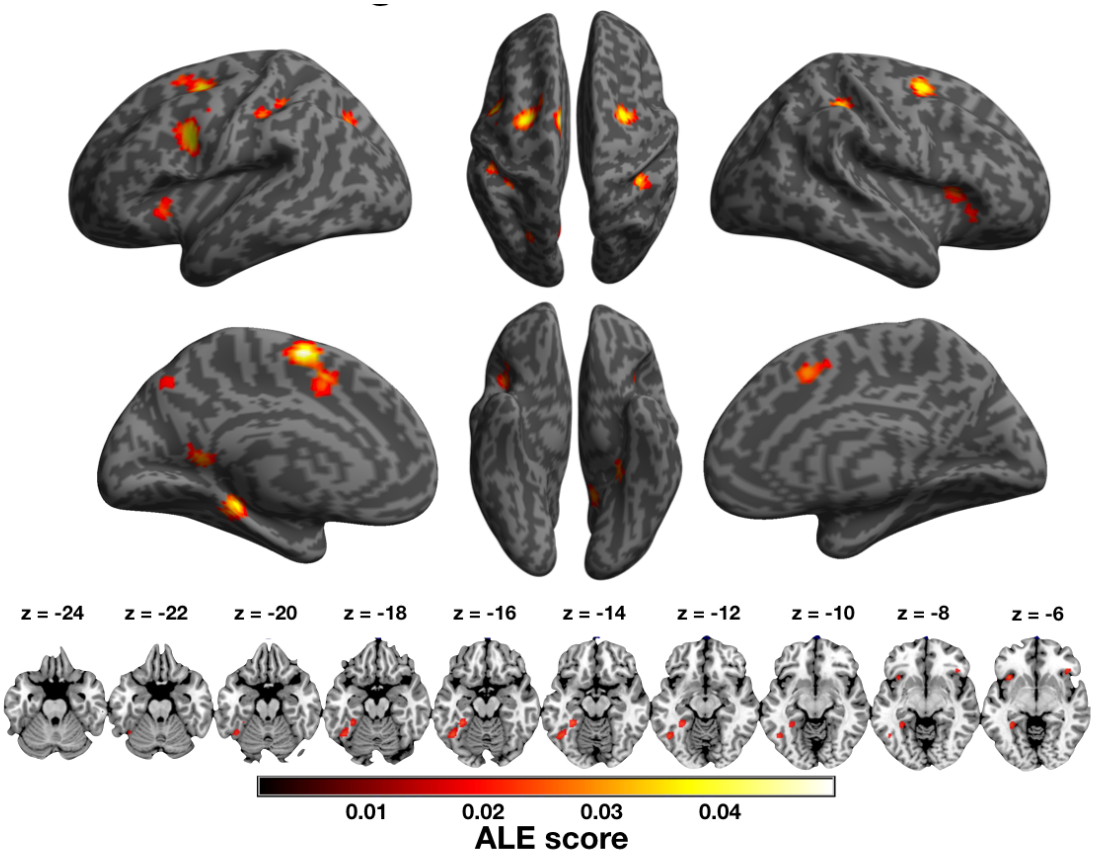

Figure 3. *Brain regions showing consistently increased activation associated with mental imagery (across all the domains of VMI > Control, VMI > Perception, and MMI > Control).*

The meta-analysis of the 27 experiments included in the VMI *vs* Control condition showed activation increases in bilateral superior frontal gyri, in the left anterior insular cortex, in the bilateral inferior parietal lobe / extending to the superior portion of the left middle occipital gyrus (BA19), in the left superior parietal lobe, in the left middle frontal gyrus, in the left fusiform gyrus, as well as regions lateralized to the right hemisphere, including the angular gyrus, the supplementary motor area / anterior cingulate cortex. **Figure 4** shows the surface views of brain regions showing consistent activation in the VMI *vs* Control condition, while **Table 5** reports the coordinates of common activation in the VMI *vs* Control condition.

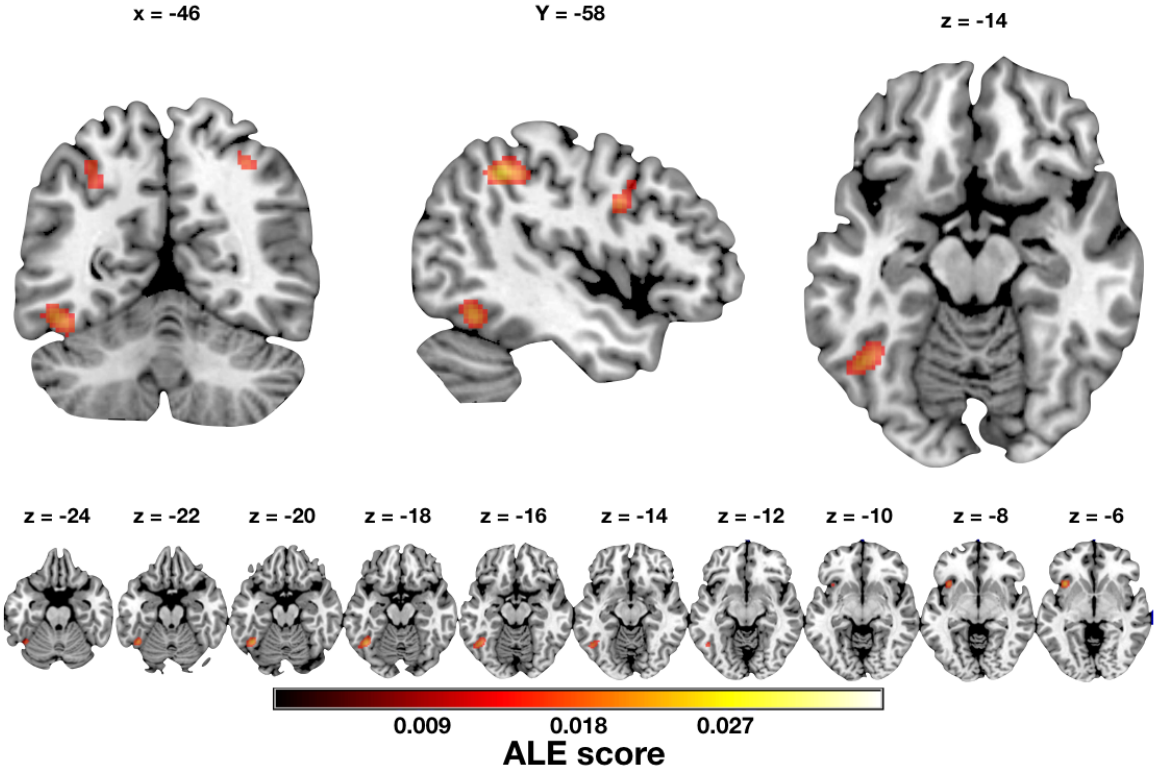

Figure 4. *Brain regions showing consistently increased activation associated with the contrast VMI > Control condition.*

The meta-analysis of the 4 experiments included in the VMI *vs* Perception condition showed the activation increase in the insular cortex and in the supplementary motor area / anterior cingulate cortex, bilaterally. **Figure 5** shows the surface views of brain regions showing consistent activation increase in the VMI *vs* Perception condition, while **Table 6** reports the coordinates of common activation in the VMI *vs* Perception condition.

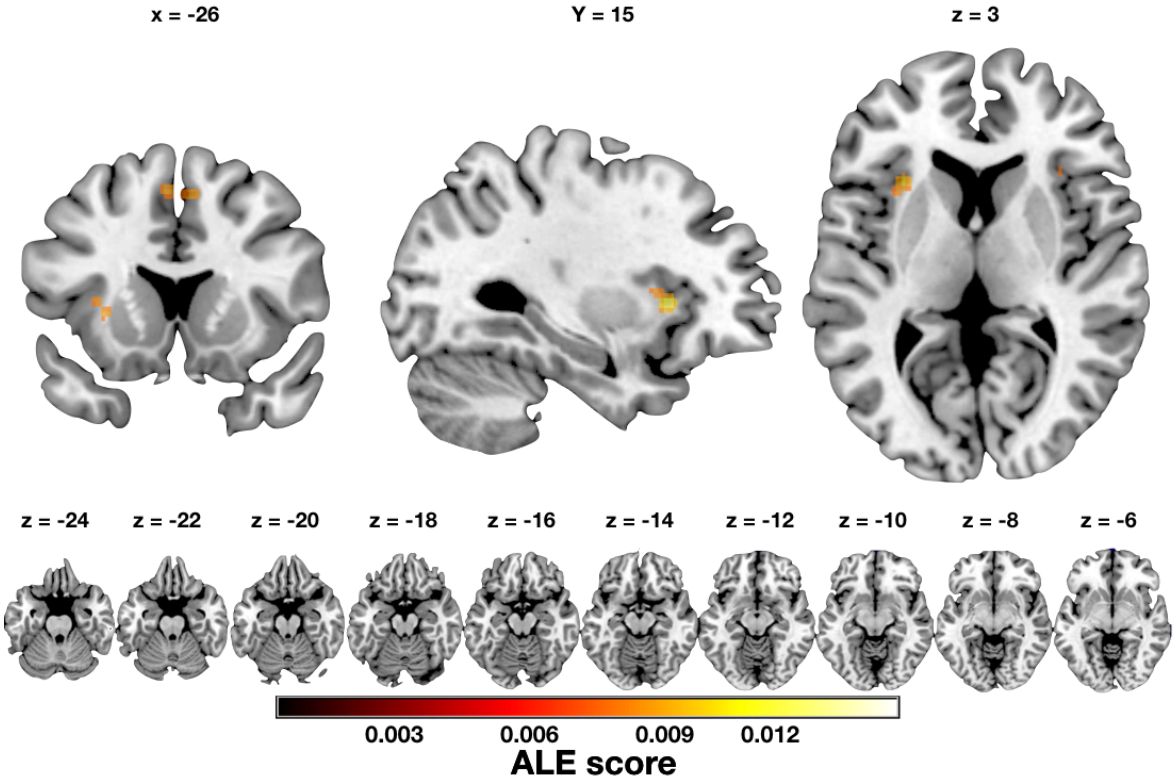

Figure 5. *Brain regions showing consistent increased activation associated with the contrast VMI > Perception condition.*

The meta-analysis of the 15 experiments included in the MMI *versus* Control condition showed activation increases in the superior frontal gyri bilaterally, of the cerebellum bilaterally, and of the left supplementary motor area, of the anterior portion of the left calcarine sulcus, and of the parahippocampal / fusiform gyri. **Figure 6** shows the surface views of brain regions showing consistent activation increase MMI *vs* Control condition, while **Table 7** reports the coordinates of common activation in the MMI *vs* Control condition.

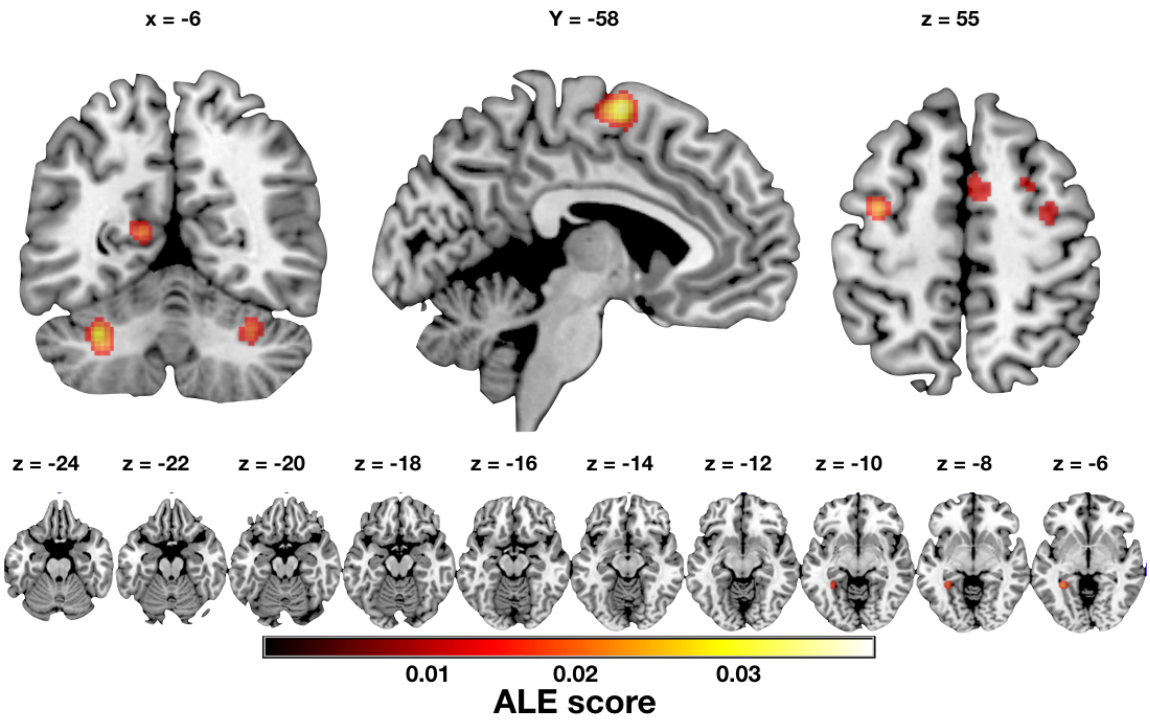

Figure 6. *Brain regions showing consistent increased activation associated with the contrast MMI > Control condition.*

To further investigate common areas of activation among the VMIs contrasts, we conducted conjunction and disjunction analyses between the VMI *versus* Control and VMI *versus* Perception contrasts (20 experiments). Results of the conjunction analysis showed activation increases in the left anterior insular cortex and in the bilateral supplementary motor area. Results of the both disjunction analyses showed no significant cluster of activation for the ((VMI > Control) > (VMI > Perception)) contrast. **Figure 7** shows section views of the brain showing region with consistent activation increase in the conjunction analysis between the VMI > Control and VMI > Perception contrasts. No significant activation foci were found from either disjunction analysis. **Table 8** lists for the coordinates of common activation in the conjunction analyses.

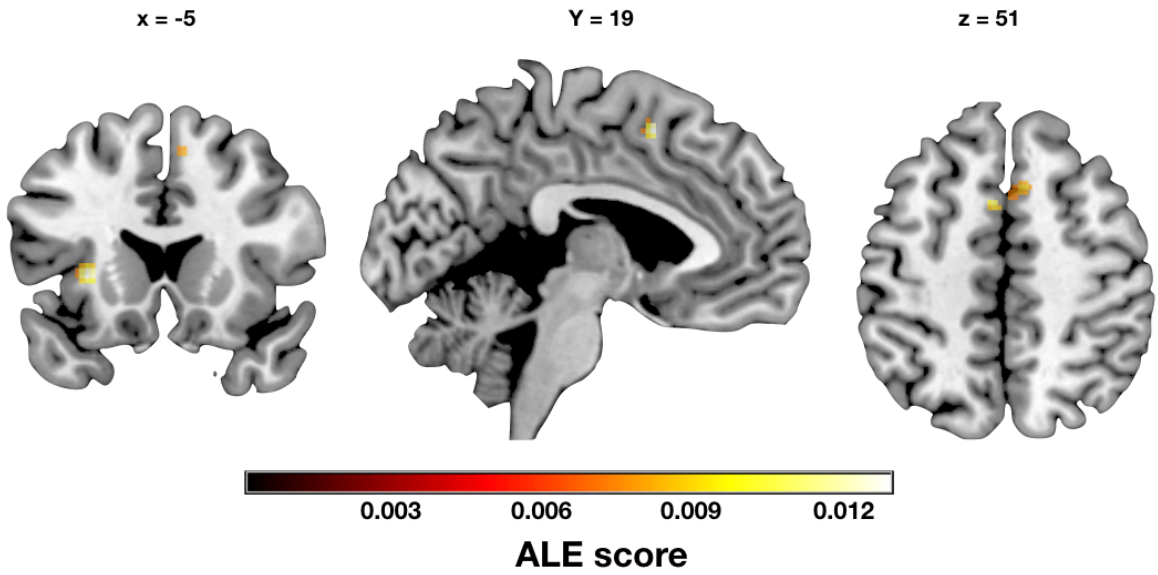

Figure 7. *Brain regions showing consistent increased activation in the left anterior insular cortex and in the bilateral supplementary motor area / anterior cingulate cortex associated with the conjunction analysis between VMI versus Control condition and VMI versus Perception condition. See Table 8 for the coordinates of common activation in the conjunction analysis.*

The meta-analysis of the conjunction between the VMI *versus* Control and MMI *versus* Control contrasts (42 experiments) showed activation increases in the superior frontal gyri and in the supplementary motor area bilaterally. **Figure 8** shows the surface views of brain region showing consistent activation increase in the conjunction and disjunction analyses between the VMI > Control and MMI > Control contrasts. See **Table 9** for the results of the conjunction and disjunction analyses.

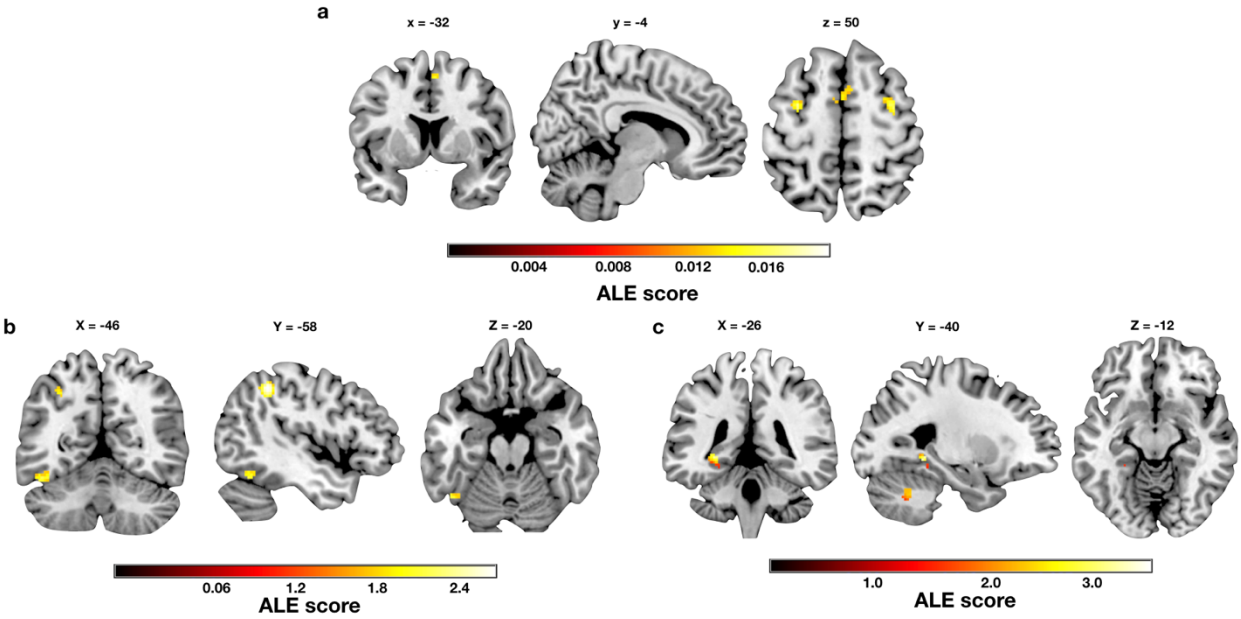

Figure 8. *Results from the conjunction analysis between VMI>Control and MMI > Control contrasts; See Table 9 for the results of the conjunction and disjunction analyses.*

The Spatial Bayesian Latent Factor Regression for the VMI > Control condition

Figure 9 shows the BF values estimated using the spatial Bayesian latent factor regression model for the contrast VMI > Control. Of particular interest for the present study, values in the early visual areas bilaterally were below the lower cut-off of 0.33, indicating the absence of consistent activation associated with VMI across the studies included in this meta-analysis.

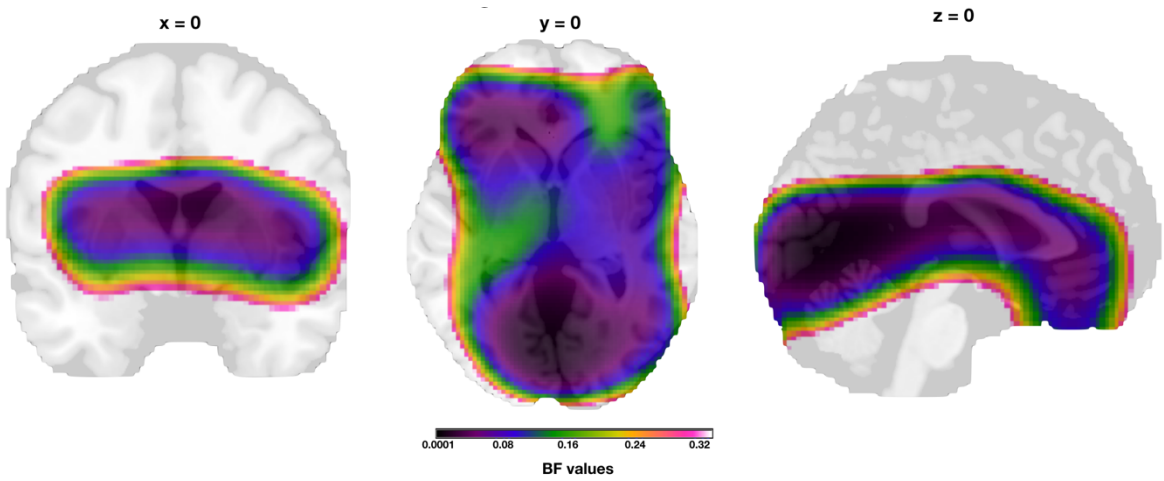

Figure 9. *Results from the Bayes Factor analysis of the VMI > Control condition overlaid over three views of the brain. The area with color shading identifies BF values < 0.33, providing evidence for the absence of activation in that area. The area shaded in white indicates identifies brain regions with BF values above 0.33.*

Discussion

1. Lack of increased activation in primary visual and motor cortices during mental imagery

The dominant model of VMI stipulates a functional and anatomical equivalence between VMI and visual perception [56]. According to this view, VMI and visual perception should rely upon the same cortical areas across the ventral cortical visual stream [18,56]. Progression of visual information would occur in a bottom-up fashion during perception, and in a reversed, top-down direction during VMI. Indeed, results from hemodynamic neuroimaging in healthy volunteers demonstrate the engagement of early, occipital visual areas for VMI in some studies, but not in others. Notably, one study [57] actually showed a relative *decrease* of BOLD signal in occipital cortex during VMI, and the differences between the dynamics associated with visual imagery and perception were shown by two recent studies [12,13]. On the other hand, TMS interference on V1 was shown to impact VMI [21], but this effect might have resulted from modulation of downstream visual areas. The dominant model also provides a principled account of inter-individual differences in VMI, because the level of activation in low-level visual areas seem to correlate with the subjective experience of "vividness" of visual mental images [22]. Recent support to this claim came from the finding that the content of VMI can be decoded from V1 activity [58]. However, in all the decoding studies visual stimuli were presented before asking subjects to imagine them. Thus, one cannot exclude potential effects of "leakage" of perceptually-related activity during the VMI conditions. More generally, even the decoding studies are correlational and not causal in nature; their findings might thus reflect nonfunctional byproducts, instead of the true neural bases of VMI. In addition, a decoding study investigating

face VMI [59] reported that only voxels in the temporal lobe supported above-chance decoding of imagined faces, whereas occipital and frontoparietal regions did not perform above chance. Our Bayesian analysis indicates that we can confidently accept the hypothesis that VMI does not increase BOLD signal in occipital cortex when VMI is compared with control conditions. This result is unlikely to depend on different regions of V1 being implicated in different domains of VMI, because many of the included studies used items such as objects, words and faces, which are preferentially processed in foveal vision. The present evidence, together with the extensive evidence from brain-damaged patients with intact VMI after lesions restricted to the occipital cortex [24], strongly suggests that VMI does not need activity in early visual areas.

We also note that for the motor imagery contrast we found no evidence of involvement of the primary motor cortex (BA4), consistent with previous meta-analytic results [60]. The lack of primary motor cortex activation might have been related to methodological differences in the tasks used in the studies included in the meta-analysis. Due to the topographical organization of BA4 [61,62], different subregions, controlling different parts of the body, are meant to be activated by different tasks (e.g., drawing with the right hand should have activated the hand-portion of M1 in the left hemisphere, while a different region might have been activated for walking). Ultimately, this null effect may also reflect the obvious fact that actual movement execution has to be inhibited in motor mental imagery.

2. *Evidence for left fusiform implication in VMI*

The present demonstration of robust activity in the left fusiform gyrus during VMI is remarkable in view of the wide variety of methods used in the included studies, and because of its striking agreement with the evidence from brain-damaged patients. Impaired VMI in these patients typically occurs after extensive damage to the temporal lobe, and especially in the left hemisphere at least for form and color VMI [23,24,41]. A recently described case report [63] provides additional, converging causal evidence on the role of the left fusiform gyrus in VMI. After a

bilateral stroke in the territory of the posterior cerebral artery, an architect, who before the stroke could easily imagine objects and buildings, spontaneously reported to have become virtually unable to visualize items. He had now to rely on computer-aided design for his work, because he needed to see items that he could previously imagine. The stroke had provoked extensive damage to the right hemisphere, including the occipital pole, the lingual gyrus, the fusiform gyrus and the parahippocampal region. In the left hemisphere, the lesion was smaller and affected only the medial fusiform gyrus and lingual gyrus. The authors compared the location of his lesions with those of other patients with strokes in the same arterial territory, who had spared VMI. The results showed that the patient with impaired VMI had selective damage in the right lingual gyrus and in the left posterior medial fusiform gyrus. The fusiform lesion was located in area FG3 [64], and partially overlapped with the hotspot we found in the present meta-analysis (**Figure 10**). This fusiform region might act as an interface between semantic processing in the anterior temporal lobe [65] and perceptual information coming from the occipital cortex.

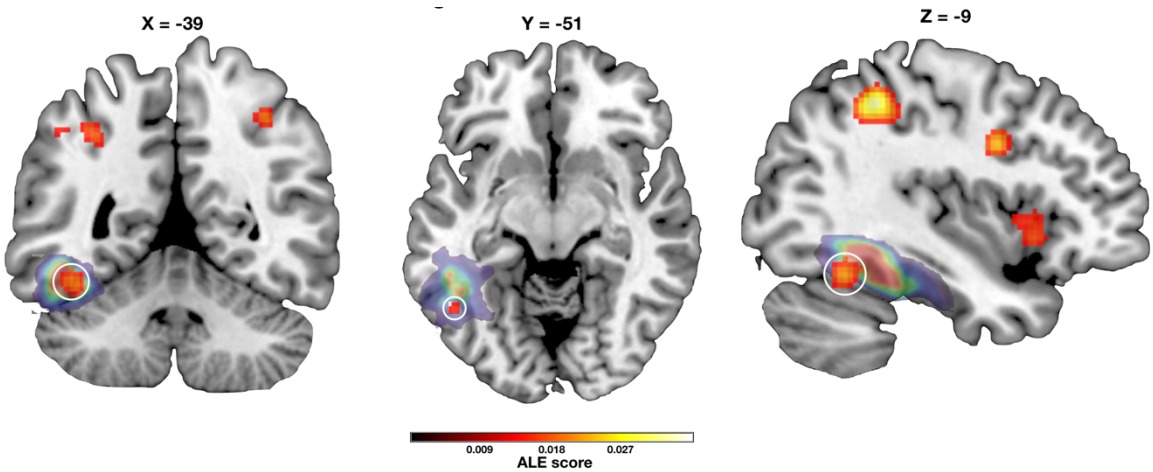

Figure 10. *The FG3 activation found in our meta-analysis (colored in red and circled in white), overlaid to the mask of the probability distribution of the FG3 as shown in the coordinates of Ref.* [64] *(colors ranging from purple to red).*

3. *The role of fronto-parietal networks*

Conjunction analysis between the VMI and the MMI showed the consistent activation of the bilateral superior and middle frontal gyri, extending to the frontal eye fields. This result suggests a possible role for these prefrontal regions in a supramodal function in VMI, a role also observed in the attention literature [66-70]. Alternatively, the role of these areas might be related to eye movements associated with scanning a visual object, whether physically present or imagined [71,72]. In this respect, the increased frontal eye field activation in VMI vs. perception contrast seems consistent with the behavioral evidence that more saccades are produced when imagining a geographical map, than when visually exploring the same map [72]. Another interesting result involving the motor imagery contrast is the observation of the consistent bilateral activation increase in the cerebellum. Although outside the main scope of the current study, this result adds more evidence to the existing literature showing the involvement of the bilateral cerebellum in internally simulated movements [73-76].

In addition to the supramodal fronto-parietal activation, modality-specific activations emerged in the left parahippocampal and fusiform gyri and in the parietal lobe bilaterally for VMI-related contrasts, and in the cerebellum bilaterally, in the left parahippocampal / fusiform gyri, in the anterior cingulate cortex bilaterally, and in the lingual gyrus for motor imagery tasks.

The activation of areas within the fronto-parietal [77-79] and cingulo-opercular [80-83] networks, bilaterally, suggests that mental imagery requires the activation of task-positive neural substrates supporting high-level cognitive functions, including those for attentional control[49,77,84,85] and visual working memory [86,87]. Also, the implication of fronto-parietal networks in VMI is broadly consistent with lesion location in spatial neglect for visual mental images [37], which typically goes far beyond the occipital cortex, and implicates the fronto-parietal networks in the right hemisphere [88-90].

Results from the contrast between VMI and perception showed that the activation of the bilateral cingulo-opercular network (i.e., the anterior cingulate cortex and the anterior insular

cortex) was greater in VMI than in perception. This result should, however, be interpreted with caution, given the low number of studies that fit our inclusion and exclusion criteria for the VMI > Perception contrast (n = 4).

Taken together, the results from this meta-analysis shed further light on the neural correlates of VMI, and suggest a left-hemisphere superiority that is in line with neuropsychological evidence [35,38,41,91]. Functional lateralization is a fundamental organization principle of the brain, and spans across the anatomical and functional realm [92]. Besides adding additional evidence regarding the potential lateralization of VMI, this result can be put in relation to attention processes, another family of functions showing various types of brain lateralization [49,93-99]. Putting together the high degree of similarity between the regions of the brain showing a consistent increase of activation associated with VMI and those associated with visual attention, it is likely that these two functions share a common bilateral neural substrate in the rostral frontal regions; a right hemisphere bias might emerge when directing attention towards external stimuli (as in visual cued tasks) [49], while a left hemisphere bias might arise when directing attention towards internally-generated stimuli [100] (as in the case of mental imagery).

Given the prominent role of fronto-parietal attention networks in attention-mediated conscious processing [101-103] and in neural models of consciousness [104], it is tempting to speculate that individual differences in subjective vividness of visual mental images might in part depend on different degrees of engagement of fronto-parietal networks in VMI, or on their degree of anatomical and functional connectivity with the ventral temporal cortex. For example, vivid re-experiencing of traumatic memories in post-traumatic stress disorder might depend in part on poor prefrontal control on medial temporal lobe activity [17].

4. The Brain Networks of Visual Mental Imagery - a revised model

The present results, together with the evidence from neurological patients, invite a revision of the neural model of VMI (**Figure 11**).

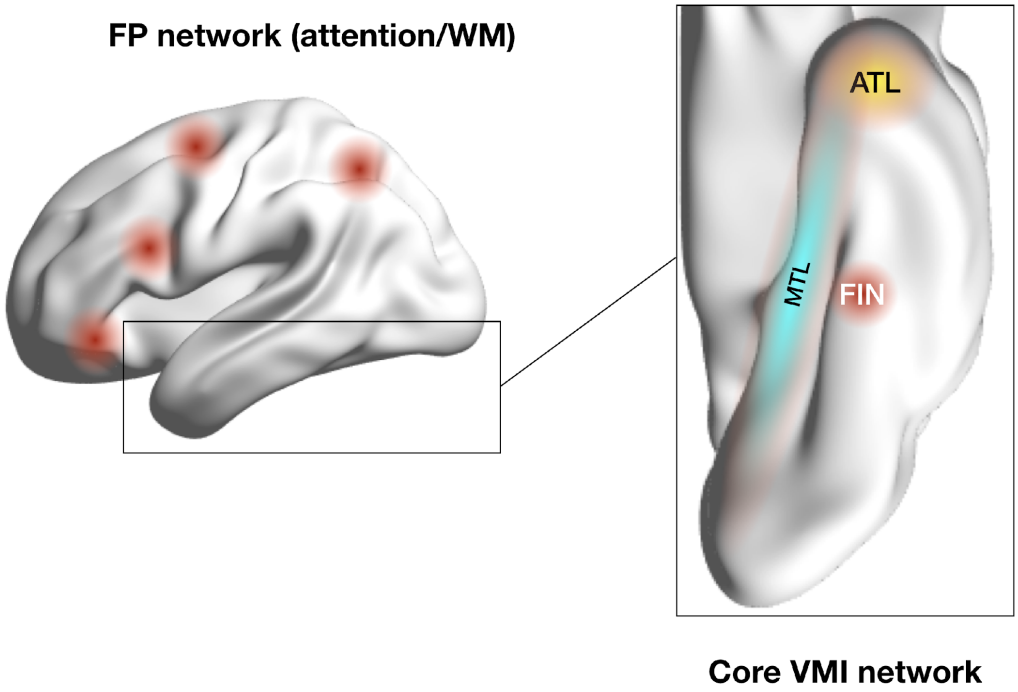

Figure 11. *Schematic depiction of a revised neural model of VMI. FP, fronto-parietal; WM, visual Working Memory; FIN, Fusiform Imagery Node; ATL, Anterior Temporal Lobe; MTL; Medial Temporal Lobe.*

We propose that a core network of VMI builds upon a region in the FG3 area [64] of the left fusiform gyrus, which may be labeled as Fusiform Imagery Node (FIN), in analogy with other domain-preferring regions in the ventral temporal cortex [105]. More anterior regions of the left temporal lobe (ATL) provide the FIN with semantic information [65]. During VMI, prefrontal circuits might engage activity in this core network. The FIN is part of the ventral cortical visual pathway; during perception, it receives visual information from more posterior regions. Medial temporal lobe (MTL) structures may provide a neural substrate for recombining elements of past experiences to generate episodic simulations in VMI [106,107]. MTL structures, together with the posterior cingulate, and perhaps with the fronto-parietal attention networks, may contribute to the phenomenal experience of VMI as "quasi-visual" in nature (sometimes referred to as "vividness" of visual mental images) [7]. The degree of this integration may differ among individuals. Functional disconnection of the MTL components of the network may lead to impaired

phenomenal experience associated with VMI (aphantasia). In these cases, some recovery of visual information (without VMI experience) may still be provided by the ATL-FIN portion of the VMI network. Dysfunction of the ATL-FIN component may lead to VMI deficits, as suggested by the patterns of performance of patients with extensive left temporal damage [24]. A homologue network in the right hemisphere might contribute to aspects of VMI for faces [108]. Activity in the temporal lobe components is initiated, modulated and maintained by fronto-parietal networks subserving attention and working memory. Dysfunction of right hemisphere fronto-parietal networks, coupled with their disconnection from the left FIN [89], but with normal functioning of the left hemisphere portions of the network, may provoke neglect for the left side part of visual mental images, with spared processing of their right side (imaginal or representational neglect) [37,88]. In this case, visual mental images are built by the left hemisphere VMI network, but the attentional impairment resulting from right fronto-parietal dysfunction determines the incomplete exploration or maintenance of the left portion of mental images [89].

5. *Conclusions*

Altogether, the long-standing neuropsychological evidence of the past 30 years, together with more recent neuroimaging evidence analyzed here, invites a reappraisal of the dominant model of visual mental imagery, based on a substantial functional and structural overlap between visual mental imagery and visual perception. The available evidence suggests a different scenario, where prefrontal regions are to initiate the imagination process by recruiting the stored information to-be-recalled from semantic circuits involving the left temporal lobe, together with high-level ventral stream areas of the left fusiform and parahippocampal gyri, and then activates networks important for attention and visual working memory, which maintain the recalled images to perform the task at hand (whether a simple inspection, a rotation, or a judgement). This alternative model seems better equipped to deal with dramatic patterns of double dissociation between perception and imagery abilities in brain-damaged patients. In particular,

the present finding of FIN activity in VMI is strikingly consistent with the observation of imagery deficits occurring not after occipital damage, but after extensive left temporal damage [24,41,63]. Further neuroimaging and neuropsychological research is needed to determine the brain correlates of specific domains of VMI (faces, object form or color, places, orthographic material). Furthermore, a clear description of these fast-occurring dynamics can only be achieved by employing techniques with adequate spatiotemporal resolution (such as magnetoencephalography or intracerebral recordings), to trace feedback and feedforward sweeps of activation in the model we propose.

Authors Contribution

P.B. and A.S. conceived the study. A.S., D.H., and J.L. extracted the coordinates from the source articles. A.S. and D.H. conducted the analysis on Ginger ALE. A.S. and J.L. conducted the Bayesian Analyses. All the authors contributed to the writing of the manuscript. Raw Coordinates included in each of the contrasts, instructions to reproduce the figures, and supplementary videos can be found on the Github page of A.S..

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Tables

Table 1. List of studies (n = 27) showing the first author's name, publication year, manuscript title, contrast used, and number of subjects (n = 340) that were included in the ALE meta-analysis for the contrast Visual Mental Imagery > Control condition. Fixed or Random Effects and Corrected or Uncorrected variables were used as covariates in the Bayesian Analysis. A total of 372 activation foci were included in the analysis for this contrast.

	Name and Year	Manuscript title	Contrast	Category	Table	N	Mean Age ±SD (min:max)	Gender	Handedness	FFX / RFX	Corrected / Uncorrected
1.	Anderson et al. 2019	*Visual imagery during real-time fMRI neurofeedback from occipital and superior parietal cortex*	Visual Imagery vs no imagery	A	4	21	24.15 (19:31)	10M	Unknown	RFX	Corrected
2.	Belardinelli et al. 2009	*An fMRI investigation on image generation in different sensory modalities: The influence of vividness*	Visual imagery vs abstract sentences	A	3	9	25.2 ± 3.7	9F	Right	RFX	Corrected
3.	Boccia et al. 2015	*A Penny for Your Thoughts! Patterns of fMRI Activity Reveal the Content and the Spatial Topography of Visual Mental Images*	Visuospatial mental imagery vs. Rest baseline	A	1	15	24.67 ± 2.16	7F	Right	RFX	Corrected
4.	Boly et al. 2007	*When thoughts become action: An fMRI paradigm to study volitional brain activity in non-communicative brain injured patients*	Face imagery vs. Rest baseline	B	2	12	24 ± 4	12M	Unknown	RFX	Corrected

5.	D'Esposito et al. 1997	*A functional MRI study of mental image generation*	Face imagery vs. Rest baseline	B	1	18-37	7M	Right	FFX	Corrected	
6.	Gardini et al. 2005	*Different neuronal pathways support the generation of general and specific mental images*	Words Imagery vs. No Imagery of pseudo words	A	1	15	25.93 ± 8.87 20:51;	6F	Right	RFX	Corrected
7.	Handy et al. 2004	*Visual imagery and memory: Do retrieval strategies affect what the mind's eye sees?*	Visual imagery vs. Rest epochs	A	1	15	18 ± 29	10F	Right	RFX	Uncorrected
8.	Huijbers et al. 2011	*Imagery and retrieval of auditory and visual information: Neural correlates of successful and unsuccessful performance*	Successful vs. unsuccessful visual mental imagery	A	4	21	22	16F	Right	RFX	Uncorrected
9.	Ishai et al. 2000	*Distributed Neural Systems for the Generation of Visual Images*	Visual Imagery vs no imagery	A/B	4	9	28 ± 5	5F	Right	RFX	Corrected
10.	Kaas et al. 2009	*Imagery of a moving object: The role of occipital cortex and human MT/V5+*	Imagery of visual motion vs. no imagery control (auditory tone)	A	1	12	20:34	8F	Unknown	RFX	Corrected
11.	Kilintari et al. 2016	*Brain activation profiles during kinesthetic and visual imagery: an fMRI study*	Visual imagery vs. Rest	A	4	14	18:41	10F	Right	RFX	Corrected

12.	Kukolja et al. 2006	*Neural mechanisms underlying spatial judgements on seen and imagined visual stimuli in the left and right hemifields in men*	Imagine the Clock angle vs. catch trials	A	3(D)	20	24.5 ± 3.2 21:32	20M	Right	RFX	Corrected
13.	Lambert et al. 2002	*Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement — an fMRI study*	Visual Imagery of animals vs. 20 abstract words not conducive to MI	A	2	6	24±3.5; 19 :25	4F	Right	RFX	Corrected
14.	Logie et al. 2011	*Low and high imagers activate networks differentially in mental rotation*	Mental rotation of 3D abstract object vs. 0° identical objects and 0° mirror images	A	1	21	20:35	14F	Right	RFX	Corrected
15.	Mazard et al. 2005	*Neural impact of the semantic content of visual mental images and visual percepts*	Imagery of objects vs. listening to letters or numbers	A	1	15	18:27	4F	Right	FFX	Corrected
16.	Pyke et al. 2017	*When math operations have visuospatial meanings versus purely symbolic definitions: Which solving stages and brain regions are affected?*	Visuospatial mental solving of math problems vs. purely symbolic solving	A	1	40	23.6 ± 4.9	36F	Right	FFX	Uncorrected

17.	Sack et al. 2002	*Tracking the Mind's Image in the Brain II: Transcranial Magnetic Stimulation Reveals Parietal Asymmetry in Visuospatial Imagery*	Imagine the Clock angle vs. Baseline	A	1,2	6	27.8 ± 5.7	3F	Right	FFX	Corrected
18.	Sasaoka et al. 2013	*Dynamic Parieto-premotor Network for Mental Image Transformation Revealed by Simultaneous EEG*	Imagine the Clock angle vs. Baseline	A	1	23	Unknown	23M	Right	RFX	Corrected
19.	Seurinck et al. 2011	*Mental Rotation Meets the Motion Aftereffect: The Role of hV5/MT+ in Visual Mental Imagery*	Perform mental rotation vs. Baseline	A	1	16	24 ± 2.0; 21:28	16M	Right	RFX	Corrected
20.	Slotnick et al. 2005	*Visual Mental Imagery Induces Retinotopically Organized Activation of Early Visual Areas*	Perform mental rotation vs. Baseline	A	1	6	21 ± 1.1	3F	Unknown	FFX	Corrected
21.	Slotnick et al. 2011	*Visual memory and visual mental imagery recruit common control and sensory regions of the brain*	Visual Imagery vs. abstract words not conducive to MI	A	1	12	18.6 :22.2	8F	Unknown	RFX	Corrected
22.	Soddu et al. 2009	*Reaching across the abyss: recent advances in functional magnetic resonance imaging and their potential relevance to disorders of consciousness*	Visual imagery versus eyes-closed. resting state	A/B	1	8	Unknown	Unknown	Unknown	RFX	Corrected

23.	Thompson-Schill et al, 1999	*A neural basis for category and modality specificity of semantic knowledge*	Visual semantic imagery vs. nonsense auditory stimuli	C	1	5	Unknown	1F	Unknown	FFX	Corrected
24.	Trojano et al. 2000	*Matching Two Imagined Clocks: the Functional Anatomy of Spatial Analysis in the Absence of Visual Stimulation*	Imagery of clock angle vs Baseline	A	2	4	27; 23:32	2F	Right	RFX	Uncorrected
25.	Yomogida et al., 2004	*Mental Visual Synthesis is Originated in the Fronto-temporal Network of the Left Hemisphere*	Visual mental imagery vs. Baseline condition	A	1	23	18:31	Unknown	Unknown	FFX	Corrected
26.	Zeman et al. 2010	*Loss of imagery phenomenology with intact visuo-spatial task performance: A case of 'blind imagination'*	Imagery of faces vs. nonsense letter string control	B	4	10	63.4; 55:76	Males	Right	RFX	Corrected
27.	Zvyangintsev et al. 2013	*Brain networks underlying mental imagery of auditory and visual information*	Visual imagery vs baseline (counting backward)	A	2	15	25.1 ± 5.7	7F	Right	RFX	Corrected

Category: A = Object Form; B = Faces; C = Orthographic Material.

Table 2. List of studies (n = 4) showing the first author's name, publication year, manuscript title, contrast used, and number of subjects (n = 52) that were included in the ALE meta-analysis for the contrast Visual Mental Imagery > Perception condition. Fixed or Random Effects and Corrected or Uncorrected variables were used as covariates in the Bayesian Analysis. A total of 62 activation foci were included in the analysis for this contrast.

	Name and Year	Manuscript title	Contrast	Table	N	Mean Age ±SD (min:max)	Gender	Handedness	FFX / RFX	Corrected / Uncorrected
1.	Arzy et al. 2009	*Subjective mental time: the functional architecture of projecting the self to past and future*	Mental time imagery - self projection in different time points and events vs. Face discrimination	1	12	33.7 ± 4.2 (29:38)	5F	Right	FFX	Corrected
2.	Daselaar et al. 2010	*Modality-specific and modality-independent components of the human imagery system*	Visual Imagery vs. Visual Perception	2	16	21	10F	Right	RFX	Uncorrected
3.	Kukolia et al. 2006	*Neural mechanisms underlying spatial judgements on seen and imagined visual stimuli in the left and right hemifields in men*	Visual Imagery vs. Visual Perception	3	20	24.5 ± 3.2 (21:32)	20M	Right	RFX	Corrected
4.	Trojano et al. 2000	*Matching Two Imagined Clocks: the Functional Anatomy of Spatial Analysis in the Absence of Visual Stimulation*	Visual imagery vs. spatial matching of visually presented clocks	3	4	27; (23:32)	2F	Right	FFX	Uncorrected

Table 3. List of studies (n = 16) showing the first author's name, publication year, manuscript title, stimuli used, and number of subjects (n = 282) that were included in the ALE meta-analysis for the contrast Motor Mental Imagery > Control condition. Fixed or Random Effects and Corrected or Uncorrected variables were used in the Bayesian Analysis. A total of 346 activation foci were included in the analysis for this contrast.

	Name and Year	Manuscript title	Stimuli used	Table	N	Mean Age ±SD (min:max)	Gender	Handedness	FFX / RFX	Corrected / Uncorrected
1.	Boly et al. 2007	*When thoughts become action: An fMRI paradigm to study volitional brain activity in non-communicative brain injured patients*	Playing tennis imagery vs. Rest; Spatial navigation imagery vs. Rest	2	12	24 ± 4	12M	Unknown	RFX	Corrected
2.	Cremers et al. 2012	*Hemispheric Specialization During Mental Imagery of Brisk Walking*	Brisk walking imagery vs. Standing; Brisk walking imagery vs. Lying	1, 2	18	22.9 ± 2.5	7F	Right	RFX	Corrected
3.	Fernandez-Espejo et al. 2014	*The Clinical Utility of fMRI for Identifying Covert Awareness in the Vegetative State: A Comparison of Sensitivity between 3T and 1.5T*	Imagery of playing tennis vs. Rest; Spatial navigation imagery vs. Rest	2,4	15	23 ± 3	6F	Right	RFX	Corrected
4.	Harrington et al 2009	*The neural basis for simulated drawing and the semantic implications*	Imagery of drawing familiar and non familiar objects vs. Rest	1	8	32.8 (20–52)	7F	Right	FFX	Corrected

5.	Jahn et al. 2008	*Imaging human supraspinal locomotor centers in brainstem and cerebellum*	Imagine body movement: lying (rest condition), standing, walking and running	1,2,3	26	33.7; (21– 61)	12F	Right	FFX	Corrected
6.	Jahn et al. 2008	*Supraspinal locomotor control in quadrupeds and humans*	Imagery of running vs. Lying; Imagery of standing vs. Lying; Imagery of walking vs. Lying;	1	38	Unknown	Unknown	Unknown	FFX	Corrected
7.	Jancke et al. 2001	*The Role of the Inferior Parietal Cortex in Linking the Tactile Perception and Manual Construction of Object Shapes*	Motor imagery vs. actual squeezing; Motor imagery vs. actual modeling	2,3	12	36	2F	Right	FFX	Corrected
8.	Kilintari et al. 2016	*Brain activation profiles during kinesthetic and visual imagery: an fMRI study*	Kinesthetic mental imagery vs. Rest	3	14	(18 – 41)	10F	Right	RFX	Corrected
9.	La Fougèere et al. 2010	*Real versus imagined locomotion: A [18F]-FDG PET-fMRI comparison*	Imagery of walking vs. Imagery of lying	2	16	61.3 ± 7.8; (51-73)	7F	Right	RFX	Corrected
10.	Piefke et al. 2009	*Neurofunctional Modulation of Brain Regions by Distinct Forms of Motor Cognition and Movement Features*	Motor imagery vs. Observation of movements	5	12	25.18 ± 4.25	14M	Right	RFX	Corrected
11.	Sauvage et al. 2011	*Reevaluating brain networks activated during mental imagery of*	Motor Imagery vs. Rest	2	8	24.4 ± 4	2F	Right	RFX	Corrected

		finger movements using probabilistic Tensorial Independent Component Analysis (TICA)								
12.	Soddu et al. 2009	*Reaching across the abyss: recent advances in functional magnetic resonance imaging and their potential relevance to disorders of consciousness*	Motor Imagery vs. Rest	1	14	Unknown	Unknown	Unknown	RFX	Corrected
13.	Wagner et al. 2008	*Mind the bend: cerebral activations associated with mental imagery of walking along a curved path*	Motor Imagery vs. Imagery of Standing	1,2,3,4, 5	12	33.5 (21– 51)	7F	Right	RFX	Corrected
14.	Whittingstall et al. 2013	*Structural network underlying visuospatial imagery in humans*	Motor Imagery vs. Count Backwards	1	18	(20-28)	3F	Right	FFX	Uncorrected
15.	Zu Eulenburg et al. 2013	*On the recall of vestibular sensations*	Motor Imagery vs. Rest	1	16	26.3 ± 3	8F	Right	RFX	Corrected

Table 4. Brain regions showed consistent increased activation across all the mental imagery domains (46 studies, 787 foci, 671 subjects).

Region	L/R	BA	x	y	z	Z	K
Supp. Motor Area	L	6	-4	-2	64	0.05	1020
Precentral Gyrus[a]	R	6	30	-4	54	0.04	463
Insular Cortex	L	47	-30	22	4	0.04	336
Precentral Gyrus[a]	L	6	-28	-4	56	0.04	511
Inferior Parietal Lobe	L	40	-38	-42	46	0.04	503
Insular Cortex	R	47	34	22	2	0.03	357
Inferior Parietal Lobe	R	40	40	-42	48	0.03	297
Middle Occipital Gyrus	L	19	-26	-76	38	0.03	741
Cerebellum Crus1	L	0	-32	-60	-36	0.03	189
Precentral Gyrus	L	6	-52	6	36	0.03	436
Precuneus	R	7	16	-68	50	0.03	114
Calcarine Sulcus	L	17	-12	-56	10	0.03	266
Fusiform Gyrus	L	37	-46	-58	-14	0.02	149
ParaHippocampal Gyrus	L	37	-32	-44	-4	0.02	161

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] comprises the Frontal Eye Fields.

Table 5. Brain regions showed consistent increased activation in the VMI *versus* Control condition (27 studies, 376 foci, 380 subjects).

Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Precentral Gyrus	R	6	30	-4	54	0.03	270
Inferior Parietal Lobe	L	40	-40	-44	46	0.03	910
Superior Parietal Lobe	L	7	-16	-64	52	0.02	
Middle Occipital Gyrus	L	19	-28	-74	30	0.02	
Supp. Motor Area	R	32	8	14	50	0.03	273
Precentral Gyrus	L	6	-26	-2	60	0.02	308
Precentral Gyrus	L	44	-52	10	38	0.02	270
Insular Cortex	L	47	-36	18	-2	0.02	238
Fusiform Gyrus	L	37	-42	-54	-18	0.02	166
Inferior Parietal Lobe	R	40	40	-42	48	0.02	310
Angular Gyrus	R	7	32	-66	48	0.02	

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] comprises the Frontal Eye Fields.

Table 6. Brain regions showed consistent increased activation in the VMI *versus* Perception condition (4 studies, 62 foci, 52 subjects).

Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Insular Cortex	R	47	34	22	0	0.01	76
Insular Cortex	L	48	-30	18	2	0.01	68
Supp. Motor Area[a]	L	6	-4	10	52	0.01	88

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] This cluster extended bilaterally.

Table 7. Brain regions showed consistent increased activation in the MMI *versus* Control condition contrast (15 studies, 340 foci, 239 subjects).

Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Supp. Motor Area	L	6	-2	-2	66	0.04	604
Cerebellum	L	0	-32	-58	-32	0.03	181
Cerebellum	R	0	32	-62	-30	0.03	135
Precentral Gyrus	L	6	-36	-4	56	0.02	123
ParaHippocampal Gyrus	L	37	-32	-44	-4	0.02	100
Calcarine Sulcus	L	17	-16	-52	12	0.02	143
Middle Frontal Gyrus	R	6	32	0	60	0.02	167

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] comprises the Frontal Eye Fields.

Table 8. Brain regions showed consistent increased activation in the conjunction and disjunction analyses between VMI > Control condition (27 studies, 376 foci, 380 subjects) and VMI > Perception condition (4 studies, 62 foci, 52 subjects).

Conjunction (VMI > Control) and (VMI > Perception)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Anterior Insular Cortex	L	48	-30	18	2	0.0156	248
Supp. Motor Area[a]	L	6	-4	10	52	0.01	51
Disjunction (VMI > Control) > (VMI > Perception)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
No cluster found							
Disjunction (VMI > Perception) > (VMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
No cluster found							

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] extending bilaterally.

Table 9. Brain regions showed consistent increased activation in the conjunction and disjunction analyses between VMI > Control condition (27 studies, 376 foci, 380 subjects) and MMI > Control condition (15 studies, 340 foci, 242 subjects).

Conjunction (VMI > Control) and (MMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Precentral Gyrus	L	6	-32	-4	50	3.00	54
Precentral Gyrus	R	6	34	-8	52	2	56
Supp. Motor Area [a]	L	6	-8	0	64	0.02	79
Disjunction (VMI > Control) > (MMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Fusiform Gyrus	L	37	-46	-58	-20	3.00	60
Superior Occipital Lobe	R	7	28	-78	44	2.00	61
Inferior Parietal Lobe	L	40	-50	-46	40	1.00	110
Disjunction (MMI > Control) > (VMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Suppl. Motor Area	L	6	-10	-8	70	13.00	450
Suppl. Motor Area	R	6	8	2	52	1.00	
Precentral Gyrus	L	6	-36	-6	48	6.00	52
Cerebellum Crus1	R	0	30	-64	-36	5.00	104
Fusiform Gyrus	L	37	-26	-40	-12	4.00	106
Cerebellum Crus1	L	0	-32	-58	-38	3.00	151
Lingual Gyrus	L	18	-14	-56	4	2.00	157

Note: x, y, z: coordinates of the corresponding peak in MNI space, in units of millimeter. Abbreviations: ALE, activation likelihood; BA, Brodmann area; K, cluster size in number of voxels; L, left; R, right. [a] extending bilaterally.

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