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

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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. 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 52 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 bilaterally, as well as of the left fusiform gyrus. Results from the VMI *versus* Perception contrast showed the association between VMI and activation increase of areas lateralized to the left hemisphere, including the superior and inferior frontal gyri, as well as the fusiform gyrus. Conjunction analyses between the VMI *versus* Control and the VMI Mental Imagery *versus* Perception contrasts showed the activation of the left anterior insular cortex. Results from the Motor Mental Imagery *versus* Control contrast showed that mental motor imagery increases the activation of the cerebellum bilaterally, of the precentral gyrus bilaterally, of the left supplementary motor area, and of the left fusiform sulcus. Conjunction analyses between the

VMI *versus* Control and the Motor Mental Imagery *versus* Control contrasts showed the activation of the right superior frontal gyrus. 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 evidence from brain-damaged patients. Our evidence suggests a revision of the VMI model. A Fusiform Imagery Node 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, in connection with the medial temporal lobe, important for a vivid VMI episodic experience. 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 of patients with brain damage.

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

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].

The dominant model of VMI [3] proposes common neural substrates underlying VMI and visual perception, spanning across the ventral cortical visual stream. Neuroimaging studies in healthy volunteers supported this model by demonstrating the engagement of early, occipital visual areas in VMI [17,18]. Further, TMS interference on V1 was shown to impact VMI [19]. 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 [5,20] (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 [21-23]. Whereas the model would predict a systematic co-occurrence of perceptual and imaginal deficits after brain damage [24], patients with brain damage restricted to the occipital cortex often have spared VMI abilities [25-28], with spared subjective VMI

vividness despite damaged early visual cortex [29], even in the case of bilateral cortical blindness [25,30,31]. Instead, deficits of VMI for object form, object color, faces or orthographic material typically arise as a consequence of more anterior damage [24,32-38], often extensively including the temporal lobes, especially in the left hemisphere [21,22,39]. Such a strong evidence of dissociation is at odds with models proposing an overlap between perception and imagery and suggests an engagement in VMI of higher-order associative areas, especially in the left hemisphere, rather than early visual cortex. Also, accumulating evidence shows that the temporal dynamics of VMI and perception are different [12,40-42]. 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 [43]. Also this evidence suggests that VMI and visual perception rely on (at least partially) different brain mechanisms. However, the precise identity of these mechanisms, and of the underlying brain networks, remains unknown. 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 [40,44,45]. This evidence suggested that what VMI shares with visual perception is not the passive, low-level perceptual aspect, but the active, exploratory aspects of vision [22,23,46], such as those sustained by visual attention [47].

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. As a control for modality-specific *versus* 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) [48]. 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) non-first hand empirical studies such as review articles (excluded n = 7); (2) 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); (3) single-subject studies (excluded n = 2); (4) studies that could not be clearly classified into one of our three subdomains, or reporting contrasts not of interest for this study (n = 15); (5) studies not using fMRI (e.g., voxel based morphometry studies or DTI studies; n = 14); (6) studies using analytic approaches not of interest for this study (e.g., ROI analyses, multivariate pattern analysis, functional or effective connectivity analysis)(n = 14). The resulting final number of studies included in the meta-analysis was 44.

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. 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, eight of the 44 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 52. Specifically, we found (1) 23 experiments (325 foci from a total of 303 subjects) reporting contrasts regarding the difference in activation between VMI and rest or control condition; (2) 13 experiments (92 foci from a total of 149 subject) reporting contrasts regarding the difference in activation between visual mental imagery and perception, and (3) 16 experiments (353 foci from a total of 279 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.

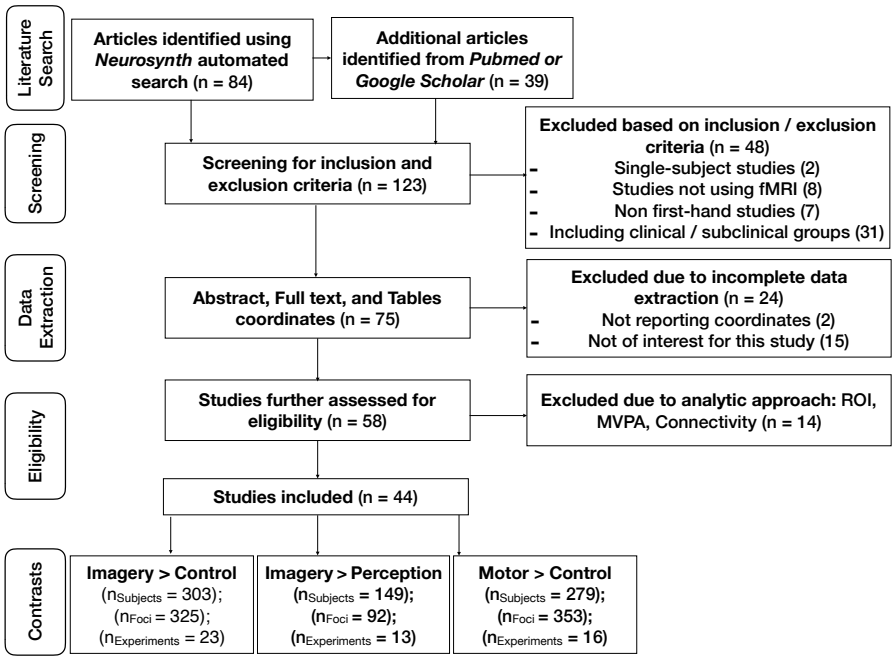

Figure 1. Flow chart of the selection process conducted in the present meta-analysis showing the following steps: 1) identification of studies through literature searches (studies repeated in the two searches were included only once); 2) screening for inclusion and exclusion criteria; 3) assessment for 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); 6) attribution of the included studies to one or more contrasts (i.e., some of the studies reported coordinates contrasts that could be included in more than one contrasts). **Figure 2** shows the published activation foci from the included studies projected onto an inflated cortical surface for the contrast of a) MI *vs* all, b) VMI > Control, c) VMI > Perception, d) MMI > Control. See the supplementary video for a dynamical representation of the foci included in the VMI > Control analysis.

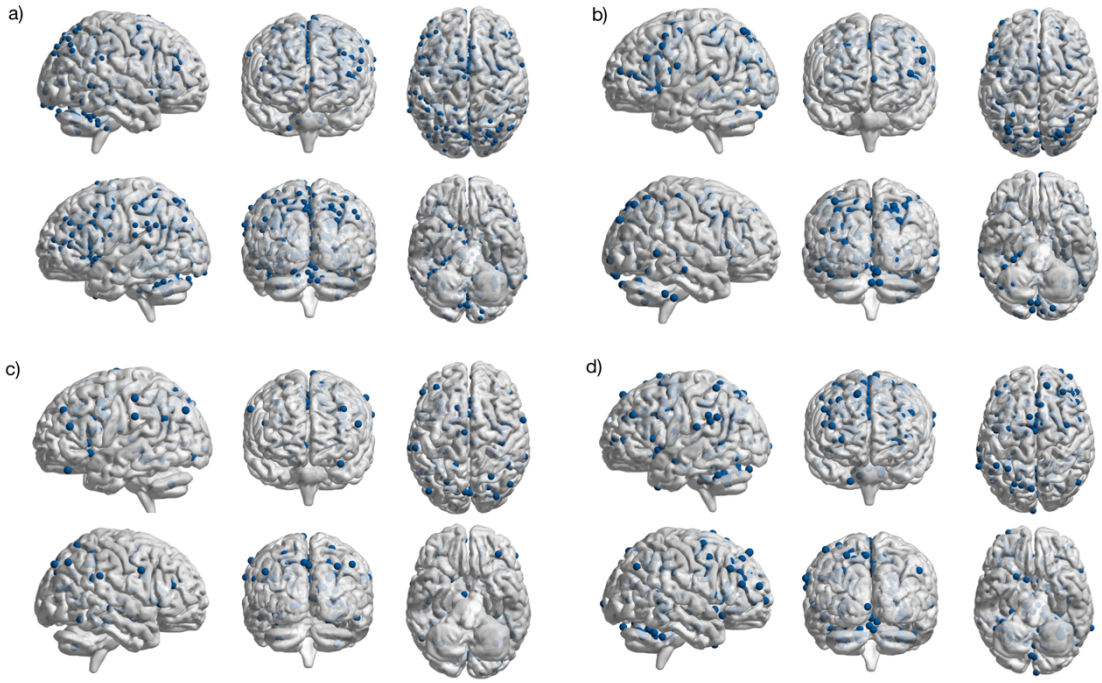

Figure 2. Activation foci reported in the studies included in the present meta-analysis for the contrasts a) mental imagery vs all, b) VMI > Control, c) VMI > Perception, d) MMI > Control.

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 [49-51]. 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 [49]. **Tables 1, 2,** and **3** report author names, publication year, type of stimuli used in the study, 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 [49,50]. 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 $p < .01$ 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 test whether the contribution of V1 / V2 is necessary 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 a focus, $\mathrm{p(v)}$, is modeled via a doubly stochastic Poisson process [52]. The study-specific log intensity function is characterized as a linear combination of a high-dimensional basis set. To test the activation degree of each voxel, the null hypothesis ($\mathrm{H_0}$) stated that the voxel was specifically activated as a focus during VMI vs Control condition. We took the posterior probability $\mathrm{p(v)}$ as the probability of null hypotheses for each voxel. The alternative hypothesis ($\mathrm{H_1}$) 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. [52] for additional details about the method and a general discussion of the properties of this model). We defined Bayes Factors [53] for accepting and rejecting the null hypothesis. To compute the odds hypothesis conditionally on observed data: $\text{Bayes Factors} = \mathrm{Pr(H0|data)}/\mathrm{Pr(H1|data)}$. 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 23 studies on VMI > Control condition for a total of 325 foci (see **Table 2** 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 $2mm^3$ 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 2,500 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 52 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 cingulo-opercular network (including the bilateral anterior cingulate and anterior insular cortices). In addition, unilateral activation increases consistent across the studies were found in the left middle and inferior frontal gyrus, in the left precuneus and the anterior portion of the calcarine sulcus, in the left parahippocampal / fusiform 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.

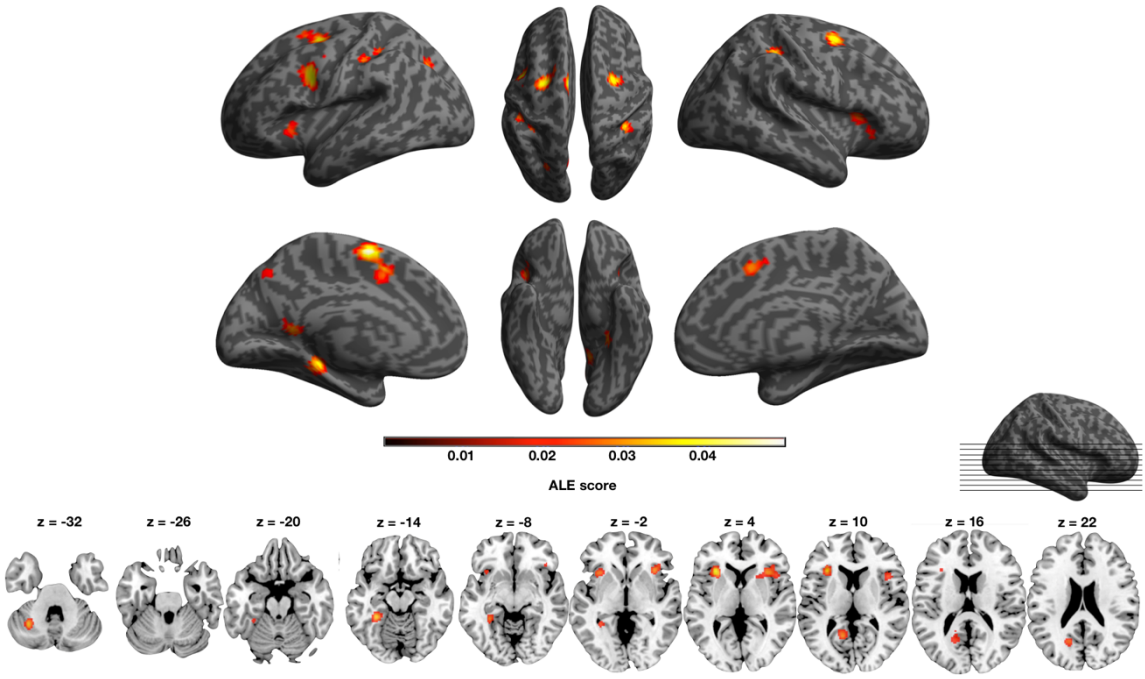

Figure 3. *Brain regions showing consistent increased activation associated with mental imagery (across all the domains of VMI > Control, VMI > Perception, and MMI > Control).*

The meta-analysis of the 23 experiments included in the VMI *vs* Control condition showed activation increases in bilateral superior frontal gyri, bilateral inferior parietal cortex, bilateral anterior insular cortex, and in regions lateralized to the left hemisphere, including the middle occipital gyrus (BA19), cerebellum, inferior parietal lobe, the superior occipital lobe, and the fusiform gyrus. **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.

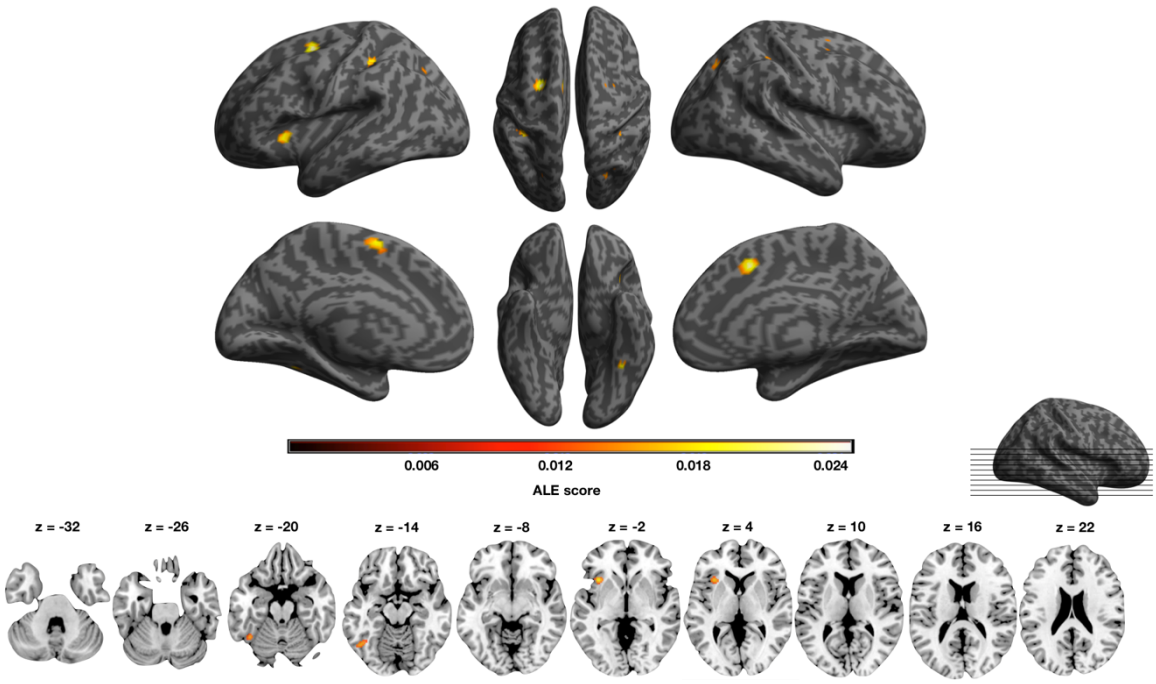

Figure 4. *Brain regions showing consistent increased activation associated with the contrast VMI > Control condition.*

The meta-analysis of the 13 experiments included in the VMI *vs* Perception condition showed the activation increase in regions lateralized to the left hemisphere, including the middle and inferior frontal gyrus and the fusiform gyrus. **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 VMI *vs* Perception condition.

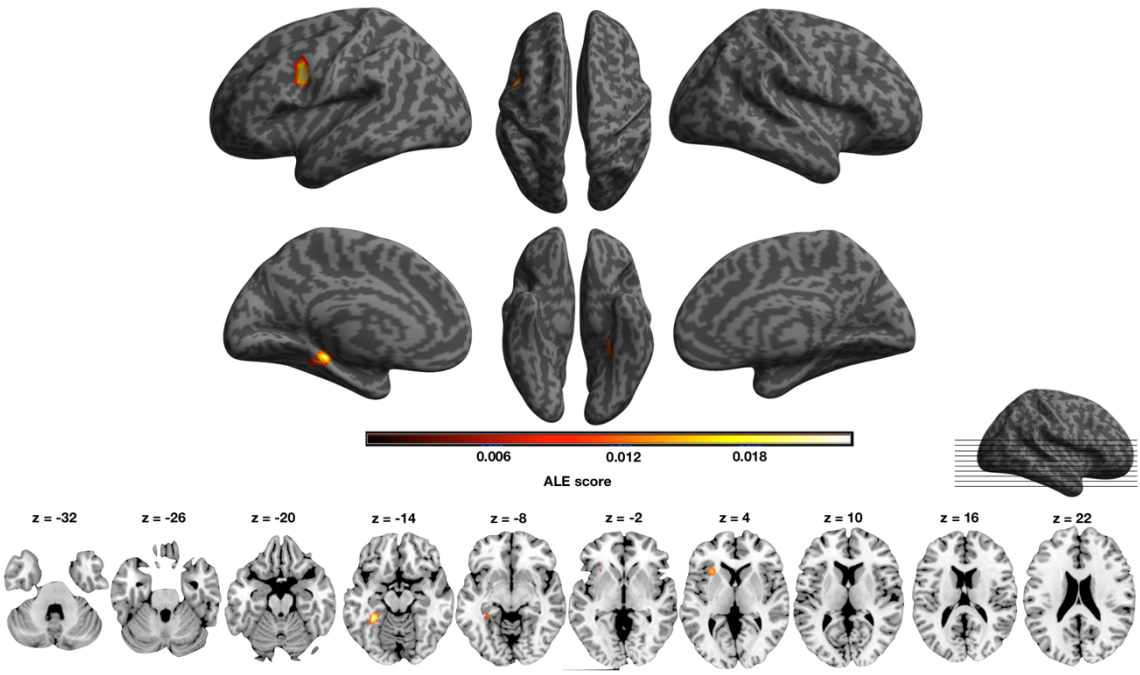

Figure 5. *Brain regions showing consistent increased activation associated with the contrast VMI > Perception condition.*

The meta-analysis of the 16 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.

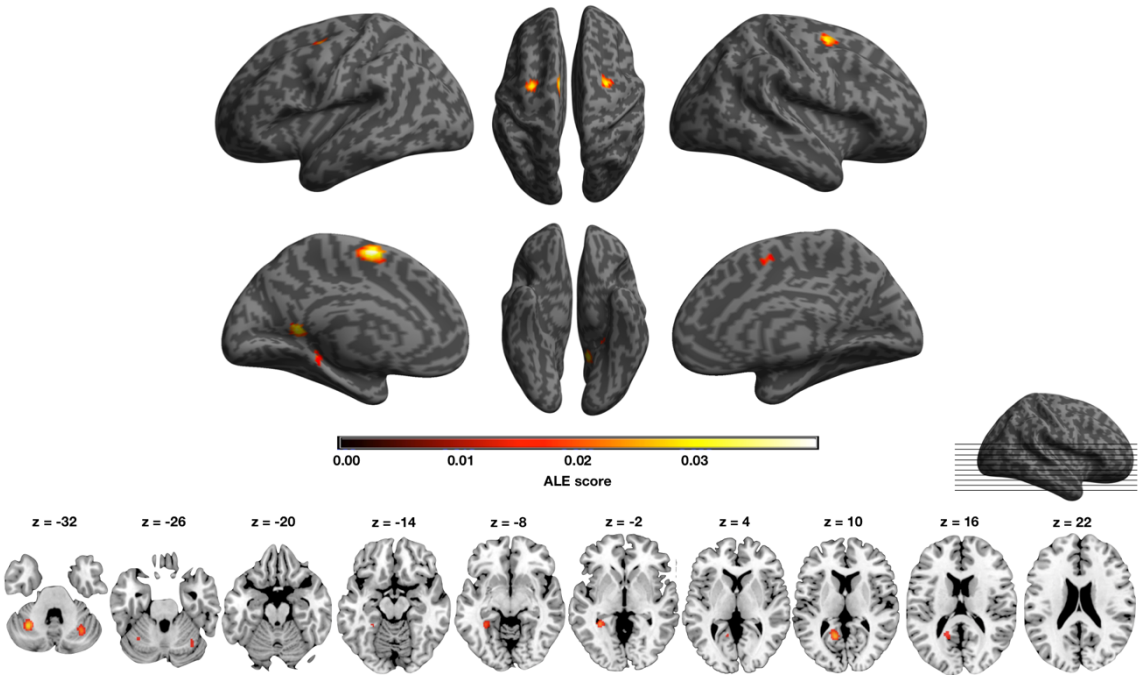

Figure 6. *Brain regions showing consistent increased activation associated with the contrast MMI > Control condition.*

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 (36 experiments). Results of the conjunction analysis showed activation increases in the left anterior insular cortex. Results of the disjunction analyses showed no significant cluster of activation for the ((VMI > Control) > (VMI > Perception)) contrast, and activation increases in the left precentral gyrus and in the left fusiform gyrus for the ((VMI > Perception) > (VMI > Control)) contrast. **Figure 7** shows the surface views of brain region showing consistent activation increase in the conjunction analysis between the VMI > Control and VMI > Perception contrasts. See **Table 8** for the coordinates of common activation in the conjunction and disjunction analyses.

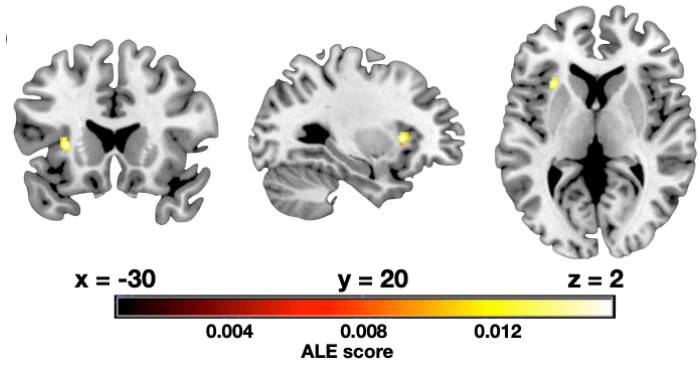

Figure 7. *Brain regions showing consistent increased activation in the left anterior insular cortex associated with the conjunction analysis between VMI versus Control condition and VMI versus Perception condition. See Table 8 for the coordinates of common activation in the conjunction and disjunction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

The meta-analysis of the conjunction between the VMI *versus* Control and MMI *versus* Control contrasts (23 experiments) showed activation increases in the superior frontal gyri, bilaterally and in the left supplementary motor area. **Figure 8** shows the surface views of brain region showing consistent activation increase in the conjunction analysis between the VMI > Control and MMI > Control contrasts. See **Table 9** for the coordinates of common activation in the conjunction and disjunction analyses.

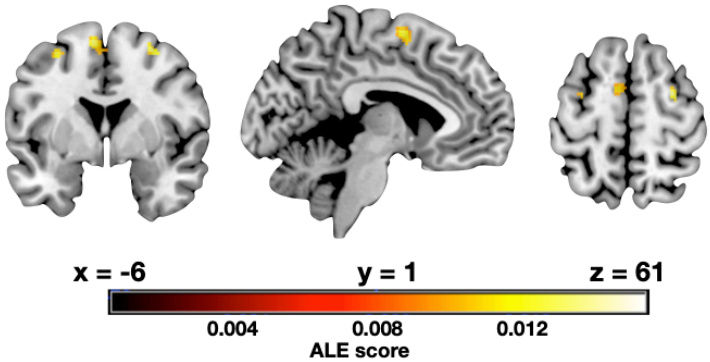

Figure 8. *Brain regions showing consistent increased activation in the bilateral superior frontal gyrus and in the left supplementary motor area associated with the conjunction analysis between VMI versus Control condition and MMI versus Control condition. See Table 9 for the coordinates of common activation in 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. Values in both the inferior and middle temporal gyri were above the lower cut-off of 0.33; BF values across the whole occipital cortex where instead below 0.33, which allows to accept the alternative hypothesis of an absence of early visual activation associated with VMI.

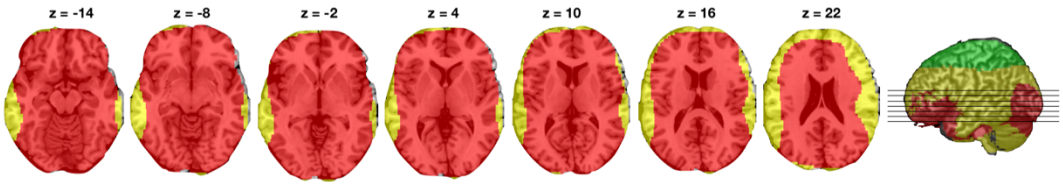

Figure 9. *Sections of the brain showing results from the Bayes Factor analysis of the VMI > Control condition overlaid over the surface. The area covered in red shows BF values below 0.33, indicating the absence of activation for visual mental imagery compared to control condition. The area covered in yellow shows BF values between 0.33 and 3, indicating no evidence for either the null or the alternative hypothesis (values covering the inferior temporal gyrus were BF > 1, and thus supported the hypothesis of VMI-related activation). The area covered in green shows BF values above 3, indicating substantial evidence for VMI-related activation.*

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 [54]. According to this view, VMI and visual perception should rely upon the same cortical areas across the ventral cortical visual stream. 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 [55] actually showed a relative *decrease* of BOLD signal in occipital cortex during VMI. On the other hand, TMS interference on V1 was shown to impact VMI [19], 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 [20]. Recent support to this claim came from the finding that the content of VMI can be decoded from V1 activity [56]. 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. Furthermore, another decoding study [57] found that only the temporal voxel selection supported above-chance decoding of VMI for faces. 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 rest conditions. This result, together with the extensive evidence from brain-damaged patients with intact VMI after lesions restricted to the occipital cortex [22], 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 [58]. 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 [59,60], 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 in striking agreement with the evidence from brain-damaged patients. Impaired VMI in these patients typically occurs after extensive damage to the temporal lobe, especially in the left hemisphere for object form and color VMI [21,22,39]. A recently described case report [61] 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 patients 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 [62], and partially overlapped with the hotspot we found in the present meta-analysis (**Figure 10**). This region, which was more active in VMI than in visual perception, might act as an interface between semantic processing in the left temporal lobe and perceptual information coming from the occipital cortex.

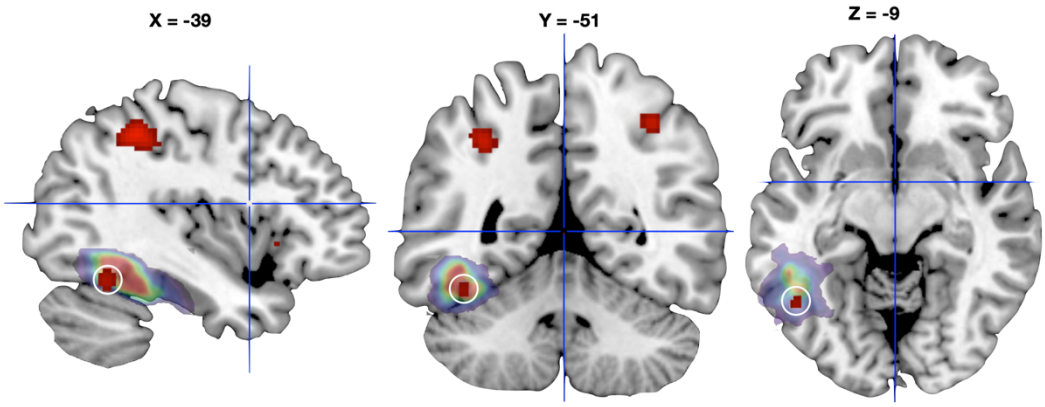

Figure 10. *The FG3 activation found in our meta-analysis (circled in white), and an overlapping mask of the probability distribution of the FG3 as shown in Ref.* [62] *(colors ranging from purple to red).*

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 observed also in the attentional literature [63-67]. Alternatively, the role of these areas might be related to eye movements associated with scanning a visual object, whether physically present or imagined [68,69]. 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 [69]. Another interesting result involving the motor imagery contrast is the observation of the consistent activation increase in the bilateral cerebellum for the motor imagery condition. 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 [70-73].

The consistent activation increases of fronto-parietal regions, especially lateralized to the left hemisphere, was associated with a variety of mental imagery tasks, and appeared to be

supramodal (irrespectively of whether visual or motor)[66,67]. In addition, modality-specific activation was also found in the left parahippocampal and fusiform gyri for VMI-related contrasts, and in the cerebellum bilaterally for motor imagery tasks.

The activation of areas within the fronto-parietal [74-76] and cingulo-opercular [77-80] networks, bilaterally, suggests that mental imagery requires the activation of task-positive neural substrates supporting high-level cognitive functions, including those for attentional control[47,74,81,82] and visual working memory [83,84]. Also, the implication of fronto-parietal networks in VMI is broadly consistent with lesion location in spatial neglect for visual mental images [35], which typically goes far beyond the occipital cortex, and implicates the fronto-parietal networks in the right hemisphere [85-87].

Results from the contrast between visual mental imagery and perception further shed light on the neural correlates of this function, pointing at a left-hemisphere superiority that is in line with neuropsychological evidence [33,36,39,88]. Specifically, the middle frontal gyrus (part of the fronto-parietal networks), the anterior insular cortex (part of the cingulo-opercular network), and the high-level visual component of the fusiform gyrus of the left hemisphere were consistently activated in the VMI vs Perception contrast. Functional lateralization is a fundamental organization principle of the brain, and spans across the anatomical and functional realm [89]. Besides adding additional evidence regarding the lateralization of VMI, this result can be put in relation to attention processes, another family of functions showing various types of brain lateralization [47,90-96]. 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 may emerge when directing attention towards external stimuli (as in visual cued tasks), while a left

hemisphere bias might arise when directing attention towards internally-generated stimuli (as in the case of mental imagery).

Given the prominent role of fronto-parietal attention networks in attention-mediated conscious processing [97-99] and in neural models of consciousness [100], 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.

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**).

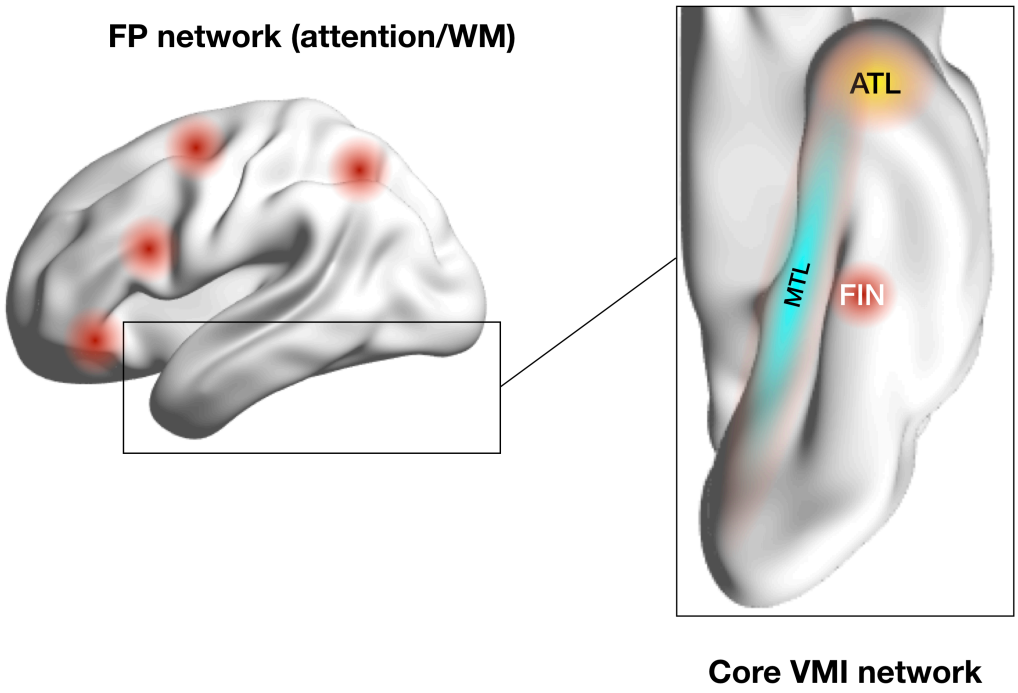

Figure 11. *Schematic depiction of a revised neural model of VMI. WM, visual Working Memory; FIN, Fusiform Imagery Node; ATL, Anterior Temporal Lobe; MTL; Medial Temporal Lobe.*

We propose that a core network of VMI includes a region in the FG3 area [62] of the left fusiform gyrus, which may be labeled Fusiform Imagery Node (FIN), in analogy with other domain-preferring regions in the ventral temporal cortex [101]. More anterior regions of the left temporal lobe (ATL) provide the FIN with semantic information [102]. This core network would be activated by prefrontal regions in VMI. The FIN is part of the ventral cortical visual pathway; during perception, it receives visual information from more posterior regions. Middle temporal lobe (MTL) structures may provide a neural substrate for recombining elements of past experiences to generate episodic simulations in VMI [103]. MTL structures such as the parahippocampal gyri, 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, recovery of VMI-related information may still be provided by the ATL-FMI portion of the VMI network. Dysfunction of the ATL-FMI component may lead to VMI deficits for object form and color, as suggested by the patterns of performance of patients with extensive left temporal damage [22]. A homologue network in the right hemisphere might contribute to aspects of VMI for faces [104]. 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 [86], and 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 the right side (imaginal or representational neglect) [35,85]. In this case, visual mental images are built by the left hemisphere VMI network, but the

attentional impairment resulting from the right fronto-parietal dysfunction determines the incomplete exploration or maintenance of the left portion of mental images [86].

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 [22,39,61]. It is plausible that a clear description of these fast-occurring dynamics will be achieved by employing techniques with adequate spatiotemporal resolution (such as magnetoencephalography), 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.

Tables

Table 1. List of studies (n = 23) showing the first author's name, publication year, manuscript title, stimuli used, and number of subjects (n = 303) 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 325 activation foci were included in the analysis for this contrast.

	Name and Year	Manuscript title	Stimuli used	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*	Imagery of flickering checkerboard	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*	Generating visual mental images	A	3	9	25.2 ± 3.7	9F	Right	RFX	Corrected
3.	Boly et al. 2007	*When thoughts become action: An fMRI paradigm to study volitional brain activity in non-communicative brain injured patients*	Generating visual mental images	B	2	12	24 ± 4	12M	Unknown	RFX	Corrected
4.	Gardini et al. 2005	*Different neuronal pathways support the generation of general and specific mental images*	Generating visual mental images	A	1	15	25.93 ± 8.87 20:51;	6F	Right	RFX	Corrected

5.	Huijbers et al. 2011	*Imagery and retrieval of auditory and visual information: Neural correlates of successful and unsuccessful performance*	Generating visual mental images	A	4	21	22	16F	Right	RFX	Uncorrected
6.	Ishai et al. 2000	*Distributed Neural Systems for the Generation of Visual Images*	Imagery of objects categories: faces, houses, and chairs	A/B	4	9	28 ± 5	5F	Right	RFX	Corrected
7.	Kaas et al. 2009	*Imagery of a moving object: The role of occipital cortex and human MT/V5+*	Imagery of moving object	A	1	12	20:34	8F	Unknown	RFX	Corrected
8.	Kilintari et al. 2016	*Brain activation profiles during kinesthetic and visual imagery: an fMRI study*	Generating visual mental images	A	4	14	18:41	10F	Right	RFX	Corrected
9.	Kukolia et al. 2006	*Neural mechanisms underlying spatial judgements on seen and imagined visual stimuli in the left and right hemifields in men*	Adaptation of the O'Clock Test	A	3(D)	20	24.5 ± 3.2 21:32	20M	Right	RFX	Corrected
10.	Lambert et al. 2002	*Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement — an fMRI study*	Generating visual mental images	A	2	6	24±3.5; 19 :25	4F	Right	RFX	Corrected

11.	Logie et al. 2011	*Low and high imagers activate networks differentially in mental rotation*	Mental rotation task	A	1	21	20:35	14F	Right	RFX	Corrected
12.	Mazard et al. 2005	*Neural impact of the semantic content of visual mental images and visual percepts*	Generating visual mental images	A	1	15	18:27	4F	Right	FFX	Corrected
13.	Sack et al. 2002	*Tracking the Mind's Image in the Brain II: Transcranial Magnetic Stimulation Reveals Parietal Asymmetry in Visuospatial Imagery*	Mental clock task	A	1,2	6	27.8 ± 5.7	3F	Right	FFX	Corrected
14.	Sasaoka et al. 2013	*Dynamic Parieto-premotor Network for Mental Image Transformation Revealed by Simultaneous EEG*	Mental clock task	A	1	23	Unknown	23M	Right	RFX	Corrected
15.	Seurinck et al. 2011	*Mental Rotation Meets the Motion Aftereffect: The Role of hV5/MT+ in Visual Mental Imagery*	Mental rotation task	A	1	16	24 ± 2.0; 21:28	16M	Right	RFX	Corrected
16.	Slotnick et al. 2005	*Visual Mental Imagery Induces Retinotopically Organized Activation of Early Visual Areas*	Imagery of flickering checkerboard	A	1	6	21 ± 1.1	3F	Unknown	FFX	Corrected

17.	Slotnick et al. 2011	*Visual memory and visual mental imagery recruit common control and sensory regions of the brain*	Generating visual mental images	A	1	12	18.6 :22.2	8F	Unknown	RFX	Corrected
18.	Soddu et al. 2009	*Reaching across the abyss: recent advances in functional magnetic resonance imaging and their potential relevance to disorders of consciousness*	Counting down, describing a face, describing own thoughts	A/B	1	8	Unknown	Unknown	Unknown	RFX	Corrected
19.	Thompson-Schill et al, 1999	*A neural basis for category and modality specicity of semantic knowledge*	Retrieval of visual and non-visual knowledge	C	1	5	Unknown	1F	Unknown	FFX	Corrected
20.	Trojano et al. 2000	*Matching Two Imagined Clocks: the Functional Anatomy of Spatial Analysis in the Absence of Visual Stimulation*	Mental rotation task	A	1, 2	4	27; 23:32	2F	Right	RFX	Uncorrected
21.	Yomogida et al., 2004	*Mental Visual Synthesis is Originated in the Fronto-temporal Network of the Left Hemisphere*	Generating visual mental images	A	1	23	18:31	Unknown	Unknown	FFX	Corrected
22.	Zeman et al. 2010	*Loss of imagery phenomenology with intact visuo-spatial task performance: A case of 'blind imagination'*	Perception and imagery of famous faces	B	4	10	63.4; 55:76	Males	Right	RFX	Corrected

23.	Zvyangintsev et al. 2013	*Brain networks underlying mental imagery of auditory and visual information*	Generating visual mental images	A	2	15	25.1 ± 5.7	7F	Right	RFX	Corrected

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

Table 2. List of studies (n = 13) showing the first author's name, publication year, manuscript title, stimuli used, and number of subjects (n = 192) 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 149 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.	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	1	12	33.7 ± 4.2 (29:38)	5F	Right	FFX	Corrected
2.	Berger et al. 2014	*The Fusion of Mental Imagery and Sensation in the Temporal Association Cortex*	Visual perception and then imagery of objects (i.e. cercle, radius 20mm)	1	21	29.09 ± 5.56	10F	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*	Imagery of Campus maps, Rome city maps and clock task	1	15	24.67 ± 2.16	7F	Right	RFX	Corrected
4.	Daselaar et al. 2010	*Modality-specific and modality-independent components of the human imagery system*	Imagine and perception task: imagined an image associated with the word or observed an image associated with the word	2	16	21	10F	Right	RFX	Uncorrected

5.	D'Esposito et al. 1997	*A functional MRI study of mental image generation*	Mental image generation task of objects with words stimuli		7	18-37	7M	Right	FFX	Corrected
6.	Ganesh et al. 2015	*Disentangling neural processes of egocentric and allocentric mental spatial transformations using whole-body photos of self and other*	Mental spatial transformation task		23	23 ± 4	12F	Right	RFX	Corrected
7.	Handy et al. 2004	*Visual imagery and memory: Do retrieval strategies affect what the mind's eye sees?*	Perception and Visual imagery of objects by audio and words stimuli	1	15	18 ± 29	10F	Right	RFX	Uncorrected
8.	Kukolia et al. 2006	*Neural mechanisms underlying spatial judgements on seen and imagined visual stimuli in the left and right hemifields in men*	Adaptation of the O'Clock Test	3	20	24.5 ± 3.2 (21:32)	20M	Right	RFX	Corrected
9.	Mazard et al. 2005	*Neural impact of the semantic content of visual mental images and visual percepts*	Perception and imagery of object drawing and non-object drawing task	3	15	18:27	4F	Right	RFX	Corrected
10.	Shuhama et al. 2016	*Behavioral and neuroimaging responses induced by mental imagery of threatening scenarios*	Imagined scenarios of potential and imminent threats	4	16	28.5 ± 4.1	17F	Unknown	RFX	Corrected

11.	Sung-Eun et al. 2007	*The neural mechanism of imagining facial affective expression*	Imagery of emotional facial expressions as compared to neutral facial expressions	2	21	25.4±2.6; (18:35)	10F	Right	RFX	Uncorrected
12.	Trojano et al. 2000	*Matching Two Imagined Clocks: the Functional Anatomy of Spatial Analysis in the Absence of Visual Stimulation*	Visual imagery of two clocks	1	4	27; (23:32)	2F	Right	FFX	Uncorrected
13.	Trojano et al. 2000	*Matching Two Imagined Clocks: the Functional Anatomy of Spatial Analysis in the Absence of Visual Stimulation*	Visual imagery of two clocks	2	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 > rest	2	12	24 ± 4	12M	Unknown	RFX	Corrected
2.	Cremers et al. 2012	*Hemispheric Specialization During Mental Imagery of Brisk Walking*	Imagined body movement: brisk walking, standing or 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*	Motor imagery and spatial navigation	2,4	15	23 ± 3	6F	Right	RFX	Corrected
4.	Harrington et al 2009	*The neural basis for simulated drawing and the semantic implications*	Imagine drawing familiar and non-familar objects	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*	Mental imagery of locomotion	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*	Tactile perception and imagery of palpated three-dimensional objects	2,3	12	36	2F	Right	FFX	Corrected
8.	Kilintari et al. 2016	*Brain activation profiles during kinesthetic and visual imagery: an fMRI study*	Motor act imagery task using kinesthetic or visual imagery	3	14	(18 – 41)	10F	Right	RFX	Corrected
9.	La Fougèere et al. 2010	*Real versus imagined locomotion: A [18F]-FDG PET-fMRI comparison*	Real *versus* imagined locomotion task	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*	Perception and mental imagery of meaningful face and limb movements with or without objects.	5	12	25.18 ± 4.25	14M	Right	RFX	Corrected
11.	Pyke et al. 2017	*When math operations have visuospatial meanings versus purely symbolic definitions: Which solving*	Problem solving task on novel math operations with symbolic or mental visuospatial strategy	1	40	23.6 ± 4.9	36F	Right	FFX	Uncorrected

		stages and brain regions are affected?								
12.	Sauvage et al. 2011	*Reevaluating brain networks activated during mental imagery of finger movements using probabilistic Tensorial Independent Component Analysis (TICA)*	Finger tapping execution with the nondominant left hand (execution task), and finger tapping imagery with the left hand (imagery task)	2	8	24.4 ± 4	2F	Right	RFX	Corrected
13.	Soddu et al. 2009	*Reaching across the abyss: recent advances in functional magnetic resonance imaging and their potential relevance to disorders of consciousness*	Imagery task: imagining opening and closing the left hand, Counting down, Imaging preparing luggage, Imaging walking from home to work Describing a face, Imaging filling a check, Describing own thoughts	1	14	Unknown	Unknown	Unknown	RFX	Corrected
14.	Wagner et al. 2008	*Mind the bend: cerebral activations associated with mental imagery of walking along a curved path*	Mental imagery task of walking along a curved path, walking straight ahead, and upright stance	1,2,3,4,5	12	33.5 (21– 51)	7F	Right	RFX	Corrected
15.	Whittingstall et al. 2013	*Structural network underlying visuospatial imagery in humans*	Roland's Hometown walking task	1	18	(20-28)	3F	Right	FFX	Uncorrected
16.	Zu Eulenburg et al. 2013	*On the recall of vestibular sensations*	Their vestibular task focused on the per-rotary stimulation only		16	26.3 ± 3	8F	Right	RFX	Corrected

Table 4. Brain regions showed consistent increased activation across all the mental imagery domains (52 studies, 827 foci, 774 subjects).

Region	L/R	BA	x	y	z	Z	K
Suppl. Motor Area	L	6	-4	-2	64	0.05	1008
Precentral Sulcus	R	6	30	-4	54	0.04	463
Precentral Sulcus	L	6	-28	-2	56	0.04	465
Inferior Parietal	L	40	-36	-42	46	0.04	1369
Middle Occipital Gyrus	L	19	-26	-76	40	0.03	
Insular Cortex	L	47	-30	22	4	0.04	341
Precentral Sulcus	L	6	-52	6	36	0.04	520
Fusiform Gyrus	L	37	-30	-40	-14	0.03	237
Inferior Parietal	R	40	40	-42	48	0.03	304
Insular Cortex	R	47	34	22	2	0.03	369
Cerebellum	L		-32	-58	-32	0.03	158
Calcarine Sulcus	L	17	-12	-56	10	0.03	251
Precuneus	R	7	16	-68	50	0.02	134

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.

Table 5. Brain regions showed consistent increased activation in the VMI *versus* Control condition (23 studies, 325 foci, 303 subjects).

Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**K**
Precentral Sulcus	R	6	30	-4	54	0.02	267
Inferior Parietal	L	40	-38	-42	46	0.02	525
Inferior Parietal	L	7	-28	-64	40	0.02	
Supp. Motor Area	R	32	8	16	48	0.02	113
Middle Frontal Gyrus[a]	L	6	-26	-2	56	0.02	226
Angular Gyrus	R	7	34	-56	50	0.02	306
Insular Cortex	L	47	-36	20	-2	0.02	129
Inferior Parietal	L	7	-22	-76	44	0.02	132
Supp. Motor Area	L	6	-8	0	64	0.02	152
Fusiform Gyrus	L	37	-42	-56	-18	0.02	105

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 (13 studies, 92 foci, 149 subjects).

Region	**Lat**	**BA**	**x**	**y**	**z**	**Z**	**K**
Precentral Gyrus	L	6	-50	2	32	0.02	265
Fusiform Gyrus	L	37	-32	-40	-14	0.02	152
Inferior Frontal Gyrus	L	47	-30	20	2	0.02	83

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.

Table 7. Brain regions showed consistent increased activation in the MMI *versus* Control condition contrast (16 studies, 353 foci, 279 subjects).

Region	**Lat**	**BA**	**x**	**y**	**z**	**Z**	**K**
Supp. Motor Area	L	6	-4	-2	66	0.04	565
Cerebellum	L		-32	-58	-32	0.03	172
Calcarine Sulcus	L	17	-14	-56	10	0.02	168
ParaHippocampal Gyrus	L	37	-32	-44	-4	0.02	115
Precentral Gyrus	L	6	-34	-4	56	0.02	146
Superior Frontal	R	6	32	-2	60	0.02	135
Cerebellum	R		32	-62	-30	0.02	110

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 (23 studies, 325 foci, 303 subjects) and VMI > Perception condition (13 studies, 92 foci, 149 subjects).

Conjunction (VMI > Control) and (VMI > Perception)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm3**
Anterior Insular Cortex	L	48	-30	20	2	0.0156	248
Disjunction (VMI > Control) > (VMI > Perception)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm3**
No cluster found							
Disjunction (VMI > Perception) > (VMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm3**
Precentral Gyrus	L	6	-51	0	34	2.64	336
Fusiform Gyrus	L	37	-30	-46	-13	2.6	80

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.

Table 9. Brain regions showed consistent increased activation in the conjunction and disjunction analyses between VMI > Control condition (23 studies, 325 foci, 303 subjects) and MMI > Control condition (16 studies, 353 foci, 279 subjects).

Conjunction (VMI > Control) and (MMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm3**
Precentral Gyrus	L	6	-32	-4	50	3.00	54
Precentral Gyrus	R	6	34	-8	52	2	55
Supp. Motor Area	L	6	-8	0	64	0.02	79
Disjunction (VMI > Control) > (MMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm^3**
Superior Parietal Lobe	R	7	35	-71	47	2.51	632
Inferior Parietal Lobe	L	40	-46	-45	45	2.58	440
Medial Frontal Gyrus	R	32	9	17	4	0.01	432
Disjunction (MMI > Control) > (VMI > Control)							
Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**mm3**
Medial Frontal Gyrus	R	6	3	-2	67	3.89	2248
Lingual	L	18	-14	-56	4	3.89	728
Cerebellum	L		-26	-58	-36	80	584
Cerebellum	R		33	-56	-30	1	288
ParaHippocampal Gyrus	L	37	-26	-42	-12	7	544

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.

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