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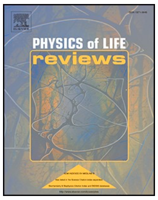

Review

Visual mental imagery: Evidence for a heterarchical neural architecture

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ABSTRACT

Theories of Visual Mental Imagery (VMI) emphasize the processes of retrieval, modification, and recombination of sensory information from long-term memory. Yet, only few studies have focused on the behavioral mechanisms and neural correlates supporting VMI of stimuli from different semantic domains. Therefore, we currently have a limited understanding of how the brain generates and maintains mental representations of colors, faces, shapes - to name a few. Such an undetermined scenario renders unclear the organizational structure of neural circuits supporting VMI, including the role of the early visual cortex. We aimed to fill this gap by reviewing the scientific literature of five semantic domains: visuospatial, face, colors, shapes, and letters imagery. Linking theory to evidence from over 60 different experimental designs, this review highlights three main points. First, there is no consistent activity in the early visual cortex across all VMI domains, contrary to the prediction of the dominant model. Second, there is consistent activity of the frontoparietal networks and the left hemisphere's fusiform gyrus during voluntary VMI irrespective of the semantic domain investigated. We propose that these structures are part of a domain-general VMI sub-network. Third, domain-specific information engages specific regions of the ventral and dorsal cortical visual pathways. These regions partly overlap with those found in visual perception studies (e.g., fusiform face area for faces imagery; lingual gyrus for color imagery). Altogether, the reviewed evidence suggests the existence of domain-general and domain-specific mechanisms of VMI selectively engaged by stimulus-specific properties (e.g., colors or faces). These mechanisms would be supported by an organizational structure mixing vertical and horizontal connections (heterarchy) between sub-networks for specific stimulus domains. Such a heterarchical organization of VMI makes different predictions from current models of VMI as reversed perception. Our conclusions set the stage for future research, which should aim to characterize the spatiotemporal dynamics and interactions among key regions of this architecture giving rise to visual mental images.

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1. Introduction

There is no limit to human imagination, according to Willy Wonka: *"... If you want to view paradise, Simply look around and view it, Anything you want to, do it..."*. This notion captures the essence of Visual Mental Imagery (VMI), enabling us to envision people, places, and objects not physically present [55,125]. Within scientific literature, the term VMI serves as a broad umbrella, encompassing various phenomena and processes associated with mental imagery. For instance, VMI can be placed at the core of human cognition. Mental images derived from long-term memory enable us to anticipate suitable behavioral responses in our environment [26,82]. However, a comprehensive review of studies exploring potential differences in imagining stimuli from various domains is missing. Such an exploration could contribute to resolving ongoing questions and debates regarding the mechanisms underlying VMI.

This review begins by probing a fundamental question: how is VMI studied? Subsequently, it delves into another pivotal question concerning the relationship between VMI and perception. Does imagining an object pose greater difficulty than perceiving it? Assessing whether such an increase in difficulty exists, and whether it remains consistent across various visual perceptual domains can shed light on the comparable mechanisms underlying imagery and perception with a greater detail than our current understanding allows.

The last question concerns the neural architecture supporting VMI across different domains. Past propositions suggested a hierarchical architecture supporting VMI, with frontal regions occupying the highest level in this hierarchy [35,58], early sensory regions at its lowest level, and a reversed flow of information compared to perception [33,35,130]. However, this model has faced recent scrutiny, with persistent unanswered questions. For instance, neurological patients typically display VMI deficits after left inferior temporal lobe damage but not after early visual cortex damage (e.g., [94], see reviews [125] and [6]). On the other hand, we recently discussed the case of a stroke patient with preserved mental imagery and right homonymous hemianopia, alexia without agraphia, and color anomia [55]. Patient RDS regions in the Ventro-Temporal Cortex (VTC) and associated white matter tracts were spared by the lesion. How can this evidence be reconciled within models proposing the complete spatial overlap between imagery and perception? Moreover, disparities in early stages of imagery and perception processes in terms of brain regions activated and temporal dynamics [22,34,35] pose further challenges. We recently uncovered the reduced functional connectivity between frontoparietal and ventral temporal cortex (VTC) regions in subjects with aphantasia but preserved visual perception [82,147], suggesting VMI generation dependence on specific network connectivity. How does this finding go along with previously stipulated imagery as vision in reverse [100]? Current evidence fails to definitively map the neurocognitive architecture of VMI within a hierarchical structure, beyond identifying sequential processing stages (ie., a cascade; [33]). Yet, identifying a sequence of neural events does not imply a hierarchy among them, but highlights the order in which the events typically occur under certain stimulus-specific conditions. Each step is essential and contributes to the final result, and none of them is inherently more essential or necessary than the others.

Altogether, this evidence suggests that while there might be shared neural substrates between imagery and perception, they are not entirely overlapping both in time and in space.

Long-standing evidence links brain regions in the ventral temporal cortex (VTC) to the processing of domain-specific visual information by responding more strongly to stimuli of a preferred type (hereafter, domain-preferring regions). Generation and maintenance of visible stimuli relies on occipito-temporal circuits along well-charted territories in the dorsal and ventral cortical visual streams [84,148]. These regions seem to play a similar role between imagery and perception, being a potential candidate for the overlap between these two processes. For example, activation of the fusiform face area in the right hemisphere is associated with both imagery (e.g., [67]) and perception [69] of faces. Similarly, patients with prosopagnosia due to lesions of the occipitotemporal region encompassing the fusiform face area can develop selective deficits in face imagery [13]. Brain activation associated with perception and imagery of colors overlaps in regions such as the fusiform gyrus and in the insular cortex [63]. Color perception is also associated with activation of the primary visual cortex, while color imagery is not [63,82]. This complex scenario challenges existing models that propose a unidirectional signal flow between prefrontal regions and the primary visual regions for all visual imagination. Addressing these complexities and nuances in neurocognitive models is essential to develop a more detailed understanding of VMI across diverse semantic domains.

In summary, to draw a revised neurocognitive model of VMI, it becomes imperative to (1) re-evaluate existing literature by clarifying the necessity of VTC regions and their interplay in VMI, (2) accommodate differences between imagery and perception by stipulating alternatives to single-stream reverse-hierarchy models, and (3) offer testable predictions for various domains of mental imagery. A heterarchical organization could provide such alternatives to the current hierarchical neural model. Heterarchical systems, first introduced by neurophysiologists [89], mix hierarchy (vertical connections) with horizontal processes (lateral connections), allowing top-down and bottom-up feedback signals to co-exist within a model. Hence, this architecture stands out as a potential candidate for VMI sub-networks to interact with each other following previously discovered processing stages (e.g., [33,130]). At the same time, it would free the model from making predictions regarding the importance of nodes within this architecture. Further, this model could produce testable predictions regarding VMI of specific domains by linking domain-general and domain-preferring regions (see Fig. 1).

Here, we review the literature on five semantic domains used in VMI literature [6,49] to highlight the similarities between behavioral and neural findings observed across these studies. As of January 1st, 2023, we identified over 60 articles focused on VMI: visuospatial imagery (rotations and trajectories; n = 22 articles), faces (n = 13 articles), colors (n = 11 articles), shapes (n = 9 articles), and letters (n = 9 articles). This effort aims at understanding how VMI is studied, what makes it different from perception, and what organizational structure supports it. We will highlight evidence in favor of the hierarchical model (see Pearson et al., for a list of predictions) and a heterarchical model of VMI. This model predicts that a region located in the left fusiform gyrus, the fusiform imagery

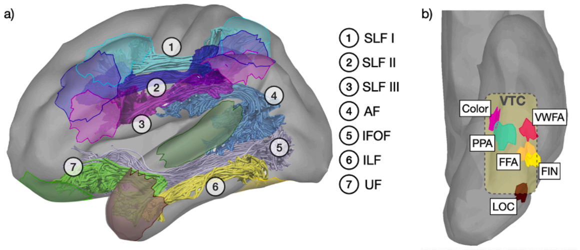

Fig. 1. Diagram of a heterarchical model of VMI. a) Brain regions and connecting fiber bundles supporting domain-general mechanisms of visual mental images. (b) Domain-preferring regions located in the VTC neighboring to the Fusiform Imagery Node (FIN) a domain-general hub for the visualization of mental images. LOC = Lateral Occipital Complex (-41, -73, -9) coordinates from [50]; PPA = Parahippocampal Place Area (-29, -45, -22) coordinates from Epstein and Kanwisher [39]. Color = Color-biased region (anterior patch: -34. -36, -14) coordinates from Lafer-Sousa et al. [78]. FFA = Fusiform Face Area (-42, -54, -17) from Kanwisher et al. [69]. FIN = Fusiform Imagery Node (-46, -58, -14) from Spagna et al., [126]. VWFA = Visual Word Form Area (-45, -41, -18) from Szwed et al. [131]. Coordinates in MNI space.

node (FIN) [127] is a central hub for VMI. The FIN connects high-level visual areas processing domain-specific information with other regions in the temporal lobe implicated in memory- and semantic-related processes. Direct lesion or disconnection of the FIN from more anterior regions should produce domain-general deficits of VMI [8]. Regions processing domain-specific information for mental imagery are also located in the VTC. The model predicts activation of fusiform face area (FFA) and parahippocampal place area (PPA) during imagery of faces and places, respectively, activation of the lateral occipital complex (LOC) for shape imagery, in the visual word form area (VWFA) for letter imagery, and in the color-biased region for color imagery. Lesion or disconnection of domain-preferring regions in the VTC should instead produce domain-specific deficits of VMI [9]. This model also predicts that greater vividness of mental imagery would be associated with higher connectivity between FIN and frontoparietal regions linked by the superior longitudinal fasciculus and by the arcuate fasciculus. Collectively, the divergent predictions stemming from the models provide an ideal arena for exploration within this review.

2. Visuospatial mental imagery (trajectories and rotation)

With the term visuospatial imagery, we refer to a wide range of abilities, including visualizing and manipulating objects (e.g. rotations and spatial trajectories) as well as evaluating their spatial features (viewpoint and relative position, relative distance, and configuration) [110,111].

Shepard & Metzler [117] devised a mental construction task (CONS) to assess the *rotation* aspect of visuospatial imagery. Participants saw pairs of three-dimensional objects made out of cubes attached together and forming an arm-like shape were presented on the screen. They were asked to mentally visualize the entire object for 5 seconds and to indicate whether two visually presented images were congruent (possible) or incongruent (impossible) rotations. The results demonstrated that the average rate at which participants could rotate an object was roughly 60 degrees per second, with the time required to indicate the congruency between constructed and depicted images linearly increasing as a function of angle rotation. Mellet et al. [91] used PET to unveil the neural bases of performance on this task, and observed the activation of a widespread bilateral occipito-fronto-parietal network for the mental construction condition compared to rest, as well as in the right inferior temporal cortex and left fusiform gyrus. In an fMRI study using the same task, Logie et al., [83] divided participants into low and high imaging ability based on a self-report Vividness of Visual Imagery Questionnaire (VVIQ, [85]). Participants' processing time and error rate increased as the angle of mental rotation increased, an effect especially prominent between 20 and 60 degrees. When compared with a control condition (0 degrees of rotation), mental rotation induced stronger bilateral activation over the supplementary motor area. This effect was particularly evident in the group of low imagers, who also activated neural resources in the visual system located in the middle occipital / inferior temporal gyri. On the other hand, high imagers showed increased activation in frontal regions. Lamp et al. [79] used fMRI to examine the neural activity patterns associated with the maintenance aspect (working memory) of mental rotations. The procedure consisted of a 1-back task, in which participants viewed a series of arm-shaped stimuli interleaved by a masking noise. In the maintenance task, participants judged whether the current image was a repeat of the previous one. In the maintenance plus rotation task, participants indicated whether the current image was a repeat and rotated version of the previous one (congruent condition) or not (incongruent condition). At the end of the fMRI scan, participants provided a rating of how difficult they found the task to be, on a Likert scale from 1 to 5. Participants rated the maintenance plus rotation task to be relatively difficult to complete compared to the maintenance only task, and that difficulty ratings negatively correlated with accuracy scores. Neuroimaging results demonstrated that completion of the maintenance only task was associated with greater right-lateralized parietal activation for incongruent over congruent trials, while the same contrast in the maintenance plus manipulation task was associated with bilateral parietal and left fusiform activation.

The Mental Clock Task is another commonly used task to study the rotation aspect of visuospatial imagery [51,77,97,112]. Participants are asked to imagine two analog clock faces based on acoustically presented times, and to judge at which of the two times the clock hands formed the greater angle. Comparison response time increased with decreasing angular size differences, while accuracy in position matching remained high [43,77,98,136]. There were asymmetries in performance across the imagined visual field, but they were not consistent in different studies. Formisano et al. [43] observed slower RT for mental clocks imagined on the right side of the imagined visual field, while Kukolja et al. [77] showed the opposite results on the left side (ie.. slower but not less accurate for clock hands on the left side of the clock). In a Modified Mental Clock Task, Sasaoka et al. [112] asked participants to mentally rotate clock hands for various time periods at a specific speed from an initially auditorily presented position and then to match the position to the visually presented clock hands. They reported a main effect for both amount of rotation and direction of rotation, but not an interaction between the two. From a neural perspective, the first study that used fMRI and the mental clock task [136] investigated whether the neural correlates associated with perceptual transformations are also in charge of visuospatial rotations. Results converged over the role of the parietal lobes in visuospatial rotations, while there was no activation of the primary visual cortex. Later fMRI studies on the mental clock task have shown activation in the bilateral supplementary motor area [43,111], prefrontal and anterior cingulate cortex [77], frontal eye fields and precuneus [111], posterior parietal cortex [43,77,111], left primary motor cortex [111], and cerebellum [77]. Performance of the Modified Mental Clock task was associated with activation in the frontal lobe along the medial and lateral frontal surface over the left hemisphere and in the left inferior parietal lobe extended from the supramarginal gyrus to a part of the anterior intraparietal sulcus [112].

Alivisatos and Petrides [2] used PET to investigate mental rotation of alphanumeric stimuli. This experiment encompassed three conditions: in the control condition, participants saw an alphanumeric stimulus (e.g., the number ‘2’) presented on the screen and were asked to indicate which stimulus was presented by pressing a corresponding button. In the mirror-image discrimination condition, the same alphanumeric stimuli were used as in the control condition, but participants pressed a button to indicate whether the stimulus appeared either in their canonical form or backwards. The mental rotation condition consisted of the same alphanumeric stimuli and task as in the mirror-image condition, but the stimuli presented were rotated to 120, 180, or 240 degrees. Results showed activity changes in the posterior parietal cortex for both the mirror image discrimination and the mental rotation condition, including the left inferior parietal lobe and the parieto-occipital junction.

Seurinck et al. [115] used fMRI to investigate mental rotation abilities using motion aftereffects (MAE). Participants first underwent an induction phase, during which sinusoidal gratings rotating clockwise or counterclockwise were presented for 5 secs. They then judged whether an alphanumeric stimulus presented on the screen was in a canonical or mirror configuration. In congruent trials, the direction of MAE rotating induced from the presentation of a sinusoidal grating was identical (vs. opposite in incongruent trials) to that of the required imagined visual rotation of the stimulus. There was a significant interaction between angular disparity and MAE congruency in error rates with only the largest angular disparity group showing a significant difference, while the main effect of MAE congruence in RT was observed. Neuroimaging results showed a linear increase in neural activity with increasing angular disparity, a plausible neural substrate underlying the behavioral effect of mental rotation found in Mellet et al., [91] and in Shepard & Metzler [117]. This activation spanned across a network of visual, parietal, and frontal areas, and greater activation in the left hV5/MT+ for trials when the MAE rotation was incongruent.

Dhindsa et al. [32] used fMRI to explore visuospatial rotations in the egocentric and allocentric space. Participants first learned stimuli configurations during a virtual reality session outside the scanner. They then completed three tasks: 1) in the reference viewpoint task, participants pointed towards an imagined object from a familiar point of view learned during the virtual reality session. 2) in the rotation viewpoint task, participants imagined facing an object and then rotate themselves towards a second object. 3) In the judgment of the relative direction task (JRD), participants imagined standing in the position of one object and facing another object, and then rotated themselves towards a third object. Participants were highly accurate in the reference viewpoint task, and less accurate in the rotation viewpoint and JRD tasks, indicating that rotations of allocentric viewpoints were more complex to perform. This pattern was associated with increased activation in a circuit of parietal and medial temporal regions (ie., hippocampus and parahippocampal area) for the JRD condition compared to the baseline conditions.

The stimuli used to explore imagined visuospatial *trajectories* include moving gratings [122], geometric shapes [68], arrows [102], spatial locations, and navigation of maps [15,17,18,75,107,139].

Kosslyn et al., [75] investigated the pictorial nature of mental imagery by testing whether greater time is required to mentally scan further distances compared to shorter ones. Participants first memorized a map of a fictitious island consisting of 7 object locations presented auditorily, then mentally scanned the entire map from the first object location to the second in the shortest straight line. Results showed that the time employed to complete the map consistently increased with increasing distance during the mental scanning. In a series of studies, Bourlon and colleagues [14–18] studied eye movements to further elucidate the similarities between mental and perceptual exploration of maps. Participants were asked to conjure up a mental image of the map of France, and to indicate whether towns or regions presented in the auditory modality were situated left or right of Paris (e.g., participants heard "Paris," "Bordeaux,", the answer is left). Results from eye tracking showed that participants tended to produce similar eye movements on the imaginal and on the perceptual conditions of the task. Saccades mirrored not only the direction of mental exploration, but also the side of exploration. Regional cerebral flow changes associated with mental navigation of a familiar route was studied using PET [107]. Participants were instructed to recall one of 6 familiar walking routes and to mentally navigate through it. Participants reported being able to look around 3-dimensional imagined scenery and zoom in on certain details, change direction multiple times over distances spanning thousands of meters, and imagine environments in color. Neuroimaging results showed increased activity in superior and lateral frontal cortex, and in posterior parietal cortex along the lateral and medial (precuneus) surfaces. Boccia et al., [15] combined the scanning of a map, as in Kosslyn et al. [75], and navigation of a map, as in Roland et al. [107], to distinguish between egocentric and allocentric map navigation. They used fMRI while participants imagined the spatial location of three categories of stimuli. Stimuli tapped on topographical & navigational abilities (e.g., landmarks within their college campus), topographical & geographical abilities (e.g., towns on a map of their country), and non-topographical abilities (different times on a clock). Participants were highly accurate in answering each set of questions (greater than 85 % on average). Activities in the bilateral fusiform gyrus, left lingual gyrus, and bilateral calcarine sulcus were associated with performance in both the topological-navigational and topological-geographical conditions. Frontal activation was associated with the topological-geographical and non-topographical spatial conditions. The contrast between topographical versus non-topographical stimuli showed an increased activation in the left angular gyrus. In another study, Whittingstall et al. [139] used another navigation of familiar maps tasks along with fMRI and found activation in cortical areas across both the dorsal (extrastriate, parietal and prefrontal areas) and ventral (temporal and lingual areas) pathways, bilaterally. They also observed moderate deactivation in the striate visual cortex and V1.

Early visual cortex activation associated with visuospatial mental imagery was observed by Slotnick et al. [122] in a study using consisting of three tasks: 1) a perception task associated with a standard retinotopic mapping procedure, in which two flickering checkerboard wedges were rotated around a central fixation point. 2) An imagery *plus* attention task, in which only the outer arcs of the wedges of the flickering checkerboards were presented; participants were asked to mentally visualize the stimulus wedges while using the stimulus arcs as a guide. (3) An attention task in which participants either distributed attentional resources across the entire visual display or focused attention to where the stimulus wedges were. Participants were slower and less accurate performing imagery tasks than perception tasks, particularly for stimuli imagined in the right visual field. Neuroimaging results obtained using fMRI revealed similar retinotopic maps and similar activation of the area MT for both imagery tasks and perception tasks, indicating a role for this area that is independent of whether the imperative stimulus is imagined or visible.

Motion imagery and its effect on the activation of higher-order visual areas was studied by Kaas et al. [68] using fMRI. An auditory cue tone with an ascending or descending pitch was used to instruct participants to imagine a blue ball moving back and forth in the upper right (IM-UR) or lower left (IM-LL) visual hemifield. Participants indicated the position of the imagined ball with respect to two target squares presented on the screen by selecting the square that was closer to the imagined ball. Compared to the control condition (auditory cues with a stable frequency), imagery of a moving object was associated with increased activation of the bilateral frontoparietal regions, right anterior insula, right basal ganglia, and left middle occipital gyrus, and with the activation of the primary visual cortex.

Pyke et al. [102] used fMRI to analyze the link between visuospatial abilities and arithmetic. Participants solved arithmetic problems either using symbolic (i.e., mathematical symbols and numbers) or visuospatial (i.e., rectangular 3D blocks) novel math operators while undergoing fMRI recordings. Visuospatial and symbolic solving strategies followed a similar learning curve with increased accuracy rate and shorter RT for both tasks after successive training sessions. Neuroimaging results demonstrated that solving arithmetic problems using a visuospatial strategy activated regions in both the lateral and medial surfaces of the parieto-temporal lobes, including the bilateral angular gyrus, and in the left fusiform / lingual gyrus. Conversely, solving the arithmetic problems using mathematical operation was associated with increased activation in frontal (superior, middle, and inferior) as well as middle temporal and right angular areas.

[3] used fMRI to design a neurofeedback protocol to assess individuals' capacity to self-regulate brain activity linked to visuospatial mental imagery. While in the scanner, participants performed tasks in two conditions: (1) a stimulus localizer condition, requiring to fixate on a central cross while a flickering checkerboard pattern was presented to the top right or left quadrant; (2) an imagery localizer condition, requiring to imagine a flickering circle in one of the two quadrants or to stop imagining during rest blocks. For real-time feedback, participants either imagined the upper right imagery block or stopped imagining during the rest block. Behavioral performance was measured outside of the scanner, by means of a modified vividness questionnaire (VVIQ) with an added self-reported measure for focus levels. Vividness scores were significantly correlated with activation in the parietal lobe, but not the early visual cortex.

Overall, from reviewing the literature of visuospatial mental imagery, our three initial questions (ie., how is VMI studied? Is it more difficult than perception? What is the neurocognitive architecture supporting VMI?) find the following conclusions. First, stimuli used to manipulate the rotation component included bi-dimensional mental clocks [43,51,52,77,83,98,111,112,136], three-dimensional cubes [91,117], flickering [3] and rotating gratings [115]. Trajectory tasks, on the other hand, included moving arrows [102], objects [68], maps [15,17,75], or one's own body in space [107]. Second, subjective (self-report) and objective (accuracy and RT) measures of participant performance often indicate that visuospatial imagery tasks are more difficult to perform compared to visuospatial perceptual tasks (e.g., [79,122]), even though accuracy measures in these visuospatial VMI are well above chance level (~85 % of correctness; [15]). Third, as also discussed in previous reviews and meta–analysis of visuospatial mental imagery [47,58], among a plethora of regions activated by visuospatial tasks, the most consistent finding seems to be the involvement of the bilateral parietal cortex [2,32,43,77,79,83,91,102,111,112,115], often in tandem with more anterior, frontal, regions [68,83]. Further, the activation of the fusiform gyrus has been a recurrent finding associated with visuospatial imagery, although it is still unclear whether this activation is restricted only to the left hemisphere [79,102], to the right hemisphere [122], or is observed bilaterally [15,91]. Lastly, a lack of activation [3,83,91,122] or the deactivation [139] of the early visual cortex has been observed, although evidence for the opposite result has also been reported [122].

Overall, the ability to visualize and manipulate objects as well as evaluating their spatial features is supported by activation of inferior temporal regions and frontoparietal networks. On the basis of the evidence reviewed, it is possible to begin discerning among activation of brain regions supporting the processing of specific types of stimuli (e.g., hV5/MT for rotations: [68,102,115,122]; parahippocampal gyrus for trajectories and egocentric perspectives: [32,139]). This evidence aligns with the involvement of regions in the dorsal stream pathway for high-level perception of spatial relations, object recognition and shape perceptions [4]. Frontoparietal activation is also observed irrespective of the type of stimulus employed in these studies (e.g., high imagers in [79,83,111,139]), in the fusiform gyrus (e.g., Mellet et al, [15,79]) and in the lingual gyrus (e.g., [15,102,139]) suggesting a potential domain-general role of these regions in visuospatial mental imagery.

3. Mental Imagery of Faces

The ability to visualize whole or parts of people's faces [96], is involved in a variety of every-day activities [45]. For instance, mental imagery of faces can be used to visualize the face of our neighbor, but it also contributes to prejudicial schemas based on a subjective representation of how our new neighbor should look.

Ishai et al. [67] used fMRI to compare the activation of brain regions between visual imagery and perception associated with faces, houses and chairs. Results of face imagery and perception tasks showed opposite patterns of hemispheric lateralization in the VTC, with greater activation in the left hemisphere for imagery tasks, and greater activation in the right hemisphere activation for perception tasks. Bilateral activation of the lateral fusiform gyrus was observed for visual imagery but not perception of faces. Additionally, activation associated with face imagery was observed in a network of regions, including parietal (i.e, the intraparietal sulcus, superior parietal lobe, and precuneus) and frontal (caudal anterior cingulate cortex, superior frontal sulcus, and inferior, mid and superior frontal gyri) regions, as well as the cerebellum. In another fMRI study investigating visual mental imagery of famous faces, Ishai et al. [66] showed that face-selective regions in the inferior occipital gyri, lateral fusiform gyri, superior temporal sulci, and amygdala were activated during imagery tasks as well as perception tasks. The number of voxels activated in those regions was greater for perception than in imagery, indicating both overlap and differences between these two processes. Further, the direct comparison between imagery and perception showed that amygdala activation was left lateralized for imagery and bilateral in perception. Last, imagery of faces interacted with attentional load such that focusing attention on facial features (e.g., eyes, lips, or nose) resulted in greater activation in the frontoparietal regions of the right hemisphere (IPS and IFG). Frontoparietal and occipitotemporal activation associated with mental imagery of faces, places, and letters was also observed by Dijkstra et al. [34]. In line with findings from [66], this study further elucidated the substantial overlap in activation of frontal and parietal regions for perception and imagery of faces. This widespread brain activation was modulated by self-reports of imagery vividness and was stronger in the frontal and prefrontal cortex for imagery compared to baseline; activation in the more posterior areas (visual cortex) was greater for perception compared to baseline. In another study, participants imagined the face of a known person (from a list provided by the participants), in as much detail and as vividly as possible [119]. Participants reported greater vividness for the recall of people than of places; this effect was associated with activation for faces and places along a medial-lateral axis in the ventral temporal cortex (VTC - with face selectivity associated with a more lateral patch).

Further evidence for the role of regions within the VTC (encompassing the fusiform gyrus / fusiform face area) in face mental imagery stems from the studies using multivariate voxel pattern analysis of fMRI data to decode imagined stimuli from brain activity [16,103,105,137]. For example, Reddy et al. [105] asked participants to either see or imagine stimuli from four domains (shapes, tools, faces, and places) and then estimated activity patterns from object-responsive voxels separately from the perception and imagery tasks. Results showed above-chance level classification performance from domain-preferring regions in the VTC (e.g., fusiform face area - FFA for faces) - but not in retinotopically-organized voxels in the primary visual cortex - for both imagined and perceived objects. Object-responsive voxels in the VTC overlapped significantly between imagery and perception. Similar results were observed in Ragni et al., [103], with significantly above-chance decoding accuracy observed from the left fusiform face area, the bilateral para-hippocampal place area, and frontoparietal regions, but not in early visual cortex regions. Evidence for successful decoding of face imagery from VTC regions has also been demonstrated by Boccia et al. [16] using representational similarity analysis. Results showed that activation patterns in high-level visual areas (ie., bilateral fusiform face area, bilateral occipital face area, and left occipito-place area) could be observed across imagined stimuli categories. At odds with the previous evidence are results from a study using deep generative neural networks on BOLD fMRI activity to train a brain-decoding system to reconstruct imagined or perceived faces [137]. Decoding accuracy for seen and imagined faces was instead significantly above chance for both occipital and temporal regions, but not from frontoparietal regions, suggesting that these regions did not store information regarding the represented stimulus.

Neuropsychological cases highlight these similarities between processes and neural substrates supporting perception and imagery faces. Barton and Cherkasova [13] tested nine prosopagnosic patients by asking them to imagine the faces of two famous individuals and indicate which one had a certain visual property (e.g. *who has a wider mouth: Sophia Loren or Ingrid Bergman*?). Results showed that lesions to the anterior right fusiform gyrus might impair mental imagery for faces. Grüter et al. [53] compared behavioral performances in mental imagery vividness of 53 individuals with congenital prosopagnosia to those of 88 neurotypical individuals. A follow up comparison of 12 prosopagnosia patients and 12 age-matched controls showed a significantly lower ability to discriminate imagined faces - but not imagined houses - in the prosopagnosic group compared to controls. Clinical prosopagnosia, often linked to lesions of the right fusiform gyrus ([13,132]; but also see the discussion of a clinical case in [108]), is often associated with face imagery deficits. However, face imagery deficits do not seem to follow lesions to the primary visual cortex, as described by Bridge et al. [19], or to the connections between the occipital and the temporal lobe [10]. Bridge et al. [19] compared behavioral and neuroimaging performance of a patient with damage selectively affecting the gray matter of the calcarine sulci with a group of 8 age-matched controls. Results from subjective reports as well as BOLD responses associated with imagined face stimuli (as well as imagined houses) were comparable between the patient and the control group, indicating that damage to the primary visual cortex had left this function unimpaired. Consistent with previous research, activation in bilateral fusiform face area and in the frontoparietal network (mostly left lateralized) was associated with face imagery.

Results from these fMRI studies using general linear modeling, more recent analytic methods such as multivariate pattern analysis, and group comparisons with lesion patients, are at least partly consistent with a human electrophysiology study conducted using intracerebral recordings of VTC units published by Khuvis et al. [72]. The authors examined whether neuronal activation exhibited during encoding of faces is also observed during recall or imagination of those same faces, and the role of top-down endogenous mechanisms in this reactivation. Participants first looked at full color photographs of famous faces and scenes. They then put a blindfold on and performed a short 1-back interference task (counting back from 150 in steps of 5) and then freely recalled as many pictures as possible, focusing on one category (faces/scenes) at a time. Activity in face-selective neural units in the right fusiform gyrus began increasing around 2 seconds before participants began describing a face. After peaking, activity then returned to near baseline as the subjects began to speak. Evidence for similar activity patterns during recall and initial face presentation suggested the possibility of predicting the identity of the face to be recalled by matching activity of these units before a recall event to their activity during presentation [72]. Altogether, results demonstrate that circuits centered in the fusiform gyrus (in either hemisphere) were implicated in face imagery.

The interactions between mental imagery of faces and social processes, such as stereotyping, have rarely been studied (reviewed in Eisenstadt, Spagna, Stroessner, *in prep*), despite images of social categories (e.g., race and gender) underlie how groups and their members are understood, evaluated, and treated (e.g., [149]). Dotsch et al. [36] used a face imagery task to explore this issue, and concluded that participants' representations of ethnic faces are related to their level of prejudice. Participants completed a two-alternative forced choice task featuring two faces placed side by side on the screen. On each trail, they then were asked to select the more Moroccan-looking face out of the two by imagining a stereotypical face. Hence, this task could only be completed by voluntarily activating a stereotypical mental image with certain characteristics and comparing it with the two images on the screen. The prejudice level for the image chosen in this construction phase was later assessed. Participants in high prejudice subgroups choose a mental image with stronger negative associations (more criminal-like and less trustworthy), indicating that visual imagery plays an essential role in intergroup relations.

The observed depth of research on mental imagery of faces might be due to the plethora of studies investigating face / place differential activation in the VTC during perception [96]. As such, stimuli used to study face imagery and perception overlap, and include imagining faces of famous people [67,119], of familiar people [67,119], as well as stereotypical and prototypical traits related to race [36]. As relevant to the question of differences between imagery and perception, participants seem to complete face imagery tasks without difficulty, even when required to visualize only details of a stimulus (e.g., the nose as opposed to the entire face) or to use facial representations to inform social judgment. Such seeming similarity between imagery and perception is surprising and warrants additional investigation, as faces are often considered complex stimuli [45]. Findings converge over the importance of regions within the ventral temporal cortex (e.g., the fusiform face area) either lateralized to of the right hemisphere [72,119] or bilateral [66], as well as potential involvement of frontal and parietal regions in face imagery. Altogether, these correlational findings are in line with neuropsychological evidence [13,19,53], indicating the partial overlap of the neural substrates supporting perception and imagery of faces in the inferior temporal lobe, with a lateralization pattern remaining unclear. Hence, activation in the VTC region along with frontoparietal network and fusiform gyrus observed for face imagery parallels what observed for the visuospatial imagery domain reviewed above, and further strengthens the evidence in favor of a distinction of domain-specific (FFA) and domain-general (FPN and FIN) roles of these regions in VMI.

4. Mental Imagery of Colors

Color mental imagery has been defined as the ability to recall and manipulate colors at will [7,11,40]. Color imagery can be used to enhance the creativity of the mind's eye. For example, painters might use color imagery to envision how a painting might look and what it can become. The literature on mental imagery of color features several single case studies of patients who have sudden vision loss and sudden color blindness but are still able to mentally visualize color (recently reviewed in Bartolomeo [150]). Below, we summarize the literature on clinically normal individuals and then discuss how this relates to evidence from lesion neuropsychology.

Howard et al. [63] used fMRI to disentangle the functional anatomy of color perception and color imagery. Participants either perceived colors or generated visual mental images of colors in order to complete a relative darkness judgment task (e.g., is the red shade of a strawberry darker than that of a raspberry). While behavioral results were comparable between imagery and perception, neuroimaging results showed a clear dissociation between perception and imagery of colors. Specifically, brain activation associated with color perception was observed in the bilateral fusiform gyrus, bilateral insular cortex, right sided lingual gyrus, and primary visual cortex. Color imagery, however, was associated with activation in areas in the temporal lobe (including the right parahippocampal gyri, hippocampus, and right anterior fusiform gyrus) as well as left insula, but not in primary visual cortices. Similarly, Bannert and Bartels [5] observed no behavioral difference in performance related to imagined and perceived colors along with a lack of significant decoding accuracy in the primary visual cortex for imagined colors. Participants completed two tasks: a color-related perception task, in which participants viewed three different colors and indicated whenever the color changed brightness, and a color imagery task, in which participants memorized colored objects and mentally visualized the object indicated by a visually-presented cue word. In the imagery task, participants then indicated whether the object they just imagined matched (congruent condition) or did not match (incongruent condition) the color of a visual object. Decoding accuracy from activity in the striate cortex did not reach statistical significance for color imagery, while color could be decoded from all retinotopically mapped visual areas. Activity from human V4 successfully predicted which color participants had imagined on a trial by trial basis when classifiers were trained on responses to physical colors [5]. This result centers hV4 as a key region in the mental representation of colors, whether perceived or imagined.

Evidence for the lack of a role of early sensory cortices in imagery of color also comes from neuropsychological evidence in patients with acquired achromatopsia. For example, Shuren et al. [118] administered three color tasks to patient E.H, a 63 year old man who noted that everything looked gray and devoid of color after a cerebral angiogram following a year of living with ataxia. In the Mental Color Imagery Task, the patient was told the names of 15 objects whose color name is uncommon. He was asked to imagine the object and name its appropriate color (e.g. "What color is a U.S. mailbox?"). In the Mental Hue Comparison Task, Patient E.H was given 15 verbal pairs of colors and asked which of the pair had more of one color than the other (e.g. "plum and eggplant, which has more red in it?"). In the Color Odd-Man-Out Task, patient E.H was given 15 verbal triads of objects, two of which had the same or similar color. He was asked which two objects had the same color. Compared to control subjects, E.H. showed preserved color imagery and color naming of visually imaged colors across the three tasks. This led the authors to conclude the existence of a dissociation between top-down and bottom-up processing in a single visual system that mediates both color imagery and color perception. Similar results were described in another case of acquired achromatopsia with preserved mental imagery for colors [11]. Zago et al. [145] compared performance from P.B., an 86 year old who was hospitalized in 2008 for sudden vision loss due to bilateral occipital lobe infarction and *Anton syndrome* (ie, anosognosia for blindness: the patient was unaware of his blindness and claimed to be able to see), with age-matched male controls. Participants were required to mentally visualize symbols, objects, animals, and colors and to answer a pool of questions regarding their structural characteristics. P.B. had no visual imagery disorders when compared with the performance of healthy participants. This result further supports the lack of a role of the primary visual cortex in color imagery ability.

Hsu et al. [65] used fMRI to examine brain activation during retrieval of color knowledge and to identify factors such as context (e.g., finding the strawberries in a fruit salad that also includes either raspberries or watermelon) and cognitive style (i.e., a preference for visualization or verbalization) that can influence it. Participants saw the names of three items and asked participants to indicate which two of the three items were most similar in terms of color while they underwent fMRI recordings. The options either differed by color categories (ie., comparing *paprika* and *pencil* to *ladybug*) or within the same color category (eg., comparing *butter* and *egg yolk* to *school bus*). While the authors discussed results from this study in the context of memory retrieval and semantics, an imagery component may also be required to visualize and compare names of colors from their written form. In line with findings from Bannert and Bartels [5], performance for items in different color categories was better than that for items within the same color category, both in terms of response times and accuracy. Neuroimaging results showed increased activation in the left fusiform and lingual gyri for the same compared to different color categories. In subsequent work, Hsu et al. [64] investigated potential differences in making a luminance judgment (lighter/darker) on a named pair of chromatic (e.g., lemon and basketball) or achromatic (eg. coal and snow) objects. Participants were faster in responding to achromatic blocks compared to chromatic blocks, an effect that the authors ascribe to the function of color retrieval. Yet, this task cannot be completed without using mental imagery. After completing the knowledge retrieval task, a color perception task was used as a functional localizer of brain regions involved in color perception. Participants saw stimuli from the Farnsworth-Munsell 100 Hue stimuli, and had to identify whether the wedges making up colored or grayscale wheels were ordered from lightest to darkest sequentially. Neuroimaging results showed an increase of BOLD fMRI activation in the left lingual gyrus while participants were performing either the perception or the memory retrieval tasks, highlighting that a chromaticity effect reliant on VTC high-level visual areas known to be involved in color perception [78].

Color imagery has also been studied in absence of color structure (i.e., pure color imagery; [23,24,138]). For instance, Chang et al. [23] examined whether color imagery could occur without the compound (or confound) of shapes and form (ie., imagining a red square instead of pure red). As a measure of the interfering effects of background luminance, participants followed a visual cue prompting them to imagine a color during either an imagery condition (the background remained black), or the background luminance condition (the background rapidly brightened over a short period, remained at full brightness, and then ramped off). After the imagery interval, a colored rivalry stimulus (ie., two low-luminance differently colored Gaussians curves) was presented, and participants reported the dominant color by pressing the corresponding numbered keys. Mental imagery of pure colors had a priming effect on subsequent binocular rivalry: participants' prior color imagery and perception biased perceptual dominance, with little to no difference between imagined and perceived colors. In a second experiment, the authors observed this priming effect of imagined colors over perceptual dominance only when both processes occurred in the same retinotopic location. These results suggest that perceptual and imagery processes involving color stimuli influence each other, adding additional evidence regarding their shared mental processes. In another study, participants were visually cued with a color name or image and instructed to mentally generate an image of that color Wantz et al. [138]. They were then presented with 6 different color patches and had to select the one that was either congruent or incongruent with the initial cue. Results from this study showed how color imagery can benefit conscious visual processing of colored stimuli. The effect of imagery on subsequent color perception of the pop out effect was also observed by Cochrane et al. [24]. The pop-out effect occurs when a target in a visual display stands out from surrounding distractors due to a single distinguishing feature [135]. The researchers conducted five experiments in which they manipulated the pop-out effect using a priming procedure that involved repeating a target feature between trials to improve performance. To manipulate participants' expectations, the authors used mental imagery and found that the pop-out effect could be reversed when participants imagined a color that was opposite to the target color from the previous trial. Performance was better when the imagined color (e.g. green, opposite to the previous red target) and the color of the target in the next trial (e.g., green) happened to be the same.

The possibility to use color imagery to guide attentional selection of stimuli during a visual search was the object of investigation in a series of experiments conducted by Moriya [93]. In these experiments, participants were asked explicitly to generate a certain color in their mind either directly or through an object closely associated with it. Then, they were presented with 2, 4, or 6 Landolt-C-like squares, each with one gap on the side. Only the target stimuli (but not the distractor) had the gap at either the upper or the lower location and participants had to identify it through pressing the designated key. In valid trials, the imagined color was the same as the target stimuli while in invalid trials it was the same as the distractor stimuli; in neutral trials, this color was absent. Increased response times in invalid trials compared to valid trials, an effect that was not observed in a control experiment in which participants were not explicitly instructed to imagine the color. The authors concluded that attentional resources had been allocated towards the imagined stimuli.

Overall, three interim conclusions can be drawn: 1) color mental imagery has been extensively studied using either colors embedded in objects (e.g., the yellow of a banana) or pure color imagery (a red patch). Further, there is an abundance of evidence regarding the effects that color imagery has on subsequent color perception [24,138] and attention [93]. 2) The most consistent finding seems to be the activation of the lingual gyrus in color imagery, although the extent of hemispheric lateralization is unclear (right hemisphere: [63]; left hemisphere: [64,64,106]). Activation of the lingual gyrus was also anecdotally observed in visuospatial navigation tasks requiring the exploration of familiar routes - often imagined in color [15,139]. 3). Evidence for activation of the fusiform gyrus (right: [63]; left: [65]) and hV4 region [5,106] of the visual cortex, as well as the lingual gyri has also been demonstrated. Last, both neuropsychological (reviewed by [11,118,145,150]) and neuroimaging studies [63] indicate the absence of a role for primary sensory areas in color imagery. Taken together, the consistent activation observed in the lingual gyrus [15,64,65,139] might suggest a domain-specific role for this region in color imagery. Yet, some evidence suggests that the anterior patch of this region may process both color and shapes [78,120,121]. Activation of the hV4 [5] and para-hippocampal areas [63] is frequently observed during color imagery, opening to the possibility that these three regions form a domain-specific color-imagery sub-network. The recurrence of fusiform gyrus activation observed for this domain provides compelling further support for the hypothesized domain-general role of this region in VMI.

5. Mental Imagery of Shapes

Mental imagery of shapes has been defined as our ability to elaborate mental images of a precise object without its external presence [29]. This ability is foundational for the construction, transformation, and rotation of complex three-dimensional scenarios necessary for visuospatial mental imagery.

We begin by reviewing results from a series of fMRI studies on mental imagery of shapes that share the same criticality: a lack of behavioral response that allows objectively distinguishing whether participants performed the mental imagery task correctly or not. D'Esposito et al. [31] used fMRI to investigate mental imagery generation using word shapes as stimuli. Participants either actively imagined (concrete condition; e.g., 'apple', 'house', 'horse') or passively listened to (abstract condition; e.g., 'treaty', 'guilt', 'tenure') auditorily presented words while undergoing fMRI recordings. Because participants were not required to perform any overt response, the study did not report behavioral results. Neuroimaging results showed that for all seven participants, an increase of BOLD fMRI activation was observed in the left inferior temporal lobe (particularly in the fusiform gyrus) in the concrete condition compared to that in the abstract condition. In another study, Handy et al [57] used fMRI to evaluate whether visual cortex activation associated with visual mental imagery is modulated by the memory retrieval strategy used to activate the to-be-imagined content. Participants visualized objects by either recalling pictures encoded during a familiarizing session (i.e., picture task) or their common knowledge (i.e., nouns task) while undergoing fMRI recordings [57]. Then, they subjectively reported their success in visualization during each fMRI run (approximately 6 minutes in duration). Neuroimaging results from the contrast between the conditions of imagery of pictures vs rest and imagery of nouns vs rest showed comparable results. Neural activity was observed across the anterior (frontal, bilateral) and posterior (inferior temporo-occipital and inferior parietal) cortices. Further, results showed greater activation of the left fusiform gyrus in both tasks vs rest, while no temporal activation was observed when comparing the two (contrast picture vs nouns). In another study, Yomogida et al., [143] examined how individuals use mental imagery to synthesize known information and create new mental objects. Participants underwent fMRI recordings while generating a visual image by synthesizing two items (words or drawings) and to indicate the completion of this imagery process by button press. Outside of the scanner, they then drew what they imagined on a piece of paper. Both the imagining and synthesizing items based on words or drawings were associated with the activation of the left inferior frontal lobe and the left inferior temporal region. The study by Gardini et al. [48] shares the same criticality highlighted for the studies D'Esposito et al., [31], Handy et al., [57], and Yomogida et al. [143]. In the Specificity Task, visual mental imagery was elicited by means of visually presented words indicating a highly familiar item (e.g., a cat) while participants underwent fMRI recordings. Familiarity of the list of items used was assessed in a separate sample of college students in the authors' institution. The task had three conditions: 1) a nonspecific imagery condition where participants were told to imagine the stimulus in an imprecise, nonspecific manner; 2) a specific imagery condition where they imagined the stimulus in a specific and detailed manner; 3) a baseline condition where participants were given abstract words and pressed a button after reading each word. In either active condition, participants pressed a button when they completed the image generation. Response time for imagined nonspecific images being shorter than specific images. Neuroimaging results comparing nonspecific image generation with the baseline condition were associated with the activation of the left frontal lobe, including the medial and superior frontal gyri. Compared to the baseline condition, specific image generation activated the left superior frontal gyrus, and both the anterior and the posterior cingulate. Lastly, the contrast between specific vs nonspecific imagery was associated with activation in the frontal regions along the lateral and medial surface, and in the right middle occipital gyrus.

Trial by trial responses to shape imagery were collected by Mazard et al. [88], Kashihara and Nakahara [70], Belardinelli et al. [14], and Palmiero et al. [99]. Mazard et al. [88] studied mental imagery of shapes by using five two alternative-forced-choice tasks concurrently with fMRI recordings: 1) a baseline task (listening of letters or numbers and indicate vowel or even by button press), 2, 3) two imagery tasks, requiring to imagine whether or not an object (e.g., a bottle) or non-object (e.g., a random shape) presented auditorily has the properties described in a statement (e.g., higher than wide) by reporting a true/false response; and 4, 5) perception tasks, using the same items and commission of the imagery tasks, but with visually presented stimuli. Results showed better performance for objects compared to non-objects, both for imagery (higher accuracy and lower response times) and for perception (higher accuracy). Neuroimaging results from the contrast between imagined objects compared to non-objects showed a left-lateralized activation in the occipito-temporal regions and in the inferior frontal region. Kashihara and Nakahara [70] used a delayed match-to-sample procedure to examine participants' performance on four mental imagery tasks using 2D and/or 3D geometrical shapes while undergoing electroencephalographic recordings. Participants were asked to store 2D (tasks 1 and 2) or 3D (tasks 3 and 4) shapes in working memory to perform a true/false judgment. Yet, task 3 required to mentally rotate the 3D figure based on various 2D viewpoints to indicate whether a new figure, presented after a delay, matched or not the initial one. Participants' performance was reduced by the additional operation of mentally rotating the shape, in terms of both RT and accuracy. These results were associated with increased theta-band activity detected from frontal lobe sensors. In two fMRI studies ([14] and [99])), participants completed the Questionnaire of Mental Imagery (QMI) [109] to assess the vividness of their mental images. They then completed a mental imagery task while undergoing neuroimaging recordings. The task required them to create a mental image based on the meaning of an auditorily presented statement and maintain that image until the next sentence was delivered. Statements tapped on different imagery modalities (e.g., visual: "to see a candle"; auditory: "to hear a shot"; tactile: "to touch something hard"; olfactory: "the smell of alcohol"; gustatory: "the salty taste"; somatic: "the sensation of fatigue"; kinesthetic: "the activation of writing"; abstract - non imagery: "racial prejudice"). Neuroimaging results from the BOLD fMRI contrast including all imagery modalities vs the abstract condition showed the activation of the left fusiform gyrus. Further, comparing activation in high-vivid vs low-vivid imagers based on the QMI ratings allowed the observation of modality-specific activation in primary and secondary sensory areas (e.g., occipital for visual; anterior insula for gustatory), suggesting that the neural processes underlying modality-specific perception may also be used for imagery when evoking vivid images. In another study, Dijkstra et al. [34] investigated the relationship between vividness of shape imagery (as well as letters and faces - discussed in their respective sections) and BOLD fMRI responses. Results showed an effect of mental imagery vividness on lateral occipital and inferior temporal cortices.

The relationship between visual mental imagery of shapes and visual memory was investigated by Slotnick et al. [123]. Participants first familiarized with a list of objects (drawings) and later recalled (memory task) or visualized (imagery task) objects from the familiarization list. While in the memory task, participants reported whether they remembered, were familiar with, or did not remember the object; in the imagery task, they reported whether the image had a high, moderate, or low vividness. In some trials, participants were also presented with one of three control words (left, right, center), and were asked to press a corresponding button. Participants were highly accurate in performing the three tasks. In line with results from another study investigating the interrelations between visual imagery and memory [57], performance on the imagery task was associated with increased BOLD fMRI activation in occipital-temporal regions, including the fusiform gyrus and frontoparietal domain-general regions.

Lesion studies further elucidate the causal role of the left inferior temporal regions with visual mental imagery. Mehta et al. [90] first linked mental imagery deficit with temporo-occipital lesion causing visual agnosia. In this study, nine neurotypical individuals and one agnosic patient completed six tasks, out of which two tapped on mental imagery and employed written words presented on the screen. In one task involving object imagery, participants visualized the shape of three auditorily presented objects and identified which two were more similar (e.g., hammer, ax, saw - with the correct answer being hammer and ax). The other task involved mental imagery word-shapes, and required visualizing the shape of three words written in lowercase that were presented in uppercase, and identify which two were more similar in shape (e.g., BOOK, TAIL, HEAD - which in lowercase look like book, tail, head - and the correct response being book and head). The patient with visual agnosia due to bilateral (mostly right-sided) lesions performed significantly worse in both the object imagery and word-shape imagery tasks than 9 neurotypical controls. The first of these two tasks was also used by Hayakawa and Keysar [59] to evaluate the effect of bilingualism on the vividness of mental imagery. The vividness of imagined shapes cued by words visually presented in a foreign language was reduced compared to that of words presented in the native language. In the Shape Mental Imagery Task [29], participants with early blindness (i.e participants who lost sense of sight before the age of 6) were given everyday objects (e.g., toothbrush, teapot, etc.) for tactile exploration and familiarization outside of the PET scanner. During PET acquisitions, subjects then built a mental image of the shape of the object by an auditory cue presented, and to answer a series of questions on the visual aspect of the target (e.g., for the word "scissors", they were asked whether or not its holes are of equal size). Participants' performance was satisfactory in the amount of details the subjects could retrieve (around 80 %). Neuroimaging results from the contrast between the imagery condition (auditory cue words) vs control condition (noise sounds instead of cue words) showed activation in lateral occipito-temporal areas, including the left posterior part of the fusiform gyrus, and the posterior part of the inferotemporal gyrus. The focus of activity also extended medially to the border between the fusiform gyrus, the lingual gyrus, and the posterior part of the cerebellar vermis. More recently, an indirect link between mental imagery of 3D objects from 2D figures has been also shown in a clinical case of an architect who lost the ability to imagine following bilateral strokes in the posterior cerebral artery territories [133]. The authors compared the neuropsychological profile of five individuals with bilateral ($n = 4$; 3 non-aphantasic patients and one aphantasic architect) or right-lateralized ($n = 1$; a non-aphantasic architect) posterior cerebral artery strokes. Loss of mental imagery was observed only in the aphantasic architect, a deficit that was associated with a lesion in the left fusiform gyrus and in the right lingual gyrus.

Overall, two main conclusions can be drawn from the literature regarding shape mental imagery. First, tasks employed the shape of the object [31,90,143] the shape of a word [90], or the manipulation of the shape of an object through varying specificity [48], viewpoint of an object [70], or changing of the shape [143]. Interestingly, the ability to imagine shapes appears to be a logical prerequisite for mentally visualizing trajectories and rotations of objects. However, despite this apparent connection, no research has directly yet examined this relationship, nor have we found evidence of a direct comparison between shape imagery and perception. Second, brain regions activated were often located in the temporal lobe [14,29,31,88,123], particularly the left fusiform, and in the frontal [48] and parietal [143] lobes.

To summarize the literature on shape imagery, domain-specific activation can be observed in occipito-temporal regions (e.g., [88]; Yomogida et al. [143]) while domain-general activation stems from left fusiform (e.g., [31,57]) and frontoparietal regions [48,57,143].

6. Mental Imagery of Letters

Letter imagery acts as a bridge between language-specific processes related to phonology and morphology by allowing us to make judgment about words and single characters starting from their sounds [74]. Letter imagery also acts as a tool that aids in simple thought processes, and has been shown to help adolescents to excel in the development of literacy and written language comprehension [25]. For example, in the study conducted by CabáN et al. [21], participants who used the mental image approach scored higher on spelling tests than participants who did not partake in the mental image task. These results were interpreted as indicating that the quality of spelling instruction for eighth grade students was better improved by the mental imagery method than the other two standard approaches to spelling instruction.

Podgorny and Shepard [101] showed behavioral differences between imagined and perceptual processes using a letter task. Participants were either shown a 5 × 5 grid or a 5 × 5 box with no grid lines. Participants either saw or imagined specific squares of the grid to be darkened in order to form a letter stimulus (e.g. a darkening of the box forming the letter F). Then, a blue dot was presented somewhere on the grid, and participants pressed a pedal once they determined if the dot was on a darkened square or not. Response time increased with more complex letter stimuli (i.e. the letter E has more darkened squares than the letter L), and for off-letter dots. In a follow up experiment, participants were instructed to view or imagine letter stimuli “L” or “F” placed in different locations throughout the grid. However, this time they were sometimes shown two dots in two different squares or two dots in the same square. Participants decided if any dot presented to them were in the letter stimuli. Response times were faster when the letter stimuli were in the left part of the grid (see Formisano et al., [43] visuospatial imagery study for a similar asymmetry). Participants also displayed faster RT for seen stimuli than for imagined ones. Further, dots that were on the letter resulted in faster RT than off-letter dots. Error rates increased as off-figure dots got closer to the figure. Similarly, Kosslyn et al. [[73,74] exp. 3] found that imagining smaller letters was more challenging for participants compared to imagining larger letters, as suggested by their slower response times. Further, the authors used PET recordings to show that this pattern was associated with activation in the primary visual cortex along the medial surface (area 17), with an anterior / posterior gradient of activation for large / small letters [74]. Mentally formulating large letters also activated regions in the left superior and middle temporal gyrus, while mentally building small letters activated the left precentral gyrus and the right dorsolateral prefrontal area. In another PET study, Gulyás [54] examined the behavioral and neural correlates of reading by asking participants to perform under three conditions: 1) listing the letters of the Hungarian alphabet in due order and internally reciting the national anthem; 2) visualizing the letters of the alphabet; 3) and visualizing the capital letter of the first verse of the Hungarian anthem internal listing. Participants visualized the letters of the anthem more easily compared to letters of the alphabet, a behavioral effect associated with increased metabolic activity of the anterior cingulate cortex. Yet, results from PET scans showed that both task conditions (*anthem* and *alphabet*) were associated with increased activation of regions along the bilateral intraparietal sulcus compared to rest. Further, visualizing letters of the alphabet was associated with left-lateralized activation spanning across the middle, medial, and superior frontal gyrus, as well as of the lateral occipital gyrus. Activation of frontal regions was also observed by Stokes, Thompson, Nobre et al. [129], who developed a task requiring participants to imagine either the letter X or O as instructed by an auditory cue. Participants reported being able to imagine the stimulus in most trials, and this effect was associated with the bilateral activation of frontoparietal regions. The involvement of frontoparietal and VTC regions associated with mental imagery of letters was also observed by Dijkstra et al. [34]. Mental imagery vividness of letters modulated the activation of right-lateralized intraparietal sulcus and inferior temporal gyrus.

The role of the neurons in the inferior temporal gyrus in imagery of letters was further illustrated in a study conducted on a epileptic patient who underwent intracranial electroencephalographic recordings [56]. The patient performed two working memory tasks (delayed match-to-sample tasks for visuospatial or verbal stimuli) and a visual imagery task (requiring to mentally visualize letters being drawn on a blank sheet of paper). The quality of the mental imagery was assessed by patients’ self-report on how well they performed the task, what they were actually imagining and how difficult it was for them to follow the instructions. Increase in gamma band activity was observed in contacts located on the lateral side of the fusiform gyrus during visual mental imagery but not perception of letters. Contacts responding solely to letter perception were located along the medial surface of the fusiform gyrus. The authors concluded that neural networks supporting imagination and perception are distinct.

Characterizing the mechanisms underlying letter imagery can also serve as a way to further our understanding of clinical conditions during both development and adulthood. For example, Soulières et al. [124] showed that children diagnosed with autism display enhanced abilities to create visual images of letters compared to non-autistic IQ-matched control children. In their study, participants were instructed to imagine a letter inside a circle, and then indicate which of two highlighted portions of the circle would contain the greater proportion of that letter. The group of individuals with a diagnosis of autism was more accurate - though this difference was only marginally significant - compared to the group of participants with typical development, suggesting that enhanced abilities to create and compare visual mental images may be associated with this neurodevelopmental condition. Enhanced visualization abilities were also observed in individuals with schizophrenia by Matthews et al. [87].

Overall, visualizing and examining letters in “the mind’s eye” is often reported to be harder than merely identifying letters in a display [74] or listing single letters and words [54]. In addition, visualizing the letters of a national anthem, a meaningful text with emotional connotations, resulted in more of a gradual build up of activity in the frontoparietal networks associated with even greater reported difficulty [54]. Letter imagery recruits frontoparietal regions [54,129], and areas in the inferior temporal areas [129] especially the fusiform gyrus [56]. Recent evidence obtained using ultra-high field fMRI [82] indicates that letter/word imagery recruits both the domain-preferring visual word form area [30] and the domain-general FIN in a partially overlapping, but distinct region. More precisely, the anatomical location of the FIN tended to be more mesial, rostral and ventral than the VWFA. Activity in early sensory areas was also observed to be associated with letter imagery in some studies [73,74] but not in others (e.g., [54]). The engagement of V1 and V2 in visual imagery of letters is also suggested by recent reports showing the possibility to decode imagery of letters from early visual cortex activation [114], warranting additional future studies. Altogether, imagery of letters is supported by the activation of domain-preferring and domain-general regions in the VTC, and by a domain-general frontoparietal network.

7. Discussion

Over the past three decades, the field of human mental imagery has witnessed substantial advancements. We reviewed the findings derived from studies exploring visual mental imagery (VMI) across five domains. At the outset, we formulated three objectives: 1) examining the methodologies employed in VMI research, 2) comparing behavioral results between imagery domains and perception, and 3) reviewing evidence regarding the neurocognitive architecture supporting VMI. In the subsequent discussion, we will provide a concise overview of our findings regarding these questions.

7.1. How is VMI studied?

We have identified more than 50 distinct experimental manipulations that were developed to explore various aspects of visual mental imagery. These investigations spanned over 60 individual articles. Most studies focused on one perceptual domain or category at a time (e.g., navigating a familiar route [107], clock rotations using imagined clocks [51], letters [54], and colors [23]). This approach resulted in two distinct unintended outcomes that were nevertheless interrelated. First, the act of imagining a specific stimulus, such as a familiar route, can be accompanied by activation of additional domains, for instance, envisioning that path in color [16,139]. This intriguing and unexplored area of research questions the automaticity of cross-domain activation in VMI (e.g. does imagining a strawberry activate various attributes such as color and shape?). Furthermore, it prompts researchers to explore the corresponding brain activation patterns involved. Second, using a hard-lined distinction between domains appears to be insufficient, since many of these domains are interdependent. For instance, shape imagery might serve as the foundation for visuospatial abilities, as well as face imagery. Therefore, the following follow up questions emerge: does a lower-dimensional space underlie these VMI domains? What weight do conclusions drawn from studies utilizing a single set of imagined stimuli hold? Do these findings pertain exclusively to the specific perceptual domain or extend across a wider spectrum of visual perceptual domains within VMI? Exploring the potential existence of this lower-dimensionality could involve employing unsupervised clustering methods (e.g., t-SNE or k-means clustering). These methods would enable the clustering of participants' responses based on single-trial behavioral performance and neuroimaging data. Such analysis might reveal variances in domain-specific performance between imagery and perception, offering insights into potential disparities in their underlying cognitive mechanisms.

Only a limited number of VMI studies have concurrently explored multiple visual perceptual domains (e.g., faces, houses, and chairs, [66]; faces, letters and places [34]; faces, letters, and shapes [33]). These investigations offered initial insights into both domain-specific and domain-general mechanisms associated with visual mental imagery, illuminating distinctions from visual perception. However, these studies primarily employed a subtractive logic of activation, comparing activation across different conditions (e.g., letters vs. shapes). Consequently, the extent to which multiple imagery domains co-occur in response to a single cue word remains largely unexplored. Furthermore, the inquiry into the lower-dimensional space underlying these mental imagery domains remains entirely unaddressed.

We also observed differences in the methodologies used to study each VMI domain. Most studies within the visuospatial domain followed one of two methodological tracks: clock tasks [43,51,77,97,111,112,136] and map tasks [15,17,18,75,107,139]. Color mental imagery utilized more general approaches, such as comparison tasks (e.g. which color is darker) [5,63,64,118] or, less commonly, distractor tasks (e.g. imagine a color, then perceive an incongruent color) [24,93,138]. Some studies within the face domain employed common stimuli sets, such as famous faces [13,66,72,80,119]. We did not observe any distinct methodology within shape mental imagery, but experiments generally varied in the specificity with which participants imagined and judged stimuli. Letter imagery, aside from containing letters from various alphabets, also failed to have any distinct methodologies. Given the fewer number of studies within the shape and letter domains, this observation is not surprising.

Clinical conditions present opportunities to learn more about the neural regions associated with domain-specific and domain-general visual mental imagery. Specific conditions, such as prosopagnosia [13,53] and achromatopsia [11,118] result in domain-specific deficits. Alternatively, general loss of mental imagery abilities in conditions such as in aphantasia [133] allow for a domain-general study of VMI deficits. Lesion patients also present unique opportunities to localize domain-specific and domain-general deficits [72,90]. In this review, we highlighted the similarities in findings across domains, opening to advance our understanding of both visual mental imagery as a whole, and clinical conditions presenting imagery deficits circumscribed to one or few domains (e.g., imaginal neglect: [9,18,151–156]).

7.2. Is it more difficult to imagine than to perceive?

Contrary to our hypothesis, we did not observe consistent evidence for the increased difficulty for imagery compared to visual perception tasks. Specifically, performance differences favoring perception over imagery were found for visuospatial trajectories [122] and rotations [79], letters [54,74] but not for colors [63]. Yet, it must be noted that the lack of evidence may be due to the scant literature directly comparing behavioral findings on imagery and perception of an individual stimulus category, while most studies focused on within-category comparisons (e.g., imagining small vs large letters), within-imagery comparisons (e.g., imagining colors vs shapes), or their neural substrates. This endeavor warrants further investigations, as we believe it may shed light on the similarities of the computational mechanisms underlying VMI and visual perception.

7.3. What is the neurocognitive architecture supporting VMI?

Our inquiry into the neural architecture supporting VMI aimed to discern whether existing evidence more strongly aligned with a hierarchical or a heterarchical model. However, this review did not yield clear support for the reverse hierarchy model due to two main reasons: 1) contrary to the proposed complete spatial overlap between imagery and perception, numerous studies reveal a lack of activation in the early visual cortex during imagery tasks (e.g. [3,63,136]). In addition, the observed double dissociations in neural circuits underlying imagery and perception in neurological patients challenge the model's premise of complete overlap. 2) While neurobehavioral systems typically exhibit a hierarchy of processes involving information merging or nesting during sequential stages [41,46,60] evidence supporting such structured processes in VMI remains absent. For instance, in perception, tasks evolve over sequential stages of increasing complexity, demonstrating nesting processes [42,61]. However, current data lack evidence for similar nesting processes in VMI. The term 'Merge,' defining a linguistic computation that combines elements into a syntactic hierarchical structure, exhibits parallels in language processing [46]. For example, in the sentence "Imagine an apple", a determiner "an" and a noun "apple", individual elements, are merged together to form a higher-level element. The most posterior portion of Broca's area might be the neural substrate implementing Merge computations [144]. Yet, no direct evidence indicates a parallel 'Merge' process in VMI, despite the possibility that mental images are assembled in an as-yet-unidentified manner. In summary, this review did not find evidence for mental imagery processes being either nested - contrary to evidence for visual perception - or merged - as shown in language. The lack of evidence showing that VMI features either nesting or merging processes challenges the claim that imagery is the reverse hierarchical process of perception.

7.4. Heterarchy in VMI: Heterarchical Interactions among domain-General and -Preferring **Imagery** Networks (HeXaGeN)

The evidence reviewed here seems instead consistent with a heterarchical organization (see Fig. 2) of interconnected sub-networks [128]. High-level visual cortex appears to provide central nodes of such an architecture. A possible alternative model of visual mental imagery emerges, centered on high-level visual cortices: the Heterarchical Interaction among domain-General and -Preferring Imagery Networks (HeXaGeN). HeXaGeN makes the following testable predictions. (1) Visual mental imagery is "ignited" [86] by top-down feed-forward attentional processes. VMI ignition would be supported by domain-general prefrontal and parietal sub-networks linked by branches of the superior longitudinal fasciculi (see [126] for a discussion on this point). (2) The visualization process is shaped by the interplay between domain-general and domain-preferring regions within the VTC. (3) A domain-general node is located in the fusiform gyrus of the left hemisphere (the fusiform imagery node, FIN). The strategic location of the FIN between the temporal pole and domain-preverring VTC regions makes it a candidate for generating mental images by bridging semantic, episodic memory, and domain-specific information. (4) Domain-preferring activations in the ventral and dorsal cortical visual streams support domain-specific processing, such as in the case of FFA plus FIN for imagery of faces or lingual gyrus plus FIN for imagery of color. The vertical connections typical of heterarchical organizations [89] are provided by fibers of the arcuate fasciculus linking the FIN and frontal regions [55]. (5) The maintenance of imagery over time is facilitated by working memory processes supported by frontoparietal networks. (6) A sub-network supporting episodic memory functions that simulate events where multiple stimuli are presented together, with a key node being the hippocampal region [20,26,113,146]. (7) Sub-networks located in the anterior temporal and superior temporal gyri support semantic processes [159,160] associated with VMI. Horizontal fibers of the inferior longitudinal fasciculus link the FIN with anterior temporal regions. (8) Domain-preferring orbitofrontal regions integrate memories, value attribution, and decision making [1,158], connected to the anterior temporal lobe by the Uncinate Fasciculus [157].

The HeXaGeN model revolves around some of the key structures discussed in a model of visual conscious perception, the *global neuronal workspace* (GNW - [86]). According to GNW, the horizontal, recurrent connections that link structures in the prefrontal,

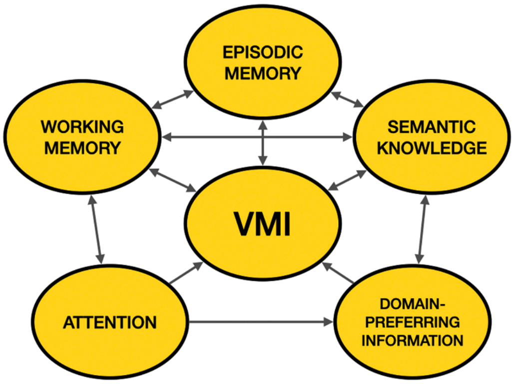

Fig. 2. A schematic depiction of HeXaGeN. This model includes vertical and horizontal connections among domain-general (eg, the *fusiform imagery node* in VMI) and domain-preferring (eg, FFA for faces, PPA for places) neural mechanisms. This flexible model allows mechanisms non-specific to VMI (e.g., attention, working and episodic memory, semantic knowledge) to be included in the architecture to support activation, maintenance, and use of VMI.

temporal, and occipital lobes are responsible for igniting and maintaining information. This information is then made globally accessible to local processors. Below, we will further detail the role of the three sub-networks directly involved in VMI visualization and highlight similarities between HeXaGeN and the GNW model.

7.5. Frontoparietal networks initiate and maintain imagery across multiple stimuli domains

In this review, we discussed evidence regarding *voluntary* visual mental imagery. It is therefore unsurprising that we observe activity in frontal and parietal regions associated with these results. The link between voluntary processes and frontoparietal activation is well-established [134]. For example, frontoparietal activity has been linked to the functioning of a *task-positive network* [44], which is activated when individuals are actively engaged in *any* task, and balances activation from the default mode network [104]. Others conceived the existence of a *multiple-demand system* [37] supported by wider brain networks compared to the task-positive network and including frontal, prefrontal, and parietal activity [116] and associated white matter fibers [71]. The multiple-demand system supports complex, multi-component behaviors [37] and has been specifically tied to human fluid intelligence [140]. Right-lateralized frontoparietal networks [126,142] and associated white matter tracts (Thiebaut [27,28]) support visuospatial attention [12]. Bilateral activation of the frontoparietal networks, and in particular the prefrontal cortex, has been associated with working memory [92,95]. Also, parietal activation contributes to aspects of shape perception [4], further complicating the picture. Hence, which of these constructs is instantiated by this frontoparietal involvement in VMI, and whether the same frontoparietal regions are associated with imagery activation and maintenance is still elusive.

Nonetheless, frontoparietal activation is observed consistently across all VMI studies, which invites the conjecture that these regions are part of a cognitive system that supports VMI activation and maintenance in relative independence of perceptual domain. Support for this claim comes from studies that focused on decoding stimulus-specific information from brain activity patterns. For instance, three studies reviewed here [15,105,137] were unable to decode stimulus-specific information from frontoparietal activity, although successful decoding was possible in another study [103]. The claim regarding the involvement of frontoparietal regions in the ignition of attentional mechanisms first and of the active maintenance later would be in line with (a) recent evidence showing attentional circuits directing attention towards internal thought or external objects [71]; (b) evidence showing frontoparietal activation in nonvisual mental imagery (e.g., olfactory, gustatory, kinesthetic; [99]); (c) the attentional ignition role of this frontoparietal activation [86]. Last, the role of frontoparietal networks in activation and maintenance of VMI could be tested using neuroimaging methods with high spatiotemporal resolution, such as magnetoencephalography (MEG) or stereotactic EEG (sEEG). MEG could track whole-brain connectivity patterns among domain-general and domain-preferring modules and subnetworks supporting attentional processes igniting visual mental imagery, directed from frontoparietal areas to brain networks supporting semantic and episodic memory processes. The greater spatial resolution of sEEG would complement this knowledge by dissociating across time and space between neuronal populations activated by the visual mental imagery prompts from those associated with maintenance of the mental images in working memory. Researchers have investigated the spatiotemporal dynamics of mental imagery and its similarity with perception using computational models [130], magnetoencephalography [33,35] and electroencephalography [141]. Altogether, results from these studies showed increased top-down modulation for mental imagery (of faces, letters, and shapes) compared to perception, while bottom-up modulation increases for perception compared to imagery [33], a pattern that the authors later highlighted as a reversal of the computational cascade [33] and that is linked to alpha oscillations [33,141].

7.6. The role of the FIN: a domain-general node bridging visual and semantic information

The second most consistent neuroimaging result in the reviewed literature is the activation of the fusiform gyrus (often left-lateralized) observed across different stimulus modalities and in 20 out of 64 articles. A crucial role of the left temporal lobe in mental imagery has been initially suggested by case reports of neurological patients (reviewed by [6]). Our recent meta-analysis of fMRI studies [127] pinpointed a specific VTC region in the mid-fusiform gyrus (Tailarach coordinates: -40, -55, -11), which we named as the Fusiform Imagery Node (FIN). In the present review we further specify this pattern. Activation in the fusiform gyrus was associated with visuospatial mental imagery [15,88,102,122], faces imagery [16,66,67,72,103,105,119,137], color imagery [63,65], shape imagery [14,29,31,57,99,123]. VMI of letters seems to be a special case, because only one study found activation of the fusiform gyrus [56]; the proximity of the FIN with the visual word form area, combined with the use of subtractive logic in the fMRI contrasts, might have canceled out the fusiform activation.

Activation of the FIN was observed predominantly in the left hemisphere, in an area neighboring with domain-preferring regions in the VTC. The strong lateralization of the FIN to the left hemisphere has recently been discussed in an article reviewing the hemispheric asymmetry of voluntarily generated visual mental imagery [81], and is also supported by tractography evidence on the anatomical connectivity of the FIN, showing preferential connections to the perisylvian language network through the arcuate fasciculus [55]. The current review, our previous meta-analysis [127], and our recent ultra-high field fMRI study [82], concur in showing a consistent activation of the FIN across different domains of VMI. This leads us to propose a domain-general role in visual mental imagery also for the FIN. In contrast with the domain- and modality-general role ascribed to frontoparietal activity leading to ignition and maintenance of mental images, activity in the FIN could process the visual features of semantic information (“visualization”). The spatial location of this region - neighboring with domain-preferring regions of the VTC, hippocampus for episodic memory, anterior temporal lobe for semantics, and perisylvian regions for language [55] - further points towards the potential bridging role of the FIN in VMI.

Gathering further evidence on the functional and anatomical connectivity of the FIN can assess the merit of the prediction made by the HeXaGeN model of the FIN as an *interface* between top-down influences from the frontoparietal and horizontal connections within the VTC. An interface enables the interaction between objects or mental representations without forcing each other to transform into a common code [62]. Interfaces create a third code or representation that is unrelated to the code used by (at least two) communicating processes. Therefore, an hypothesis could be advanced suggesting that the FIN acts as the VMI interface allowing, for instance, amodal semantic memories and visual information from domain-preferring regions to affect behavior.

Outstanding open questions are 1) what additional evidence would indicate that the FIN is a domain-general node in this heterarchical model of VMI? 2) Do we observe a third code in FIN neuronal populations, further confirming the role of this region as the interface? The most fundamental evidence for the domain-general role of the FIN would be provided by an increased functional connectivity between the FIN and domain-preferring regions under each domain. In other words, we should expect increased connectivity between FIN and FFA for face imagery (and not for other domains), while increased connectivity between FIN and LOC should be observed for shape imagery (and not for other domains). A well-powered study should also be able to decode which mental imagery domain was presented to participants on a given block of trials by the pattern of connectivity between FIN and domain-preferring regions. The above-mentioned testable predictions could be answered using whole-brain MEG recordings paired with tasks tapping on domains of mental imagery. Evidence for the role of the FIN as an interface could be obtained using sEEG, by investigating the existence of neuronal connecting processes within and outside a network located in the VTC and supporting imagery (e.g., domain-preferring and semantic information) populations coding.

7.7. Domain-preferring activation in domain-preferring regions

Domain-preferring VTC regions constitute another sub-network of HeXaGeN. Evidence regarding dissociations in performance across various imagery domains among neurological patients [6,49] led us to select the five domains reviewed: visuospatial, faces, colors, shapes, and letters mental imagery. For all five domains, imagery-related activations overlapped with some of the perceptual-related activations in high-level VTC visual areas, with the exception of the activation of the parietal lobe in visuospatial mental imagery. The involvement of domain-preferring regions in the VTC such as the fusiform face area (FFA) and the parahippocampal place area (PPA) was observed in imagery of faces and places, respectively [72,96]. These regions partly overlap with the corresponding domain-preferring circuits in visual recognition [30,38,69,76,78,84]. Further studies examining the degree of overlap between regional activation associated with domain-preferring perceptual and imagery processes should employ methods with the highest spatial resolution available. Yet, a balance will need to be sought for between individual anatomical subject variability and millimetric overlap in neural patches associated with VMI [82]. Functional connectivity analyses between these domain-preferring regions and domain-general regions may be challenging, because of the concurrent requirement of high temporal and spatial resolution. Space- and time-resolved techniques such as sEEG can provide the necessary evidence to assess these issues, provided that patients with suitable electrode placement can be recruited.

8. Conclusion

In summary, the complexities of visual mental imagery defies simple accounts invoking “a reverse” of visual perception, or a top-down only process. Rather, activation of domain-preferring regions, attentional and working memory mechanisms, and episodic memory and semantic processes all contribute to this complex cognitive function. Domain-general regions for activation and generation of mental images located in the frontoparietal networks interplay with a domain-general region in the left fusiform gyrus supporting visualization and bridging with semantics and episodic memory processes. A VTC network encompasses the relevant domain-preferring areas. Further, while not apparent in neuroimaging contrasts, semantic and memory processes must be involved in certain aspects of imagination. A heterarchical architecture seems to be more apt to support visual mental imagery, encompassing a distributed network spanning across several large-scale brain circuits, with still largely unknown spatiotemporal dynamics. We advance **a new model of VMI, HeXaGeN,** that distinguishes between domain-general and domain-preferring functions within the VTC, integrating neuroimaging and neuropsychological findings. This model not only presents a comprehensive perspective but also lays the groundwork for investigating its testable predictions.

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Declaration of competing interest

The authors declare the absence of any conflict of interest.

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