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I can see where you would be: Patterns of fMRI activity reveal imagined landmarks

Maddalena Boccia [a,b,*], Valentina Sulpizio [a,b], Liana Palermo [c], Laura Piccardi [b,d], Cecilia Guariglia [a,b], Gaspare Galati [a,b]

[a] Department of Psychology, "Sapienza" University of Rome, Rome, Italy
[b] Cognitive and Motor Rehabilitation Unit, IRCCS Fondazione Santa Lucia of Rome, Rome, Italy
[c] Department of Medical and Surgical Sciences, University Magna Graecia, Catanzaro, Italy
[d] Department of Life, Health and Environmental Sciences, L'Aquila University, L'Aquila, Italy

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ABSTRACT

Visual mental imagery arises when perceptual information is accessed from memory, originating the experience of "seeing with the mind's eye". Different content-dependent brain areas in the human ventral visual stream are activated during visual mental imagery, similarly to what happens during visual perception. The neural patterns within these regions, but not in the early visual cortex, are similar during imagery and perception, suggesting that, in the absence of perceptual stimulation, content-dependent brain areas are able to re-instantiate specific neural patterns allowing for mental imagery. However, it remains unknown whether these areas contain adequate neural representations that create mental images or need to interact with other regions in the brain, such as the hippocampus (HC), to access the necessary information from memory. To test this hypothesis, we used functional magnetic resonance imaging and both multivoxel pattern classification and psychophysiological interaction analyses. Participants were scanned while viewing or imagining scenes of familiar environments. We found that the identity of familiar places can be decoded from the neural patterns in the parahippocampal place area (PPA), retrosplenial complex/parieto-occipital sulcus (RSC/POS) and HC, during both imagery and perception, and that item-specific information from perceived places was re-instantiated during mental imagery of the same places and vice versa. Furthermore, the right PPA significantly interacted with the right HC and RSC/POS according to the performed task. Specifically, the functional coupling between PPA and HC was higher during mental imagery, whereas the functional coupling between PPA and RSC/POS was higher during perception. Our investigation provides an important contribution to the understanding of how the brain uses previously acquired knowledge to build a mental representation of the world.

Introduction

Mental imagery concerns the human ability to access previously encoded perceptual information from memory (Farah, 1989; Kosslyn, 1980), together with the associated details, to create a complex and sophisticated mental experience of objects, people, or places. Functional magnetic resonance imaging (fMRI) studies show that different content-dependent areas of the ventral visual stream are activated during visual mental imagery depending on the content of the image, similarly to what happens during visual perception (Ganis et al., 2004). For example, imagining a face leads to activation of the fusiform face area (FFA), a brain area related to face perception, whereas imagining a scene leads to the activation of the parahippocampal place area (PPA), a brain area known to be related to place and scene perception (O'Craven and Kanwisher, 2000). Recent fMRI studies, adopting an information based approach aimed to identify cognitive states on the basis of multivoxel regional signals (Kriegeskorte and Bandettini 2007a, b), have been able to decode the items participants were imagining starting from the neural patterns of specific content-dependent brain areas in the ventral visual stream (Naselaris et al., 2015; Johnson and Johnson, 2014), similarly to what happens during decoding of perceived visual stimuli (Kriegeskorte et al., 2007). The PPA and the retrosplenial complex, i.e., the brain region encompassing both the retrosplenial cortex proper (Vann et al., 2009) and the anterior bank of the parieto-occipital sulcus (hereafter called RSC/POS; Sulpizio et al., 2016a), also contain a neural code for the position of

* Correspondence to: Department of Psychology, "Sapienza" University of Rome, 00185 Rome, Italy.
E-mail address: maddalena.boccia@uniroma1.it (M. Boccia).

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imagined familiar places (Boccia et al., 2015b) and the heading assumed on a particular trial (Vass and Epstein, 2016).

The finding that the neural patterns during imagery and perception are similar within the content-dependent brain areas of the ventral visual stream, but not in the early retinotopic brain areas (Reddy et al., 2010), strongly supports the idea that, in the absence of perceptual stimulation, these regions are able to re-instantiate specific neural patterns which allow for mental imagery. However, it remains unclear whether these regions contain neural patterns coding for the identity of previously experienced stimuli (e.g., familiar places or faces) which are part of the individual's episodic knowledge, or whether they must interact with other regions, such as the hippocampus (Eichenbaum et al., 2012; Moscovitch et al., 2005), to access and associate perceptual information for creating mental images.

Interestingly, PPA, RSC/POS and HC, together with a set of areas in the caudal inferior parietal lobe, are nodes of a dedicated parieto-medial temporal lobe network underpinning spatial navigation in both monkeys (Kravitz et al., 2011) and humans (Margulies et al., 2009; Boccia et al., 2015a), and their functional interactions predict individual navigational abilities (Sulpizio et al., 2016b). Within this neural network each region plays a different and complementary contribution. The PPA and the RSC/POS are thought to play separate and complementary roles in human navigation (Epstein et al., 2007; Iaria et al., 2007), i.e., the representation and the localisation of visual scenes, respectively (Epstein, 2008). According to one influential model (BBB model: Burgess, Becker, King, & O'Keefe, 2001; Byrne et al., 2007), the posterior parietal lobe provides an egocentric "window" into long-term spatial memory, serving mental imagery, planning and navigation, whereas the medial temporal lobe allows for allocentric coding, with the parahippocampal gyrus building allocentric representations and the HC storing them into long-term spatial memory. Finally, the RSC would allow accessing spatial representations stored in an allocentric format by the egocentric parietal window, and vice versa. Along this model, medial temporal lobe areas are mutually interconnected to allow pattern completion/recall of "full" representation of a place, which consists of observer's location, landmarks and their visual appearance (Byrne et al., 2007). The HC has also been shown to be essential for memory consolidation (Eichenbaum et al., 2012) and encoding of coherent representations. Specifically, following Horner et al. (2015), the HC a) binds event elements coded in distinct cortical regions into coherent "event engrams" and b) allows re-experiencing and holistically retrieving all aspects of such events, by means of hippocampal pattern completion and cortical re-instatement.

The dynamic interaction among the above-mentioned brain areas serving mental imagery and actual navigation/perception is largely unknown. Here we aimed to assess a) whether similar neural mechanisms underlie visual perception and visual imagery of familiar places (hereafter called landmarks) within the brain areas involved in scene perception (PPA and RSC/POS) and memory (HC); b) whether in these areas specific neural patterns encode landmark identities; c) whether visual mental imagery re-instantiates the same neural patterns as during visual perception; and d) whether scene-selective brain areas (i.e., PPA and RSC/POS) interact with the HC during visual imagery and visual perception of familiar landmarks. With these aims we developed an fMRI carry-over design (Aguirre, 2007), which allows for analysing data

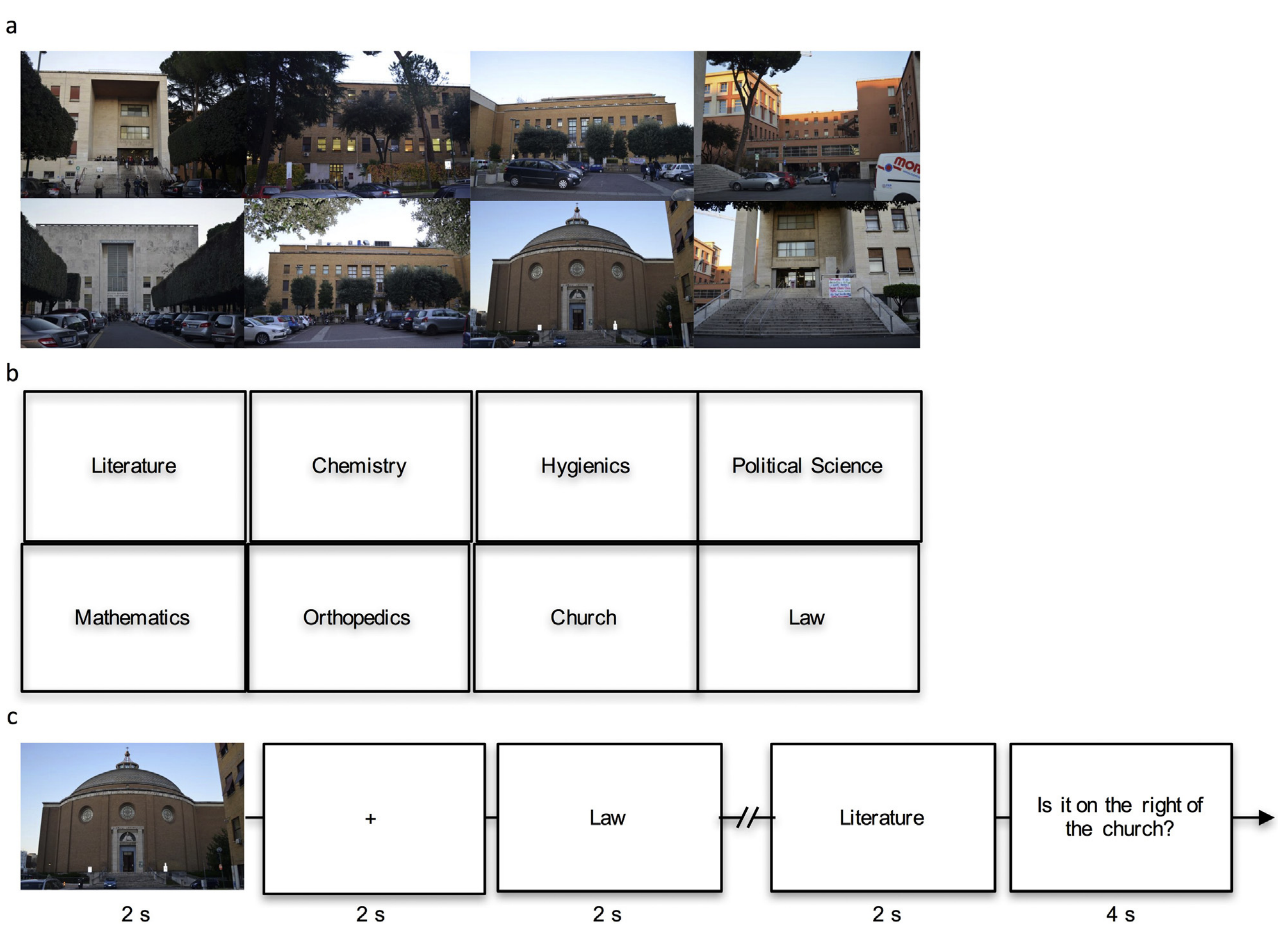

Fig. 1. Stimuli and Task. A, perceptual trials. B, imagery trials. C, experimental trials and timeline.