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How landmark suitability shapes recognition memory signals for objects in the medial temporal lobes

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ABSTRACT

A role of perirhinal cortex (PrC) in recognition memory for objects has been well established. Contributions of parahippocampal cortex (PhC) to this function, while documented, remain less well understood. Here, we used fMRI to examine whether the organization of item-based recognition memory signals across these two structures is shaped by object category, independent of any difference in representing episodic context. Guided by research suggesting that PhC plays a critical role in processing landmarks, we focused on three categories of objects that differ from each other in their landmark suitability as confirmed with behavioral ratings (buildings > trees > aircraft). Participants made item-based recognition-memory decisions for novel and previously studied objects from these categories, which were matched in accuracy. Multi-voxel pattern classification revealed category-specific item-recognition memory signals along the long axis of PrC and PhC, with no sharp functional boundaries between these structures. Memory signals for buildings were observed in the mid to posterior extent of PhC, signals for trees in anterior to posterior segments of PhC, and signals for aircraft in mid to posterior aspects of PrC and the anterior extent of PhC. Notably, item-based memory signals for the category with highest landmark suitability ratings were observed only in those posterior segments of PhC that also allowed for classification of landmark suitability of objects when memory status was held constant. These findings provide new evidence in support of the notion that item-based memory signals for objects are not limited to PrC, and that the organization of these signals along the longitudinal axis that crosses PrC and PhC can be captured with reference to landmark suitability.

Introduction

The ability to discriminate between previously encountered and novel objects, i.e., recognition memory, is a critical component of adaptive human behavior. A considerable body of research conducted with humans and non-human animals has focused on characterizing medial temporal lobe (MTL) contributions to recognition memory. There is consensus in the neuroscience literature that the integrity of perirhinal cortex (PrC) is critical for performance on recognition memory tasks (Meunier et al., 1993; Eacott et al., 1994; Brown and Aggleton, 2001; Bowles et al., 2007; Eichenbaum et al., 2007; Murray et al., 2007; Squire et al., 2007; Martin et al., 2011, 2012). It has also been suggested that PrC supports recognition memory in a manner that is distinct from the role of the hippocampus and parahippocampal cortex (PhC), with particular emphasis placed on its role in item-based recognition memory (also referred to as familiarity-based recognition memory), rather than recovery of contextual information about specific item encounters (Vargha-Khadem et al., 1997; Mayes et al., 2002; Yonelinas et al., 2002; Bastin et al., 2004; Quamme et al., 2004; Aggleton et al., 2005; Holdstock et al., 2008; Turriziani et al., 2008; Jäger et al., 2009; see Montaldi and Mayes, 2010; Ranganath, 2010; Wixted et al., 2010; Yonelinas et al., 2010; for review and discussion). An issue that has received limited consideration and investigation is whether the role of PrC in recognition memory is comparable across all object categories, and how object properties shape the differential involvement of MTL structures to recognition memory. The majority of results linking item-based recognition memory to PrC come from functional magnetic resonance imaging (fMRI) studies in which mixed word lists served as stimuli, and categorical structure of

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object representations was not systematically considered (for review, see Diana et al., 2007; Kim, 2013). Moreover, even when studies have addressed category-effects in the MTL with non-verbal stimuli, they have typically not focused on memory signals, i.e., on patterns of activation in relation to the outcome of recognition-memory judgments (Diana et al., 2008; Litman et al., 2009; Liang et al., 2013; Huffman and Stark, 2014; but see Martin et al., 2013; Kafkas et al., 2017).

Concerning the functional role of PhC in the MTL, a large body of evidence argues for an involvement in processing scene stimuli. Much of this research has focused on a region that shows a preferential response to scenes over objects, and that crosses the anatomical boundary between PhC and more posterior medial ventral visual pathway regions (see Epstein, 2008; for review). Scene specific responses in PhC have contributed to the proposal that this structure represents episodic context in recognition memory and recall (Davachi, 2006; Eichenbaum et al., 2007). Evidence from fMRI research conducted using non-mnemonic tasks suggests, however, that PhC also plays a role in representing items from some object categories (Epstein and Kanwisher, 1998; Bar and Aminoff, 2003; Cate et al., 2011; Mullally and Maguire, 2011; Konkle and Oliva, 2012; Troiani et al., 2012; Bastin et al., 2013; Harel et al., 2013; Konkle and Caramazza, 2013; Epstein and Vass, 2014; Bainbridge and Oliva, 2015; Lescroart et al., 2015). Indeed, understanding the stimulus properties that determine the contributions of PhC to object processing is an area of active neuroimaging investigation. Prominent dimensions that have been discussed include real-world size, permanence (i.e., fixedness in location), and the sense of surrounding three-dimensional space that an object evokes (Mullally and Maguire, 2011; Konkle and Oliva, 2012; Troiani et al., 2012). Consideration of these properties has led to the suggestion that the extent to which an object can be a suitable landmark for navigation may be a critical determinant of PhC involvement in object processing (Janzen and van Turennout, 2004; Troiani et al., 2012; Epstein and Vass, 2014).

Prior fMRI studies have linked PhC to recognition-memory for landmarks that were previously encountered through navigation in virtual environments (Janzen and van Turennout, 2004; Janzen et al., 2008; Wegman and Janzen, 2011). In these studies, landmark status was established based on navigational history rather than inherent object characteristics. Differential engagement of PhC in memory for landmarks was revealed by comparing activity when participants made judgments about objects previously encountered in proximity to decision points as compared to objects in other locations. Critically, objects were randomly assigned to both conditions. Consequently, there were no inherent properties that distinguished landmarks from non-landmark objects. Differential PhC activity has also been observed during recognition memory decisions pertaining to landmarks previously encountered in the real world (Schinazi and Epstein, 2010). Although these fMRI findings implicate PhC in landmark processing, it is possible that the observed activation reflects episodic recollection of navigational context rather than item-based memory signals. One important open question is whether landmark suitability, as an object property, shapes recognition-memory signals in PhC as well.

Results from recent research using multi-voxel pattern analysis (MVPA) of fMRI data from our laboratory provide some initial evidence that PhC does indeed carry item recognition-memory signals for some object categories when scene and prior navigational context play no role (Martin et al., 2013, 2016; see also Kafkas et al., 2017). Specifically, we found item-based recognition memory signals for faces in PrC and corresponding signals for buildings in PhC, with item-recognition signals for chairs present in both structures. These findings suggest that object category is an important factor in the organization of item-based memory representations across PrC and PhC. Moreover, the observation of signals for chairs in both structures could suggest that there are no sharp functional boundaries between PrC and PhC, as is typically assumed in theoretical models (e.g., Eichenbaum et al., 2007; Montaldi and Mayes, 2010; Ranganath and Ritchey, 2012). Indeed, it has been suggested that there may be an anatomical gradient, perhaps related to differential connectivity (Wang et al., 2016; Zhuo et al., 2016), that crosses both structures (Litman et al., 2009; Staresina et al., 2011; Liang et al., 2013; Liang and Preston, 2017).

In the current fMRI study we aimed to shed further light on the organization of item-based recognition-memory signals in PrC and PhC. Our primary interest was to seek further evidence for such signals in PhC, and to determine whether and how they are shaped by landmark suitability. Towards this end, we employed three categories of objects that differ in their landmark suitability as confirmed with behavioral ratings (buildings, trees, and aircraft). As in our previous research, we primarily focused on patterns of activity that distinguish between perceived familiar versus novel items across these different object categories (see Martin et al., 2013, 2016; for further rationale).

Materials and methods

Participants

Twenty right-handed participants took part in the fMRI study (21–29 years of age, mean age = 24.3 years, 13 females). They were screened for the absence of a history of neurological disorders. Participants received financial compensation for their participation and provided informed consent according to procedures cleared by the Western University Health Sciences Research Ethics Board.

Stimuli

This study used 360 color images depicting objects that were evenly distributed across three stimulus categories: buildings, trees, and aircraft. Representative stimuli are presented in Fig. 1A. All images were obtained from the internet using Google image search; building stimuli were adapted from Martin et al. (2013). Scenic elements (e.g., ground, horizon, and other non-target objects or features) were removed from each image and objects were centered on a white background (375 × 250 pixels). As such, stimuli qualified as objects by virtue of being displayed as discrete entities that were bounded by a single contour in an image without background elements or a marked horizon (see also Troiani et al., 2012; Bastin et al., 2013). The images did not include any extra-object pictorial cues that could provide information pertaining to relative object size, such as distance from viewer. Final stimulus selection was guided by results from behavioral pilot experiments conducted to equate item-based recognition performance across categories.

Stimuli were rated on several attributes in order to help with characterization of stimulus dimensions that differed between object categories. Ratings were obtained for all 120 objects from each of the three stimulus categories used in the fMRI study. Each dimension was probed in a separate sample of 16 participants. All ratings required use of a 10-point scale. Specifically, these ratings allowed for characterization of our stimuli with respect to five properties that have previously been linked to object processing in PhC.

1. Landmark Suitability: (with 1 = low, 10 = high). Participants were asked to judge whether they could use each object as a landmark to make way-finding decisions (Auger and Maguire, 2013; Troiani et al., 2012).
2. Permanence (with 1 = low, 10 = high). Participants were told that this judgment relates to the geographical stability of object as a whole (e.g., plane), rather than features or parts (e.g., propeller; see Auger and Maguire, 2013).
3. Real-world size (with 1 = small, 10 = large). Participants were asked to consider real world-size independent of image size (see Konkle and Oliva, 2012).
4. Spatial definition (with 1 = low, 10 = high). Participants were informed that objects scoring high on this dimension help define the space around them, while objects that score low provide less