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Research report

Assessing the mechanism of response in the retrosplenial cortex of good and poor navigators☆

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ABSTRACT

The retrosplenial cortex (RSC) is consistently engaged by a range of tasks that examine episodic memory, imagining the future, spatial navigation, and scene processing. Despite this, an account of its exact contribution to these cognitive functions remains elusive. Here, using functional MRI (fMRI) and multi-voxel pattern analysis (MVPA) we found that the RSC coded for the specific number of permanent outdoor items that were in view, that is, items which are fixed and never change their location. Moreover, this effect was selective, and was not apparent for other item features such as size and visual salience. This detailed detection of the number of permanent items in view was echoed in the parahippocampal cortex (PHC), although the two brain structures diverged when participants were divided into good and poor navigators. There was no difference in the responsivity of the PHC between the two groups, while significantly better decoding of the number of permanent items in view was possible from patterns of activity in the RSC of good compared to poor navigators. Within good navigators, the RSC also facilitated significantly better prediction of item permanence than the PHC. Overall, these findings suggest that the RSC in particular is concerned with coding the presence of every permanent item that is in view. This mechanism may represent a key building block for spatial and scene representations that are central to episodic memories and imagining the future, and could also be a prerequisite for successful navigation.

1. Introduction

The retrosplenial cortex (RSC) comprises Brodmann areas 29/30 and is part of an extended network of brain regions engaged during fMRI studies of autobiographical memory, spatial navigation, imagining fictitious and future experiences and scene processing (Addis, Wong, & Schacter, 2007; Epstein, 2008, 2011; Maguire, 2001a, 2001b; Hassabis, Kumaran, & Maguire, 2007; Spreng, Mar, & Kim, 2009; Svoboda, McKinnon, & Levine, 2006; Troiani, Stigliani, Smith, & Epstein, 2012). RSC is particularly interesting because damage that involves this region in humans can result in significant memory and navigation deficits (Aggleton, 2010; Maguire, 2001b; Vann, Aggleton, & Maguire, 2009), while the earliest metabolic decline in Alzheimer's disease is centred on RSC (Minoshima et al., 1997; Nestor,

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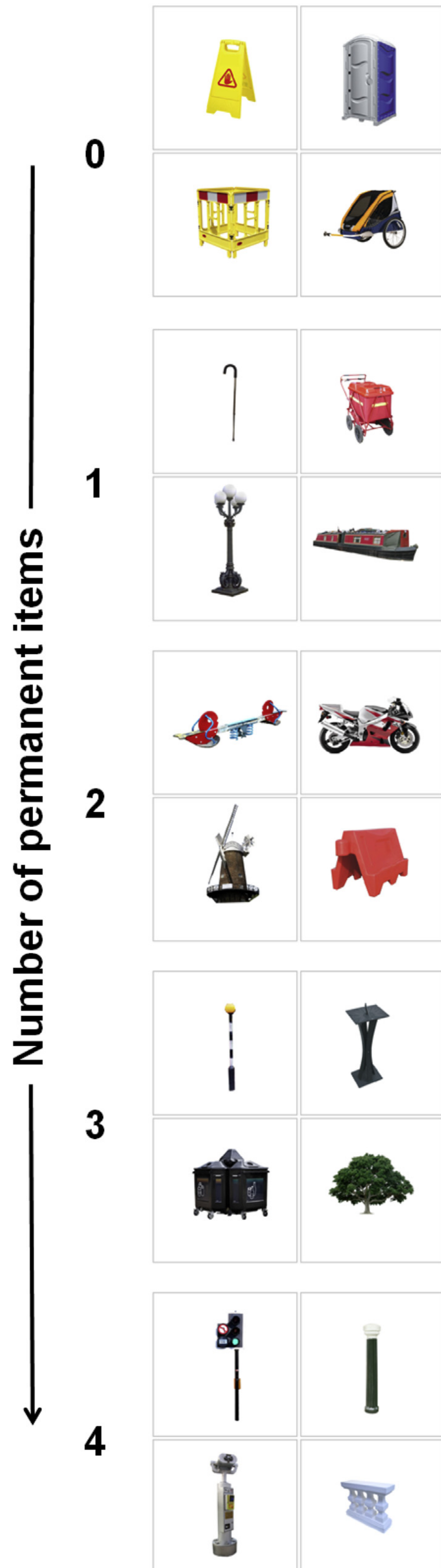

Fig. 1 – Examples of the stimuli. Categories varied according to the number of permanent, 'never moving', items they contained. One example stimulus from each of the five permanence categories is shown here, ranging from no permanent items in the top stimulus, to all four items being permanent in the bottom stimulus.

Fryer, Ikeda, & Hodges, 2003; Pengas, Hodges, Watson, & Nestor, 2010; Villain et al., 2008). Yet despite this, its precise function remains elusive.

In a recent fMRI study by Auger, Mullally, and Maguire (2012) we offered another insight into the role of RSC. We examined different features of items that are normally found outdoors in the everyday environment, including their size, visual salience and the permanence or stability of their location. Participants viewed images of these items one at a time, with RSC responding to only the most permanent, never moving, items. Therefore, even when complex memories, navigation or scenes were not involved, a robust RSC response was evident at the level of single, permanent landmarks. We then examined participants who were good or poor navigators, and found that the latter were much less reliable at identifying the most permanent items. Moreover, when responses to the most permanent items were examined using fMRI, poor navigators had significantly reduced responses in RSC. This suggested that the RSC's contribution may be to provide input regarding permanent items upon which other brain areas can then build effective spatial and scene representations (Auger et al., 2012).

Our previous study (Auger et al., 2012) focussed on single items; however, in the real world, we do not normally encounter items in isolation. In order to promote a proper understanding of the role of the RSC, we need to test its reaction to multiple items, as this will inform whether its responsivity is item-specific or more general. Therefore, the question we addressed here was whether RSC is simply engaged by the presence of permanence per se, irrespective of the number of permanent items being viewed, or whether is it mechanistically more nuanced, tracking the specific number of permanent items. Adjudicating between these two options is important, as going forward it could guide how we conceptualise the function of the RSC and probe the mechanisms that may operate therein. If RSC codes for just the presence of permanence, then its input into spatial and scene representations would be limited. However, if RSC represents each permanent item in a given view, then it could play a key role in detecting and mapping individual landmarks as we encounter them in our surroundings. This operation could be crucial for successful navigation, as the very building blocks of any representation of an environment are the most stable items within it.

To test the nature of RSC processing, we had good and poor navigators view quartets of outdoor items (Fig. 1). The stimuli differed in terms of how many of their four items were permanent, i.e., with a fixed location in the environment – they contained either no, 1, 2, 3, or 4 permanent items. We used multi-voxel pattern analysis (MVPA; Chadwick, Bonnici, & Maguire, 2012; Haynes & Rees, 2006; Norman, Polyn, Detre, & Haxby, 2006) to assess whether information about the number of permanent items in view could be decoded from activity in RSC and, if so, whether this differed between good and poor navigators. The quartets were carefully designed such that