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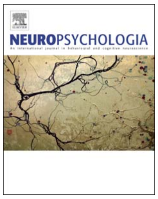

Efficacy of navigation may be influenced by retrosplenial cortex-mediated learning of landmark stability

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ABSTRACT

Human beings differ considerably in their ability to orient and navigate within the environment, but it has been difficult to determine specific causes of these individual differences. Permanent, stable landmarks are thought to be crucial for building a mental representation of an environment. Poor, compared to good, navigators have been shown to have difficulty identifying permanent landmarks, with a concomitant reduction in functional MRI (fMRI) activity in the retrosplenial cortex. However, a clear association between navigation ability and the learning of permanent landmarks has not been established. Here we tested for such a link. We had participants learn a virtual reality environment by repeatedly moving through it during fMRI scanning. The environment contained landmarks of which participants had no prior experience, some of which remained fixed in their locations while others changed position each time they were seen. After the fMRI learning phase, we divided participants into good and poor navigators based on their ability to find their way in the environment. The groups were closely matched on a range of cognitive and structural brain measures. Examination of the learning phase during scanning revealed that, while good and poor navigators learned to recognise the environment's landmarks at a similar rate, poor navigators were impaired at registering whether landmarks were stable or transient, and this was associated with reduced engagement of the retrosplenial cortex. Moreover, a mediation analysis showed that there was a significant effect of landmark permanence learning on navigation performance mediated through retrosplenial cortex activity. We conclude that a diminished ability to process landmark permanence may be a contributory factor to sub-optimal navigation, and could be related to the level of retrosplenial cortex engagement.

1. Introduction

Behavioural and brain differences between good and poor navigators have been widely reported (Auger et al., 2012; Auger and Maguire, 2013; Baumann et al., 2010; Epstein et al., 2005; Hartley et al., 2003; Janzen et al., 2008; Maguire et al., 2000; Ohnishi et al., 2006; Sulpizio et al., 2016; Wegman and Janzen, 2011; Woollett and Maguire, 2011), but the specific causes of navigation variability have been more difficult to determine (Wolbers and Hegarty, 2010). Effective navigation relies upon the formation and utilisation of accurate environmental representations, the bedrock of which are stable landmarks (Burnett et al., 2001; Lynch, 1960; Siegel and White, 1975). These landmarks can be distal, global cues (Doeller et al., 2008) or more proximal objects (Committeri et al., 2004; Galati et al., 2010; Lew, 2011; Marchette et al., 2015, 2014; Yoder et al., 2011), but whatever the size or salience of these permanent, non-moving environmental features, how they are processed by the brain may be related to a person's general navigation ability (Auger et al., 2012; Auger and Maguire, 2013).

A previous functional MRI (fMRI) study demonstrated that the retrosplenial cortex (RSC) was responsive to the permanence of common everyday landmarks (Auger et al., 2012). Moreover, processing of permanence appeared to be automatic, being implicitly registered even when attention was not directly drawn to this landmark feature. Interestingly, relative to good navigators, poor navigators had a specific deficit in reliably identifying the most permanent, non-moving items in the environment, and reduced responses to permanent landmarks in the RSC (Auger et al., 2012). It has also been shown that RSC codes for the specific number of permanent items in view, and the RSC of good navigators contained more discriminative representations of these permanent landmarks (Auger and Maguire, 2013). Other work has revealed that representations of permanence in RSC developed rapidly for completely novel items, and RSC responses directly tracked the emerging knowledge of landmark permanence (Auger et al., 2015).

Processing of other landmark features, such as whether or not items are encountered at navigationally relevant 'decision points' in an environment (Janzen and van Turennout, 2004; Schinazi and Epstein,

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2010), whether they evoke a sense of surrounding space (Mullally and Maguire, 2011), their size and visual salience (Auger et al., 2012; Konkle and Oliva, 2012), have been found to engage other brain regions, in particular the parahippocampal cortex (PHC). Responses in PHC have also been linked to general navigation abilities (Wegman and Janzen, 2011).

The hippocampus (HC) is the other brain region where there is extensive evidence for a role in navigation ability (Bohbot et al., 2007; Hartley et al., 2003; Iaria et al., 2008; Janzen et al., 2008; Maguire et al., 2000; Schinazi et al., 2013; Wegman and Janzen, 2011; Woollett and Maguire, 2011). Unlike RSC and PHC, however, the HC has not been found to operate at the basic level of individual landmark features. Instead, the HC appears to be associated with the processing of more detailed spatial information related to knowledge of where landmarks are situated in an environment overall (Auger et al., 2015), consistent with its often reported role in retrieving spatial location information about objects (Baumann et al., 2010; Ekstrom et al., 2011; Manns and Eichenbaum, 2009; Save et al., 1992).

Thus, there are numerous examples of MRI studies linking RSC, PHC and HC with navigation ability, and also with landmark features, in particular permanence. However, no study has directly examined the relationship between good and poor navigation and the learning of landmark permanence, along with the concomitant fMRI activity. To address this issue, we first needed to identify groups of good and poor navigators by objectively measuring their wayfinding in an environment that they had all learned, and then somehow retrospectively assess how they had come to learn about the permanence of landmarks within that environment, all while in an MRI scanner. It was also important that the landmarks in question were novel, so that participants did not have prior knowledge or expectations about their permanence status, but had to acquire this knowledge when learning the environment.

We therefore created a virtual reality environment containing five overlapping paths and landmarks of which participants had no prior experience (Fig. 1). Participants learned the layout of this environment while undergoing fMRI scanning knowing that their knowledge of the environment would be tested in a variety of unspecified ways after scanning. Crucially, of the environment's 60 landmarks, some remained fixed in their locations while others changed position each time they were seen (Auger et al., 2015). Participants' knowledge of landmark identity (recognition memory) and permanence was assessed during and after the fMRI learning scan. Also after scanning, we examined how well they knew the overall layout of the environment and, importantly, their ability to navigate within it.

We reasoned that the most obvious and naturalistic way to divide participants into good and poor navigator groups was based on their ability to find their way within the environment after the learning phase in the scanner. We could then look back at both the learning and fMRI data that were acquired during scanning to examine whether there were any differences between good and poor navigators. Given previous reports (Auger et al., 2012; Auger and Maguire, 2013), we predicted that poor, relative to good, navigators would be significantly worse at learning landmark permanence. We also expected that this would be accompanied by reduced activity specifically in the RSC of poor navigators during learning.

2. Materials and methods

2.1. Participants

Thirty two subjects (16 female, mean age 23.7 years, SD 2.4) took part in the experiment. All were right handed and healthy with normal vision. The participants and experimental design have been reported previously (Auger et al., 2015) in a study that was focused on a different set of questions which did not involve the data presented here. All experimental protocols were approved by the University College London Research Ethics Committee. The experimental methods were carried out in accordance with the approval of the Ethics Committee. Informed written consent was obtained from all participants.

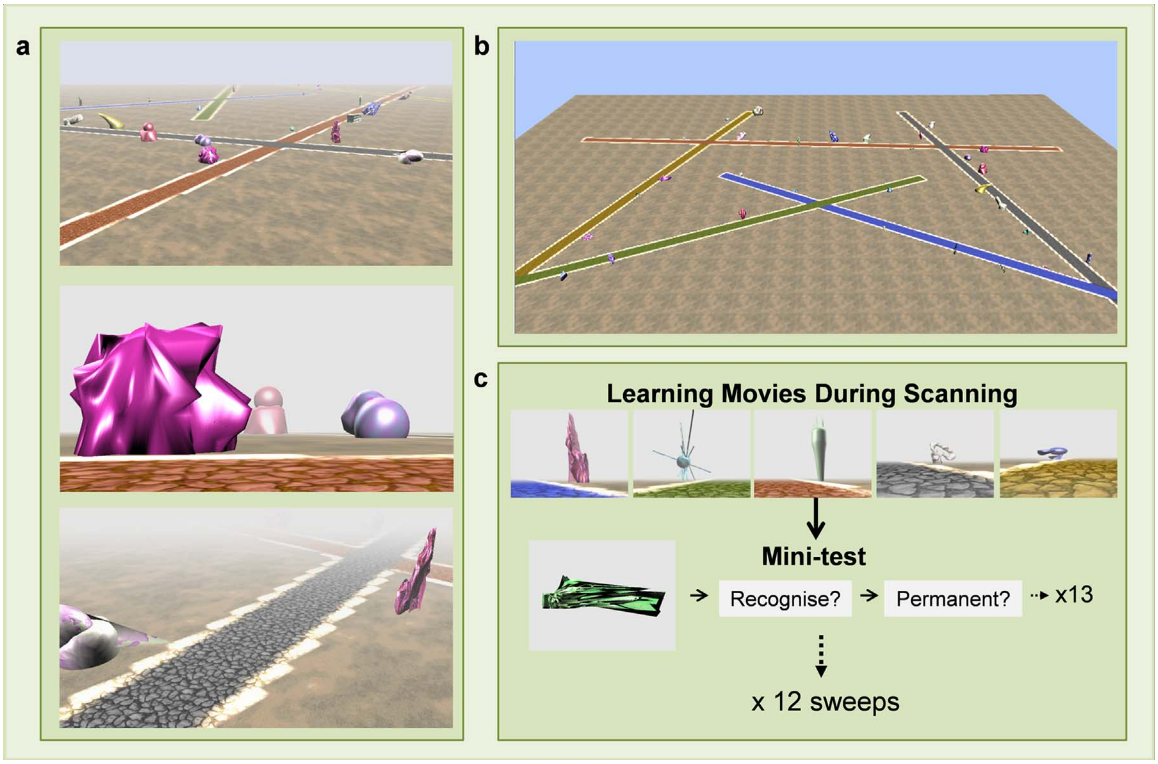

Fig. 1. *The virtual reality environment and fMRI task.* (a) Screenshots showing landmarks situated alongside the 5 different coloured paths. Fog was used to control subjects' exposure to the environment. (b) An aerial perspective without fog showing how the 5 paths related to one another. (c) The learning phase during fMRI consisted of 12 learning "sweeps".