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Egocentric and allocentric visuospatial working memory in premotor Huntington's disease: A double dissociation with caudate and hippocampal volumes

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ABSTRACT

Our brains represent spatial information in egocentric (self-based) or allocentric (landmark-based) coordinates. Rodent studies have demonstrated a critical role for the caudate in egocentric navigation and the hippocampus in allocentric navigation. We administered tests of egocentric and allocentric working memory to individuals with premotor Huntington's disease (pmHD), which is associated with early caudate nucleus atrophy, and controls. Each test had 80 trials during which subjects were asked to remember 2 locations over 1-sec delays. The only difference between these otherwise identical tests was that locations could only be coded in self-based or landmark-based coordinates. We applied a multiatlas-based segmentation algorithm and computed point-wise Jacobian determinants to measure regional variations in caudate and hippocampal volumes from 3 T MRI. As predicted, the pmHD patients were significantly more impaired on egocentric working memory. Only egocentric accuracy correlated with caudate volumes, specifically the dorsolateral caudate head, right more than left, a region that receives dense efferents from dorsolateral prefrontal cortex. In contrast, only allocentric accuracy correlated with hippocampal volumes, specifically intermediate and posterior regions that connect strongly with parahippocampal and posterior parietal cortices. These results indicate that the distinction between egocentric and allocentric navigation applies to working memory. The dorsolateral caudate is important for egocentric working memory, which can explain the disproportionate impairment in pmHD. Allocentric working memory, in contrast, relies on the hippocampus and is relatively spared in pmHD.

1. Introduction

Our brains code spatial information separately in allocentric (landmark-based) or egocentric (self-based) coordinates. The allocentric reference frame represents the spatial relationships between landmarks, independent of the position of the self, and is important for developing cognitive maps (Maguire et al., 1998; O'Keefe and Nadel, 1978). The egocentric reference frame represents object locations in reference to the position of the self, is updated during movement, and is important for navigating toward a visible landmark and learning stimulus-response associations and fixed routes (Aguirre and D'Esposito, 1999; Chersi and Burgess, 2015; Redish, 1999). These representational systems operate largely in parallel, and individuals favor one system or the other when solving a navigation task (Bohbot et al., 2007; Iaria et al., 2003).

Egocentric and allocentric representational systems have been studied extensively in the context of navigation learning. Well-established rodent paradigms, including the Morris Water Maze, the plus

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maze, and the radial arm maze, have been manipulated to test the integrity of either system. For example, maze targets can be positioned relative to other landmarks to measure allocentric navigation, or to the rodent's starting position to measure egocentric navigation. Lesion and neuronal activation studies show a double dissociation in the neural bases of these strategies such that the hippocampus is critical for allocentric navigation and the caudate for egocentric navigation (Kesner and Gilbert, 2006; McDonald and White, 1994; Packard and Knowlton, 2002; Packard and McGaugh, 1996; Pearce et al., 1998; Vann et al., 2000).

Human studies that have adapted these paradigms in real-space (delpolyi, et al., 2007; Hort et al., 2007) and virtual environments (Doeller et al., 2008; Etchamendy and Bohbot, 2007; Hartley et al., 2003; Iaria et al., 2007; Possin et al., 2016) demonstrate that the role of the hippocampus in allocentric navigation may translate, to some degree, to humans. For example, transgenic mice expressing human amyloid precursor protein and patients with mild cognitive impairment with the predicted pathology of Alzheimer's disease show similar impairments on analogous versions of an allocentric Morris Maze (Possin et al., 2016). Performance on an allocentric Morris Maze correlates with right hippocampal volumes in patients with amnestic mild cognitive impairment or Alzheimer's disease (Nedelska et al., 2012) and with the size of CA1 hippocampal lesions in acute transient global amnesia (Bartsch et al., 2010). In functional neuroimaging studies, the medial temporal lobe activates in relationship to the spatial layout of virtual environments (Aguirre et al., 1996; Maguire et al., 1998; Mellet et al., 2000). The hippocampus contribution to human navigation is not only allocentric, however. Direct projections from parietal cortex provide a large amount of egocentric information to the hippocampus (Boccia et al., 2016; Kravitz et al., 2011), and hippocampal hypoactivation in amnestic MCI has been associated with decreased performances in both egocentric and allocentric navigation (Boccia et al., 2016). Beyond navigation, a leading view is that the hippocampus encodes events by mapping the relationships between objects and actions within spatial contexts Eichenbaum and Cohen, 2014).

The caudate appears to play an important role in egocentric forms of human navigation. Navigating based on memory for prior responses is associated with caudate nucleus activation (Iaria et al., 2003) and individuals who spontaneously adopt an egocentric response (versus allocentric) strategy on a radial maze task have larger caudate and smaller hippocampal volumes (Bohbot et al., 2007). Also, patients with early stage Huntington's disease (HD), which is associated with caudate atrophy, have shown less caudate activation and greater hippocampal activation than controls on a route-learning task, suggesting that the hippocampus may compensate during navigation for functional degradation of the caudate (Voermans et al., 2004). However, in this same study, the HD patients did not differ from controls in their navigation accuracy, and further, Majerová et al. (2012) demonstrated normal navigation in HD patients with mild motor symptoms and parallel deterioration in allocentric and egocentric navigation in patients with moderate motor symptoms.

There are limitations to investigating the allocentric - egocentric distinction in navigation. Navigation learning is complex, involving basic perceptual and memory related processes as well as the integration and manipulation of multisensory information over time and space (Wolbers and Hegarty, 2010). Performance can be compromised by impairment in any of the component processes. Also, although widely-used egocentric and allocentric navigation paradigms usually favor one strategy, they can often be solved by either strategy (Ekstrom et al., 2014; Neggers et al., 2006; Wolbers and Wiener, 2014). Further, egocentric navigation has been inconsistently defined. Judgment of the order of landmarks, the novelty of landmarks, and landmark appearance, and way-finding along habitual routes and memory for responses, have all been considered forms of egocentric navigation (Boccia et al., 2014).

In a model presented by Wolbers and Hegarty (2010), navigation relies on various sensory cues, computational mechanisms, and both online and offline spatial representations. Online spatial representations, in their model, include both egocentric self-to-object directions and distances, and allocentric object-to-object directions and distances. Consistent with their model, there is some evidence that spatial information may be distinctly represented by the egocentric and allocentric reference frames, and there may be caudate-hippocampal underpinnings that parallel those of more complex navigation learning. Postle and D'Esposito (2003) presented healthy young adults with blocks of allocentric working memory trials (the subjects briefly remembered the distance between a square and an adjacent line) and egocentric working memory trials (the subjects remembered where a square was relative to their own gaze with allocentric reference points disrupted). Caudate activity was greater during the delay period of the egocentric trials only. Individuals with HD have shown impaired immediate memory for arm movements or hand movements (Davis et al., 2007, 2003), whereas patients with hippocampal damage have shown impaired perception and brief memory for topographical information (Hartley et al., 2007). Both individuals with hippocampal damage and individuals with HD have shown impaired memory for locations on a grid (Davis et al., 2003; Olson et al., 2006), which can be represented in either allocentric or egocentric coordinates.

The possibility of measuring the allocentric - egocentric distinction in working memory by using an experimental design that facilitates one strategy while preventing the other is compelling. Working memory, when tested in its most basic form with simple stimuli and brief delays, could allow for a more pure measure of the reference frames. Furthermore, working memory is an essential component of all navigation tasks; one cannot navigate using either reference frame without online spatial representations. Thus, the distinction measured in working memory would have relevance for understanding the distinction in navigation learning.

The purpose of this study was to evaluate whether the allocentric - egocentric distinction existed in the context of simple visuospatial working memory with a hippocampal - caudate dissociation that paralleled the literature on navigation learning. We adapted the Postle and D'Esposito working memory tests that require subjects to briefly represent locations relative to a landmark or relative to their own position (2003). The working memory tests were otherwise identical, which allowed us to independently evaluate and compare the integrity of working memory in each reference frame. We compared performance on the tests in individuals with premotor Huntington's disease (pmHD) and neurologically healthy controls. HD is an autosomal dominant inherited disorder caused by an expansion of the trinucleotide repeat cytosine-adenine-guanine (CAG). Individuals with pmHD do not yet exhibit the motor symptoms including chorea, but can exhibit cognitive or psychiatric changes (Epping et al., 2015; Paulsen et al., 2013), including working memory impairments (You et al., 2014). Caudate volume loss is present more than a decade before HD diagnosis and contributes robustly to cognitive impairment, whereas hippocampal volumes are relatively preserved and do not predict cognitive impairment (Aylward et al., 2013, 2004). We correlated accuracy on each test with regional caudate and hippocampal volumes. We hypothesized that individuals with pmHD would show greater impairment on egocentric working memory. Also, we hypothesized that atrophy in the dorsolateral head of the caudate, a region that receives projections from dorsolateral prefrontal regions important for goal directed actions (Bonelli and Cummings, 2007), would be associated with egocentric working memory accuracy. We hypothesized that the posterior hippocampus, a region with place cells, strong connections to parahippocampal cortex and posterior parietal cortex, and an important role in spatial processing and navigation (Fanselow and Dong, 2010; Poppenk et al., 2013), would be associated with allocentric working memory accuracy.

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