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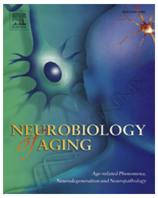

How age-related strategy switching deficits affect wayfinding in complex environments

Mathew A. Harris [a,b,*], Thomas Wolbers [c]

[a] Centre for Cognitive and Neural Systems, University of Edinburgh, Edinburgh, UK
[b] Centre for Cognitive Ageing and Cognitive Epidemiology, University of Edinburgh, Edinburgh, UK
[c] German Center for Neurodegenerative Diseases, Otto von Guericke University Magdeburg, Magdeburg, Germany

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ABSTRACT

Although most research on navigation in aging focuses on allocentric processing deficits, impaired strategy switching may also contribute to navigational decline. Using a specifically designed task involving navigating a town-like virtual environment, we assessed the ability of young and old participants to switch from following learned routes to finding novel shortcuts. We found large age differences in the length of routes taken during testing and in use of shortcuts, as, while nearly all young participants switched from the egocentric route-following strategy to the allocentric wayfinding strategy, none of the older participants stably switched. Although secondary tasks confirmed that older participants were impaired both at strategy switching and allocentric processing, the difficulty in using shortcuts was selectively related to impaired strategy switching. This may in turn relate to dysfunction of the prefrontal-noradrenergic network responsible for coordinating switching behavior. We conclude that the large age difference in performance at the shortcutting task demonstrates for the first time, how strategy switching deficits can have a severe impact on navigation in aging.

1. Introduction

Aging impairs a range of cognitive abilities to varying degrees, and navigation may be among those most severely affected. This is partly attributable to degeneration of multiple involved brain areas, such as the hippocampus (Driscoll et al., 2003; Lister and Barnes, 2009; West, 1993) and entorhinal cortex (Du et al., 2003, 2006). This degradation leads to decline in the numerous navigational processes supported by these areas, for example cognitive mapping (Iaria et al., 2009; Moffat et al., 2006; Rosenzweig et al., 2003) and path integration (Allen et al., 2004; Harris and Wolbers, 2012; Mahmood et al., 2009). However, real-world navigation is often dependent on using more than one of these component processes during a single journey (Wolbers and Hegarty, 2010), because of changes in availability of cues, or to make use of features of different reference frames. We have therefore previously suggested that a deficit in switching between navigational strategies may also contribute to age-related navigation impairments (Harris et al., 2012).

Strategy switching is thought to be coordinated by regions of prefrontal cortex (PFC), as mediated by noradrenaline (NA) produced by the locus coeruleus (LC), in response to changes in rewards associated with the current behavioral strategy (Aston-Jones and Cohen, 2005; Bouret and Sara, 2005). Supporting studies have demonstrated that depletion of prefrontal NA—by lesioning of noradrenergic fibers projecting from LC to PFC (Tait et al., 2007) or by infusion of a NA receptor antagonist into medial PFC (Caetano et al., 2013) — does seem to produce a deficit in switching between different strategies. Further evidence shows that aging degrades LC and disrupts NA function (Grudzien et al., 2007; Manaye et al., 1995), while the frontal aging hypothesis suggests that various aspects of age-related cognitive decline may be attributable to PFC degradation (Pfefferbaum et al., 2005; West, 1996). It might be expected that these changes in the brain that occur with aging induce deficits in strategy switching; and indeed these deficits have been demonstrated in aged animals and humans using attentional and conceptual set shifting tasks (Ashendorf and McCaffrey, 2008; Moore et al., 2003; Young et al., 2010).

Within the context of navigation, strategies may be described as allocentric—in relation to a fixed external coordinate system; or egocentric—in relation to the body's changing position and orientation. For example, an allocentric strategy might involve using distal landmarks to find a novel route, whereas an egocentric

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* Corresponding author at: Centre for Cognitive and Neural Systems, University of Edinburgh, 1 George Square, Edinburgh, EH8 9JZ, UK. Tel.: +44 131 650 3520; fax: +44 131 651 1835.
E-mail address: m.a.harris-2@sms.ed.ac.uk (M.A. Harris).

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strategy may involve following a familiar route encoded as a sequence of body movements. Allocentric and egocentric strategies have been associated with the hippocampus and caudate nucleus, respectively (Cook and Kesner, 1988; Hartley et al., 2003; Iaria et al., 2003; O'Keefe, 1990). Both systems constantly provide input to PFC, which then appears to determine how each influences behavior (Doeller et al., 2008), based on the appropriate navigational strategy.

Switching between these 2 types of strategy has previously been studied in rodents using a "plus maze" (Ragozzino, 2007; Rich and Shapiro, 2007), which involves finding a reward using either an allocentric place strategy, or an egocentric response strategy, and periodically switching between the two. Importantly, inactivation of regions of medial PFC impairs performance of strategy switches, but not reversals (Ragozzino et al., 1999; Rich and Shapiro, 2007; Young and Shapiro, 2009). We recently used a virtual adaptation of the plus maze (VPM) to investigate navigational strategy switching in young and old human subjects. While we also demonstrated a specific impairment in performing strategy switches but not reversals, the deficit was actually even more specific, affecting only switches from the response to the place strategy (Harris et al., 2012). We suggested that this "switch-to-place" deficit may relate to a reduction in functional connectivity between the prefrontal-noradrenergic switching network and the hippocampus in aging. However, how accurately switching from the response to the place strategy within the VPM corresponds to engaging an allocentric strategy during real-world navigation is uncertain, as the nature of the task and the 2 strategies used in the VPM is relatively simplistic.

The aim of the present study was therefore to demonstrate that switching from an egocentric to an allocentric strategy is still impaired within a more realistic context. We developed a novel virtual reality task, in which participants were repeatedly trained to follow long, indirect routes to goal locations. Participants were then required to switch to finding shorter, more direct routes by taking shortcuts during testing. We hypothesized that older participants would experience greater difficulty in switching from an egocentric route-following to an allocentric wayfinding strategy. We also administered a shortened version of the VPM (sVPM), hypothesizing that it would again demonstrate a deficit among older participants in switching to the place strategy, and that switch-to-place performance during the sVPM would relate to wayfinding performance during the shortcutting task.

2. Methods

2.1. Participants

Twenty-five (12 female) young participants (aged 18–29 years, mean 21.84 years) and 25 (11 female) old participants (aged 61–79 years, mean 68.68 years) were recruited through local advertising and from an existing database of psychology research volunteers within the local Edinburgh community, and were reimbursed for their time at a rate of £7.00 per hour. Most had prior experience of participating in research, and all had normal or corrected-to-normal vision and no known cognitive deficits or neurological disorders.

2.2. Procedure

Participants provided information on their age and gender, before completing the Montreal cognitive assessment (MoCA; Nasreddine et al., 2005; scored out of 30) to screen for mild cognitive impairment using a cut-off of 23 (Luis et al., 2009), the National Adult Reading Test (NART; Nelson, 1982; scored out of 50) as a measure of crystallized intelligence, and a computer-based version of the Corsi blocks task (Corsi, 1972; Kessels et al., 2000; maximum sequence length 9) as a measure of spatial working memory. They then completed the main shortcutting task, followed by the sVPM, each presented on a 24-inch widescreen monitor by a standard desktop computer, providing input through a standard keyboard. Finally, participants completed a simple cognitive mapping test as a measure of allocentric processing, which involved labeling landmarks encountered during the shortcutting task on paper maps of the task's virtual environments (VEs), similar to those shown in Fig. 1, and gave a combined score out of 17. All participants were made fully aware of the details of the study and provided consent before participating.

2.2.1. Shortcutting task

This task was based in 2 realistic virtual town environments designed in 3ds Max (Autodesk, San Rafael, CA, USA) each consisting of houses and salient buildings (supermarkets, restaurants, and so forth.) as landmarks along roads in a grid formation (Fig. 1). The task, programmed and run in Vizard (WorldViz, Santa Barbara, CA, USA), involved training participants on long, indirect routes to 4 goal locations, then testing their ability to find available shortcuts. The first 2 routes each ran from a different start point to a different goal location, but overlapped in the middle of the first VE, and included 4 junctions between start and end points. The other 2 routes ran through and overlapped in the middle of the second VE, and included 6 junctions.

During training, participants actively navigated the routes by using arrow keys to choose whether to go left, right, or straight ahead at each junction, but were not allowed to deviate from the set routes, which, to begin with, were indicated by arrows at each junction. Training also incorporated probe trials, which involved placing the participants at a point in the VE facing a particular landmark and asking them to point to another landmark, again using the arrow keys. These probe trials were designed to both promote and test the use of landmark information and allocentric processing while the routes were being learned. Each training cycle consisted of a traversal of each of the 4 routes in turn twice, followed by a set of 3 probe trials for each of the 2 VEs. Participants progressed to testing once they were able to traverse all 4 routes without directions or errors, and to respond correctly to a full set of probe trials for each VE. Route learning was also measured in terms of the number of training cycles before able to navigate each route without directions or errors. As the direction arrows gradually disappeared throughout the first 2 training cycles, the minimum number of training cycles was 3, while the maximum, due to time constraints, was 7.

Participants were then tested on each of the 4 original routes, and 4 new routes, which crossed from each start point to the opposite goal location in the same VE. These 8 trials were presented in a random order twice, producing a total of 16 test trials. Before testing, participants were explicitly informed that they were no longer restricted to the long training routes, and that the objective during testing was to find the shortest route to each goal location, which they were reminded of at the start of every trial. We assessed task performance in terms of the lengths of the routes taken to each goal location in number of junctions (adjusted for VE differences in route length), and whether the shortcut was used on each trial.

2.2.2. Short virtual plus maze task

The sVPM, also designed, programmed and run in 3 ds Max and Vizard, was derived from a previous virtual plus maze task (VPM; cf. Harris et al., 2012), in turn based upon the rodent plus maze task (e.g., Rich and Shapiro, 2007). As in the standard plus maze task,