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

**Citation for published version:**
Harris, MA & Wolbers, T 2014, 'How age-related strategy switching deficits affect wayfinding in complex environments' Neurobiology of Aging, vol. 35, no. 5, pp. 1095-1102. DOI: 10.1016/j.neurobiolaging.2013.10.086

**Digital Object Identifier (DOI):**
10.1016/j.neurobiolaging.2013.10.086

**Link:**
Link to publication record in Edinburgh Research Explorer

**Document Version:**
Peer reviewed version

**Published In:**
Neurobiology of Aging

**Publisher Rights Statement:**
This is an author manuscript that has been accepted for publication.

# 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, 1 George Square,
Edinburgh, EH8 9JZ, UK
m.a.harris-2@sms.ed.ac.uk

[b] Centre for Cognitive Ageing and Cognitive Epidemiology, University of Edinburgh, 7
George Square, Edinburgh, EH8 9JZ, UK

[c] German Centre for Neurodegenerative Disorders, Otto von Guericke University Magdeburg,
Leipziger Strasse 44, Haus 64, 39120 Magdeburg, Germany
thomas.wolbers@dzne.de

[*] Corresponding author:
Mathew Harris, Centre for Cognitive and Neural Systems, University of Edinburgh, 1 George
Square, Edinburgh, EH8 9JZ, UK
m.a.harris-2@sms.ed.ac.uk
tel:  +44 131 650 3520
fax  +44 131 651 1835

## Abstract

While most research on navigation in ageing 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 behaviour. 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 ageing.

Keywords: Ageing, navigation, strategy switching, shortcutting, route learning, virtual reality

## 1. Introduction

Ageing 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 (West, 1993; Driscoll et al., 2003; Lister & Barnes, 2009) and entorhinal cortex (Du et al., 2003; Du et al. 2006). This degradation leads to decline in the numerous navigational processes supported by these areas, for example cognitive mapping (Rosenzweig et al., 2003; Moffat et al., 2006; Iaria et al., 2009) and path integration (Allen et al., 2004; Mahmood et al., 2009; Harris & Wolbers, 2012). However, real world navigation is often dependent on using more than one of these component processes during a single journey (Wolbers & Hegarty, 2010), due to changes in availability of cues, or in order 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 behavioural strategy (Aston-Jones & Cohen, 2005; Bouret & Sara, 2005). Supporting studies have demonstrated that depletion of prefrontal NA – by lesioning of noradrenergic fibres 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 ageing degrades LC and disrupts NA function (Manaye et al., 1995; Grudzien et al., 2007), while the frontal ageing hypothesis suggests that various aspects of age-related cognitive decline may be attributable to PFC degradation (West, 1996; Pfefferbaum et al., 2005). It might be expected that these changes in the brain that occur with ageing induce deficits in strategy switching; and indeed these deficits have been demonstrated in aged animals and humans using attentional and conceptual set shifting tasks (Moore et al., 2003; Ashendorf & McCaffrey, 2008; 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 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 & Kesner, 1988; O'Keefe, 1990; Hartley et al., 2003; Iaria et al., 2003). Both systems constantly provide input to PFC, which then appears to determine how each influences behaviour (Doeller et al., 2008), based on the appropriate navigational strategy.

Switching between these two types of strategy has previously been studied in rodents using a 'plus maze' (Ragozzino, 2007; Rich & 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 & Shapiro, 2007; Young & 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 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 ageing. 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 two 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 (VR) 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 hypothesised 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), hypothesising 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. Materials and methods

### *2.1. Participants*

25 (12 female) young participants (aged 18-29, mean 21.84) and 25 (11 female) old participants (aged 61-79, mean 68.68) 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 (MCI) 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 crystallised 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 primary shortcutting task, followed by the sVPM, each presented on a 24in 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 labelling landmarks encountered during the shortcutting task on paper maps of the task's virtual environments (VEs), similar to those shown in fig.1a, 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 two realistic virtual town environments designed in 3ds Max (Autodesk, San Rafael, CA) each consisting of houses and salient buildings (supermarkets, restaurants, etc.) as landmarks along roads in a grid formation (*fig.1*). The task, programmed and run in Vizard (WorldViz, Santa Barbara, CA), involved training participants on long, indirect routes to four goal locations, then testing their ability to find available shortcuts. The first two routes each ran from a different start point to a different goal location, but overlapped in the middle of the first VE, and included four junctions between start and end points. The other two routes ran through and overlapped in the middle of the second VE, and included six 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 four routes in turn twice, followed by a set of three probe trials for each of the two VEs. Participants progressed to testing once they were able to traverse all four 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 two training cycles, the minimum number of training cycles was three, while the maximum, due to time constraints, was seven.

Participants were then tested on each of the four original routes, as well as four new routes, which crossed from each start point to the opposite goal location in the same VE. These eight 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), as well as whether or not the shortcut was used on each trial.

### *2.2.2. Short virtual plus maze task*

The sVPM, also designed, programmed and run in 3ds 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 & Shapiro, 2007). As in the standard plus maze task, trials were grouped into blocks, with the strategy being switched (e.g. from 'go to the north arm' to 'turn left') or reversed (e.g. from 'turn left' to 'turn right') between blocks, and on each trial participants approached the central junction of the plus maze from one of two opposing start arms and decided whether to go left or right to one of two goal arms, where a reward was presented if coherent with the current strategy. As in our previous VPM, the sVPM was set in a mountain scenery VE, participants used the arrow keys to provide a response, and a visual cue was used to signal reward, which also increased a visible running total score. The original VPM was shortened by reducing the length of each trial and the number of trials (155) in terms of both trials per block (15 or 20, varied pseudorandomly) and total blocks (nine, allowing four switches and four reversals). We also ensured that the task started with a block of place strategy trials for all participants, rather than pseudorandomising starting strategy across participants, in order to avoid exaggerating any age-related allocentric processing deficits. Performance was assessed in terms of the average number of correct trials for each block type.

### *2.3. Data analysis*

Data were analysed in Matlab (Mathworks, Natick, MA). Results of the MoCA, NART, Corsi blocks task and cognitive mapping test were each represented as a single-value or percentage score. Cognitive mapping test scores were corrected to account for the fact that it was impossible to get only one incorrect. Results of the sVPM were processed in terms of the number of correct trials for each block. For the shortcutting task, we assessed route learning in terms of number of training cycles, and testing performance in terms of route length and shortcut use. We performed mixed model ANOVAs and paired t-tests to assess group differences across routes and VEs, and correlated shortcutting task performance with secondary measures. For multiple comparisons, p values were corrected using the Holm-Bonferroni method (following corrected p values are denoted $p_{HB}$). Participants were to be excluded if they scored below 24 on the MoCA, if they failed to learn all of the routes in the maximum training period allowed, or if their average testing route length was further than 2SDs from the group mean, but no participants met any of these exclusion criteria.

We also employed a Bayesian learning analysis technique (Smith et al., 2004), run in WinBUGs (Lunn et al., 2000) through the “matbugs” Matlab function. This approach can be used to estimate, at each point throughout a series of trials, the likelihood that responses to all subsequent trials will be coherent with a certain strategy, based on observed responses. The point at which the lower 95% confidence interval of this estimation first exceeds and remains above the chance probability of an individual coherent response corresponds to the point at which the appropriate strategy has been stably acquired. We used this to determine whether each block of sVPM trials had been learned, as well as to identify if and when each participant switched to an allocentric wayfinding strategy in the shortcutting task.

## 3. Results

All participants scored 24 or above on the MoCA so none were excluded for showing signs of MCI. The older group performed significantly better than the young at the NART ($t_{48}$=5.018, p<.001), as observed in previous studies (Strauss et al. 2006), and significantly worse than the young at the Corsi blocks task ($t_{48}$=4.729, p<.001), indicating that our participants represented typical samples of the young and old populations. We later found that performance at the NART and Corsi blocks task did not correlate with shortcut use throughout the shortcutting task.

### *3.1. Shortcutting*

The young group generally learned the routes of the shortcutting task in the lowest number of training cycles possible, while the older group took slightly longer (*fig.2*). A mixed model ANOVA revealed a significant main effect of age group on route learning ($F_{1,48}$=28.330, p<.001), and post-hoc t-tests demonstrated that this was due to a significant difference in the number of training cycles taken to learn the two routes in the more complex VE (route 1 [VE1]: $t_{48}$=2.025, $p_{HB}$=.097; route 2 [VE1]: $t_{48}$=1.877, $p_{HB}$=.067; route 3 [VE2]: $t_{48}$=3.222, $p_{HB}$=.009; route 4 [VE2]: $t_{48}$=2.882, $p_{HB}$=.018). However, while the older group took slightly longer than the young to learn the routes, most participants learned the routes reasonably quickly, and all successfully learned all routes during the training period. There were no gender differences within either the young group ($t_{23}$=1.174, p=.477) or the old group ($t_{23}$=1.649, p=.113) in route learning. On the other hand, while most participants – 22 young and 18 old – managed to respond correctly to a full set of probe trials for at least one of the VEs, many – nine young and 23 old – did not do so for both VEs, and consequently performed the maximum number of training cycles.

During testing, the older group took longer routes (as a proportion of the shortest possible route in number of junctions) than the young to reach the goal locations (*fig.3 top*). A mixed model ANOVA with age and VE as factors demonstrated a significant main effect of age on test route length ($F_{1,48}$=104.937, p<.001) and post-hoc t-tests confirmed that older participants took significantly longer routes in both VE1 ($t_{48}$=6.796, $p_{HB}$<.001) and VE2 ($t_{48}$=8.061, $p_{HB}$<.001). This may indicate that the old tended to use the newly available shortcuts less often than the young. We confirmed this by assessing shortcut use directly, for which there was an even stronger age effect ($F_{1,48}$=199.538, p<.001), again driven by differences in both VEs (VE1: $t_{48}$=11.405, $p_{HB}$<.001; VE2: $t_{48}$=12.561, $p_{HB}$<.001). As illustrated (*fig.3 bottom*), while the young group used the available shortcuts on the majority of test trials, the older group used the shortcuts on only a small proportion of trials. In terms of number of junctions, both groups took longer routes in VE2 simply because routes through this VE included more junctions, but after adjusting the measure of route length to account for this difference, there was no significant effect of VE ($F_{1,48}$=.072, p=.789). VE did however seem to have a small effect on shortcut use ($F_{1,48}$=4.617, p=.037), but this difference was not significant for each age group individually (young: $t_{24}$=1.297, $p_{HB}$=.207; old: $t_{24}$=1.789, $p_{HB}$=.173). Again, there were no gender differences within either the young ($t_{23}$=.541, p=.594) or old ($t_{23}$=.696, p=.493) group.

In the probe trials, participants had to point to unseen landmarks, hence successful completion indicated that they had formed a survey representation of that particular VE. This means that, as some participants were unable to complete all the probe trials successfully, the deficit in shortcut use among older participants might have been caused by an inability to learn the layout of the environments. To address this problem, we performed an additional analysis in which we compared shortcut use between younger and older participants only for those VE’s for which participants correctly responded to a full set of probe trials during training. This analysis confirmed a large age difference in use of shortcuts across both VEs ($t_{38}$=14.331, p<.001).

Finally, we applied the Bayesian learning analysis described above to the data on shortcut usage in order to assess whether each participant stably switched from an egocentric route-following strategy to an allocentric wayfinding strategy during testing. Based on the results, we were able to divide all participants into four categories: those that switched immediately and used the shortcuts for all test trials; those that switched at some point during testing and used the shortcuts for all subsequent trials; those that used the shortcuts on some trials, but either not enough or not consistently enough to suggest that they had stably switched to a wayfinding strategy; and those that never used the shortcuts (*fig.4*). The vast majority of young participants stably switched to the allocentric strategy either immediately or at some point during testing, with only one participant using the shortcuts inconsistently. On the other hand, not one of the older group stably switched to the allocentric strategy, although most did use the shortcut on at least one test trial.

### *3.2. Strategy switching and cognitive mapping*

The results of the sVPM also suggest that the older group was less able to switch between egocentric and allocentric strategies (*fig.5 top*). A mixed ANOVA showed main effects of age ($F_{1,38}$=10.105, p=.003) and change type (switch-to-place [S-P], switch-to-response [S-R], reverse-place [R-P] & reverse-response [R-R]; $F_{1,38}$=7.783, p=.008) on the proportion of correct responses to sVPM trials, as well as a significant interaction ($F_{1,38}$=6.715, p=.014), which seemed to be due to impaired performance among the older group during blocks following a switch ($t_{38}$=3.467, $p_{HB}$=.003). More specifically, this difference was significant for switch-to-response blocks ($t_{37}$=3.197, $p_{HB}$=.011), although, after correcting for multiple comparisons, not for switch-to-place blocks ($t_{34}$=2.013, $p_{HB}$=.156). However, post-hoc tests revealed no significant differences in performance between different change types, including between switch-to-place and switch-to-response blocks ($t_{34}$=.204, $p_{HB}$=.840). There were no gender differences in overall VPM performance (young: $t_{22}$=.911, p=.372; old: $t_{15}$=1.096, p=.291), nor in cognitive mapping (young: $t_{23}$=.854, p=.402; old: $t_{23}$=1.705, p=.108).

However, there was also a significant age difference in performance at the cognitive mapping test ($t_{48}$=7.298, p<.001; *fig.5 bottom*), suggesting that an allocentric processing deficit may have contributed to the age difference in use of shortcuts. To assess the effects of strategy switching and cognitive mapping on shortcut use, we performed a general linear model analysis, modelling use of shortcuts in terms of age group, VPM switching performance and cognitive mapping score. While both age group (β=-.548, $t_{36}$=-6.432, p<.001) and strategy switching (β=.445, $t_{36}$=2.383, p=.023) showed significant independent effects on use of shortcuts, we did not observe a significant contribution for cognitive mapping (β=.001, $t_{36}$=.918, p=.365). These results are consistent with the results reported in section 3.1, which show that shortcut use was deficient in older adults even where successful probe trial performance indicated that they had formed an allocentric representation of the VE. Although these combined findings do not rule out the possibility that allocentric impairments may have affected use of shortcuts, they do suggest that it was mainly a strategy switching deficit that led to impaired performance at our shortcutting task in the older group.

### *3.3. Crossing routes*

Finally, we explored the effects of the novel testing routes, which involved crossing from the start point of one training route to the end point of another. As these new test routes were not repetitively trained, we expected that they would make it easier for participants to switch from using a route-following strategy, and to start using the available shortcuts. We investigated this by assessing the trial type upon which each participant first used a shortcut. Participants who never used the shortcuts could not be included in this analysis. Of those that did use a shortcut during testing, 17 of 25 young and six of 19 old participants first did so on a crossing route test trial ($\chi^2_1$=21.184, p<.001), suggesting only the young were prompted to start using shortcuts. We also assessed the effect of crossing routes on the length of routes taken during testing (excluding trials on which the shortcut was taken), but found no significant differences.

## 4. Discussion

We used a novel VR task to demonstrate a deficit among older people in switching from an egocentric route-following strategy to an allocentric wayfinding strategy when navigating in a complex environment. During training, older participants learned long routes to goal locations almost as quickly as the young, demonstrating a significant difference only for the more complex routes. However, during testing, when shortcuts to the goal locations were available and participants were instructed to take the shortest available route to each goal location, the older group took longer routes, primarily because they used the available shortcuts much less often than the young group. Furthermore, while the vast majority of young participants stably switched from using a route-following strategy to a wayfinding strategy either on the first test trial or at some point during testing, the older participants used the shortcuts either sporadically or not at all, so that not one could be said to have stably switched to the wayfinding strategy. Crossing routes during testing may have prompted young participants to use the shortcuts, but old participants were not affected in the same way. The older group's perseveration with the route-following strategy may still have been due either to a reluctance to use an allocentric strategy (due to deficits in allocentric processing), or to an impaired ability to switch strategies. However, their much lower use of the shortcuts was predicted by switching performance, as measured by the VPM, but not allocentric processing ability, as measured by the cognitive mapping test. Our results therefore demonstrate that, while allocentric impairments may still play a role, strategy switching deficits in old age have a direct impact on wayfinding in everyday environments.

Our main finding, that older people were less able to switch from following a learned route to finding a novel shortcut, is consistent with both our primary hypothesis and our previous VPM work demonstrating a specific deficit in switching from an egocentric to an allocentric navigational strategy (Harris et al., 2012). This study therefore corroborates this earlier finding, but also, due to the more realistic nature of the shortcutting task, provides support for the assumption that a strategy switching deficit observed in the relatively abstract VPM does translate to a real-world navigational impairment. As strategy switching is thought to be coordinated by PFC and the LC-NA system (Aston-Jones & Cohen, 2005; Bouret & Sara, 2005; Caetano et al., 2013), this navigational strategy switching deficit can be explained in terms of age-related dysfunction of PFC (West, 1996; Pfefferbaum et al., 2005), perhaps causing an underlying deficit in the ability to decide which strategy to use, and/or the LC-NA system (Manaye et al., 1995; Grudzien et al., 2007), affecting the ability to engage the correct strategy. More specifically, if the deficit only affects switching from an egocentric to an allocentric strategy, it may relate to reduced functional interconnectivity between the prefrontal-noradrenergic strategy switching network and the hippocampus, the neural substrate of allocentric processing (O'Keefe, 1990; Hartley et al., 2003; Iaria et al., 2003). Unfortunately, due to the complex nature of our shortcutting task, assessing switching in the opposite direction could not be easily incorporated while maintaining a reasonable experimental duration, which meant that it was unable to confirm the specificity of the switching deficit.

However, the sVPM did assess switching in the opposite direction and, contrary to our hypotheses and to our previous VPM work, switching to the response strategy was impaired. In fact, the apparent age difference in switching to the place strategy did not remain significant after correcting for multiple comparisons, although there was no significant difference between these two change types. These results are more concordant with a general strategy switching deficit, which would not relate to reduced prefrontal-hippocampal connectivity, as previously suggested, but instead to dysfunction within the LC-NA system or PFC, as above. Our previous findings may have been due to a discrepancy between the two strategies in terms of difficulty (Floresco et al., 2008), which we may have alleviated in this study by ensuring that all participants started on the more difficult place strategy. As our general linear model also demonstrated an age-independent relationship between switching performance and use of shortcuts, we argue that the observed impairment in shortcutting reflects a general strategy switching deficit, rather than a specific deficit in engaging an allocentric strategy. Our main findings may therefore relate more directly to previous work on age-related switching deficits in other cognitive domains (Moore et al., 2003; Ashendorf & McCaffrey, 2008; Young et al., 2010).

In addition to deficits in switching between strategies, the large age difference in performance on the cognitive mapping test is indicative of an allocentric processing deficit. Such cognitive mapping tests have been criticised because survey maps can theoretically be generated from a quantitatively scaled route representation (Montello et al., 2004), but the results are consistent with previous work demonstrating allocentric processing deficits in older people (Begega et al., 2001; Moffat et al., 2006; Antonova et al., 2009; Iaria et al., 2009; Wiener et al., 2012). Furthermore, many more older participants than young failed to respond correctly to a full set of probe trials for both VEs, also indicating an impairment in formation or use of a cognitive map. It seems likely that an allocentric processing impairment would have contributed to the age difference in use of shortcuts, as older people may have been less able to use a wayfinding strategy, and/or less inclined to attempt to switch to one. However, while only two older participants responded correctly to a full set of probe trials for both VEs, most of them managed to do so for at least one VE, suggesting that they were able to form and use allocentric representations of the environments. Moreover, when only assessing shortcut use within VEs for which each participant *did* pass a set of probe trials, we still found a large age difference, suggesting that older participants failed to switch to a wayfinding strategy even when they had formed an allocentric representation of the environment. Similarly, while none of the older participants stably switched to the wayfinding strategy, the majority did use a shortcut at least once, confirming that they were able to do so. Furthermore, navigating overlapping routes has been shown to depend more heavily upon the hippocampus (Brown et al., 2010), yet older participants did not seem to find the crossing routes more difficult. Finally, while our general linear model demonstrated an age-independent effect of strategy switching, it did not show a specific effect of cognitive mapping ability on use of shortcuts. This does not prove that allocentric processing deficits did not affect use of shortcuts, and in fact it is likely that they did; but if older people were less able or less willing to switch to a wayfinding strategy due to impaired allocentric processing, cognitive mapping, as a measure of such, would be expected to predict use of shortcuts. Together, our results indicate that shortcutting was more dependent on strategy switching, suggesting that the large age difference we observed in use of shortcuts does reflect a strategy switching deficit.

Our study was limited by its cross-sectional design, because the older sample could have contained cases of borderline cognitive impairments that were not detected with only one neuropsychological assessment. This could be addressed with a longitudinal study involving more extensive neuropsychological testing, which our results suggest would be worthwhile. In addition, studying shortcutting using neuroimaging could also be useful in determining the neural mechanisms that underlie deficits in switching to an allocentric navigational strategy.

### *4.1. Conclusions*

In summary, our findings illustrate a large effect of age on the ability to switch from following a known route to using a novel shortcut in order to take the optimal route to a goal location. This confirms that the age-related deficit in navigational strategy switching that we previously identified using the VPM does affect performance at a more realistic navigational task and provides an example of how real-world navigation may be affected by this deficit. Older participants also showed evidence of allocentric processing difficulties, which are likely to contribute as well, but their perseveration with the route-following strategy was more closely related to strategy switching performance, confirming that it can be at least partly explained in terms of a general strategy switching impairment. This impairment may result from degradation of PFC or dysfunction of the LC-NA system, causing underlying deficits in decision making or in engaging a behavioural strategy, although exactly how age-related changes in function of this prefrontal-noradrenergic network lead to navigational strategy switching deficits remains to be explored. Overall, our findings show how a relatively subtle age-related impairment in a single executive process can contribute to much more substantial effects on navigational performance and on the everyday lives of older people.

## Acknowledgements

This study was funded by the University of Edinburgh and the Biotechnology and Biological Sciences Research Council (BBSRC). Thanks also to Ella Feltham, Emma Hall and Kelly Leslie for help with data collection.

## Disclosure statement

The authors have no conflicts of interest to declare. This study was approved by the University of Edinburgh Psychology Research Ethics Committee and conducted in accordance with the declaration of Helsinki.

## References

Allen, G.L., Kirasic, K.C., Rashotte, M.A., 2004. Aging and path integration skill: kinesthetic and vestibular contributions to wayfinding. Percept. Psychophys. 66, 170-179.

Aston-Jones, G., Cohen, J.D., 2005. An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. Annu. Rev. Neurosci. 28, 403-450.

Antonova, E., Parslow, D., Brammer, M., Dawson, G.R., Jackson, S.H., Morris, R.G., 2009. Age-related neural activity during allocentric spatial memory. Memory 17, 125-143.

Ashendorf, L., McCaffrey, R.J., 2008. Exploring age-related decline on the Wisconsin Card Sorting Test. Clin. Neuropsychol. 22, 262-272.

Begega, A., Cienfuegos, S., Rubio, S., Santin, J.L., Miranda, R., Arias, J.L., 2001. Effects of ageing on allocentric and egocentric spatial strategies in the Wistar rat. Behav. Proc. 53, 75-85.

Bouret, S., Sara, S.J., 2005. Network reset: a simplified overarching theory of locus coeruleus noradrenaline function. Trends Neurosci. 28, 575-582.

Brown, T.I., Ross, R.S., Keller, J.B., Hasselmo, M.E., Stern, C.E., 2010. Which way was I going? Contextual retrieval supports the disambiguation of well learned overlapping navigational routes. J. Neurosci. 30, 7414-7422.

Caetano, M.S., Jin, L.E., Harenberg, L., Stachenfeld, K.L., Arnsten, A.F., Laubach, M., 2013. Noradrenergic control of error preservation in medial prefrontal cortex. Front. Integr. Neurosci. 6, 125.

Corsi, P.M., 1972. Human memory and the medial temporal region of the brain. Diss. Abstr. Int. 34, 819B.

Cook, D., Kesner, R.P., 1988. Caudate nucleus and memory for egocentric localization. Behav. Neural Biol. 49, 332-343.

Driscoll, I., Hamilton, D.A., Petropoulos, H., Yeo, R.A., Brooks, W.M., Baumgartner, R.M., Sutherland, R.J., 2003. The aging hippocampus: cognitive biochemical and structural findings. Cereb. Cortex 13, 1344-1351.

Doeller, C.F., King, J.A., Burgess, N., 2008. Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. Proc. Natl. Acad. Sci. USA. 105, 5915-5920.

Du, A.T., Schuff, N., Chao, L.L., Kornak, J., Jagust, W.J., Kramer, J.H., Reed, B.R., Miller, B.L., Norman, D., Chui, H.C., Weiner, M.W., 2006. Age effects on atrophy rates of entorhinal cortex and hippocampus. Neurobiol. Aging 27, 733-740.

Du, A.T., Schuff, N., Zhu, X.P., Jagust, W.J., Miller, B.L., Reed, B.R., Kramer, J.H., Mungas, D., Yaffe, K., Chui, H.C., Weiner, M.W., 2003. Atrophy rates of entorhinal cortex in AD and normal aging. Neurology 60, 481-486.

Floresco, S.B., Block, A.E., Tse, M.T., 2008. Inactivation of the medial prefrontal cortex of the rat impairs strategy set-shifting, but not reversal learning, using a novel, automated procedure. Behav. Brain. Res. 190, 85-96.

Grudzien, A., Shaw, P., Weintraub, S., Bigio, E., Mash, D.C., Mesulam, M.M., 2007. Locus coeruleus neurofibrillary degeneration in aging, mild cognitive impairment and early Alzheimer's disease. Neurobiol. Aging 28, 327-335.

Harris, M.A., Wiener, J.M., Wolbers, T., 2012. Aging specifically impairs switching to an allocentric navigational strategy. Front. Aging Neurosci. 4, 29.

Harris, M.A., Wolbers, T., 2012. Ageing effects on path integration and landmark navigation. Hippocampus 22, 1770-1780.

Hartley, T., Maguire, E.A., Spiers, H.J., Burgess, N., 2003. The well-worn route and the path less traveled: distinct neural bases of route-following and wayfinding in humans. Neuron 37, 877-888.

Iaria, G., Palermo, L., Committeri, G., Barton, J.J.S., 2009. Age differences in the formation and use of cognitive maps. Behav. Brain Res. 196, 187-191.

Iaria, G., Petrides, M., Dagher, A., Pike, B., Bohbot, V.D., 2003. Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. J. Neurosci. 23, 5945-5952.

Kessels, R.P., van Zandvoort, M.J., Postma, A., Kappelle, L.J., de Haan, E.H., 2000. The Corsi Block-Tapping Task: standardization and normative data. Appl Neuropsychol. 7, 252-258.

Lister, J.P., Barnes, C.A., 2009. Neurobiological changes in the hippocampus during normative aging. Arch. Neurol. 66, 829-833.

Luis, C.A., Keegan, A.P., Mullan, M., 2009. Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. Int J Geriatr Psychiatry 24, 197-201.

Lunn, D.J., Thomas, A., Best, N., Spiegelhalter, D., 2000. WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. Stat. Comput. 10, 325-337.

Mahmood, O., Adamo, D., Briceno, E., Moffat, S.D., 2009. Age differences in visual path integration. Behav. Brain Res. 205, 88-95.

Manaye, K.F., McIntire, D.D., Mann, D.M., German, D.C., 1995. Locus coeruleus cell loss in the aging brain: a non-random process. J. Comp. Neurol. 358, 79-87.

Moffat, S.D., Elkins, W., Resnick, S.M., 2006. Age differences in the neural systems supporting human allocentric spatial navigation. Neurobiol. Aging 27, 965-972.

Montello, D.R., Hegarty, M., Richardson, A.E., Waller, D., 2004. Spatial memory of real environments, virtual environments, and maps. In: Allen GL (Ed.), Human spatial memory: remembering where. Lawrence Erlbaum Associates, Mahwah, NJ, pp.251-285.

Moore, T.L., Killiany, R.J., Herndon, J.G., Rosene, D.L., Moss, M.B., 2003. Impairment in abstraction and set shifting in aged rhesus monkeys. Neurobiol. Aging 24, 125-134.

Nasreddine, Z.S., Phillips, N.A., Be, V., Collin, I., Cummings, J.L., Chertkow, H., 2005. The Montreal cognitive assessment, MoCA: A brief screening tool for mild cognitive impairment. J. Am. Geritatr. Soc. 53, 695-699.

Nelson, H.E., 1982. The National Adult Reading Test (NART): test manual. NFER Nelson, Windsor, UK.

O'Keefe, J., 1990. A computational theory of the hippocampal cognitive map. Prog. Brain Res. 83, 301-312.

Pellizzer, G., Bâ, M.B., Zanello, A., Merlo, M.C., 2009. Asymmetric learning transfer between imagined viewer- and object-rotations: evidence of a hierarchical organisation of spatial reference frames. Brain Cogn. 71, 272-278.

Pfefferbaum, A., Adalsteinsson, E., Sullivan, E.V., 2005. Frontal circuitry degradation marks healthy adult aging: Evidence from diffusion tensor imaging. Neuroimage 26, 891-899.

Ragozzino, M.E., 2007. The contribution of the medial prefrontal cortex, orbitofrontal cortex, and dorsomedial striatum to behavioural flexibility. Ann. N. Y. Acad. Sci. 1121, 355-375.

Ragozzino, M.E., Detrick, S., Kesner, R.P., 1999. Involvement of the prelimbic-infralimbic areas of the rodent prefrontal cortex in behavioural flexibility for place and response learning. J. Neurosci. 19, 4585-4594.

Rich, E.L., Shapiro, M.L., 2007. Prelimbic/Infralimbic Inactivation Impairs Memory for Multiple Task Switches, But Not Flexible Selection of Familiar Tasks. J. Neurosci. 27, 4747-4755.

Rosenzweig, E.S., Redish, A.D., McNaughton, B.L., Barnes, C.A., 2003. Hippocampal map realignment and spatial learning. Nat. Neurosci. 6, 609-615.

Smith, A.C., Frank, L.M., Wirth, S., Yanike, M., Hu, D., Kubota, Y., Graybiel, A.M., Suzuki, W.A., Brown, E.N., 2004. Dynamic analysis of learning in behavioral experiments. J. Neurosci. 24, 447-461.

Strauss, E., Sherman, E.M.S., Spreen, O., 2006. A Compendium of Neuropsychological Tests: Administration, Norms, And Commentary, third ed. Oxford University Press, Oxford, UK.

Tait, D.S., Brown, V.J., Farovik, A., Theobald, D.E., Dalley, J.W., Robbins, T.W., 2007. Lesions of the dorsal noradrernergic bundle impair attentional set-shifting in the rat. Eur. J. Neurosci. 25, 3719-3724.

West, M.J., 1993. Regionally specific loss of neurons in the aging human hippocampus. Neurobiol. Aging 14, 287-293.

West, R.L., 1996. An application of prefrontal cortex function theory to cognitive aging.

Psychol. Bull. 120, 272-292.

Wiener, J.M., de Condappa, O., Harris, M.A., Wolbers, T., 2013. Maladaptive bias for extrahippocampal navigation strategies in aging humans. J. Neurosci. 33, 6012-6017.

Wiener, J.M., Kmecova, H., de Condappa, O., 2012. Route repetition and route retracing: effects of cognitive aging. Front. Aging Neurosci. 4, 7.

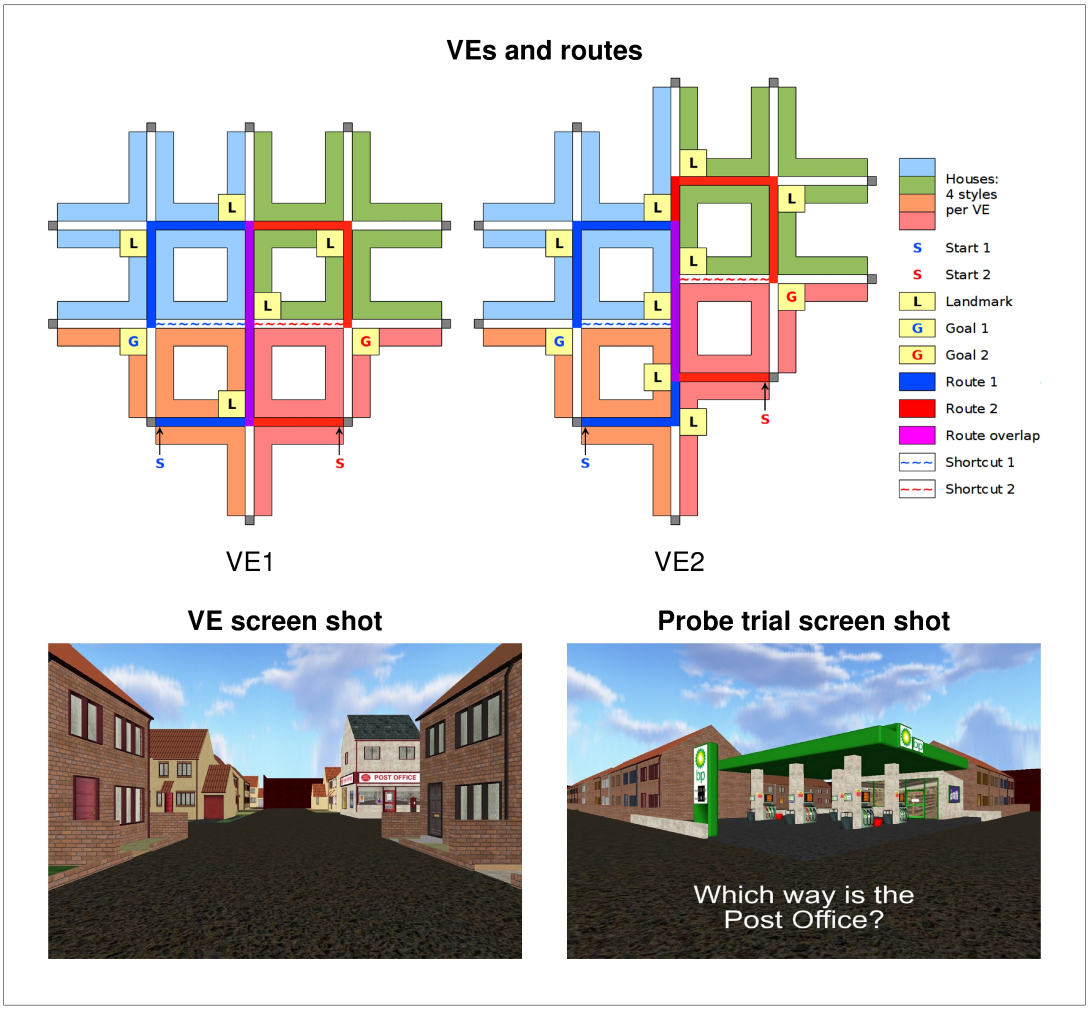
Wolbers, T., Hegarty, M., 2010. What determines our navigational abilities? Trends Cogn. Sci. 14, 138-146.

Young, J.J., Shapiro, M.L., 2009. Double dissociation and hierarchical organization of strategy switches and reversals in the rat PFC. Behav. Neurosci. 123, 1028-1035.

Young, J.W., Powell, S.B., Geyer, M.A., Jeste, D.V., Risbrough, V.B., 2010. The mouse attentional-set-shifting task: a method for assaying successful cognitive ageing? Cogn. Affect. Behav. Neurosci. 10, 243-251.

Zaehle, T., Jordan, K., Wüstenberg, T., Baudewig, J., Dechent, P., Mast, F.W., 2007. The neural basis of the egocentric and allocentric spatial frame of reference. Brain Res. 1137, 92-103.

## Figures and legends



VEs and routes

VE screen shot

Probe trial screen shot

**Figure 1** Shortcutting task. *Top:* Maps of the two VEs, with the four long routes to each goal location (followed during training) and the shortcuts (available during testing) marked. *Bottom left:* Screen capture from VE 1 during training, approaching one of the goal locations. *Bottom right:* Screen capture illustrating a probe trial (in which the post office was directly to the left).

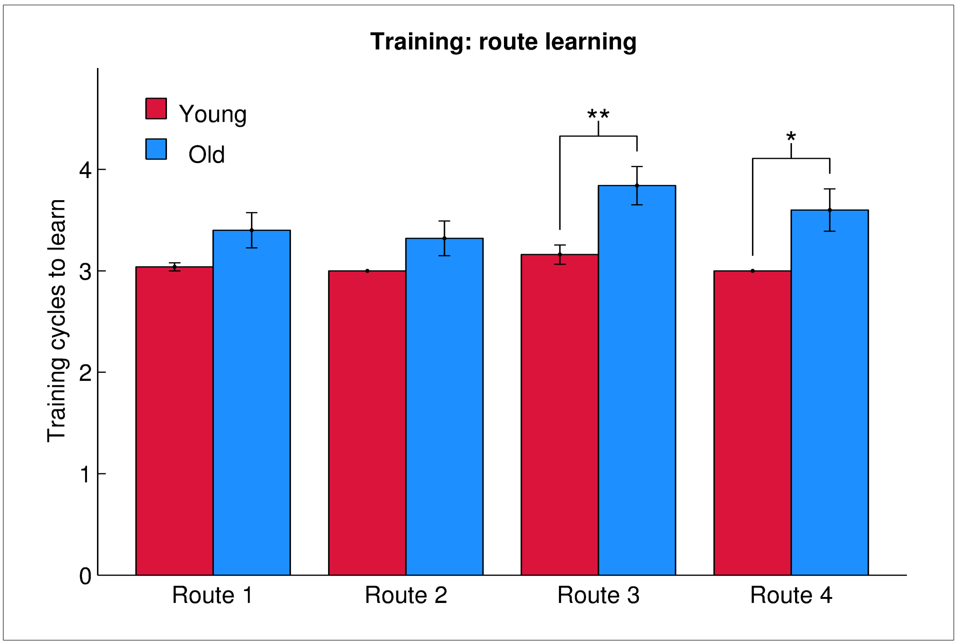


**Figure 2** Speed of route learning during training by route and age group, in terms of mean number of training cycles until the route could be followed without directions or errors. As directions were present throughout the first two cycles, the minimum possible number of training cycles in which this criterion could be reached was three. The younger group is represented by red bars, the older group by blue bars. Error bars represent standard error of the mean. Asterisks indicate significant differences at the $p_{HB}<.05$ (*) and $p_{HB}<.01$ (**) levels.

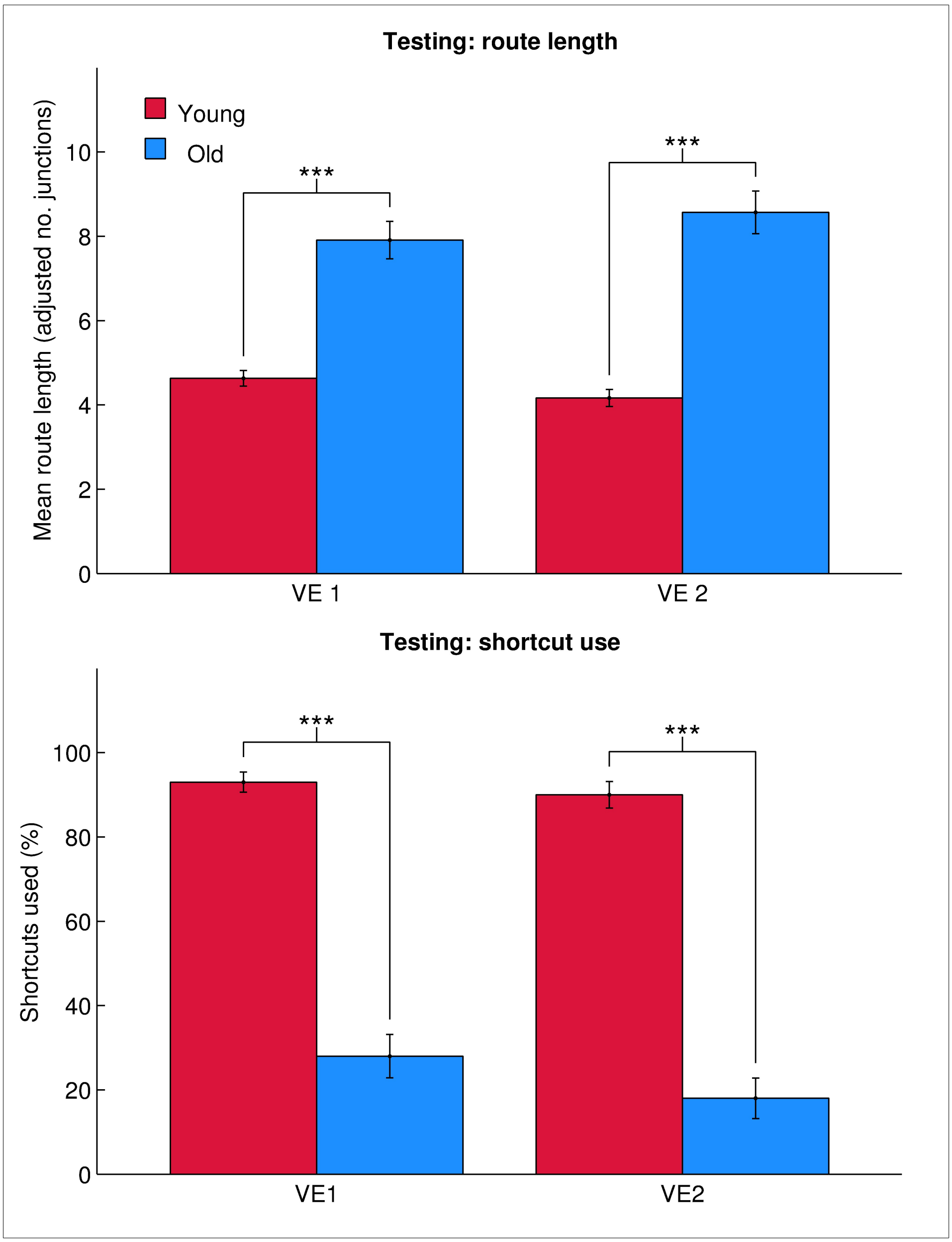


**Figure 3** Shortcutting task performance by VE and age group, in terms of mean length of route to goal location in number of junctions (adjusted for VE differences in route length; *top*) and mean percentage of test trials on which the available shortcut was used (*bottom*). The younger group is represented by red bars, the older group by blue bars. Error bars represent standard error of the mean. *** indicates a significant difference at the $p_{HB}<.001$ level.

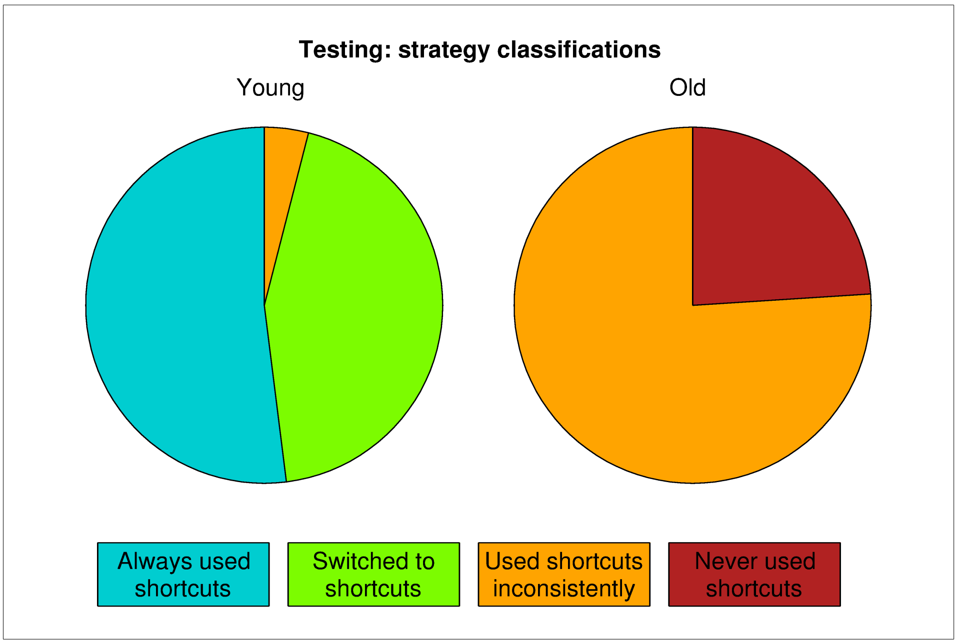


**Figure 4** Strategy use classifications by age group. *Always used shortcuts:* Participants that used the available shortcuts from the first test trial and throughout testing. *Switched to shortcuts:* Participants that followed the long training routes at the beginning of testing, but stably switched to a shortcutting strategy at some point during testing. *Used shortcuts inconsistently:* Those that occasionally used the available shortcuts, but not consistently enough to be classified as having stably switched to a shortcutting strategy. *Never used shortcuts:* Those that employed a route following strategy throughout testing and never used the shortcuts.

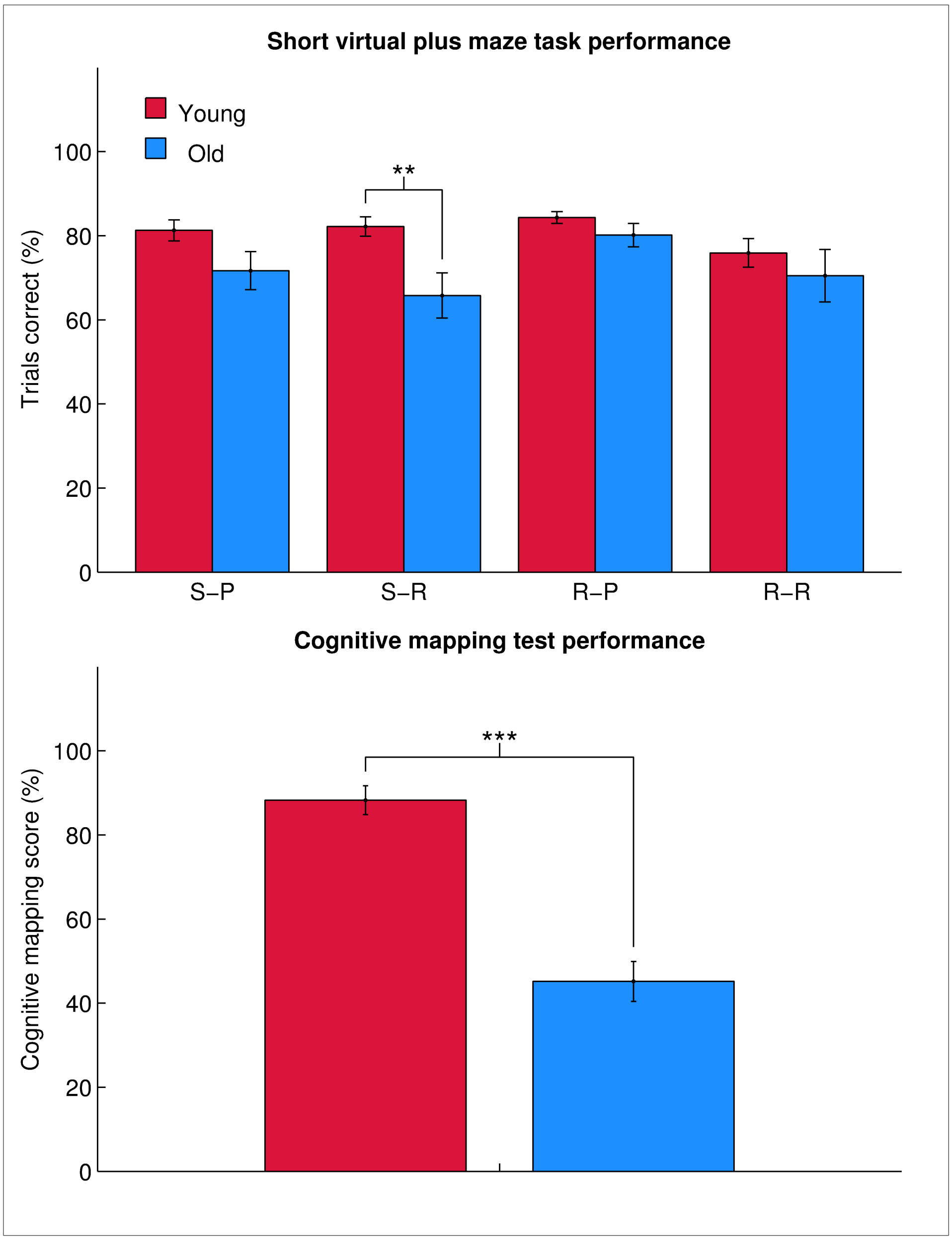


**Figure 5** sVPM task and cognitive mapping test results. *Top:* sVPM performance, in terms of mean percentage of trials correct, by age group and for switch-to-place (S-P), switch-to-response (S-R), reverse-place (R-P) and reverse-response (R-R) trial blocks. *Bottom:* Cognitive mapping task performance by age group, in terms of mean percentage of landmarks correctly labelled. The younger group is represented by red bars, the older group by blue bars. Error bars represent standard error of the mean. Asterisks indicate significant differences at the $p_{HB}<.05$ (*) and $p_{HB}<.001$ (***) levels.