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The contribution of visual attention and declining verbal memory abilities to age-related route learning deficits

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ABSTRACT

Our ability to learn unfamiliar routes declines in typical and atypical ageing. The reasons for this decline, however, are not well understood. Here we used eye-tracking to investigate how ageing affects people's ability to attend to navigationally relevant information and to select unique objects as landmarks. We created short routes through a virtual environment, each comprised of four intersections with two objects each, and we systematically manipulated the saliency and uniqueness of these objects. While salient objects might be easier to memorise than non-salient objects, they cannot be used as reliable landmarks if they appear more than once along the route. As cognitive ageing affects executive functions and control of attention, we hypothesised that the process of selecting navigationally relevant objects as landmarks might be affected as well. The behavioural data showed that younger participants outperformed the older participants and the eye-movement data revealed some systematic differences between age groups. Specifically, older adults spent less time looking at the unique, and therefore navigationally relevant, landmark objects. Both young and older participants, however, effectively directed gaze towards the unique and away from the non-unique objects, even if these were more salient. These findings highlight specific age-related differences in the control of attention that could contribute to declining route learning abilities in older age. Interestingly, route-learning performance in the older age group was more variable than in the young age group with some older adults showing performance similar to the young group. These individual differences in route learning performance were strongly associated with verbal and episodic memory abilities.

1. Introduction

Age-related differences in route learning abilities are now firmly established (Cushman, Stein, & Duffy, 2008; Hartmeyer, Grzeschik, Wolbers, & Wiener, 2017; Head & Isom, 2010; Lipman, 1991; O'Malley, Innes, & Wiener, 2018; Varner, Dopkins, & Philbeck, 2016; Wiener et al., 2012, 2013; Wilkniss, Jones, Korol, Gold, & Manning, 1997; Zhong & Moffat, 2016), however the underlying mechanisms are still poorly understood. Here we study whether differences in control of visual attention – required to select navigationally-relevant information – correlate with age-related declines in route learning performance. In addition, we use a series of neuropsychological assessments to investigate whether declines in specific cognitive functions can predict performance differences between age groups.

Route navigation, arguably the most frequent human navigation task, is the prototypical egocentric navigation task, as the underlying knowledge is typically conceptualised as a series of recognition-triggered responses ("Turn left at Fire Station") or direction changes ("Left, right, left, straight"; Waller & Lippa, 2007), both of which utilise a body-based reference frame. Route knowledge depends on striatal structures such as the caudate nucleus (Hartley et al., 2003), but more recently the contribution of hippocampal episodic memory mechanisms to successful route learning have been discussed (Goodroe, Starnes, & Brown, 2018). Given that both the caudate and hippocampus show similar rates of age-related neurodegenerative changes (Betts, Acosta-Cabronero, Cardenas-Blanco, Nestor, & Düzel, 2016), it is not surprising that older adults consistently show slower route learning performance than younger adults (for a recent review, see Lester, Moffat, Wiener, Barnes, & Wolbers, 2017).

The exact psychological mechanisms that could explain the declines in route learning performance in older age, however, we are only beginning to understand. Zhong and Moffat (2016) argue that weaker

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associative learning of landmarks and direction changes can explain slower route acquisition in older adults. O'Malley et al., 2018 studied whether younger and older adults use different encoding strategies by comparing route knowledge after successful learning of routes. Specifically, participants were presented with short routes until they could recall all the direction choices along the route. Their memory of the routes was then studied with a series of tests, probing knowledge of landmark direction associations, knowledge of sequence of turns and knowledge of sequence of landmarks. While older adults needed longer to learn the routes than younger adults, and while there were differences in associative knowledge between younger and those older adults that showed early signs of cognitive impairments, O'Malley and colleagues report little differences in strategies between younger and healthy older adults. Together these findings support the notion that general associative learning deficits (Naveh-Benjamin et al., 2009; Naveh-Benjamin, Brav, & Levy, 2007) contribute to age-related difference in route-knowledge acquisition.

Attentional processes have also been suggested to contribute to age-related declines in route learning. When learning novel routes, navigators primarily attend to and encode objects/landmarks located at navigationally relevant locations such as decision points (Aginsky, Harris, Rensink, & Beusmans, 1997; Janzen, 2006). Hartmeyer et al. (2017) used an auditory probe task in a simplistic virtual environment with few environmental cues to measure how attentional engagement is modulated during route learning. They reported that stronger attentional engagement with the route-learning task when approaching intersections resulted in better route learning performance in both younger and older adults.

In more complex and naturalistic environments that feature a multitude of cues, however, older adults tend to remember salient features along a route, rather than focusing on navigationally relevant situations (Lipman, 1991). This is in line with studies from other cognitive domains, suggesting that older adults have more difficulties ignoring salient, but task-irrelevant stimuli (Schmitz, Cheng, & De Rosa, 2010). For example, Tsvetanov, Mevorach, Allen, and Humphreys (2013) asked young and older participants to identify a target in either the local or global level of a hierarchical visual stimulus. In this task, older adults were less efficient in ignoring salient distractors, even if these were not task-relevant, i.e. if they were present in the non-relevant hierarchical level. These findings are in line with the inhibition deficit theory (Lustig, Hasher, & Zacks, 2007) stating that older adults are less efficient in inhibiting the processing of irrelevant or unwanted information. If these findings translate to the context of route learning, or more precisely, landmark selection, it would suggest that older participants would be less efficient in attending to and selecting navigationally relevant landmarks if these are presented alongside more salient but task-irrelevant objects.

We tested this hypothesis using eye-tracking during a route learning task. This allowed us to study the influence of attentional control and participants' ability to inhibit salient but non-relevant information on route learning performance. In the experiment, participants were transported along short routes comprised of four intersections and were asked to learn these routes. Each intersection featured two landmark objects, one of which was unique, while the other one was repeated somewhere along the route. During learning we monitored (1) how much time they spent attending to the navigationally relevant (i.e. unique objects) as compared to other environmental cues, (2) how effectively they directed their attention away from non-unique objects toward unique objects when they first encountered a repeated object and (3) whether switching of attention from non-unique to unique objects was affected by the object's saliency. After training, participants were presented with screenshots of the intersections in random order and were asked to indicate the direction in which the route continues. This procedure was repeated until participants have learned the route.

In line with earlier behavioural work (O'Malley et al., 2018 for a similar paradigm), we expected our older participant group to show slower route learning, i.e. we expected them to make more errors and to require more repetitions until they have successfully learned the routes. We expected all participants to spend more time looking at salient than non-salient objects (Lipman, 1991), especially during the first encounter with the objects. If the ability to shift attention to the unique – i.e. navigationally relevant – landmark is affected by age-related declines in route learning performance, we expected our older participant group to (1) spend less time looking at the unique landmark information during learning, and (2) to less effectively shift gaze from the non-unique to the unique landmark object, especially if the non-unique objects are the salient objects.

It is important to note at this point that age-related differences in route learning abilities are reported even though older participants are typically being screened for signs of cognitive impairments. This suggests that screening tools for early cognitive impairments such as the MoCA (Nasreddine et al., 2005), the MMSE (Folstein, Folstein, & McHugh, 1975), or the (M-)ACE (Hsieh, McGrory, & Leslie, 2015; Mathuranath, Nestor, Berrios, Rakowicz, & Hodges, 2000) are either not sensitive enough or are not targeting those cognitive mechanisms that contribute to age-related declines in route learning and navigation abilities. In addition to studying visual attentional control in this study we therefore also administered a series of assessments targeting verbal and episodic memory, spatial working memory and executive functioning to develop a better understanding of whether declines in any of these cognitive functions contribute to age-related route learning deficits. We selected these specific assessments as they cover at least some of the cognitive functions and processes that are assumed to be involved in determining human navigation abilities (Wolbers & Hegarty, 2010).

2. Material & methods

We created a virtual environment that resembled a residential development or care home. The environment was designed to look as natural as possible and was based around dementia-friendly design guidelines (Greasley-Adams, Bowes, Dawson, & McCabe, 2014; O'Malley, Innes, & Wiener, 2017). Nevertheless, to avoid recognition effects of the different corridors, pictures on walls and doors were the same for each corridor but varied between the different routes.

2.1. Participants

A total of 80 participants (32 younger adults [17 females; mean age 24.25 ± 6.38 years; range, 18–40] and 48 older adults [24 females; mean age 73.28 ± 4.82 years; range, 66–82]) took part in the experiment. Participants were administered a battery of cognitive tests to assess overall cognitive function, verbal and visual memory, and working memory (see Table 1). This assessment included: Rey-Osterrieth Complex Figure Test (ROCF; copy, immediate recall, delayed recall), Digit Span (forward & backward, WAIS IV), Word List I & II (WMS III), Spatial Span (aka "Corsi Block", forward & backward, WMS III), and the Mini-Addenbrooke's Cognitive Examination (M-ACE). The ROCF has been used to evaluate visuospatial constructional abilities, visual memory and cognitive functions (Shin, Park, Park, Seol, & Kwon, 2006), whereas the Corsi Block Task assesses the visuospatial short-term memory (Kessels, Van Zandvoort, Postma, Kappelle, and De Haan (2000). The Digit Span test was administered to evaluate the participant's verbal short-term memory (Kessels, Overbeek, & Bouman, 2015). Further, the Word List Learning test was administered to test for verbal episodic memory abilities (Beck, Gagneux-Zurbriggen, Berres, Taylor, & Monsch, 2012). The M-ACE is a brief cognitive screening tool for dementia which accesses items in the domains of orientation, memory, language, and visuospatial function (Hsieh et al., 2015). Additional questionnaires were administered to collect demographic data and to determine the participant's depression level (HADS, Zigmond & Snaith, 1983) and their sense of direction (SBSOD, Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002). Most of the younger participants

Table 1
Participant demographic characteristics and results of standardised neurocognitive assessments (SD in brackets).

	younger (n = 32)	older (n = 46)	t values (df)	p values
Sex (m/f)	15 m, 17 f	24 m, 24 f		
Handedness (r, l, b)	30 r, 2 l	42 r, 5 l, 1 b		
Age (yrs)	25.26 (6.38)	73.28 (4.82)	−36.74 (54.35)	< 0.001
Education (yrs)	16.19 (3.54)	14.64 (4.94)	1.6 1 (74.68)	0.11
computer experience (0–7)	3.66 (1.81)	1.37 (1.18)	6.22 (49.22)	< 0.001
M-ACE (/30)	28.25 (3.03)	28.72 (1.58)	−0.81 (40.84)	0.42
HADS	10.56 (4.27)	7.45 (4.49)	3.10 (69.43)	< 0.01
SBSOD (/7)	3.67 (1.04)	3.28 (1.04)	1.63 (67.41)	0.11
ROCF				
Copy (/36)	34.88 (1.64)	33.72 (3.56)	1.92 (67.34)	0.059
Immediate (/36)	22.48 (6.14)	17.24 (6.47)	3.61 (69.35)	< 0.001
30 min delay (/36)	23.06 (6.16)	17.20 (6.35)	4.08 (68.60)	< 0.001
Word List I & II				
Trials 1–4 (/48)	38.38 (5.48)	33.54 (7.12)	3.45 (74.50)	< 0.001
Immediate (/12)	10.41 (1.43)	8.48 (2.81)	4.12 (72.03)	< 0.001
30 min delay (/12)	9.97 (1.79)	8.00 (2.89)	3.80 (75.58)	< 0.001
Digit Span				
Forward (/144)	72.88 (27.57)	66.17 (23.88)	1.12 (60.38)	0.27
Backward (/112)	44.72 (18.43)	49.65 (22.86)	−1.05 (74.37)	0.30
Corsi Block				
Forward (/144)	70.22 (24.15)	45.94 (15.48)	5.04 (47.88)	< 0.001
Backward (/112)	62.10 (20.46)	46.59 (17.86)	3.46 (61.23)	=0.001

were Psychology undergraduates at Bournemouth University and were rewarded course credits for their participation. The older participants were volunteers who were receiving reimbursement for their participation in the study. Ethical approval was obtained from the Science, Technology & Health Research Ethics Panel at Bournemouth University and written informed consent was obtained from all participants, in accordance with the declaration of Helsinki (World Medical Association, 2000).

Two older participants were excluded from the analyses as they finished less than half of the twelve routes (one participant had to quit due to motion sickness and the other due to technical problems with the setup). 41 of the remaining 46 older participants completed the entire experiment and five completed at least six out of twelve routes (one: 10 routes, two: 9 routes, one: 7 routes, and one: 6 routes). All younger participants completed the entire experiment.

2.2. Apparatus

Eye movements were captured using a head-mounted eye tracker (EyeLink II, SR Research Ltd., Ottawa, Canada) sampling left eye pupil position at 500 Hz. Calibration was performed and checked for accuracy before starting the experiment using a nine-point grid. Drift

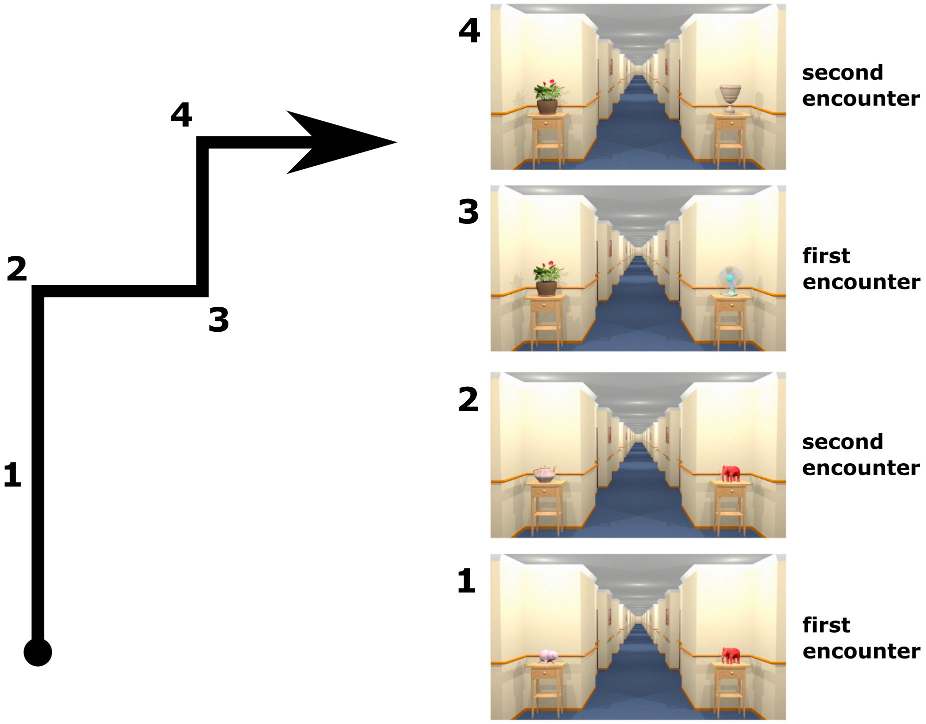

Fig. 1. Left: Schematic overview of one of the routes: Right: Screenshots of the four intersections of the route. Note that this is an example of an incongruent route as the more salient object was the non-unique object (red statue of elephant at intersections 1 and 2 and flowers at intersections 3 and 4). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

correction was performed before each stimulus presentation (video or static image). The experiment was presented on a 40″ CRT monitor with a resolution of 1920 × 1080 and a refresh rate of 100 Hz. Participants were seated 100 cm in front of the monitor. Experiment Builder (SR Research Ltd., Ottawa, Canada) was used for displaying the visual stimuli and the recording of eye-movements, as well as responses given via a standard computer keyboard.

2.3. Virtual environment

The virtual environment and the twelve routes through it were created using 3D Studio Max (Autodesk Inc., San Rafael, USA). To investigate how cognitive ageing affects people's ability to select unique objects as landmarks, two types of routes were created: congruent routes (n = 6) and incongruent routes (n = 6), each comprising four intersections with two different objects as landmarks at each intersection. At each intersection, one of the two objects was unique, appearing only once along the route, while the other one was non-unique, appearing at two of the intersections along the route (henceforth "first encounter" and "second encounter"). In other words, each route featured two non-unique objects each of which appeared twice along the route. A specific non-unique object always appeared on the same side of the intersection to ensure that participants needed to attend to the other unique object in order to disambiguate two intersections with the same non-unique objects (Fig. 1). Finally, the positions of the non-unique objects and the direction of travel was counterbalanced between routes. For congruent routes, the unique landmarks were also salient. For the incongruent routes, in contrast, the salient objects occurred twice on the route (i.e., "non-unique") and the non-salient objects were unique. The saliency of the objects was assessed using two approaches: (1) using a subjective approach, we asked 103 participants in an online survey (SurveyMonkey, San Mateo, USA) to compare 70 pairs of objects and to indicate "which of the objects stands out more" using a 7-digit scale; (2) using an objective approach, we calculated saliency maps for each of the pairs (Harel, Koch, & Perona, 2006; Itti & Koch, 2000). Objects that scored high in both approaches were chosen as salient landmarks and objects that scored low in both approaches were chosen as non-salient landmarks. Two exemplary images along with their ratings are included in Appendix A. Every route had four intersections and was comprised of at least one left turn, one right turn and one movement straight on. Turns and movements, as well as arrangement of salient/unique objects, were balanced between all twelve routes.

2.4. Procedure

For each of the twelve routes the same procedure was used: in the training phase, participants were shown the video of the route through the virtual environment. Several studies have demonstrated that route learning performance does not differ between active and passive route exploration (e.g., Cutmore, Hine, Maberly, Langford, & Hawgood, 2000; Gaunet, Vidal, Kemeny, & Berthoz, 2001), suggesting that active decision making has no reliable influence on spatial-knowledge acquisition (Chrastil & Warren, 2012). We therefore decided to passively transport participants along the routes during the learning phase. This also ensured that the visual input during the learning phase was identical for each participant. In the subsequent test phase, full-screen images of the four intersections were presented in a random order and participants had to indicate the movement direction required to continue along the route by pressing the corresponding arrow key using a standard keyboard. The images were displayed until the response was made. There was no time limit for the responses, but participants were instructed to respond quickly and accurately. By randomising the order in which intersections were presented in the test phase, we ensured that participants could not simply remember the order of turns along the route, but instead had to rely on the object information to solve the task. Training and test phase were repeated until a route was successfully learned, i.e. until all test phase responses were correct, or until the route was presented for a total of five times. The 12 routes were presented in a random order. For calibration purposes, a fixation dot was shown before each of the images and the videos.

2.5. Analysis

Behavioural data: for each route we recorded the number of repetitions (i.e. training trials) participants needed to learn the route. For each stimulus presented in the test phase, participants' responses (left, right, or up) as well as their response time were recorded. Data of all participants (46 older and 32 younger) entered the analyses.

Eye movement data: eye movements were recorded for both the training and the test phase and interest areas were defined around both objects ("left", "right") as follows: for the training phase a time window of 5 s before crossing the intersection (= 2500 frames) was chosen where both objects were fully visible. The interest areas that were created for the analysis grew dynamically while approaching the intersection, i.e. the area's size increased every 500 ms (= 250 frames; Fig. 2). These looming interest areas ensured that fixations could be assigned to the objects more precisely than using fixed sized interest areas. For the test phase, fixed interest areas of the same size each were defined around the objects. For both training and test phase, the area outside of the object interest areas was labelled as "non-objects". Due to technical issues with the eye-tracker, data from 4 older and 1 younger participant was removed from the eye movement analysis.

Fixations shorter than 80 ms were removed from the data set. Fixations were detected using SR Research's velocity and acceleration based algorithm with a fixed velocity threshold of 30°/s and an acceleration threshold of 8000°/s (Eyelink User Manual, 2005).

We report inferential statistics based on linear mixed models (LMM). We chose LMMs as sphericity was violated for many of our dependent variables. To fit the LMMs, we used the lmer function of the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) and the R Environment for Statistical Computing (R Core Team, 2017). For each factor, we report regression coefficients (b), standard errors, and t-values and we use the two-tailed criterion $|t| \geq 1.96$, corresponding to a 5% error criterion for significance for all tests (e.g., Vorstius, Radach, Mayer, & Lonigan, 2013). We centered all fixed effects and used contrast coding to do so where the factors were categorical instead of continuous. Unless specified differently, we started with intercept only models, using factors that resembled the experimental manipulation as fixed effects and participants as random effect. We then included random slopes and interactions between random slopes, but only kept these if they improved the model based on the conventional model selection Akaike Information Criterion (AIC). For each analysis we report the final model in Appendix A.

3. Results

3.1. Behavioural data

3.1.1. Number of training trials

To explore performance differences between age groups, we investigated the number of training trials participants needed to learn the routes. The model included fixed effects for age group, experiment phase, route type, and their interaction. Random factors were participants and route IDs. The successfully converged model included the full random effects structure for participants and route IDs. There was an effect of age group (b = 0.43, SE = 0.07, t = 6.18) and experiment phase (1st vs. 2nd half of experiment: b = 0.11, SE = 0.03, t = 3.66), but no effect of route type (congruent, incongruent: b = 0.07, SE = 0.08, t = 0.93) and no interactions (all $|t| < 1.96$). Specifically, older participants needed more trials to learn the routes than younger participants (2.25 vs. 1.40 training trials; Fig. 3A), participants needed more trials for the first six routes than for the rest of the routes (2.01 vs.

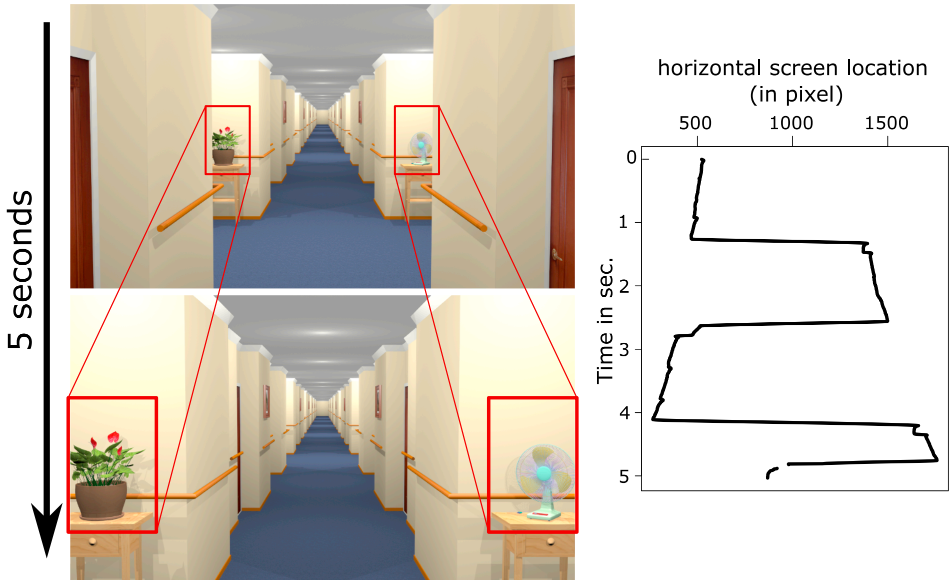

Fig. 2. Left panel: schematic depiction of the dynamically growing interest areas that were used for the gaze analysis of the training phase. The size of the interest areas increased every 500 ms. Right panel: exemplary gaze behaviour of one participant for the last five seconds when approaching the intersection.

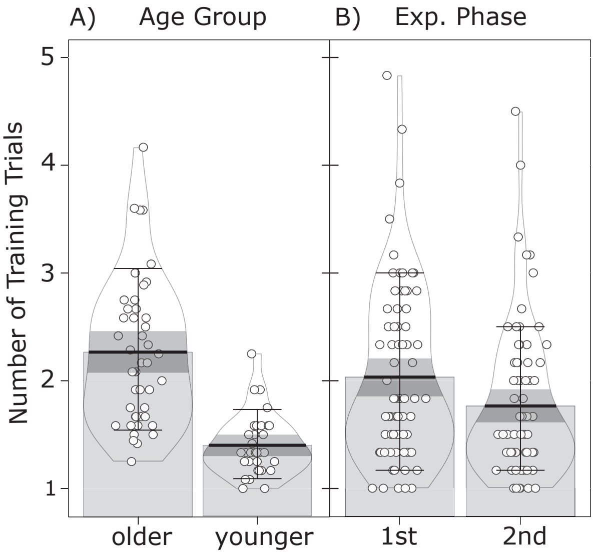

Fig. 3. Mean number of training trials per participant. Plots show individual data (dots), mean ± CI and 10th/90th quantiles of the groups. Older participants needed more training trials than younger participants (3A), all participants needed more training trials during the first six routes of the experiment compared to the rest of the routes (3B).

1.77 training trials; Fig. 3B) but similar numbers of trials for congruent routes and incongruent routes (1.81 vs. 1.97 training trials).

Visual inspection of the data in Fig. 3A also suggests that the variance was larger in the older participant group than in the younger participant group. This was confirmed using Levene's test that indicated unequal variances (F = 18.24, $p < 0.001$).

3.1.2. *Errors*

Error rates were obtained to further explore performance differences between age groups. In contrast to the number of training trials, errors allowed us to address not only the number of errors per route, but also where along the route errors were made. The model included fixed effects for age group, experiment phase, route type, intersection, and their interaction. Random factors were participants and route IDs. The successfully converged model included the full random effects structure for participants and route IDs. There was an effect of age group (b = 0.06, SE = 0.01, t = 6.11), experiment phase (1st vs. 2nd half of experiment: b = 0.01, SE = 0.01, t = 2.29) and intersection (1–4; b = 0.02, SE = 0.004, t = 4.52), but no effect of route type (congruent, incongruent: b = 0.01, SE = 0.01, t = 0.68) and no interactions (all $|t| < 1.96$). Specifically, older participants performed worse than younger participants (2.20 vs. 0.60 errors), participants performed worse in the first half of the experiment than in the second half of the experiment (1.79 vs. 1.27 errors; Fig. 4B) and errors increased along the route (average errors at 1st intersection: 0.30; average errors at 4th intersection: 0.42; Fig. 4C).

As the total number of errors per route is not independent of the number of training trials, we also calculated the average number of errors per repetition (see Fig. 4A) and reran the above analysis, but without the factor intersection, which rendered very similar results. There was an effect of age group (b = 0.20, SE = 0.03, t = 6.64) and experiment phase (1st vs. 2nd half of experiment: b = 0.04, SE = 0.02, t = 2.70), but no effect of route type (congruent, incongruent: b = 0.03, SE = 0.04, t = 0.62) and no interactions (all $|t| < 1.96$). Specifically, older participants performed worse than younger participants (0.66 vs. 0.25 errors per training trial; Fig. 4A) and participants performed worse in the first half of the experiment than in the second half of the experiment (0.54 vs. 0.44 errors per training trial).

Visual inspection of the data in Fig. 4A suggests that the variance was larger in the older participant group than in the younger participant group. This was confirmed using Levene's test that indicated unequal variances (F = 18.56, $p < 0.001$).

3.1.3. *Response time*

Times for correct responses were analysed using a model that included fixed effects for age group, experiment phase, route type, intersection, and their interaction. Random factors were participants and route IDs. The successfully converged model included a random slope of experiment phase for participants but none for route IDs. There was an effect of age group (b = 675.82, SE = 81.73, t = 8.27), experiment phase (1st vs. 2nd half of experiment: b = 198.00, SE = 42.76, t = 4.63) and intersection (1–4; b = 149.76, SE = 32.35, t = 4.63), but no effect of route type (congruent, incongruent: b = 6.05, SE = 61.17, t = 0.10) and no interactions (all $|t| < 1.96$). Specifically, older participants responded slower than younger participants (3542 ms vs. 2175 ms; Fig. 5A), responses were slower for the first six routes than for

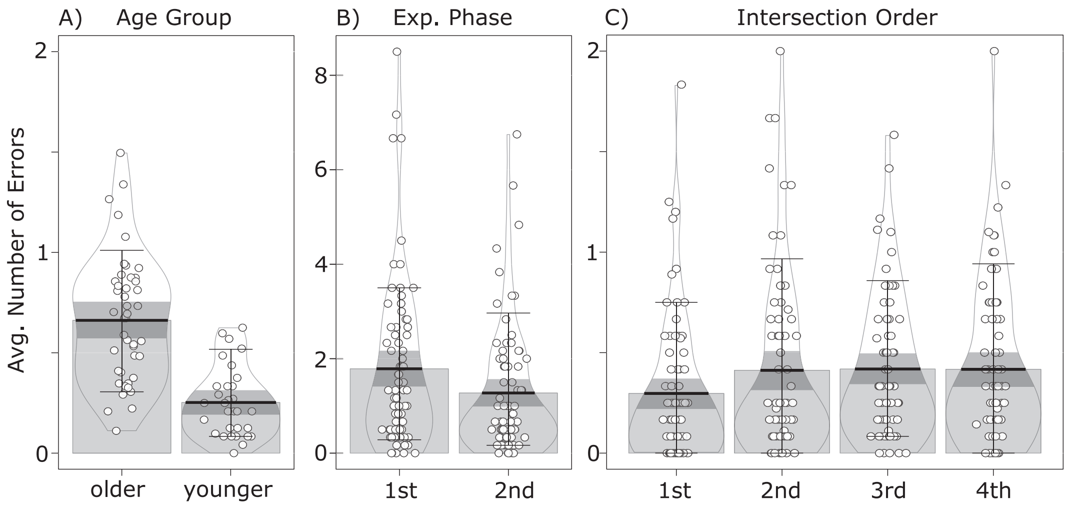

Fig. 4. (A) average number of errors per participant and training trial: older participants performed worse than younger participants. (B + C) average number of errors per participant and routes: participants made more errors during the first six routes of the experiment compared to the rest of the routes, performance was best for the first intersection that appeared on each route (i.e., order shown in training phase) and decreased with increasing appearance. Plots show individual data (dots) and mean ± CI and 10th/90th quantiles of the groups.

the rest of the routes (3165 ms vs. 2755 ms; Fig. 5B) and response times were shortest for the first intersection and increased for the remaining intersections (first intersection 2666 ms, second intersection 3005 ms, third intersection 3122 ms, fourth intersection 3133 ms; Fig. 5C). The analyses for correct and incorrect responses are included in Appendix A.

3.2. *Eye movement data*

We used an interest area analysis (see Section 2.5 and Fig. 2) to investigate how participants attended to the landmark objects in the environment when learning the routes. Specifically, we compared (1) dwell time on the landmark objects between age groups, and (2) whether both age groups efficiently shifted visual attention towards the unique objects. For both the learning and the test phase, these analyses were restricted to the first presentation of the route for a number of reasons: first, most of the younger participants needed only a single exposure to the route; second, each route featured both unique and non-unique objects; and third because only during the first presentation of the route, when participants were still unaware which of the objects were repeated, could we sensibly investigate the shift away from repeated object towards the unique objects.

We conducted three separate analyses, one for each interest area (unique object, non-unique object, non-object) with age (young, old), route type (congruent, incongruent), and encounter (1st, 2nd) as fixed effects, and dwell time in the corresponding interest area as the dependent variable. For the dwell time analyses of gaze behaviour in the test-phase we also added trial accuracy as a fixed effect. Note that during the first encounter with an object, for example at the first intersection, participants cannot know which object is unique and which is repeated (i.e. non-unique). Only upon encountering the same object for the second time can they realise which object is unique and which is repeated.

3.2.1. *Training phase*

3.2.1.1. Landmark saliency. Each intersection featured a salient and a less-salient (hereafter non-salient) object. We first analysed whether both age groups showed a tendency to dwell longer on salient as compared to non-salient objects. To isolate the effect of saliency, we restricted the analysis to the first encounter with the objects during the training phase, i.e. the first time participants saw the objects. At this point, participants did not know which object was repeated. We did not consider object uniqueness in this analysis, as uniqueness is balanced across salient and non-salient objects and is captured by route type in the further analyses below. We compared the relative dwell times towards salient and non-salient objects, i.e. dwell time towards non-objects did not enter the analysis. The successfully converged model

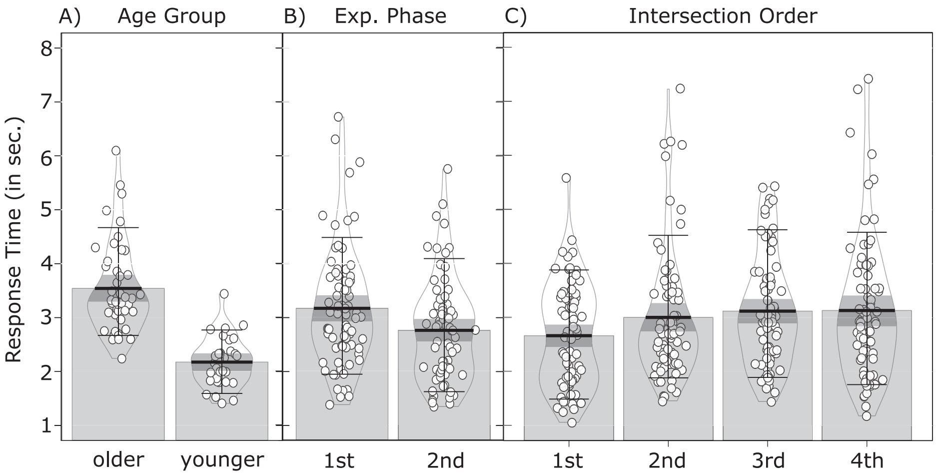

Fig. 5. Response Times for correct responses during the test phase. Plots show individual data (dots) and mean ± CI and 10th/90th quantiles of the groups. Older participants responded slower than younger participants (4A), responses were slower for the first six routes of the experiment compared to the rest of the routes (4B), response times were lowest for the first intersection that appeared on each route (i.e., order shown in training phase) and increased with increasing appearance (4C).

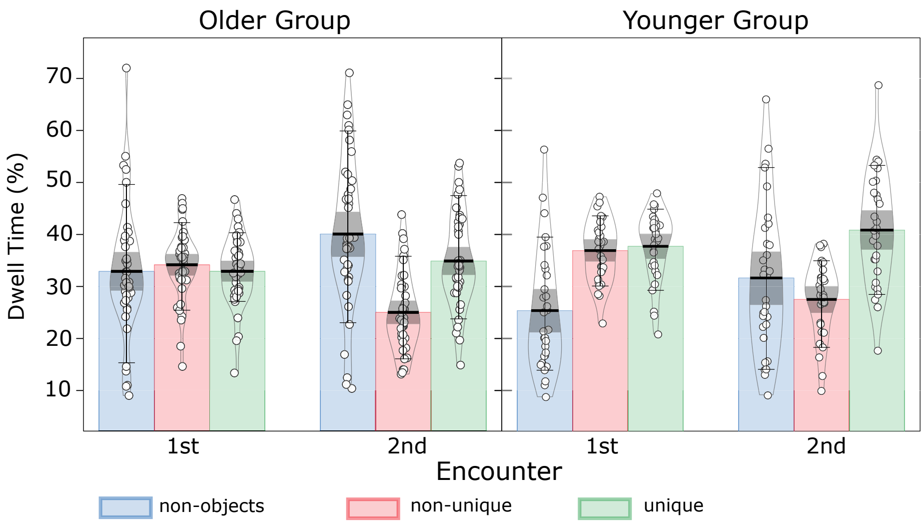

Fig. 6. Dwell Time in percent for all interest areas during the training phase. Plots show individual data (dots) and mean ± CI and 10th/90th quantiles of the groups. Gaze behaviour data was analysed of routes that were shown for the first time, i.e. no repetitions were included. Dwell time percentages for older participants are shown in the left panel and for the younger participants in the right panel. 1st Encounter = the non-unique landmark appears for the first time on the route. 2nd Encounter = the non-unique landmark appears for the second time.

was the intercept-only model with age group and interest area (salient vs. non-salient) as fixed effects. Participants spent more time looking at salient objects than at non-salient objects (52.54% vs. 47.46%; $b = -2.72$, $SE = 0.48$, $t = -5.64$), but there was no effect of age group ($b = 0.00$, $SE = 0.73$, $t = 0.00$).

3.2.1.2. Landmark uniqueness. Unique object: The successfully converged model included random slopes of encounter and route type for participants. Overall, our older participants spent less time attending to the unique objects than younger participants (33.99% vs 39.28%; $b = -2.67$, $SE = 0.90$; $t = -2.96$) and participants spent less time looking at the unique object at the first encounter than at the second encounter (34.99% vs 37.49%; $b = -1.31$, $SE = 0.40$; $t = -3.11$; Fig. 6 green bars). There was no reliable effect of route type. The interaction route type × encounter was reliable ($b = 1.39$, $SE = 0.31$, $t = -4.48$) with a larger difference between encounter 1 and encounter 2 for incongruent routes (32.96% vs 38.25%) than for congruent routes (36.96% vs 36.59%). In addition, there was a reliable interaction of age group × route type ($b = -0.96$, $SE = 0.40$, $t = -2.39$) with a larger difference between congruent routes and incongruent routes for younger participants (40.93% vs 37.64%) than for older participants (33.71% vs 34.10%). None of the other interactions were reliable (both $|t| < 1.96$).

Non-unique objects: The successfully converged model included random slopes of encounter and route type for participants. For non-unique objects there was no reliable effect of age group ($b = -1.30$, $SE = 0.74$, $t = -1.76$). Participants spent more time looking at the non-unique object at the first encounter than at the second encounter (35.36% vs 26.08%; $b = 4.65$, $SE = 0.36$; $t = 13.04$; Fig. 6 red bars) and spent less time looking at the non-unique objects on congruent routes as compared to incongruent routes (29.93% vs 31.49%; $b = -0.71$, $SE = 0.35$; $t = -1.99$) . There was a reliable interaction between route type and encounter ($b = -1.17$, $SE = 0.28$, $t = -4.10$) with a greater difference between encounter 1 and encounter 2 for incongruent routes (37.28% vs 25.70%) than for congruent routes (33.39% vs. 26.46%). The interaction between age group × route type was also reliable ($b = -0.83$, $SE = 0.36$, $t = -2.33$) and suggests that younger participants spend more time looking at non-unique objects on congruent routes than older participants (32.33% vs 28.15%) while there was little difference between the age groups for incongruent routes (32.09% vs 31.04%). The other interactions were not reliable (both $|t| < 1.96$).

Non-objects: The successfully converged model included random slopes of encounter and route type for participants. Older participants spent more time looking at non-objects than younger participants (36.39% vs 28.50%; $b = 3.98$, $SE = 1.52$, $t = 2.62$). Participants also spent more time looking at the non-object interest areas during the second encounter than during the first encounter (36.44% vs 29.66%; $b = -3.34$, $SE = 0.39$, $t = -8.55$; Fig. 6 blue bars), while route type did not render a reliable effect ($b = 0.01$, $SE = 0.59$, $t = 0.01$). Finally, we found a reliable age group × route type interaction ($b = 1.77$, $SE = 0.59$, $t = 3.00$), with a larger difference between older and younger participants for congruent routes (38.14% vs 26.74%) than for incongruent routes (34.85% vs 30.27%). None of the other interactions were reliable (all $|t| < 1.96$).

Overall, these analyses show that older participants spent less time dwelling on landmark information and consequently more time looking at non-landmark information. However, attention in both age groups is captured by the salient objects, but both age groups shift their gaze away from the non-unique objects and towards the navigationally relevant information when encountering the non-unique object for the second time.

3.2.2. Test phase

3.2.2.1. First and last fixations towards objects. As the images of the intersections were presented in random order, participants needed to attend to the objects, or more precisely to the unique object, to inform the decisions about the movement direction. We therefore analysed (1) the time from stimulus onset until participants gazed at either object and (2) whether the first fixation and (3) the last fixation before reporting the response towards either object was more likely to be directed to the unique or non-unique object. We used LMMs with age group and object type (unique vs non-unique) as fixed effects to compare the time until first fixations between the age groups and paired t-tests to analyse the number of the fixations.

Time until first fixation: Our older participants took longer from stimulus onset until fixating either object than younger participants (586 ms vs 495 ms; $b = -100.21$, $SE = 20.45$, $t = -4.90$). Neither object type (unique/non-unique) nor the interaction between object type and age groups was reliable (both $t < |1.96|$). Assuming that participants needed to overtly attend to the navigationally relevant object in order to make their response, which is supported by the fact that participants fixated the unique object in 94% of the test trials, this difference is likely to contribute to the age difference in response time reported above.

First fixation: Overall, the first fixation towards either object, was more likely to be directed to the unique than the non-unique object (52.29% against chance level [50%]: $t(71) = 2.88$; $p < 0.01$). We further analysed whether there was a difference between age groups. Our younger participants showed a stronger preference for the unique object than our older participant group (54.17% vs. 50.87%; $t = -2.06$ (58.97), $p < 0.05$).

<u>Last fixation:</u> Similarly to the first fixation, also the last fixation towards either object before reporting responses was more likely to be directed to the unique than the non-unique object (*t*-test against chance level [50%]: 54.98%: $t = 5.05$ (71), $p < 0.01$). There was no difference between age groups (55.07% vs 54.85%; $t = 0.115$ (69.16), $p = 0.91$).

3.2.2.2. Landmark saliency. Similar to the analyses of the gaze behaviour during the training phase we first analysed whether both age groups showed a tendency to direct their first fixation towards the salient object or the non-salient object. Specifically, we compared the number of first fixations towards salient and non-salient objects (fixations on non-objects did not enter the analysis). The successfully converged model was the intercept-only model with age group and interest area (salient vs. non-salient) as fixed effects. Participants tended to fixate the salient objects more than the non-salient objects (57.15% vs. 42.85%; $b = 0.16$, $SE = 0.02$, $t = 9.504$), but there was no effect of age group ($b = 0.014$, $SE = 0.02$, $t = 0.80$).

3.2.2.3. Landmark uniqueness. <u>Unique object:</u> The successfully converged model was the intercept-only model. For unique objects there were no reliable effects of age group or trial accuracy (age group: $b = -1.44$, $SE = 0.80$, $t = -1.80$; trial accuracy: $b = -0.27$, $SE = 0.42$, $t = -0.65$). Only route type rendered a reliable effect ($b = 1.19$, $SE = 0.41$, $t = 2.90$), with participants spending more time looking at the unique objects on congruent routes as compared to incongruent routes (36.46% vs 35.48%). There was also a reliable interaction between trial accuracy and route type ($b = 1.17$, $SE = 0.41$, $t = 2.84$). Specifically, on incongruent routes, participants spent slightly more time looking at unique objects when they responded correctly as compared to incorrectly (35.92% vs 32.92%). In contrast, on congruent routes, they spent less time looking at unique objects when they responded correct as compared to incorrect responses (36.35% vs 38.93%).

<u>Non-unique objects:</u> The successfully converged model included a random slope of route type for participants. For non-unique objects there were no reliable effects of age group or route type (age group: $b = -1.28$, $SE = 0.72$, $t = -1.79$; route type: $b = -0.58$, $SE = 0.39$, $t = -1.47$). Only trial accuracy rendered a reliable effect ($b = 1.65$, $SE = 0.39$, $t = 4.22$), with participants spending more time looking at the non-unique objects when they made incorrect as compared to correct responses (30.07% vs 27.23%). None of the interactions were reliable (all $|t| < 1.96$).

<u>Non-objects:</u> The successfully converged model included a random slope of route type for participants. Older participants spent more time looking at the non-objects interest area than younger participants (38.11% vs 33.40%; $b = 2.68$, $SE = 1.23$, $t = 2.17$), and participants spent more time looking at the non-object interest areas when they made correct as compared to incorrect responses (36.67% vs 33.68%; $b = -1.38$, $SE = 0.42$, $t = -3.30$). There was no reliable effect of route type. There were reliable interactions between age group and route type ($b = 1.09$, $SE = 0.48$, $t = 2.26$) and trial accuracy and route type ($b = -0.96$, $SE = 0.41$, $t = -2.13$). Further, there was a reliable three-way interaction between age group, trial accuracy and route type ($b = 0.95$, $SE = 0.41$, $t = 2.30$). Specifically, there was a larger difference between older and younger participants for congruent routes (38.42% vs 33.15%) than for incongruent routes (37.80% vs 33.65%). On congruent routes, participants spent more time looking at non-objects interest areas when they responded correct as compared to incorrect responses (36.72% vs 32.30%) , while there was little difference between correct and incorrect responses for incongruent routes (36.39% vs 35.98%). The other interaction was not reliable ($|t| < 1.96$).

3.3. Neurocognitive assessments and route learning performance

Table 2 summarises correlations between the neurocognitive assessments and route learning performance (number of repetitions and number of errors, respectively) separately for the older and the younger participants. Interestingly, none of the neurocognitive assessments was significantly correlated with route learning performance in the younger participant group, even though forward Digit Span and delayed recall of Word List learning were close (both $p < 0.1$). In the older participants, in contrast, all but Digit Span forward and ROCF delayed were (highly) significant. The lack of significant correlations in our younger age group may, at least partly, result from the lower range in their performance data and by the lower sample size in this group.

To control for variance shared between the neurocognitive assessments and to investigate the relative contributions of the various neuropsychological assessments on route learning performance (i.e. number of errors per route) simultaneously, we carried out separate LMM analyses for younger and older participants with ROCF delayed, Digit Span forward and backward, Corsi Block forward and backward and Word List learning delayed as fixed effects and participants and route ID as random effects. For both participant groups, the only reliable predictor for route learning performance was Word List learning

Table 2
Correlation between neurocognitive assessments and route learning performance (number of repetitions and number of errors). The p-values were sequentially Bonferroni corrected for multiple testing (Holm, 1979).

	Younger corr. repetitions	Older corr. repetitions	Younger corr. errors	Older corr. errors
ROCF				
copy (/36)	$r = (-0.15)$, $p = 1.65$	$r = (-0.47)$, $p < 0.01$	$r = (-0.19)$, $p = 1.55$	$r = (-0.49)$, $p < 0.01$
immediate (/36)	$r = (-0.08)$, $p = 2.01$	$r = (-0.32)$, $p = 0.10$	$r = (-0.15)$, $p = 1.22$	$r = (-0.27)$, $p = 0.21$
30 min delay (/36)	$r = 0.01$, $p = 0.97$	$r = (-0.29)$, $p = 0.10$	$r = (-0.13)$, $p = 0.98$	$r = (-0.25)$, $p = 0.19$
Word List I & II				
Trials 1–4 (/48)	$r = (-0.25)$, $p = 0.95$	$r = (-0.58)$, $p < 0.001$	$r = (-0.26)$, $p = 0.91$	$r = (-0.56)$, $p < 0.001$
immediate (/12)	$r = (-0.30)$, $p = 0.78$	$r = (-0.57)$, $p < 0.001$	$r = (-0.30)$, $p = 0.67$	$r = (-0.54)$, $p < 0.001$
30 min delay (/12)	$r = (-0.32)$, $p = 0.69$	$r = (-0.60)$, $p < 0.001$	$r = (-0.32)$, $p = 0.63$	$r = (-0.56)$, $p < 0.001$
Digit Span				
Forward (/144)	$r = (-0.33)$, $p = 0.67$	$r = (-0.16)$, $p = 0.3$	$r = (-0.33)$, $p = 0.62$	$r = (-0.14)$, $p = 0.4$
Backward (/112)	$r = (-0.26)$, $p = 1.10$	$r = (-0.44)$, $p < 0.05$	$r = (-0.32)$, $p = 0.66$	$r = (-0.41)$, $p < 0.05$
Corsi Block				
Forward (/144)	$r = (-0.05)$, $p = 1.55$	$r = (-0.42)$, $p < 0.05$	$r = (-0.07)$, $p = 0.72$	$r = (-0.40)$, $p < 0.05$
Backward (/112)	$r = (-0.19)$, $p = 1.51$	$r = (-0.40)$, $p < 0.05$	$r = (-0.18)$, $p = 1.29$	$r = (-0.38)$, $p < 0.05$

delayed (older participants: $b = -0.24$, $SE = 0.07$, $t = -3.18$; younger participants: $b = -0.09$, $SE = 0.04$, $t = -2.01$). None of the other neuropsychological assessments reliably predicted route learning performance in either or both participant groups (all $|t| < 1.96$).

4. Discussion

The overall aim of this study was to develop a better understanding of the cognitive mechanisms that contribute to age-related declines in route learning abilities. To do so, we asked a younger and an older participant group to learn a series of short routes, while recording their gaze behaviour. In addition, we administered a number of neuropsychological tests assessing a range of cognitive functions. As expected, our older participant group learned the routes more slowly than our younger participants (cf. O'Malley et al., 2018). Analysis of gaze behaviour showed some age-related differences, but importantly, both age groups efficiently shifted attention away from ambiguous towards the unique and navigationally relevant landmark information. Finally, of all the neuropsychological assessments, including those addressing spatial abilities, only Word List learning performance was a reliable predictor for route learning success.

Our older participant group made more errors and needed more exposures (repetitions) until they successfully learned the route. These results are in line with earlier studies that reported route-learning deficits in older adults (Head & Isom, 2010; O'Malley et al., 2018; Wiener et al., 2012, 2013; Zhong & Moffat, 2016, 2018). Despite these age-related differences in learning performance, both age groups showed similar performance increases in the second half of the experiment, suggesting that fatigue cannot explain slower learning in the older age group. Both age groups also made fewer errors at the first intersection as compared to later intersections, suggesting that primacy effects in route learning (cf. Waller & Lippa, 2007) are independent of age. Our older participant group also needed longer to fixate the landmarks for the first time after stimulus onset in the test phase and longer to respond than our younger participants, which is consistent with theories of age-related declines in information processing speed (Glisky, 2007; Salthouse, 1996, 2000) and suggests that performance differences are not due to a speed-accuracy trade off.

Zhong and Moffat (2016) have recently argued that declining route learning abilities in older age may be related to poorer binding of landmark knowledge with directional information, while the recognition of the relevant landmarks (i.e. landmarks at decision points) itself was not impaired (cf. Head & Isom, 2010). This interpretation is in line with more general associative memory deficits in older age (Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008), and with our results. In our study, participants were passively transported along the route and were then presented with the intersections in random order in the test phase. This procedure ensured that participants could not rely on the sequence of turns along the route. Instead, they needed to associate the correct movement directions with the relevant landmark at each intersection (associative cue strategy, see Waller & Lippa, 2007). This procedure ensured that participants had to visually attend to the landmark information and select the landmark that was navigationally relevant, i.e. unique.

The use of eye-tracking technology allowed us to investigate whether the control of visual attention contributed to age-related differences in route learning performance. We were particularly interested in the analyses of gaze behaviour during the training phase, when participants encoded the route and had to identify and select (i.e. visually attend to) the landmark object that was navigationally relevant.

When first encountering an intersection, i.e. when participants did not know which of the two landmark objects was unique, gaze in both age groups was captured by the more salient of the two landmark objects. Similarly, when presented with the test stimuli, participants first directed their gaze to the more salient object. Given the well-established role of salient stimuli in attracting visual attention (Itti & Koch, 2001), this result was expected and it demonstrates that our approach of classifying objects as salient or non-salient in the context of navigation was successful. Importantly, the magnitude of preference for the more salient object was similar between age groups, which suggests that older adults were not more distracted by a salient object (independent of its relevance) than our younger participants.

Studies from other cognitive domains, however, suggest that declining cognitive control (Amer, Campbell, & Hasher, 2016) should result in older adults having more difficulties ignoring salient, but task-irrelevant stimuli (Schmitz et al., 2010; Tsvetanov et al., 2013). In our experiment, the non-unique object was task-irrelevant, as it did not allow to disambiguate between two of the intersections along the route. We therefore expected our older participant group to have more difficulties in shifting their gaze towards the unique landmark, particularly when learning incongruent routes, where the salient object was non-unique and the non-salient object was unique. Our results, however, suggest that both age groups effectively shifted visual attention towards the unique landmark object, independent of whether or not that object was salient. These results were somewhat surprising, as earlier navigation research suggests that older adults tend to remember salient features encountered during route learning rather than navigationally relevant situations (Lipman, 1991).

We also investigated how much time participants spend gazing at unique landmark objects as compared to non-landmark information during the training phase. Here we did find a reliable difference between age groups with older adults spending less time gazing at the unique landmark objects and more time dwelling at non-landmark information, such as the floor, the walls and pictures on the wall (which were all repeated, such that they could not be used to support navigation). These results do offer novel insights into age-related differences in route learning performance, as gaze behaviour reflects selective encoding of landmarks in route learning. Specifically, Hamid, Stankiewicz, and Hayhoe (2010) showed that removing highly viewed landmarks after route learning resulted in substantial performance decrements, while removing least fixated landmarks did not affect performance. If our older adults spent less time attending to relevant landmarks, they would not have encoded these as efficiently as younger participants, which could explain why they made more errors and needed more training trials to learn the routes. These results are in line with other recent studies from our lab, which demonstrate that older adults show less focused gaze behaviour when learning a spatial layout (Segen, Avraamides, Slattery, & Wiener, 2018), and instead, spend more time than younger adults fixating environmental features that are not necessarily required to solve the task.

The analysis of gaze behaviour in the test phase highlighted some minor differences between age groups. For example, older adults were less likely to direct their gaze immediately towards the unique object after stimulus onset than our younger participants. However, both groups were more likely to gaze at the unique than the non-unique object just before they report their response. Surprisingly, the dwell time analyses on unique and non-unique objects have not revealed main effects of age, despite the differences in performance. However, similarly to the training phase, older adults spent more time looking at non-object interest area than younger participants. Importantly, all participants spent more time dwelling on the non-unique object when they made incorrect response. This is likely to reflect that they had not encoded the navigationally relevant information, i.e. the unique landmark, in trials in which they responded incorrectly.

Overall, the analyses of gaze behaviour rendered mixed results and it is not obvious how these map onto theories of age-related changes in attentional control. The inhibition deficit theory (Lustig et al., 2007) states that older participants should be less efficient in inhibiting the processing of irrelevant or unwanted information (cf. Schmitz et al., 2010; Tsvetanov et al., 2013). We therefore predicted that our older adults should find it harder to direct gaze away from salient and towards unique landmark object. However, we did not find strong differences between age groups in (1) how strongly salient objects (irrespective of their relevance) captured visual attention, (2) how effectively participants shifted attention towards the relevant object (irrespective of its salience) in the learning phase, (3) how long they dwelled on unique or non-unique objects in the test phase or (4) how likely it was they attended the unique object when reporting their decisions. During the encoding or training phase, however, our older participants spent less time gazing at the relevant objects and more time looking at non-landmark information, which could contribute to their weaker route learning performance. In summary, these findings provide little support for our hypothesis that age-related differences in the ability to inhibit the processing of salient but irrelevant information (cf. Schmitz et al., 2010; Tsvetanov et al., 2013) contributes to performance differences in our paradigm. Instead, this study and recent work from our lab (Segen et al., in preparation) suggest that older adults show less focussed gaze behaviour and attend to more of the environment when encoding spatial information. Further research is needed to explore whether these differences are related to specific age-related shifts in encoding strategy which are not uncommon in spatial cognition (e.g., Dai, Thomas, & Taylor, 2018).

To investigate which other cognitive functions were most associated with route learning performance, we assessed participants on a range of neurocognitive tests (m-ACE, ROCF, Word List, Digit Span and Corsi Block). We selected these specific assessments as they cover cognitive functions and processes that are assumed to be involved in determining human navigation abilities (Wolbers & Hegarty, 2010). Both participant groups scored similarly on the m-ACE, suggesting that our older participant group did not show any obvious signs of atypical ageing. However, in all but the Digit Span tasks (forward and backward), our older participant group performed worse than our younger participants. While this is not surprising (Hester, Kinsella, & Ong, 2004; Salthouse, 2003; Woods, Wyma, Herron, & Yund, 2016), it opens up the question whether age-related declines in any of the cognitive functions assessed by the neurocognitive test administered here is related to declining route learning performance.

Initial correlational analyses in our younger participants suggested that performance in none of the neurocognitive assessments was associated with route learning performance. In older participants, in contrast, performance in the majority of neurocognitive assessments was associated with route learning performance (see Table 2). To investigate the relative contributions of the various neuropsychological assessments on route learning performance, we ran an LMM with all neurocognitive measures as predictors. Only Word List learning performance was a reliable predictor for route learning performance, both in our younger and in our older participant group.

At the first glance it appears somewhat surprising that Word List learning performance reliably predicted route learning performance, rather than the Corsi Block Task performance, a measure of spatial working memory (Fischer, 2001). However, route knowledge has often been described as a series of landmark-direction associations (Waller & Lippa, 2007) and human navigators have been shown to use verbal codes to encode these associations (Meilinger, Knauff, & Bülthoff, 2008). This may offer an explanation for why measures of verbal learning abilities are most predictive of route learning abilities.

As discussed above, our results suggest that older adults were not impaired as compared to the younger participants in shifting visual attention away from salient toward unique landmarks objects. As this is a cognitive control function, it is not surprising that measures that tap into executive function such as the ROCF, the Digit Span backwards and the Corsi Block Task backwards, do not present reliable predictors for route learning performance.

Overall, the results from the neurocognitive assessments have implication for future ageing studies in the context of navigation. First, short screening tools such as the m-ACE (and potentially similar assessments such as the MMSE and MoCA) are not sensitive enough to pick up subtle age-related declines in cognitive functions that are relevant for spatial orientation and navigation. Second, declines in verbal and episodic memory are associated with lower performance in route learning. If future research demonstrates that word list learning tests are also predictive of real world navigation performance, they would present a very sensitive tool to assess people's ability to learn to navigate novel environments.

Note that in both route learning performance measures (errors and training trials), our older group showed significantly more variability than our younger group. While it is possible that these differences are accentuated, at least partly, from potential floor effects in the younger participants, we have seen similar patterns also in other studies. It is important to note that there was also substantial overlap between groups, with many older adults performing very similar to our younger participants (see Figs. 2A and 3A). These results suggest that ageing did not affect all participants equally, but that some of our older participants were less protected from the effects of age-related cognitive decline than others. One possible explanation for this vulnerability and the declines in route learning abilities comes from research demonstrating that people at a higher genetic risk for AD show navigation deficits already years before they potentially develop AD (Kunz et al., 2015). A likely reason for why spatial tasks and navigation tasks are so sensitive for earliest signs of atypical ageing is that the brain areas involved in navigation, in particular the entorhinal cortex (EC) and the precuneus, show presymptomatic AD-related pathology (Braak & Del Tredici, 2015; Weston et al., 2016). Further research is needed to investigate the reasons for the increased variance in performance in aged adults.

In summary, we have presented a novel paradigm to investigate the role of visual attention in age-related declines in route learning performance. As expected, we found that our older participants took longer to learn short routes, they spend less time looking at navigationally relevant landmark information, but were just as able as our younger participants to disengage from salient, but irrelevant landmark information. Route learning performance was more variable in the older participant group and was associated with verbal and episodic memory abilities.

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Appendix A. Supplementary material

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