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Research Report

Age and gender differences in various topographical orientation strategies

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ABSTRACT

Orientation in the environment can draw on a variety of cognitive strategies. We asked 634 healthy volunteers to perform a comprehensive battery administered through an internet website (www.gettinglost.ca), testing different orientation strategies in virtual environments to determine the effect of age and gender upon these skills. Older participants (46–67 years of age) performed worse than younger participants (18–30 or 31–45 years of age) in all orientation skills assessed, including landmark recognition, integration of body-centered information, forming association between landmarks and body turns, and the formation and use of a cognitive map. Among all tests, however, the ability to form cognitive maps resulted to be the significant factor best at predicting the individuals' age group. Gender effects were stable across age and dissociated for task, with males better than females for cognitive map formation and use as well as for path reversal, an orientation task that does not require the processing of visual landmarks during navigation. We conclude that age-related declines in navigation are common across all orientation strategies and confirm gender-specific effects in different spatial domains.

1. Introduction

Human topographical orientation refers to the ability of the individuals to situate themselves within a large-scale environment, enabling them to navigate through it (Gallistel, 1990). This complex and important function relies on several processes that contribute to spatial cognition, such as memory, attention, perception, mental imagery and decision-making (Berthoz and Viaud-Delmon, 1999; Brunsdon et al., 2007; Burgess et al., 2006; Corbetta et al., 2002; Davis and Coltheart, 1999; Farah, 1989; Lepsien and Nobre, 2006; Riddoch and Humphreys, 1989). The proper function of these cognitive processes allows individuals to become familiar with the environment and to adopt a variety of strategies useful for orientation (Berthoz, 2001; O'Keefe and Nadel, 1978; Redish, 1999).

The most flexible and efficient strategy that individuals can employ for orientation is the *formation and use of cognitive maps* (Wang and Spelke, 2002). A cognitive map (O'Keefe and Nadel, 1978) is formed as individuals familiarize themselves with an environment. This is a complex mental representation of the environment in which individuals may represent environmental landmarks and their spatial relationships (Byrne et al., 2007). Once formed, cognitive maps allow individuals to reach

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any location from anywhere within their environment. Without such maps individuals are limited to learning and performing a small number of routes by using other orientation strategies. For instance, *path integration*, also known as *dead reckoning* (Mittelstaedt and Mittelstaedt, 1982), consisting of continual integration of self-motion information, can be used to obtain an estimate of one's current position with respect to a starting location without using environmental landmarks (Loomis et al., 2001). In this case, distances and directions traveled are continually updated by vestibular, somatosensory and proprioceptive inputs (Mittelstaedt and Mittelstaedt, 1982). In humans, path integration is usually investigated by asking participants to return to a starting location after they have moved blindfolded or in an environment in which no relevant landmarks are available for orientation (Wolbers et al., 2007). Another strategy that individuals may adopt for orientation is the *left–right orientation strategy*. This strategy is based on traveled distances and a sequence of body turns, ignoring landmarks available in the surrounding (Iaria et al., 2003; Packard and Knowlton, 2002; Packard and McGaugh, 1996; White and McDonald, 2002) — e.g., walk two blocks, then turn right, then left, and left again. Although the use of this strategy leads to a quick procedural approach (Bohbot et al., 2007; Packard and Knowlton, 2002), where routes are navigated in an automatic manner (Hartley et al., 2003; Iaria et al., 2003, 2009a), its use is inflexible, confining the user to a specific sequence of displacements in one direction. In fact, if the starting location changes or the individual needs to perform the route in the reversed direction, the sequence of turns no longer works out in order to reach the destination. Finally, individuals may learn and perform a pathway by using the *heading orientation strategy*, which advances on the left–right strategy by incorporating landmarks in a body-referenced fashion (Aguirre and D'Esposito, 1999; Takahashi et al., 1997): subjects navigate by making associations between specific landmarks and body turns, e.g. turn right at the bank, again right at the cinema, and left at the pharmacy. This strategy requires individuals to take into account their direction of approach or perspective for the landmark, since the type of turn depends upon it. The variety of strategies that individuals may use for orientation may (or may not) be efficient according to the individual skills and the information that is available within the environment (for a review see (Wolbers and Hegarty, 2010)).

Studies in virtual environments provide evidence that there are age differences in the ability to use cognitive maps, with older participants requiring more time and being less accurate (Iaria et al., 2009b; Moffat and Resnick, 2002). In addition, functional Magnetic Resonance Imaging (fMRI) studies reveal differences in brain activity between young and older individuals while performing spatial navigation tasks (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2006, 2007). Compared to young participants, older individuals show decreased Blood Oxygenated Level Dependent (BOLD) signal change in the hippocampal, parietal and retrosplenial cortex, and increased BOLD signal change in anterior cingulate and medial frontal cortex (Moffat et al., 2006). A small number of studies have also assessed age differences in orientation in real rather than virtual environments. In one study, individuals' orientation skills have been assessed while navigating in a supermarket (Kirasic, 1991b); in this study, the authors found that older individuals were not accurate as young individuals in recognizing novel scenes but they were just as good as young participants in finding the shortest possible routes, estimating distances, and indicating the placements of items on a floor plan. In a different study in which participants were asked to follow a path shown on a map through a hospital the authors reported discrepant results (Wilkniss et al., 1997): older participants took longer to navigate through the environment and made more turning errors; however, they performed similar to young subjects in their ability to recall objects encountered during the trip. Besides the discrepancy of the results reported in the literature, an important limitation of previous studies investigating the effects of aging on the orientation skills is the use of single tasks typically assessing only one orientation strategy, or not allowing the decomposition of different strategies. In fact, it is reasonable to argue that, since different orientation strategies rely on unique information, aging may differentially affect each orientation strategy. For these reasons, a recent review of topographical orientation emphasized the importance of a comprehensive and systematic evaluation of different orientation strategies assessed independently from one another (Moffat, 2009).

In the present study, we investigated age differences in a large sample of 634 healthy volunteers who performed a comprehensive online test battery developed to assess the use of different orientation strategies in virtual environments (Iaria and Barton, 2010). Our goal was to determine if aging and gender affected topographic orientation, and if so, whether the effects were general, impairing all forms of orientation, or specific to certain orientation strategies and sparing others.

2. Results

The online battery consisted of six tests. The *Landmark Recognition test* assessed the ability to recognize landmarks encountered during navigation; the *Left/Right Orientation test* assessed the ability to learn a defined route by following left/right body turns in the absence of environmental landmarks; the *Path Reversal test* assessed the ability to recognize a route while traveling back to the original starting location in the absence of environmental landmarks; the Heading Orientation test evaluated the ability of the individuals to perform a route based on left/right turns associated with selective landmarks available in the environment; finally, the last two tests, namely the *Cognitive Map Formation test* and the *Cognitive Map Use test*, assessed the ability of the individuals to form and make use of a mental representation of the environment. See the Experimental procedure section for a more detailed description of the tests.

Participants were divided into three age groups in order to perform a factorial two-way analysis of variance (ANOVA) with Age (Group 1, Group 2, Group 3) and Gender (Females, Males) as independent factors. Group 1 included individuals between 18 and 30 years of age, Group 2 between 31 and 45 years, and Group 3 between 46 and 67 years. In the absence of a standard cut-off age range for selecting age groups defined as young, middle-age and older, the exact age range for our three groups took into account a selection aiming to include in

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each group a relatively equal numbers of participants. In the Cognitive Map Formation test we measured the amount of time that participants required to form a cognitive map of the environment; in all remaining tests we measured the number of correct responses.

Fig. 1 reports the mean scores of participants at each orientation test. The ANOVA revealed a significant main effect of age in Landmark Recognition ($F_{(2,\ 628)}=10.15$, $p<.001$), Heading Orientation ($F_{(2,\ 628)}=23.37$, $p<.001$), Left/Right Orientation ($F_{(2,\ 628)}=5.20$, $p=.006$), Path Reversal ($F_{(2,\ 628)}=8.00$, $p<.001$), Cognitive Map Formation ($F_{(2,\ 628)}=48.49$, $p<.001$) and Cognitive Map Use ($F_{(2,\ 628)}=17.31$, $p<.001$) tests. Post-hoc multiple pair-wise comparisons (Bonferroni corrected) revealed the following: in Landmark Recognition, Heading Orientation, Left/Right Orientation, Cognitive Map Formation, and Cognitive Map use, Group 3 (46–67 years) performed worse than Group 1 (18–30 years) and Group 2 (31–45 years), but the latter two groups did not differ from each other. In Path Reversal, Group 3 performed similarly to Group 2, but both groups performed worse than Group 1.

The ANOVA also revealed a main effect of gender in Path Reversal ($F_{(1,\ 628)}=25.98$, $p<.001$), Cognitive Map Formation ($F_{(1,\ 628)}=8.07$, $p=.005$) and Cognitive Map Use ($F_{(1,\ 628)}=13.65$, $p<.001$). Post-hoc t-test comparisons (Bonferroni corrected) revealed that males performed better than females in Path Reversal ($t_{(424.09)}=4.64$, $p<.001$), Cognitive Map Formation ($t_{(483.68)}=1.97$, $p=.05$), and Cognitive Map Use ($t_{(443.92)}=3.11$, $p=.002$). The main effect of Gender did not reach significance in the Landmark Recognition, Heading Orientation and Left/Right Orientation tests (see Fig. 1). No significant interaction effect was detected between age and gender in any of the six tests.

As no significant interactions were found, we performed Pearson correlations between the participants' age and their mean scores on the orientation tests to test the linear decline of aging. The results showed significant negative correlations between age and performance on Landmark recognition ($r_{(632)}=-.191$, $p<.001$), Heading Orientation ($r_{(632)}=-.308$, $p<.001$), Left/Right Orientation ($r_{(632)}=-.150$, $p<.001$), Path Reversal ($r_{(632)}=-.146$, $p<.001$) and Cognitive Map Formation ($r_{(632)}=-.247$, $p<.001$), indicating that aging was predictive of lower mean correct responses in these tests. There was also a significant positive correlation between age and Cognitive Map Formation ($r_{(632)}=.391$, $p<.001$), with aging associated with longer time required to form a cognitive map of the environment.

In order to assess which orientation tests were best at predicting the participants' age group we performed a Three-Group Stepwise Discriminant Function Analysis using

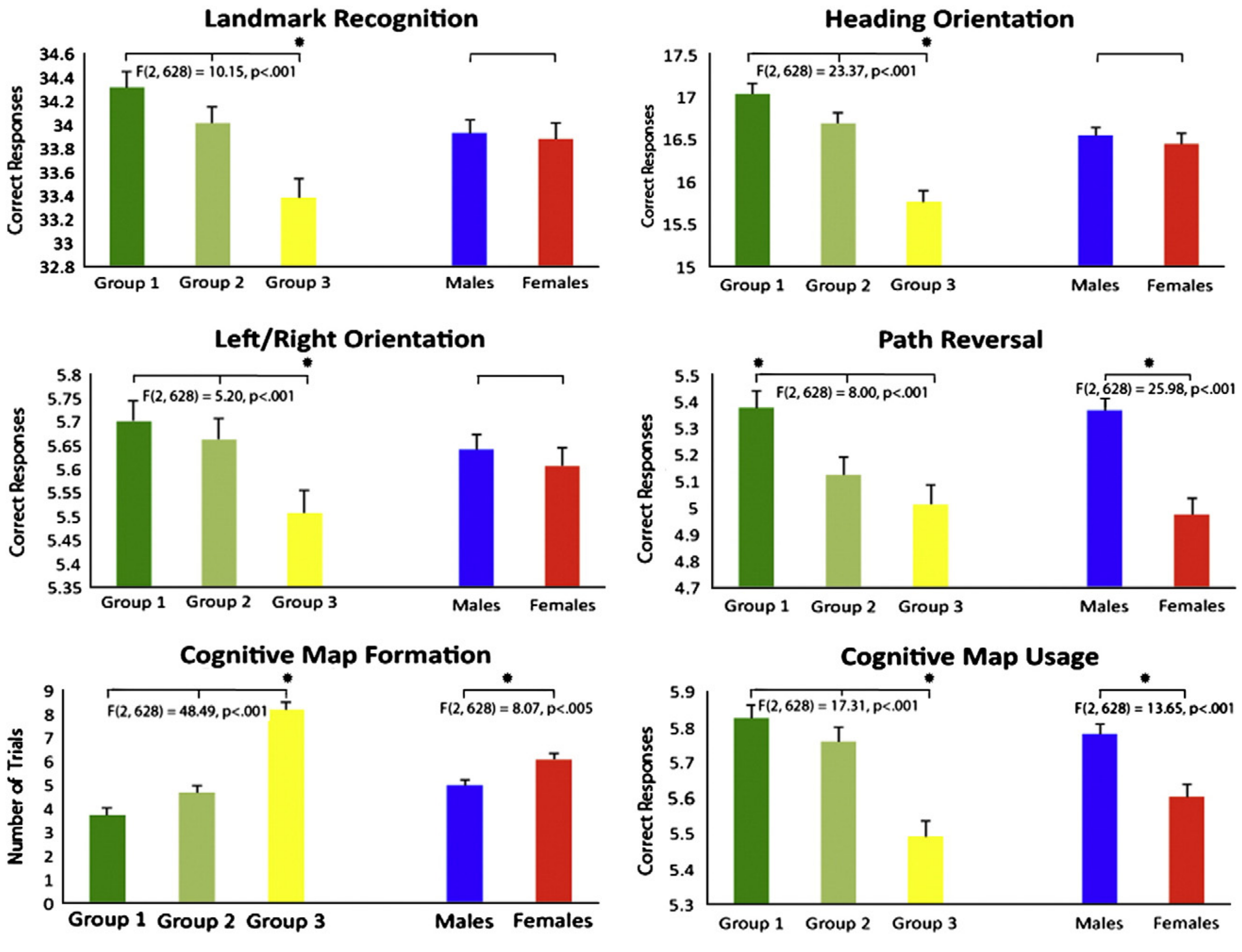

Fig. 1 – Results for each of the six orientation tests. Mean accuracy for the three age groups (Group 1 = 18–30 years, Group 2 = 31–45 years, Group 3 = 46–67 years) and two gender groups (males and females). Error bars indicate one standard error.

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participants' mean scores on the six orientation tests as predictors. Two discriminant functions were calculated. The first significant function resulted to include only the Cognitive Map Formation test (Eigenvalue = .18, Wilks's $\lambda = .182$, canonical correlation = .39, and χ^2 (4) = 105.93, $p < .001$) and accounted for 99.8% of the variance. After the removal of the first discriminant function, there was no longer a strong association between groups and predictors. The Cognitive Map test correctly classified 47.0% of the total cases included in the study (Group 1, 69.36%; Group 2, 22.05%; and Group 3, 46.15%).

Finally, we looked at the effect of practice over trials in order to investigate a possible learning effect within each test. For each test, with the exception of the Cognitive Map Formation test (which accounts for the time required to solve the task), a paired *t*-test was conducted to compare individuals' performance scores in the first and second half of the test. Overall, across groups, there was significant improvement observed for Landmark Recognition ($t_{(633)} = -4.84$, $p < .001$), Heading Orientation ($t_{(633)} = -.61$, $p < .001$), Path Reversal ($t_{(633)} = -6.91$, $p < .001$), and Cognitive Map Formation ($t_{(633)} = -3.07$, $p = .002$). There was a decrease in performance for Left/Right Orientation ($t_{(633)} = 2.28$, $p = .023$). Group 1 improved over time for Landmark Recognition ($t_{(234)} = -2.58$, $p < .001$), Path Reversal ($t_{(234)} = -2.18$, $p = .03$), and Cognitive Map Formation ($t_{(234)} = -2.36$, $p = .019$), but worsened for Left/Right Orientation ($t_{(234)} = 2.45$, $p = .015$). Group 2 improved over trials on Path Integration ($t_{(203)} = -3.58$, $p < .001$). Finally, Group 3 improved over time on Landmark Recognition ($t_{(194)} = -3.23$, $p = .001$), Path Reversal ($t_{(194)} = -6.25$, $p < .001$), and Cognitive Map Usage ($t_{(194)} = -2.16$, $p = .032$).

3. Discussion

The online approach of this study allowed evaluation of a variety of spatial orientation strategies in a large sample of healthy volunteers across an age range spanning 50 years. The results show a general age-related decline in all orientation skills examined. With one exception (Path Reversal), this decline occurred between middle (31–45 years) and older adulthood (46–67 years). Gender effects were evident and stable across the years. Females were similar to males on landmark recognition, heading orientation and left-right orientation, while males were better at path reversal, cognitive map formation and cognitive map use.

Although this is the first study of age effects on different orientation strategies, a prior study of 55 subjects showed declines in cognitive map formation and usage in subjects over age 50 (Iaria et al., 2009b). Individual differences in cognitive map formation and use are correlated with hippocampal microstructural integrity, as reflected in fractional anisotropy on diffusion tensor imaging (Iaria et al., 2008), and given the evidence that hippocampal and parahippocampal activity decline in older individuals (Antonova et al., 2009; Meulenbroek et al., 2004; Moffat et al., 2006), age-related impairments in this function could be expected. Our work advances by showing that other orientation skills are similarly vulnerable to aging between middle and late adulthood, including diverse abilities ranging from landmark recognition to left–right and heading orientation. These findings are consistent with previous studies (Iaria et al., 2009b; Kirasic, 1991a; Moffat, 2009; Moffat and Resnick, 2002; Moffat et al., 2001; Newman and Kaszniak, 2000) reporting an inverse relationship between aging and a wide range of orientation skills, including the ability to form and make use of cognitive maps as well as the ability to orient by using selective environmental landmarks. Our findings suggest that such age-related declines typically manifest in the late forties.

One possible deviation from this aging pattern was seen in the Path Reversal test. An age-related decline in this skill seemed to emerge earlier, between young (18–30 years) and middle adulthood (31–45 years). Path reversal requires a more complex set of cognitive abilities than simply recognizing body turns with or without landmarks. This may include integrating vestibular or optic flow information with mental imagery and mental rotation. While it is only speculative, it may be that the higher cognitive demands of the integration involved in this task render it more vulnerable to aging at an earlier stage. Indeed, another report has argued that cognitive demands play an important role in determining age-related declines in the use of path integration strategies (Allen et al., 2004).

With respect to gender differences, we found that men were better than women in the ability to form and make use of cognitive maps, which is consistent with previous findings (Iaria et al., 2009b; Sack et al., 2002). Differences between women and men were also revealed in the *Path Reversal* test. This finding is novel with respect to the task that we used in our study; however, this is consistent with the well-known advantage of males in the processing of distance/metric information during navigation (Ruggiero et al., 2008). No other differences were found between women and men in other orientation strategies. Together, this suggests that gender differences may be due to different degrees of familiarity that men and women may have with mentally operating on the orientation material. This is supported by several studies providing evidence that gender differences in navigational and orientation abilities are related to mental rotation skills. For instance, Moffat et al. (1998) showed that gender differences in the ability to solve a maze test in a virtual environment (men better than women) is correlated with the ability of the individuals in solving a variety of mental imagery tasks such as the *Vandenberg Mental Rotations Test* (Peters et al., 1995) , the *Guilford-Zimmerman Spatial Orientation Test* (Guilford and Zimmerman, 1956) and the *Money Road Map Test of Direction Sense* (Money et al., 1965). Similar findings are reported in studies (Astur et al., 2004; Driscoll et al., 2005) in which participants are required to solve a virtual environment version of the *Morris Water Maze* (Morris, 1981), and replicated in other studies (Coluccia and Martello, 2004; Dabbs et al., 1998; Malinowski and Gillespie, 2001; Montello et al., 1999) performed in ecological environments: in all cases, men are reported to outperform women, and the participants' performances were shown to be positively correlated with their scores at mental rotation and geographic knowledge tests. The fact that we found gender differences only in tasks that require mental imagery skills support the conclusion that gender differences in orientation strategies may due to differences in individuals' imagery skills (Palermo et al., 2008).

A possible limitation of our study is the ecological validity of testing participants in virtual environments. Practical

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considerations limit the study of orientation skills by use of "real world" environments, in which it can also be challenging to create tests that isolate one orientation strategy from the others. With technological advances, virtual paradigms are becoming an increasingly popular alternative approach. However, while virtual environments allow a high degree of experimental control, one can question the relevance of these simplified layouts to the daily experience of humans. There is evidence, however, that performance in virtual environments can correlate with "real life" ability (Iaria et al., 2009b; Lovden et al., 2005; Moffat and Resnick, 2002).

Due to the nature of the online assessment and to control for variability in motor responses, in our tests participants were able to only passively view the navigation clips, without requiring any active navigation. This is another limitation in our study since passive and active learning of spatial environments are suggested to lead to differences in performances (Hahm et al., 2007; Sun et al., 2004). This may be an important issue to address in future studies especially in older adults who require multiple sensory cues during spatial updating processes (Allen et al., 2004). An additional limitation of our study may be the lack of counter-balanced order in the administration of the tests, for which the effects of fatigue may have been an issue towards the end of the assessment. Although this may be a reasonable concern especially since the Cognitive Map Formation and Use tests occur last in the test battery, our findings are consistent with the ones reported in an earlier study in which we used a similar version of the cognitive map formation and use tests (Iaria et al., 2009b), which supports our conclusion that the decline in performance as observed in the present study is due to an aging effect.

Our findings show a general decline in all orientation strategies in the healthy aging population. However, as these results are shown at a group level, they do not establish whether these declines are universal in all subjects, or if individuals within the group show variability in the rate at which different orientation skills decline. Differential rates of decline in an individual may leave certain strategies intact, which may be exploited by substitutive approaches in rehabilitation that encourage patients to use relatively preserved abilities to compensate for impaired ones. Substitutive approaches may not be effective, however, if all orientation skills decline in step in a given patient. Hence further work is needed to determine whether certain forms of individualized rehabilitation have a substantial role to play in ameliorating the navigational difficulties of the elderly.

4. Experimental procedure

4.1. *Participants*

The sample included 634 healthy volunteers (252 females and 382 males) who had no self-reported history of neurological disorder, brain injury or psychiatric illness. Table 1 reports the participants' demographic data. Participants included in the study reported no memory defects or other cognitive difficulties interfering with everyday functioning. Although we could not test subjects directly on their visual acuity, we asked them to report whether or not they were able to read the instructions on the screen; we excluded individuals who claimed to have less than 20/60 non-corrected visual acuity. We also excluded individuals taking any medication regularly at the time of testing. The experimental protocol received ethics approval in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) as printed in the British Medical Journal (18 July, 1964). Informed consent was collected online from each participant prior to participation in the study.

4.2. *Procedure and tasks*

We recruited participants through an internet website (www.gettinglost.ca) (Iaria and Barton, 2010). After providing informed consent, participants completed a questionnaire collecting basic demographic data (gender, age, years of education) as well as handedness. Participants were then administered an online battery consisting of six tests, each with on-screen instructions of the task provided before its start. The tests assessed skills related to orientation, and were performed in virtual environments created using Game Studio three-dimensional software editor (Game Studio A6, La Mesa, CA, USA). Performance was recorded and stored in a password-protected database for offline analysis. We also recorded the duration spent by each subject from the beginning to the end of the session for the entire battery, which subjects performed in one sitting, and excluded any subject who did not completed the battery in a single session. As we obviously could not monitor performance in person, the goal of this exclusion criterion was to eliminate subjects who might have performed the test in an anomalous situation or fashion or did not complete the test battery at all.

4.2.1. *Landmark recognition test*

This test consisted of six trials. In each trial, participants first saw a 30 s video-clip showing someone navigating through a virtual environment from a first-person perspective (i.e. the navigator). During this clip, the navigator encountered three different landmarks, each displaying a unique colorful abstract image on a signpost (Fig. 2). At the end of the video-clip, participants were shown six abstract images one after another in a random order and asked to identify which were the three landmarks that have been encountered in the video-clip. The maximum score was thus 36 if participants correctly identified the 18 encountered items and correctly rejected the 18 unfamiliar items. The trial ended after their response and the next trial began with a new video-clip.

4.2.2. *Heading orientation test*

This test had six trials. As in the landmark recognition test, each trial showed a 30 s video-clip of the navigator traveling through a virtual environment and encountering three landmarks similar (but different) to those in the previous test. At the end of the video-clip, participants were presented with the same three landmarks, one at a time in random order, and asked whether the navigator made a left or a right turn at each landmark. The maximum score was thus 18.

4.2.3. *Left/right orientation test*

This test assessed the ability to learn a path from a series of turns in the absence of landmarks. The test consisted of 6 trials. In each trial, participants first saw a 30 s video-clip of the

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Table 1 – Participants' demographic information.

	Participants (N)	Age (years) mean (SD)	Education (years) mean (SD)	L-handed (N)	R-handed (N)
Group 1 (M+F)	235	24.98 (3.23)	15.86 (3.24)	21	214
Group 1 (M)	143	25.17 (3.20)	15.69 (3.32)	10	133
Group 1 (F)	92	24.70 (3.26)	16.12 (3.12)	11	81
Group 2 (M+F)	204	37.42 (4.50)	17.25 (3.48)	17	187
Group 2 (M)	112	37.18 (4.56)	16.96 (3.27)	10	102
Group 2 (F)	92	37.71 (4.42)	17.62 (3.72)	7	85
Group 3 (M+F)	195	55.41 (6.40)	16.24 (3.86)	17	178
Group 3 (M)	127	54.78 (6.44)	16.44 (3.55)	13	114
Group 3 (F)	68	56.57 (6.19)	15.87 (4.37)	4	64

navigator traveling through a virtual environment similar to the previous two tests but without any landmarks. The navigator followed a route with three randomly generated left or right turns. Immediately after, participants were shown a second 30 s video-clip in which the navigator followed a route with three left/right turns, at the end of which participants were asked if the same route had been followed in both video-clips. As the video-clips were all created within the same featureless virtual environment and the navigator traveled same distance in both video-clips, participants had to rely on the sequence of left and right turns in order to solve the task. The maximum score was 6.

4.2.4. *Path reversal test*

This test consisted of 6 trials. Each trial consisted of a 60 s video-clip. In the first 30 s part of the clip the navigator followed a route that included three randomly ordered right or left turns through a virtual environment without landmarks, just as in the Left/Right Orientation test. At the end of this route, though, the navigator stopped, turned around 180° and performed a second route that covered the same distance as the first part of the clip. At the end of the 60 s video-clip, participants were asked whether the navigator had returned to the starting location by following the same route in reverse. In 3 trials the navigator performed the same route in reverse, and in the remaining 3 trials the route was different. The maximum score was 6.

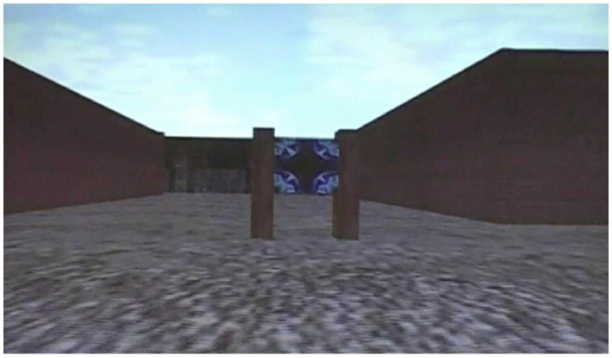

Fig. 2 – View of the environment in which landmarks (colorful abstract image displayed on a signpost) are available for orientation.

4.2.5. *Cognitive map formation test*

This test assessed the ability of the individuals to form a mental representation of the environment based on the landmarks available in the virtual environment and the spatial relations between them (Iaria et al., 2007; O'Keefe and Nadel, 1978). This test was administered in a virtual environment consisting of a 3×3 block city area with four distinct landmarks (i.e., restaurant, flower shop, hotel, and cinema), which were located in four buildings of similar sizes and identical textures (Fig. 3A). The test presented a series of exploratory trials: in each trial, participants were shown a video-clip from the first-person perspective of a pseudo-randomly generated navigation through the environment. All 4 landmarks were visited during the first trial, while subsequent trials showed 1 to 3 landmarks. There was no single location in which all four landmarks were visible to the navigator. The average duration of a video-clip was 84 s. At the end of each video-clip, participants were shown an aerial map of the virtual environment (Fig. 3B) and four different icons representing the four encountered landmarks. Participants used the mouse to drag each icon/landmark to its appropriate location on the map. The test ended when participants correctly

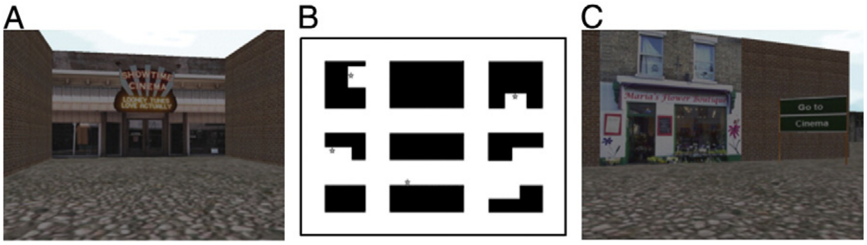

Fig. 3 – The figure displays (A) one of the four landmarks used in the Cognitive Map Formation test, (B) the top-view map of the environment in which the Cognitive Map test Formation and Use are performed (stars indicate landmarks' locations, not shown to participants during testing), and (C) the view of one of the trials administered during the Cognitive Map Use test.

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located all four landmarks in two consecutive trials (i.e. solving two consecutive trials without any feedback reduced significantly the possibility that the participants solved the task by chance). The test had a maximum of 20 trials. The number of trials needed to solve the task was an index of the time needed to form the cognitive map.

4.2.6. *Cognitive map use test*

This test assessed how effectively participants used the cognitive map formed in the previous test. The test consisted of 6 trials in each of which participants were shown video-clips from the first-person perspective of movement through the same virtual environment used in the previous test. Each video-clip started facing one of the four landmarks with a signpost indicating which of the other three landmarks was the intended destination (Fig. 3C). Next, the navigator moved through the environment and reached the intended destination. Participants were then asked whether or not the navigator had reached the destination by following the shortest route. Starting locations and destinations differed across trials. In 3 trials the navigator did reach the destination by following the shortest route, while in 3 they did not, and these were arranged in random order. The maximum score was 6.

4.3. *Analysis*

For each test, we performed a factorial two-way analysis of variance (ANOVA) with Age (Group 1, Group 2, Group 3) and Gender (Females, Males) as independent factors. The number of correct responses was used as the dependent variable in all tests except for the Cognitive Map Formation test, in which we measured the number of exploratory trials needed by the participants to solve the task. When no interactions effects were found, a Pearsons correlation analysis was used to examine the relationship between the age distribution and performance on each test. To investigate practice effects, a paired *t*-test compared performance in the first and second half of the trials.

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