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Abstract

Navigation strategy is an important component of spatial navigation. In the present study, we developed an assessment of human navigation strategy using a virtual analog of an assessment of animal navigation strategy. We examined the relationship between age, sex, and navigation strategy preference on subsequent performance of the virtual Morris Water Task (vMWT). On our novel assessment of navigation strategy, individuals were highly consistent in preferring either an allocentric or egocentric strategy. There were also substantial group differences in strategy preference with older adults overwhelmingly preferring an egocentric strategy, while younger adults were evenly divided between strategies. There were no significant sex differences in navigation strategy. On subsequent vMWT testing, allocentric strategy preference was associated with more accurate probe trial performance and enhanced cognitive mapping. These results suggest that human navigation strategy can be assessed reliably and that these strategy preferences feed forward to influence performance on independent navigation tasks.

Keywords: Navigation; strategy; humans; aging; older adults; cognitive mapping

Introduction

Age and sex differences are commonly found in both human and animal models of navigation performance (Barnes et al. 1980; Driscoll et al. 2005; Ingram 1988; McLay et al. 1999; Moffat et al. 2001; Newman and Kaszniak 2000; Wilkniss et al. 1997).

The hippocampus (HC) is part of a wide network of structures involved in spatial navigation, and has been consistently demonstrated to play a role in allocentric/world-centered spatial processing. Conversely, egocentric/self-centered processing is thought to involve primarily parietal cortex and caudate nucleus (Bohbot et al 2007; Maguire et al. 1998). Functional neuroimaging studies have demonstrated that older adult humans show less HC involvement during spatial navigation than do younger adults (Meulenbroek et al. 2004; Moffat et al. 2006; Antonova et al. 2009). In younger adults, it is thought that HC differences between males and females might underlie the widely reported finding of better male performance on spatial tasks (Astur et al., 1998).

Some researchers have theorized that reduced HC involvement in navigation in older adults might reflect changes in navigation strategy as older adults adopt extra-hippocampal strategies. (Moffat et al. 2007; Moffat et al. 2006; Iaria et al. 2009). Some preliminary evidence supports this perspective. Driscoll et al. (2005) found that self-reported allocentric strategy use declined with age.

Barnes and Colleagues (1980) investigated age differences in navigation strategy using a rat model in a modified T-maze. Rats were placed in one arm of the T-maze, and one of the remaining two arms was baited. The researchers included three types of cues in the environment that the rats could have used to learn the position of the goal: allocentric, based on objects in the environment, egocentric, based on the path taken by the rat, and cue, which took the form of a textured mat. Rats were trained to a criterion level of performance that demonstrated they had learned to reach the goal. Barnes then performed probe trials in which one of the cues was rotated 180 degrees. If the rat changed its path to "follow" the rotated cue, they were considered to be using that strategy.

Multiple probes were completed, and Barnes and colleagues were able to calculate probabilities for strategy preference for each group. Older rats were more likely than

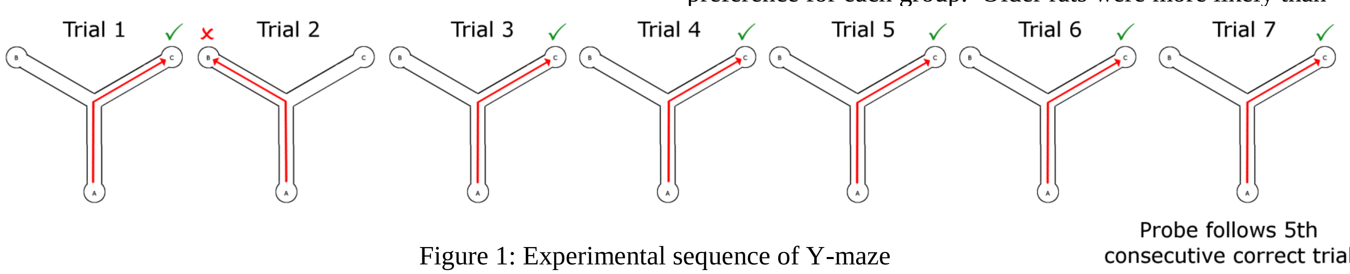

Figure 1: Experimental sequence of Y-maze tasks including sample training paths

middle-aged rats to prefer an egocentric strategy, while the reverse was true for allocentric strategy. Cue strategy was almost never used by the animals.

Some studies have attempted to use similar methods in human models (Iaria et al. 2003; Bohbot et al., 2007; Schmitzer-Torbert, 2007), and some have found group differences in navigation strategy. Schmitzer-Torbert (2007) found some evidence for sex differences in navigation strategy with males preferring an egocentric strategy and females preferring no strategy Furthermore, they are in the opposite direction of another study on sex differences in navigation strategy (Levy et el., 2005). Bohbot and colleagues (2007) have conducted a number of studies on the relevance of navigation strategy to functional activation patterns and the volume of various brain structures, finding a relationship between both volume and activity in the hippocampus and allocentric strategy, as well as a relationship between both volume and activity in the caudate nucleus and an egocentric strategy.

One classic test of human and animal navigation is the Morris Water Task (MWT; Morris et al. 1982). The MWT and its human analogue the virtual Morris Water Task (vMWT) require participants to find a hidden platform in a circular arena. The platform is always in the same location, but participant start position varies from trial to trial. It is best solved by using an allocentric strategy as there are multiple stable cues scattered throughout the environment. This is by far the most widely used test for navigation ability, and its status as a test of allocentric navigation suggests that individuals who prefer an allocentric strategy in a task such as Barnes' T-maze may perform better in the MWT.

The present study developed a navigation strategy assessment for humans, used that strategy assessment to demonstrate group differences in navigation strategy, and showed that this preference was related to navigation performance on another task.

Methods

Participants

45 older adults (60-85) and 54 younger adults (18-35) were recruited from the Metropolitan Detroit community and the Wayne State Psychology subject pool. Participants were required to be free of physiological, neurological, or psychological disorders.

Virtual Environments

All virtual environments (VE) were created using Unreal Tournament 2003 modified for use in navigation experiments (Epic Games, Rockville, MD). All environments were run on a PC and presented on a 19" monitor approximately 20" away from the face in a dark room. Participants interacted with the virtual environment using a commercially available joystick (Thrustmaster Top Gun Fox 2 Pro, Guillemot Corporation, La Gacilly Cedex, France).

All participants received joystick/VE familiarization training before the test. Additionally, a speed test was administered in which all participants were required to meet a threshold proficiency at moving through a twisting virtual hallway. Participants repeated the task until they completed it at threshold levels (<120 s).

Virtual Y-Maze Strategy Assessment (vYSA)

Following Barnes et al. (1980), we developed a strategy assessment that could be used to determine navigation strategy preferences in humans. Five Y-maze environments were developed that could be completed equally well through the use of either an allocentric or egocentric strategy. Each maze had both a stable route, providing egocentric cues, and stable extra-maze objects throughout the environment, which provided allocentric cues. Participants were told only how to know when they had completed the task correctly (hearing a major guitar chord) and that their task was to complete the task correctly as many times as possible. Participants who asked for additional instruction were not provided any additional information. This was done to prevent experimenters from using keywords such as 'place' or 'route' that might bias participants towards one strategy or another. During the training trials participants started at a given location and moved to a goal area. When participants entered the correct goal area, the pleasing tone sounded, whereas, a noxious buzzer sounded when participants entered the incorrect goal position. Training continued until participants reached a criterion level of 5 consecutive successful learning trials. See figure 1 for a diagram of this procedure.

For the probe trial, participants were placed at a third position that was neither the starting location nor the goal location for preceding training trials (figure 2). Participants were allowed to move to whichever goal position they preferred, at which point neither tone sounded.

The vYSA probe trial was designed to determine allocentric or egocentric strategy preference. Participants who, during the probe, followed the same *route* they learned in training, regardless of absolute location (e.g. turn right), were classified as using an egocentric strategy. Participants who moved to the same absolute location as trained in the learning trials, even though it required taking a different route were classified as using an allocentric strategy for that trial. Participants during prior pilot testing verbally indicated that they had noticed the change that occurred during the probe trial no matter what strategy they preferred, indicating that a participant who chose an egocentric strategy did so knowing that the environment had changed, though we did not directly assess this in the present study.

This process was completed 5 times. In order to be considered as preferring one strategy, participants were required to demonstrate the same strategy preference in at least 4 out of 5 blocks. Participants who did not prefer one

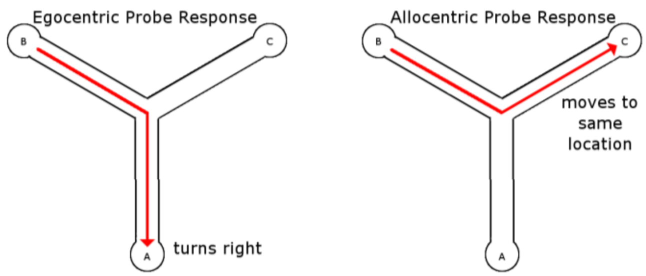

Figure 2: Routes taken by participants corresponding to egocentric and allocentric strategy, respectively.

strategy over another in 4 out of 5 blocks (N = 13) were excluded from analysis.

Virtual Morris Water Task (vMWT)

The vMWT replicated the classic Morris Water Task (Morris et al., 1982) in a virtual environment.

Participants completed 10 learning trials followed by one probe trial. For all trials, participants navigated through a circular pool contained in a large, non-symmetrical virtual room. Four objects were situated close to the edge of the pool, and two objects or features were situated more distally in the environment. For learning trials, participants were placed in the environment randomly at one of six potential starting positions inside the pool area. Participants were instructed that their goal was to find a hidden platform. When located, the platform lifted participants out of the water, accompanied by a pleasing tone. If the participant did not find the platform after 90s, a discordant buzzer tone sounded, the participants were frozen in place, and participants were allowed to look around the environment, followed by the beginning of the next trial. The dependent variable on the learning trials was the latency to reach the platform on each trial.

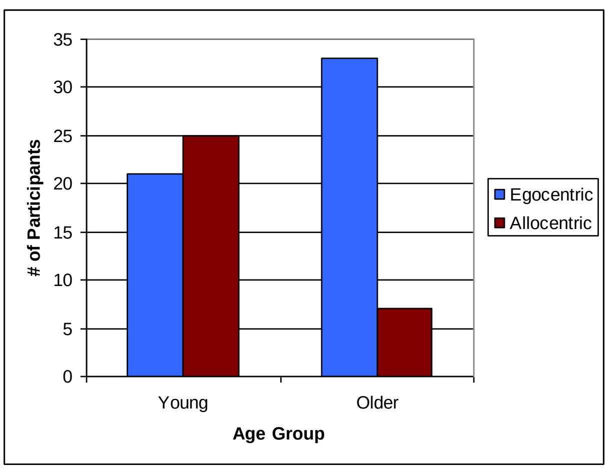

Figure 3: Strategy Preference by age group on the vYSA. Older adults overwhelmingly preferred an egocentric strategy whereas younger adults showed no marked preferences for egocentric or allocentric strategy.

In the probe trial, the platform was removed and participants began at one of the six starting locations and were instructed to locate the platform. Unlike training trials, the platform did not rise out of the water when occupied. When this occurs, participants typically assume they have made an error and attempt to cross the platform again, often multiple times. After 90 s the probe trial ended. Dependent variable on the probe trial was the number of platform intersections (number of times the participant crossed over the location that previously contained the platform).

Following the probe trial, participants were given three versions of an overhead map of the virtual environment and asked to mark with an 'X' where they believed the center of the platform to be located. The maps included a complete overhead map, a map in which only objects (and not room geometry) were shown, and a map in which only room geometry (and not objects) was shown. Platform placement error was operationalized as absolute distance from the correct center of the platform (in mm). Both platform crossings and error in placement of the platform on a map of the environment are specifically measures that have been used in the past to infer the degree to which participants were using an allocentric strategy, which is why they were chosen as the dependent variables of interest for this study.

Results

Age Differences in Strategy Preference

To investigate age differences in strategy preference, a X^2 test of independence was performed on age and strategy selection (Figure 3). Strategy preference varied by age group (X^2 = 12.43, p < .001) with older adults preferring an

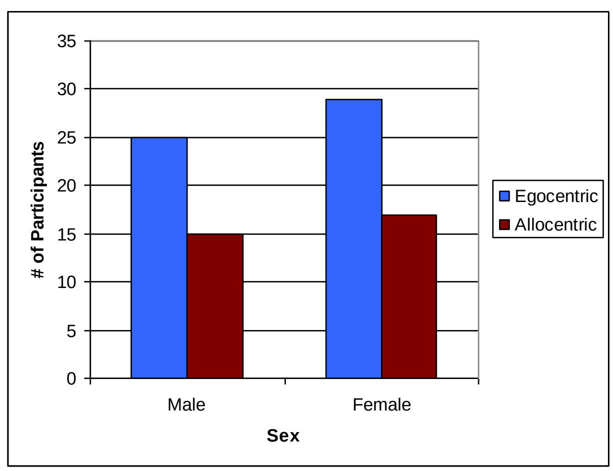

Figure 4: Strategy Preference by sex on the vYSA. There were no differences in strategy preference between males and females

egocentric strategy in 82% of cases. Younger adults were evenly divided between ego and allocentric preference. Using Cramer's V we determined that this age difference was of a very large effect size (Cramer's V= .38).

Sex Differences in Strategy Preference

A X^2 test of independence was performed on sex and strategy preference (Figure 4). Strategy did not differ as a

function of sex (X^2 = .003, *p* = .96). A very small effect size suggests that this negative finding was not due to insufficient statistical power.

Effects of Age and Strategy Preference on vMWT learning trials

The relationship between age, sex, and strategy preference on vMWT performance was investigated using a 2 (young v. old) by 2 (male v. female) by 2 (egocentric v. allocentric) Analysis of Variance. There was a main effect of age, F(1,85) = 6.04, *p* = .02; older adult latency to complete the vMWT (M = 35.68, SD = 15.67) was greater than that of younger adults who preferred an allocentric strategy on the vYSA completed the vMWT learning trials faster, on average, than all other groups. There was also a main effect for age, with older adults taking more time to complete the task than younger adults (M = 26.67, SD = 14.69). There was no significant effect of sex, F(1,85) = .66, *p* = .42, or strategy preference, F(1,85) = .60, *p* = .44.

An Age and strategy preference interaction was detected for vMWT performance F(1,85) = 4.78, *p* = .03 (Figure 5). Allocentric preferring young adults (M = 21.26, SD = 10.81) displayed lower completion latencies than egocentric preferring young adults (M = 32.10, SD = 16.67), allocentric preferring older adults (M = 38.26, SD = 16.19) and egocentric preferring older adults (M = 33.10, SD = 15.73)

Probe Trial—Platform Crossings

An investigation of the relationship between age, sex, and strategy preference on probe performance on the vMWT was completed using a 2 (young v. old) by 2 (male v. female) by 2 (egocentric v. allocentric) ANOVA with platform crossings during probe trial as the dependent variable There was a main effect of strategy preference, F(1,85) = 5.42, *p* = .02. Participants who preferred an allocentric strategy (M = 4.50, SD = 2.51) crossed the platform more times than participants who preferred an egocentric strategy (M = 3.13, SD = 2.03). There was no main effect for age, F(1,85) = 1.03, *p* = .31, or sex, F(1,85) = 2.27, *p* = .14.

Cognitive Mapping

An investigation of the relationship between age, sex and strategy preference on a measure of cognitive mapping was completed using a 2 (young v. old) by 2 (male v. female) by 2 (strategy preference) repeated measures ANOVA with Map type as the repeated measure and placement error as the dependent variable. There was a main effect of Map Type, F*(*2, 76) = 21.01, *p* < .001. A LSD post-hoc test was conducted to determine the characteristics of this difference.

Placement error on the Geometry Only Map (M = 17.31, SD = 9.31) was significantly greater than either the Objects Only Map (M = 10.43, SD = 8.26) or the Objects and Geometry Map (M = 10.85, SD = 9.13). There was no difference between objects only and objects and geometry maps.

There was also a main effect of Strategy Preference on Placement Error, F(1, 76) = 12.78, *p* = .001 (Figure 6). Participants who preferred an allocentric strategy (M = 9.80, SD = 5.21) were more accurate at placing the platform than participants who preferred an egocentric strategy (M = 14.68, SD = 6.30). There was no effect for age group, F(1,76) = .18, *p* = .67, or sex, F(1,76) = 1.19, *p* = .28.

Discussion

The present study found age—but not sex--group

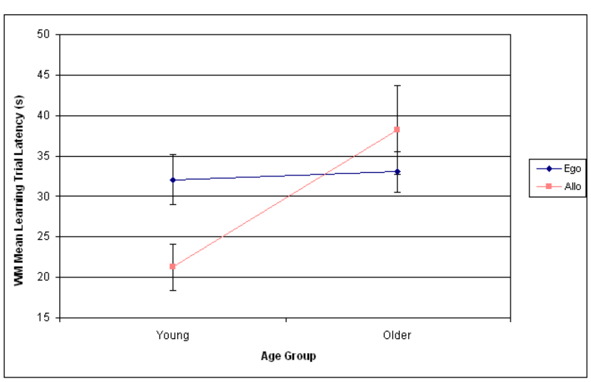

Figure 5: vMWT Mean Learning Trial Latency as a Function of Age and Strategy Preference.

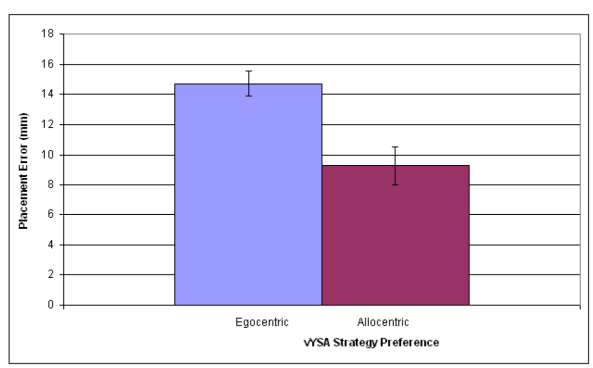

Figure 6: Platform placement error on the vMWT cognitive mapping task. Participants who preferred an allocentric strategy on the vYSA were more accurate in their platform placement error.

differences in navigation strategy using a virtual strategy assessment. Age differences were pronounced: only 18% older adults preferred an allocentric strategy during the vYSA, while younger adults were much more evenly distributed. This was conceptually similar to the results of the Barnes task, in which older rats were more likely than young to prefer an egocentric strategy.

Consistent with prior research, (Newman and Kaszniak 2000; Moffat and Resnick 2002; Driscoll et al. 2005), older adult average latency during learning trials of the vMWT was greater than in younger adults.

An important component of this study was the demonstration of a relationship between strategy preference on the vYSA and subsequent performance on the vMWT. We found that allocentric preference on the vYSA was associated with better performance on the vMWT probe trial and cognitive mapping. Allocentric vYSA preference was associated with improved vMWT learning trial performance in the young but not the older participants. Cumulatively, these results suggest that the vYSA is measuring an important preference for a spatial navigation strategy that may affect performance on subsequent independent navigation tasks.

The lack of relationship between navigation strategy and performance among older adults in the vMWT learning trials may be due to a number of factors. One possibility is that there were not enough older adults that preferred an allocentric strategy to detect a relationship between older adult strategy preference and navigation performance. Another might be related to the nature of the vMWT. The vMWT can be solved most quickly using an allocentric strategy, but older adults may no longer be capable of using an allocentric strategy effectively. This would explain the strong preference among older adults for the presumably less complex egocentric strategy. If this explanation is correct, even if an older adult preferred an allocentric strategy in the very easy vYSA, this preference may not have helped them in the much more difficult vMWT.

No relationship was found between sex and navigation strategy, which is inconsistent with other studies on the topic (Levy et al. 2005; Schmitzer-Torbert 2007). The vYSA is intentionally a very easy task for participants to complete. It is possible that there may be a ceiling effect among young adults that obscures a possible relationship between sex and strategy that would be found in a more difficult maze such as Schmitzer-Torbert's. Another possibility is that preference for one strategy over another in young adults might not reflect functional limitations, as might be the case with older adults. Further research is needed to determine what, if any, impact sex might have on navigation strategy and how this might be mediated at the neuroanatomical level. Environmental characteristics and task demands may also be important factors that warrant further investigation.

One weakness of the present study was the lack of an egocentric task to accompany the allocentric-focused vMWT. An example of such a task would be branching maze task, in which there is only one correct path through a maze with multiple intersections. It is conceivable that participants who prefer an egocentric strategy may show benefits on a subsequent egocentric task such as this.

Another weakness of this study is that because participants self-selected their strategy, cell sizes were not equal. In particular, only four older adults preferred an allocentric strategy, and three of those were male. Future studies can address this by testing greater numbers of older adults and selecting an equal number of each age, strategy, and sex combination.

In summary, the present study demonstrated age but not sex differences in strategy preference. As well, the present study demonstrated that strategy preference is related to subsequent performance on other navigation tasks, suggesting that our vYSA strategy assessment may be measuring relatively stable and generalized strategy dispositions.

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