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Quantitative and qualitative sex differences in spatial navigation

MARTIN LÖVDÉN,[1,2] AGNETA HERLITZ,[1,3] MICHAEL SCHELLENBACH,[1,4] BARBARA GROSSMAN-HUTTER,[4] ANTONIO KRÜGER[4] and ULMAN LINDENBERGER[1,2]

[1]*Center for Lifespan Psychology, Max Planck Institute for Human Development, Berlin, Germany*
[2]*School of Psychology, Saarland University, Saarbrücken, Germany*
[3]*Aging Research Center, Neurotec, Karolinska Institute, Stockholm, Sweden*
[4]*Department of Computer Science, Saarland University, Germany*

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We examined sex differences in spatial navigation performance using an ecologically relevant experimental paradigm in which virtual maze-like museums are projected in front of a treadmill. Thirty-two 20–30-year-old adults (16 women/16 men) performed a way-finding task in city-block (straight corridors) or variable (irregular corridors) topographies while walking on the treadmill. Sex differences in spatial navigation performance were reduced in variable topographies, suggesting less reliance on spatial relational learning among women. Also, spatial geometric knowledge of the mazes continued to be higher in men after all participants had attained perfect place-finding performance. Results indicate that sex differences in spatial navigation performance are modulated by interactions between environmental demands and sex differences in spatial processing.

Key words: Spatial navigation, sex differences, cognitive strategy, way-finding, spatial memory.

Martin Lövdén, Center for Lifespan Psychology, Max Planck Institute for Human Development, Lentzealleé 94, D-14195 Berlin, Germany. E-mail: loevden@mpib-berlin.mpg.de

INTRODUCTION

Sex differences favoring men are typically found in tasks assessing the ability to successfully navigate in the environment (e.g., Astur, Ortiz & Sutherland, 1998; Galea & Kimura, 1993; Moffat, Hampson & Hatzipantelis, 1998). In this study, we sought to investigate these differences, focusing on potential sex differences in cognitive processing during spatial navigation performance. Two main types of navigation processes have been suggested: spatial navigational learning and route learning. Spatial navigational learning refers to relational learning applied to the spatial domain, requiring formation and utilization of a global form of representation, or a "cognitive map" (Tolman, 1948; O'Keefe & Nadel, 1978). In other words, this form of learning is devoted to acquiring a flexible and view-point independent representation of the external world, containing information about distances and spatial relations between landmarks in allocentric space. In contrast, route learning is a navigational activity with less demand on allocentric spatial processes, involving verbal left/right serial-learning or stimulus-response-stimulus chains (e.g., Hartley, Maguire, Spiers & Burgess, 2003).

Previous studies investigating navigational performance have found large sex differences favoring men in paper-and-pencil tests (Galea & Kimura, 1993), desktop virtual reality environments (VE; Astur *et al.*, 1998; Moffat *et al.*, 1998; Sandstrom, Kaufman & Huettel, 1998), and real-world settings (Saucier, Green, Leason, MacFadden, Bell & Elias, 2002; Postma, Jager, Kessels, Koppeschaar & van Honk, 2004). Self-reports indicate that women predominantly rely on a route learning strategy when navigating in the environment. Men, on the other hand, report relying to a greater extent on Euclidean based (geometric) directions (Lawton, 1996). The notion that men, more than women, utilize spatial navigational learning, rather than route learning, is further corroborated in studies showing that men, as compared to women, have superior pointing accuracy (e.g., Holding & Holding, 1989; Lawton, 1996). In addition, men are faster at locating hidden platforms in computer-simulated Morris Water maze tests, irrespective of whether cue landmarks are available or not (Astur *et al.*, 1998), although Sandstrom and colleagues (1998) found that the magnitude of sex differences decreased when landmarks were available.

There are differences between men and women on some of the cognitive abilities underlying spatial navigation (e.g., visuo-spatial ability, episodic memory, and working memory). Most importantly, sex differences in visuo-spatial performance favoring males exist (Voyer, Voyer & Bryden, 1995) and are especially large in tasks assessing mental rotation, known to be associated with spatial navigation performance (Moffat *et al.*, 1998; Saucier *et al.*, 2002). Clearly, successful spatial navigation also requires the formation of memories, a cognitive task in which women typically outperform men (Herlitz, Nilsson & Bäckman, 1997). Sex differences in episodic memory favoring women are evident in verbal tasks but men tend to outperform women in episodic memory tasks that require a high degree of spatial processing (Lewin, Wolgers & Herlitz, 2001). Interestingly, sex differences favoring women are also found in episodic memory tasks requiring the retention of object–place associations, that is, for tasks that presumably require both spatial and verbal processing (Galea & Kimura, 1993).

The neural networks supporting human spatial navigational learning primarily involve hippocampus, parahippocampal gyrus, parietal lobe, and prefrontal cortex (see Aguirre & D'Esposito, 1999; Burgess, Maguire & O'Keefe, 2002, for reviews). With regard to sex differences, Grön, Wunderlich, Spitzer, Tomczak, and Riepe (2000) found that men primarily activate the left hippocampal region, whereas women engage right parietal and right prefrontal areas during spatial navigation. Again, these differences most likely reflect women's attempts to encode and keep landmark cues available in memory, whereas men's activation of the left hippocampal region may reflect the neural substrate of spatial navigational learning.

We sought to investigate the extent of sex differences in spatial navigation performance as well as potential sex differences in navigational strategies in an ecologically relevant setting, while maintaining a high degree of experimental control. To this end, we designed a VE maze-learning paradigm with a walking interface (see also Lövdén, Schellenbach, Grossman-Hutter, Krüger & Lindenberger, 2005). The VE, projected in front of a treadmill, was designed to give the impression of walking through an art museum. To bolster the impression of actually walking through the environment, the treadmill was synchronized with the visual flow of the VE. The task for participants was to find and remember the route from the entrance of the museum to the bistro and was completed after participants had acquired the ability to walk the shortest route from the entrance of the museum to its bistro twice in a row. To assess geometric spatial knowledge, a survey perspective of the building (without the building's internal structure) was displayed between each learning trial and participants were asked to place the museum's paintings at the correct spatial positions (henceforth, geometric knowledge test).

To address the issue of potential qualitative sex differences in navigational strategies, we varied the topography of the maze-like museum by either implementing corridors that were straight (city-block) or irregular (variable; see Fig. 1). At the same time, the number of decision points, perceptual cues, and large-scale spatial relations among the perceptual cues were kept constant. We hypothesized that, if a participant relies on spatial navigational learning for wayfinding, the irregular corridors will require continuous updating of spatial relations among key points, thereby increasing the difficulty of spatial navigational learning. In contrast, straight and variable mazes pose equal demands on route learning (e.g., landmark cue – response associations) because relevant aspects of the environment were the same. As a consequence, we expected that a spatial navigational strategy would be less effective with variable mazes than with city-block mazes, whereas a route learning strategy would be equally effective in both topographies. Since we assumed that men would rely more on spatial navigational learning than women, we predicted that men's way-finding performance would suffer more from variable relative to city-block topography than the way-finding performance of women who were assumed to preferentially rely on a route learning strategy. To validate our assumptions about sex differences in strategy preferences, we also examined acquired geometric spatial knowledge. In combination with men's greater susceptibility to topographic differences, greater geometric knowledge in men than in women would further corroborate the existence of sex differences in way-finding strategies.

METHOD

Participants

Thirty-two undergraduates from Saarland University, 16 women ($mean_{age}$ = 24.8 years; SD_{age} = 2.9) and 16 men ($mean_{age}$ = 24.7 years; SD_{age} = 3.0), received course credits or were paid 72 each for participation in this study. Table 1 summarizes scores on four unit-weighted composites (T-metric; *mean* = 50; *SD* = 10) representing performance on tests of visuo-spatial ability (mental rotations and figure folding), perceptual speed (digit letter and identical pictures), verbal memory (memory-for-text and paired associates), and verbal knowledge (vocabulary and spot-a-word) as a function of sex. The mental rotations and figure folding tests were designed for this study with the original versions as models (e.g., Vandenberg & Kuse, 1978). Detailed descriptions of the perceptual speed, verbal memory, and verbal knowledge measures are provided in Lindenberger, Mayr, and Kliegl (1993). An inspection of Table 1 suggests better performance for men relative to women on the visuo-spatial composite, but otherwise no sex differences. Univariate one-way analyses of variance (ANOVAs) for each composite were consistent with these observations: There was a marginally significant sex difference for visuo-spatial performance only, $F(1, 30) = 3.872$, $MSE = 91.5$, $p < 0.06$, $\eta^2 = 0.1$. The effects for the other measures did not approach significance: for perceptual speed, $F(1, 30) < 1$; verbal memory, $F(1, 30) < 1$; and verbal knowledge, $F(1, 30) = 1.78$, $MSE = 97.5$, $p > 0.18$. We conclude that observed sex differences were restricted to marker tests of visuo-spatial ability, suggesting that sex differences in navigation performance (see below) are unlikely to reflect more general differences in cognitive ability.

Table 1. *Cognitive characteristics as a function of sex*

	Women		Men	
Variable	Mean	*SD*	Mean	*SD*
Visuo-spatial ability	46.7	12.4	53.3	5.3
Perceptual speed	51.5	11.4	48.5	8.5
Verbal memory	50.0	10.5	50.0	9.8
Verbal knowledge	52.3	10.2	47.7	9.6

Notes: Visuo-spatial ability = *t*-scaled unit-weighted composite of Vandenberg-Kuse mental rotations test (Vandenberg & Kuse, 1978) and a figure-folding test; perceptual speed = identical pictures and digit letter; verbal memory = memory-for-text and paired-associates; verbal knowledge = spot-a-word and vocabulary.

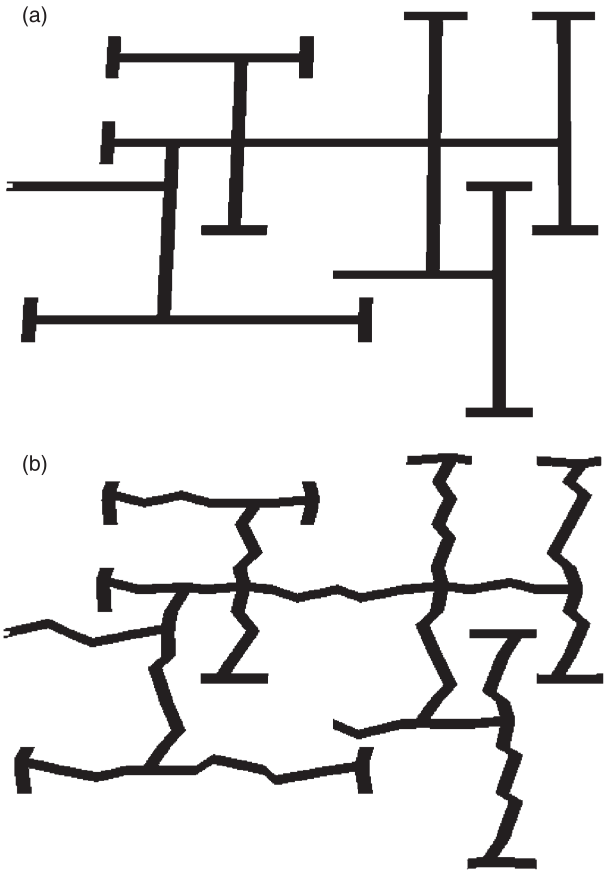

Fig. 1. (a) The city-block and (b) the variable topographies. These views were never shown to participants.

Materials

Detailed description of the general paradigm and experimental setting can be found in Lövdén *et al.* (2005). Here, we limit the description to design features relevant for this study.

Virtual environment. One practice maze and four experimental maze-like topographies were constructed. Corresponding to these five topographies, five different virtual museums of art were designed. In addition, two versions of each virtual museum were constructed: a *city-block version* (straight corridors and 90 degree turns at intersections) and a *variable* version (irregular corridors and variable degrees of turning at decision points; see Fig. 1). The lengths of the corridors were scaled to achieve comparable walking distances across the two versions.

The four experimental mazes had paintings of either van Gogh, Magritte, Breughel, or Warhol on display. The start of the maze was symbolized with a sign "Entrance to the (e.g.) van Gogh museum". The goal was symbolized with a "bistro" sign. The first, third, and fourth intersections on the correct route had paintings on display. Distributed at all intersections, unique objects that varied in texture and shape within a museum and in category across museums (chairs, ashtrays, trash bins, vases, and stools) were placed. These two types of "landmarks" were only visible in relatively close proximity of the intersections. On every corridor in the mazes, various other repetitive objects appeared (e.g., self-portraits of the artist, benches, and no smoking signs). The texture of the floor varied across museums.

The virtual scenery was projected on a 105 × 84 cm projection area allowing for approximately 39 degrees horizontal and 31 degrees vertical field of view when the participant was positioned in the normal walking position (150 cm in front of the screen).

Interface. Two handheld buttons was used to control navigation: take right (right button click), take left (left button), take straight ahead (both buttons at the same time), turn around 180 degrees via left (double click left button), and turn around via right (double click right button). Turning around was allowed in all parts of the maze and was executed by smooth changes in the virtual world. The other options were only active in close proximity of intersections. When participants approached an intersection, arrows appeared on the screen to symbolize that the buttons were active and that a decision was required.

The virtual environment was coupled with the movement of the walking area of the treadmill, in the sense that the treadmill decelerated as participants approached an intersection and came to a stop if no decision was made before reaching the intersection. In such a case, participants remained standing with a view of the intersection, including the available navigational choices, paintings, and objects until a decision was made and the movement accelerated to the maximum walking speed of 3.0 km/h.

Maze-learning task

Before starting the task, a survey perspective of the museum, displaying the outer walls, the position of entrance, and the position of bistro, but not the corridors, appeared for 15 seconds. Next, a first-person view of the entrance to the museum was displayed and the participant started walking in the museum. The task for the participant was to find and remember the way to the museum's bistro. Upon arrival at the cafeteria, the survey perspective appeared again and the participant was asked to place miniature versions of the three paintings on the correct places in the survey perspective of the museum. The three paintings were freely dragged-and-dropped with a mouse placed on a platform over the handrail. This geometric knowledge test was self-paced and participants received performance feedback after each trial in the form of a 1 to 100 scale, where 100 reflects perfect placement of the paintings.

Next, the first-person view of the entrance appeared again and the next trial started. The task was completed when participants reached the performance criterion of walking the shortest route from the entrance to the bistro twice in a row, without stopping at an intersection.

Design and procedures

The experimental design was a 2 [topography (city block/variable)] × 2 [sex] mixed factorial design. Topography was a within-subject factor and each of these cells was filled with two maze-learning tasks. The order of the conditions and the maze in each condition were rotated between individuals within the groups of men and women to form a complete counterbalancing table.

The experiment consisted of six different sessions. The individual sessions were separated by a minimum of one day and a maximum of five days.

Session I. After signing an informed-consent form, participants were interviewed and tested for a number of background variables (e.g., health and vision). After a general demographic questionnaire, several psychometric tests (reported in *Participants*) and a test of painting knowledge were administered. The painting knowledge test involved sorting pictures of the paintings used as experimental materials (three paintings times five artists) in five piles, each labeled with the names of one of the five artists. After each trial, the experimenter showed the correct solution. The participant repeated the sorting task until performance was perfect. To address potential sex differences in pre-experimental familiarity with the paintings, we performed a one-way (sex) ANOVA on the number of errors committed in the first trial. This analysis revealed no significant differences ($F < 1$).

Session II. This session started with a phase of familiarization with the treadmill and the interface, and continued with experimenter-supported practice on the maze-learning task. The practice maze of the variable format was used for this session. Participants were instructed (a) that the goal of the task was to find and remember the way to the museum's bistro; (b) that the task was completed when participants walked the shortest route from the entrance to the bistro twice in row; (c) that stopping at an intersection (i.e., not making a choice before reaching the intersection) was allowed at all times, but that a trial counted only as perfect if the shortest route to the bistro was taken without stopping; (d) that paintings appeared only on the shortest route from the entrance to the bistro, but that participants might be on the shortest route even when no painting appeared at an intersection; (e) that the paintings and the unique objects at each intersection provided important positional information; and (f) that the participant should try to remember the locations of the paintings because their memory for this information would be tested after reaching the bistro. The participant continued with the task until the performance criterion was reached.

Sessions III–VI. In each of these four experimental sessions, one maze-learning task was completed. Before the start of each maze, participants were again familiarized with the virtual environment and the interface. Next, the standardized instructions were read to the participant and the task started.

RESULTS

Maze-learning performance

Several dependent measures can be used to index performance in the maze-learning task. Here, we focus on distance traversed until the performance criterion was reached. Other dependent variables, such as the number of trials or errors, were highly colinear (rs > 0.90) with distance traversed and yielded converging results. Figure 2 displays means and standard errors for distance covered to criterion (meters) as a function of sex and navigation condition (averaged over the two tasks in each condition). An inspection of Fig. 2 suggests sex differences in favor of men. Averaged across conditions, men walked 397 meters whereas women walked 523 meters to complete the task. For men, less walking was required to reach the criterion in the mazes with city-block topography (*mean* = 322) than in the mazes with variable topography (*mean* = 472), whereas this effect was less pronounced for the women (*mean* city block = 507; *mean* variable = 539). A 2 [topography (city block/variable)] × 2 [sex] mixed ANOVA supported the above observations: The main effect of topography, $F(1, 30) = 4.77$, $MSE = 2{,}773{,}176.46$, $p < 0.04$, partial $\eta^2 = 0.14$ and sex, $F(1, 30) = 7.57$, $MSE = 3{,}373{,}899.06$, $p < 0.02$, $\eta^2 = 0.20$, were significant. The sex group by topography interaction was not significant,

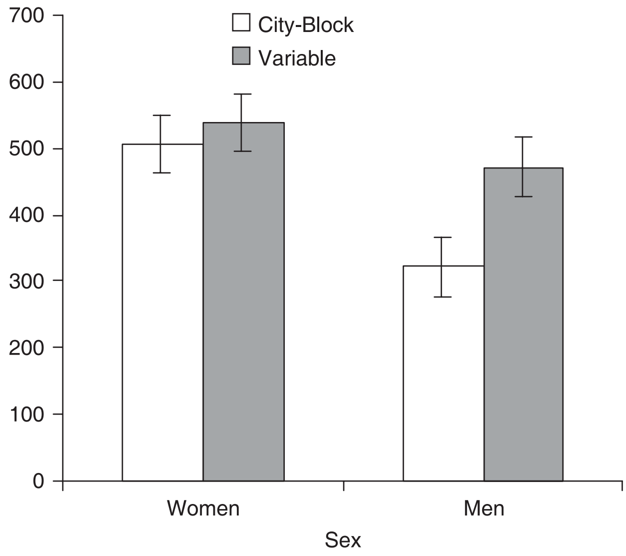

Fig. 2. Mean distance covered to criterion (±SE) as a function of sex and topography.

$F(1, 30) = 2.0$, $MSE = 2{,}773{,}176.46$, $p < 0.17$, $\eta^2 = 0.06$. Planned comparisons showed a significant effect of topography for men, $t(15) = 3.36$, $p < 0.01$, but no significant effect for women, $t(15) = 0.46$, $p > 0.65$. Related to these results, the sex differences were significant for performance in the city-block topography, $t(30) = 2.98$, $p < 0.01$, but not in the variable topography, $t(30) = 1.08$, $p > 0.29$.

Geometric knowledge

The dependent variable for this test was the log-transformed sum of the linear distances from the participant's placement of the paintings to the correct placements. We focused on performance in the last trial because we were interested in participants' mental representations of the positions of the paintings when both groups possessed efficient representations to support navigation. A 2 [topography (city block/variable)] × 2 [sex] mixed ANOVA revealed a significant main effect of sex, $F(1, 30) = 5.42$, $MSE = 0.04$, $p < 0.03$, $\eta^2 = 0.15$, as well as a significant main effect of topography, $F(1, 30) = 6.60$, $MSE = 0.02$, $p < 0.02$, $\eta^2 = 0.18$. Men (*mean* = 2.22) performed better than women (*mean* = 2.34) and performance was better for the city-block topography (*mean* = 2.24) than for the variable topography (*mean* = 2.33). The interaction was not significant, $F(1, 30) = 0.30$, $MSE = 0.02$, $p > 0.58$. Planned comparisons showed non-significant trends for effects of topography for men, $t(15) = 2.10$, $p < 0.06$ and women, $t(15) = 1.51$, $p < 0.16$. Related to these results, the sex differences were significant for performance in the city-block topography, $t(30) = 2.11$, $p < 0.05$. A non-significant trend emerged for the variable topography, $t(30) = 1.78$, $p < 0.09$.

DISCUSSION

This study yielded findings of sex differences in spatial navigation in an ecologically relevant, but experimentally well-controlled setting. Significant sex differences in spatial navigation performance were present when navigating in city-block topographies, but not when navigating in variable topographies. Sex differences in geometric knowledge persisted despite perfect navigation performance. Geometric knowledge of variable topographies was less accurate than of city-block topographies.

This study confirms previous findings of sex differences in spatial navigation performance (e.g., Astur *et al.*, 1998; Galea & Kimura, 1993; Saucier *et al.*, 2002). More importantly, however, this study indicates that the magnitude of sex differences varies as a function of environmental topography. Men's navigation performance was affected by topography but women's performance was not, resulting in significant sex differences in performance when navigating in the city-block topography only. We predicted that men's performance would be affected by topography based on the notion that continuous shifts in heading in the variable topography place greater demands on spatial navigational learning than navigation in the city-block topography. This idea was supported by the main effect of topography on geometric knowledge of the environment, indicating that it was more difficult to acquire accurate spatial allocentric representations in the variable topography. Thus, the significant effect of topography on navigation performance for men might suggests that they tend to rely more on spatial navigational learning than women, for whom the effect of topography was non-significant. In line with this notion, spatial relations were acquired less well by women than by men, even though all participants had learned to perform the navigational place finding task without error. We suggest that men might acquire better geometric knowledge than women because they rely more on spatial relational learning to support navigation, whereas women might rely more on processes involved in route learning, such as cue-response associations. This interpretation is in line with sex differences in self-reports (Lawton, 1996), male advantages in pointing accuracy (Holding & Holding, 1989; Lawton, 1996), and reductions of male advantage when proximal landmarks serve as the main source of positional information (Sandstrom *et al.*, 1998).

Interestingly, qualitative sex differences in spatial navigation processes are paralleled in contrasts between younger and older men (Lövdén *et al.*, 2005) and younger and older animals (Barnes, Nadel & Honig, 1980). Specifically, older adults show lower spatial navigation performance than younger adults, and they might also rely less on spatial navigational learning. Though it is tempting to view the difference between men and women as exclusively qualitative (women not having, or preferentially not using, the ability to engage in spatial navigational learning), older men clearly have had or have used this ability and eventually lost or stopped using it. In our view, these parallel findings, together with the present findings of effects of environmental topography, suggest that the reasons for qualitative differences in navigation behavior should be sought in the balance of the effectiveness of the underlying cognitive processes and the environmental demands on these processes. In particular, future studies should address in more detail how reliance on different forms of navigational processes is associated with the differential effectiveness of constituent processes in various environments. For example, women may adopt a more verbal strategy (i.e., route learning) because of deficiencies in spatial ability, because of efficiency of verbal abilities, or because of a combination of the two. In this vein, women with specific skills or experiential background in visuospatial ability may rely as much on spatial navigational learning as is typically found in men. These considerations are in line with the general notion that strategy choices differ not only between groups of individuals but also are malleable within individuals, and that standard experiments may underestimate the potential range of strategic variation within individuals (Baltes, Lindenberger & Staudinger, 2006; Lautrey, 2003; cf. Reuchlin, 1978).

Given the importance of self-motion (e.g., vestibular information) for developing and consolidating spatial representations (McNaughton, Barnes, Gerrard *et al.*, 1996; Waller, Loomis & Haun, 2004), the present paradigm represents an advancement over previous VE paradigms used to examine sex differences in spatial navigation (e.g., Moffat *et al.*, 1998; Sandstrom *et al.*, 1998). Self-motion information during spatial navigations has been lacking in previous studies, possibly limiting the generalizability of previous results. At the same time, the present paradigm also has some limitations. For example, body-based information was limited in this study because shifts in heading in the VE were mismatched with the actual constant direction of movement in space. Thus, information of distance covered is the only component potentially enhanced by the movement feature of the paradigm. In addition, men and women may differ with respect to amount of experience with computer games, which in turn might be related to VE navigation performance (e.g., Moffat *et al.*, 1998). Thus, differences in computer experience might have influenced the magnitude of the observed sex differences. However, our within-subject experimental manipulation ensure that ability-extraneous sex differences in computer experience cannot explain the differential magnitude of the sex differences in navigation performance between the two topographies. It is of course still possible that differential computer experience might affect the cognitive operations performed when navigating. Finally, the relatively small sample size and associated low power of this study is a potential factor behind our failure to find a significant sex by topography interaction for maze-learning performance. However, the results of the planned comparisons, indicating significant effect of topography for men but not for women, together with the residual male advantages on geometric knowledge (even though both groups had learned the place finding task to an error-free performance level), make us confident in our conclusions.

To summarize, sex differences in spatial navigation performance are reduced in variable topographies and sex differences in spatial geometric knowledge persist under conditions of equivalent navigation performance. Together, these results indicate that interactions between environmental demands and cognitive processes modulate sex differences in spatial navigation performance.

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REFERENCES

Aguirre, G. K. & D'Esposito, M. D. (1999). Topographical disorientation: A synthesis and taxonomy. *Brain*, *122*, 1613–1628.

Astur, R. S., Ortiz, M. L. & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: A large and reliable sex difference. *Behavioural Brain Research*, *93*, 185–190.

Baltes, P. B., Lindenberger, U. & Staudinger, U. M. (2006). Life span theory in developmental psychology. In W. Damon & R. M. Lerner (Eds.), *Handbook of child psychology: Vol. 1. Theoretical models of human development* (6th edn, pp. 569–664). New York: Wiley.

Barnes, C. A., Nadel, L. & Honig, W. K. (1980). Spatial memory deficits in senescent rats. *Canadian Journal of Psychology*, *34*, 29–39.

Burgess, N., Maguire, E. & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*, 625–641.

Galea, L. A. M. & Kimura, D. (1993). Sex differences in route-learning. *Personality and Individual Differences*, *14*, 53–65.

Grön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R. & Riepe, M. W. (2000), Brain activation during human navigation: Gender differential neural networks as substrates of performance. *Nature Neuroscience*, *3*, 404–408.

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

Herlitz, A., Nilsson, L.-G. & Bäckman, L. (1997). Gender differences in episodic memory. *Memory & Cognition*, *25*, 801–811.

Holding, C. S. & Holding, D. H. (1989). Acquisition of route network knowledge by males and females. *The Journal of General Psychology*, *116*, 29–41.

Lautrey, J. (2003). A pluralistic approach to cognitive dedifferentiation and development. In R. J. Sternberg & J. Lautrey (Eds.), *Model of intelligence: International perspectives* (pp. 117–131). Washington, DC: American Psychological Association.

Lawton, C. A. (1996). Strategies for indoor wayfinding: The role of orientation. *Journal of Environmental Psychology*, *16*, 137–145.

Lewin, C., Wolgers, G. & Herlitz, A. (2001). Sex differences favoring women in verbal but not in visuospatial episodic memory. *Neuropsychology*, *15*, 165–173.

Lindenberger, U., Mayr, U. & Kliegl, R. (1993). Speed and intelligence in old age. *Psychology and Aging*, *8*, 207–220.

Lövdén, M., Schellenbach, M., Grossman-Hutter, B., Krüger, A. & Lindenberger, U. (2005). Environmental topography and postural control demands shape aging-associated decrements in spatial navigation performance. *Psychology and Aging*, *20*, 683–694.

McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M., Knierim, J. J., Kudrimoti, H. S., Qin, Y., Skaggs, W. E., Suster, M. & Weaver, K. L. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology*, *199*, 173–185.

Moffat, S. D., Hampson, E. & Hatzipantelis, M. (1998). Navigation in a "virtual" maze: Sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behavior*, *19*, 73–87.

O'Keefe, J. & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.

Postma, A., Jager, G., Kessels, R. P. C., Koppeschaar, H. P. F. & van Honk, J. (2004). Sex differences for selective forms of spatial memory. *Brain & Cognition*, *54*, 24–34.

Reuchlin, M. (1978). Processus vicariants et differences individuelles [Vicarious processes and individual differences]. *Journal de Psychologie*, *2*, 133–145.

Sandstrom, N. J., Kaufman, J. & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research*, *6*, 351–360.

Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., Bell, S. & Elias, L. J. (2002). Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behavioral Neuroscience*, *116*, 403–410.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*, 189–208.

Vandenberg, S. G. & Kuse, A. R. (1978). Mental rotation, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, *64*, 907–914.

Voyer, D., Voyer, S. & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*, 250–270.

Waller, D., Loomis, J. M. & Haun, D. B. M. (2004). Body-based senses enhance knowledge of directions in large-scale environments. *Psychonomic Bulletin & Review*, *11*, 157–163.

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