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### **Proceedings of the Annual Meeting of the Cognitive Science Society**

#### **Title**

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#### **Permalink**

<https://escholarship.org/uc/item/7ws14954>

#### **Journal**

Proceedings of the Annual Meeting of the Cognitive Science Society, 27(27)

#### **ISSN**

1069-7977

#### **Authors**

Griego, Jacqueline  
Kabisch, Christiane  
Muhl, Christian

#### **Publication Date**

2005

Peer reviewed

# A Vanishing Sex Difference in the Virtual Morris Water Task

Christian Mühl, Christiane Kabisch, Jacqueline Griego

Institute for Cognitive Science, University of Osnabrück  
Osnabrück, 49069 Germany

## Abstract

Sex differences are frequently, however, not consistently found in the domain of spatial navigation in mammalian species. Using a virtual Morris water task (VMWT) we tested the hypothesis that differential use of proximal and distal cues between males and females could account for previously observed human differences. In Astur, Ortiz, and Sutherland (1998) males had faster swim latencies to a hidden platform, and smaller heading errors in the VMWT. We alternated blocks of fixed-across blocks and fixed-within blocks platform locations. Males found the hidden platform faster overall in both conditions. However the interleaved blocks eliminated the performance difference between the groups in the first trial of both the stationary and nonstationary platform blocks, indicating that females were less affected than males by the change in the reliability of the cognitive map (O' Keefe & Nadel, 1978) of the stationary blocks for the interleaved blocks. This is in line with studies indicating differential preferences and abilities to use distal or geometric cues (e.g., Sandstrom, Kaufmann, & Heutzel, 1998). Therefore, the mixed results seen in spatial navigation regarding sex differences are due in part to the cue types available in a given task environment.

**Keywords:** Sex difference; Virtual reality; Morris water task; Spatial memory, Hippocampus, Spatial ability

## Introduction

There are physical differences between human male and female brains such as those seen in gross morphology and cytoarchitecture (e.g., Toga & Thompson, 2003) that are the result of hormone regulated (e.g., Williams & Meck, 1991) and X- and Y-chromosome linked gene expression (e.g., Galfalvy et al., 2003). The significance of these manifest differences in terms of cognition are still being explored and debated. However, as we continue to define the functional relationship between brain structure and cognition, sex differences appear to be relevant parameters of the relationship. As a result of appropriate ethical considerations, much of the direct evidence in this area is obtained in animal studies. Thus the link between human and nonhuman animal studies is important to progress in cognitive science. One contemporary development is the comparison between the decades of results in spatial navigation in rodents performing maze tasks with that of human participants in virtual environments (Nadel et al., 1998)

The recent development of virtual reality environments makes possible the assessment of navigational abilities in humans with similar settings and parameters as done with

rodents. Furthermore, although studies with actual mazes have been conducted (Bohbot et al., 1994; Kállai et al., 1995), the use of virtual environments allows a tighter control of the experimental conditions and better measurement of performance: for example, regarding path trajectories and speed. To this end, rodents are now also subjects in virtual environment navigation tasks (e.g., Hölscher et al., 2005).

Investigations with human subjects in different kinds of virtual mazes have produced similar results as seen in non-virtual rodent studies, for example the acquisition of spatial knowledge (Jacobs, Thomas, & Laurence, 1997), the importance of distal cues (Jacobs et al., 1998), and the crucial involvement of hippocampal structures (Astur et al., 2002). Specific to the current study there is evidence for a general performance advantage of males in navigational ability in virtual reality mazes (Morris water maze: Astur et al., 1998; Hebb-Williams maze: Shore et al., 2001) as it was also shown for rodents (Perrot-Sinal et al., 1996; Roof, 1993; Williams & Meck, 1991).

As of yet there is not a large body of results regarding sex differences in virtual maze navigation. Therefore, the aim of the current study was twofold. First, we wanted to replicate the general sex differences of shorter swimming latencies and smaller heading errors for male navigators in a different version of a virtual environment (i.e., Astur et al., 1998; Sandstrom et al., 1998). The second was to investigate the influence interleaved nonstationary platform trials have on these sex differences in terms of differential use of allocentric and egocentric representations. A difference in the method used to construct representations of the navigation space is assumed to possibly support the use of different navigational strategies. For example, as seen in Sandstrom et al. (1998) where males and females showed no differences in navigation performance in environments with both geometric (e.g., direction and distance) and landmark cues; However, female performance was worse when there were only geometric cues.

We chose for our purposes the Morris water maze (Morris, 1981), the gold standard for assessing navigation in rodents. In the Morris water task the subject has to find a platform in a circular pool situated in a quadratic room. The platform is hidden and there are no proximal cues within the pool that could indicate the platform location. Around the pool at the walls of the room, distal cues are arranged (Fig. 1). To perform successfully the subject has to encode the platform location in relation to the distal cues, as proximal cues are essentially missing.

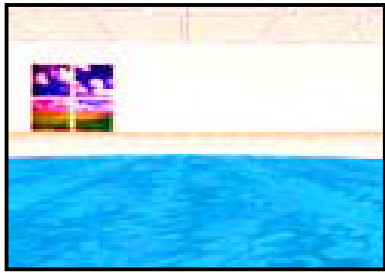


Figure 1. A view from inside the pool of the VMWT

Astur et al. (1998) showed in various experiments a reliable sex difference in the virtual Morris water task. Individuals had to escape from a virtual pool by finding a hidden platform over 20 trials after which a probe trial without platform was to be performed. Across all these experiments in which the position of the target did not change, the subjects continually improved their performance, that is, their swimming latency decreased. Overall, males were faster in finding the hidden platform, made smaller heading errors and showed a better spatial strategy in the probe trials<sup>1</sup> compared to females. Importantly in a control task with a visible platform there were no differences between male and female latencies to find the platform or in swim speed. This indicates that the sex difference was not the result of motivational, motor or sensory differences regarding the computer program, rather it could be traced back to navigational ability (Astur et al., 1998).

A possible interpretation for the sex difference would be that males and females rely on differential strategies that are based on different representations when searching for the platform. Two kinds of spatial representation, egocentric and allocentric, are potentially useful in solving the Morris water task. To navigate through the environment individuals must initially rely on an egocentric representation. That is, on a representation of distal cues in the environment relative to the one's own body. With continuous exposure to the environment, it is possible to form relations between the various cues. An allocentric representation, a cognitive map containing information about the spatial relations between diverse distal and geometric cues and the target position is built and refined gradually, supporting the navigation process (O'Keefe & Nadel, 1978). While an egocentric representation can be used to re-establish the constellation of distal cues relative to one's own body in the moment the platform was found, an allocentric representation makes it possible to derive the platform location when cues and one's own position within the environment are known. This distinction underlies the motivation for the task in our experiment. That is, interleaving a stable platform condition

with a nonstable platform condition in the same VMWT environment should disrupt the ability to use a cognitive map built across both types of blocks.

Saucier et al. (2002) presented evidence for a basic difference in the way the sexes orient in and navigate through the world, and that it may be related to the use of differential representations. They contend that the difference can be traced back to dimorphic capacity to use the two types of cues. The preference for distal cue (landmarks) use, or the relative lack of sensitivity towards geometric cues, may cause the slower acquisition of cognitive maps (i.e., absolute reckoning representation) and a stronger reliance on egocentric representations. Thus, males are more effective in construction and use of an allocentric representation of the environment relying on geometrical and distal cues, while females initially rely instead on an egocentric representation. This leads to an advantage of men in spatial navigation tasks.

Additionally, Sandstrom et al. (1998) also demonstrated that males and females differ in the kind of cues they use in tasks of spatial navigation like the Morris water maze. While men used distal and geometric cues (e.g., direction and distance) to find a hidden platform, women were mostly navigating with the help of distal cues.

In total, assuming egocentric representation to be mainly supported by parietal cortex (Colby & Goldberg, 1999), and allocentric representations by the hippocampus (Ekstrom et al., 2003; O'Keefe & Nadel, 1978), differential patterns of brain activations (Grön et al., 2000) indicate differential use of representations. While performing a complex, three-dimensional virtual reality maze, both males and females showed, besides others, strong activations in the hippocampus proper, the parahippocampal gyrus and parietal regions. This indicates that both males and females are performing on the basis of the same neural systems as outlined above. However, compatible with the differential cue use mentioned above and with the idea of different representations preferentially used, females showed stronger activations in a right parietal area and a right prefrontal area, whereas men exhibited stronger activation in the left hippocampus.

In order to investigate differential cue use we chose to use interleaved nonstationary platform location blocks within stationary platform location blocks. Subjects had to find a hidden platform in a virtual version of the MWT. While the platform location did not change over the stationary platform blocks, it was randomly assigned to a different location for each nonstationary platform block. Stationary and nonstationary blocks differed also in the distal cue design, with every-day cues (window, shelf, picture, door) and abstract cues (4 abstract pictures) randomly and evenly distributed over males and females.

We chose the nonstationary blocks to be without predictable platform location over blocks but predictable (stationary) within blocks to maximise uncertainty about the platform location. However, this minimised the possibility that individuals might conceptualize the nonstationary

<sup>1</sup> The term spatial strategy refers to the percentage of the path length that the subject spent in the quadrant where the platform was located in the practice trials. A successful spatial strategy required the subject to spent more than 40% of the path length in the target quadrant.

platform blocks as totally random (i.e., in a trial to trial randomisation). The former prevents subjects to learn one general platform location for all interleaved blocks, but for each block to learn a new location. The latter should ensure that subjects still use some kind of navigation strategy other than random navigation.

## Methods

### Participants

We tested 46 graduate and undergraduate students, 23 male students ( $M$  age = 23.3) and 23 female students ( $M$  age = 23.7), from the human sciences department. All had normal or corrected to normal vision. As compensation they received course credits for their study or took part in a lottery with the chance to win 50 €.

### Equipment

We used an implementation of a virtual Morris water task from Neuroinvestigations, Inc. Technical specifications are available at: <http://www.neuroinvestigations.com>. The experiments were done on an IBM-compatible computer with a Pentium III 800MHz processor, 256 MB RAM, a 32 MB RAM ATI Graphics Card and an IBM-compatible keyboard. The image was displayed on a 17" monitor with a resolution of 1280 x 1024 (16 Mio. colors, 85 Hz refresh).

### Design

The experiment consisted of 14 blocks, 7 of the stationary platform condition and 7 of the nonstationary platform condition, with 4 trials in each block. The blocks of the two conditions were alternating, beginning with a stationary platform condition block. In the stationary platform condition the platform was tied to the same location within the pool over all blocks, in the nonstationary platform condition the location was randomly reassigned for each block, as illustrated:

A_B.1_A_B.2_A_B.3_A_B.4_A_B.5_A_B.6_A_B.7
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Within the blocks of both conditions the platform was located at the same place over the 4 trials. However, the starting position within the pool was randomly determined for each trial.

The two platform conditions used different sets of distal cues (abstract objects: colorful abstract pictures vs. every day objects: window, bookshelf, poster, door). The cue sets made it possible for the subject to discriminate between the conditions, though not informed about the stationary/nonstationary platform design. The association of the cue types with the condition type (abstract – stationary / familiar – nonstationary vs. abstract – nonstationary / familiar – stationary) was randomly and evenly distributed over the subjects.

### Procedure

After reading an information sheet with general instructions concerning the experiment, participants signed a consent form. Then they were instructed to navigate in the virtual 3D surrounding using the arrow keys (forward, right, left) on the keyboard and to use the distal cues to orient. They were told that after 60 seconds of search the platform would appear and they were to swim to the location. It was emphasised that they should use the 5 seconds remaining to the next trial after the platform was discovered to turn and orient in the room, as this information could be helpful in the next trial. There was a 60° field of egocentric view of the virtual space, which is approximately the same as the human eye. Every 100 ms the position of the subject was recorded in the form of  $\{x,y\}$  coordinates. The latency and path length to locate the platform were determined from this data. The heading error was determined after the subject travelled a path length  $\frac{1}{4}$  of the pool diameter, or if the platform was found before this point immediately before the subject stepped on the platform.

### Results

A repeated measure 2 (Sex) by 28 (Trials) ANOVA with the mean swimming latency of all stationary trials revealed faster times for males ( $M = 14.81$ ,  $SD = 13.95$ ) than females ( $M = 22.84$ ,  $SD = 19.94$ ),  $F(1, 44) = 10.19$ ,  $p < .001$  (Fig. 2).

Furthermore a significant difference was observed for the main effect of trial,  $F(27, 1188) = 7.29$ ,  $p < .001$ . Mean latencies were reduced from the first to the last trial,  $t(90) = 6.49$ ,  $p < .001$ , reflecting learning over the blocks. There was no interaction,  $p = .392$ .

In separate repeated ANOVAs, there were no significant differences due to whether navigators were started in any one of the Cue Type (abstract or concrete objects) by Block Type (Stationary or Nonstationary),  $p = .600$ . There were also no significant differences in Heading Error between sexes,  $p = .310$ .

When we examined the latencies in all first trials of stationary platform blocks, using repeated measure ANOVA with the 7 first trials as repeating factor, we found no main effect of Sex,  $F(1, 44) = 3.02$ ,  $p > .05$ . However, a main effect of trial could be observed,  $F(6, 264) = 7.87$ ,  $p < 0.01$ , and again was shown to be caused by an decrease in latency over the blocks,  $t(90) = 3.20$ ,  $p = .002$ .

The finding of no significant sex difference in the repeated measure ANOVA above was not due to a shrunken sample size, as in an ANOVA for all second stable trials, males were again significantly faster to find the platform,  $F(1, 44) = 9.44$ ,  $p < .01$ .

However, comparing the performance of the sexes in the first trials of the stationary blocks we found an effect of the interleaved nonstationary blocks. The interleaved blocks led to a decrease in swimming latency in the first stationary trial relative to the last trial of the preceding stationary block in both sexes. This loss was larger for males than for females, therefore the swim latencies between sexes were no longer statistically different (Fig. 3).

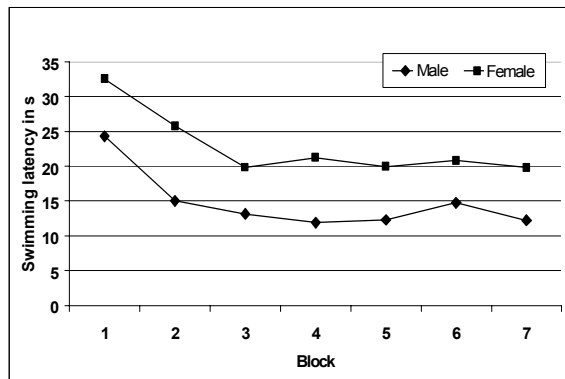


Figure 2. Development of the performance over stationary platform blocks expressed in swimming latency.

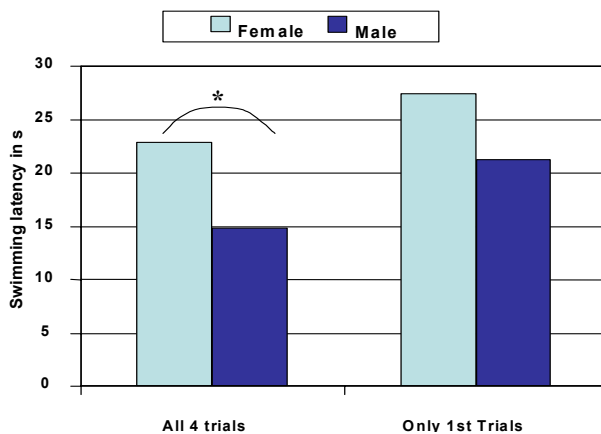


Figure 3. Mean latency to find the platform; left: performance over all four trials in the stationary blocks (\* significant contrast); right: performance over just the first trials of the stationary blocks. Nonsignificant,  $p = .09$ .

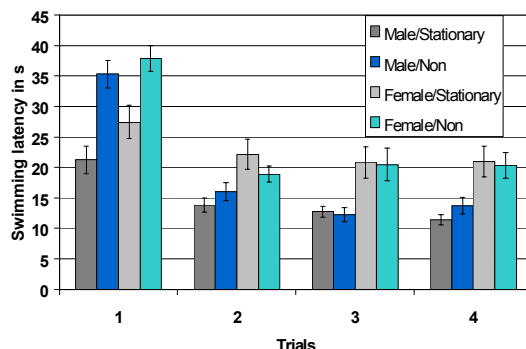


Figure 4. A profile of sex differences and similarities in performance across the four trials in each type of the block, stationary and nonstationary, whiskers are SEM.

Examining a profile of performance across the four trials shows no significant differences by sex for the first trial of the nonstationary block  $t(44) = .839, p = .41$ , in addition to the earlier result for the stationary blocks (Fig. 4). Also of note there is no difference between males and females in the second trial of the nonstationary block, indicating continued disruption for males  $t(44) = 1.501, p = .14$ . The figure includes SEM whiskers to allow for visual inspection of all trial latencies, beyond those comparisons discussed.

## Discussion

As expected, a large sex difference in the time to find a hidden platform was observed with males in general finding the hidden platform faster than females. Viewing the vanishing of the sex difference in this light suggests that the use of differential navigational strategies causes the different effects of the interleaved nonstationary blocks on performance. Not only did individuals improve in performance from first to last trial within stationary and nonstationary blocks, but also over the stationary blocks (Fig. 2 and Fig. 4).

While we took the vanishing sex difference in the first stationary trials as an indicator that males were affected relatively more than females by the change of condition, there is a possible alternative interpretation. That is, both males and females were affected to the same degree, resembling a kind of initial resetting of spatial knowledge. This implies that both would lose all their spatial knowledge about the environment and be completely disoriented. This would also be expressed as a vanishing of the sex difference because the spatial knowledge of both groups would be zero. However, this interpretation is unlikely because the general learning curve over all first stable trials implies that there is learning of spatial knowledge.

So if we assume that males and females are affected to different degrees by the interleaved nonstationary blocks, what is the cause? Assuming the stronger reliance of males on allocentric representations, and of females on egocentric, the effect could be explained by the characteristics of these representations. For example, the general advantage of males in simple tasks of spatial navigation might be a disadvantage when environmental cues change in their validity, as when the platform location changes in the interleaved blocks. In this case the cognitive maps of the two environments interfere with each other, possibly due to an automatic process of generalisation based on similar geometric cues of the two environments. Females, on the other hand, would be less affected by the change of the environment as the egocentric representation is based on the use of clearly distinguishable distal cues, and therefore it is not possible to confound the different environments.

One might question the ecological validity of the results, criticising the fact that subjects only receive minimal proprioceptive and vestibular inputs in virtual environments. Although vestibular information plays a role in spatial navigation, subjects receive optokinetic information, as for example visual motion, in virtual

environments that may compensate the lack of other information. Moreover, optokinetic information alone can induce motion sickness and vertigo, which suggests that optokinetic information is interacting with the vestibular system (Astur et al., 1998; Hamilton, Driscoll & Southerland, 2002). In our study both males and females were deprived equally of input other than the optokinetic one. It may be possible to imagine that females and males make use of differential strategies, based on cue types other than proximal and distal. In this case a differential dependency on vestibular and/or proprioceptive input may be the case, producing the sex difference. However, Waller, Knapp and Hunt (2001) compared the performance of the sexes in virtual environments and in real mazes, showing that in both differences of navigational ability can be found. This rejects the notion that the difference is merely caused by a differential dependency on vestibular or proprioceptive information.

Another point of criticism is different levels of experience with computers or computer games that might lead to the observed sex difference. Two counter arguments address this problem: Again, the demonstration of sex differences in real-world experiments rejects the idea of a mere effect of experience with computers. Furthermore, other studies using similar virtual environments showed that sex was the better predictor for spatial ability compared to computer experience (Astur et al., 1998; Shore et al., 2001).

To clarify if the vanishing sex difference is really caused by the reliance on differential representations it would be interesting to design a task employing interleaved nonstationary blocks, that forces females to build up and work with an allocentric representation. This could be done by the manipulation of the cues necessary to orient, for example removal of the distal cues and addition of geometrical cues. If males and females are using allocentric representations to navigate the Morris water task the overall sex difference should still be found, maybe even enlarged (Sandstrom et al., 1998), but more importantly also a sex difference in the first trials of the stationary blocks.

Our results indicted that interleaved blocks of a nonstationary platform condition have differential effects on the performance of males and females in the Morris water task. Though a significant overall advantage for male navigators could be observed, the interleaved blocks reduced this statistically reliable difference for the first trials of the stationary blocks to a nonreliable difference. In considering the relationship of this result to the rodent literature a similar idea has been supported in rodent studies. Kanit et al. (1998) trained rats to swim to a visible platform. When the visible platform was moved to a new location in a probe trial males swam to the location where the platform had been whereas female rats swam to the new location. This points to a strong reliance on the previously established representation in males.

## Conclusion

The investigation of sex differences in human spatial cognition has a long history and includes many components of spatial ability. For example, males perform better than females in mental rotation tasks (Tapley & Briden, 1977), the Piagetan water level task (Goodrich et al., 1993), way-finding (Lawton, 1994) and route learning (Galea & Kimura, 1993). Females have better memory for object location in static (e.g., Silverman & Eals, 1992) and dynamic environments (Tottenham, Saucier, Elias, & Gutwin, 2003).

Considering our data and those of others (cf. Astur et al., 1998; Sandstrom et al., 1998) the current study contributes to the spatial cognition literature the idea that the development of sexually dimorphic neural substrates (e.g., Williams & Meek, 1991) might result in different ways of processing environmental input during navigation, as shown in humans: for example, in patterns of effective connectivity derived from imaging studies (Grön et al., 1998). The idea of differential representation construction (i.e., egocentric and allocentric) and cue use in navigation is of course not incredibly novel. However, we point out the advantage of being able to compare rodent and human performance in similar paradigms and on similar parameters, which in turn can be tied to the neural substrate data obtained across many years of rodent brain data and finally, to functional imaging studies.

## References

- 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. *Behavioral Brain Research*, 93, 185-190.
- Astur, R. S., Taylor, L. B., Mamelak, A. N., Philpott, L., & Sutherland, R. J. (2002). Humans with hippocampus damage display severe spatial memory impairments in a virtual Morris water task. *Behavioral Brain Research*, 132, 77-84.
- Bohbot, V., Jech, R., Ruzicka, E., Bures, J., & Nadel, L. (1994). Comparison of rat and human spatial memory performance. *Society for Neuroscience Abstracts*, 361, Miami.
- Colby, C. L., & Goldberg, M. E. (1999). *Space and attention in parietal cortex*. Annual Review Neuroscience, 22, 319-349.
- Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). The cellular networks underlying human spatial navigation, *Nature*, 425, 184-187.
- Galea, L. A., & Kimura, D. (1993). Sex differences in route-learning. *Personal & Individual Differences*, 14, 53-65.
- Galfalvy, H. C., Erraji-Benchekroun, L., Smyrniotopoulos, P., Pavlidis, P., Ellis, S. P., Mann, J. J., Sibille, E., Arango, V. (2003). Sex genes for genomic analysis in human brain: Internal controls for comparison of probe level data extraction. *BMC Bioinformatics*, 4,

- Goodrich, G. A., Damin, P. B., Ascione, F. R., & Thompson, T. M. (1993). Gender differences in Piagetian visual-spatial representation of verticality and horizontality. *Journal of Genetic Psychology*, 154, 449-458.
- Grön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature Neuroscience*, 3, 404-408.
- Hamilton, D. A., Driscoll, I., Sutherland, R. J. (2002). Human place learning in a virtual Morris water task: Some important constraints on the flexibility of place navigation. *Behavioural Brain Research*, 129, 159-179.
- Hebb, D. O., & Williams, K. A. (1946). A method of rating animal intelligence. *Journal of General Psychology*, 34, 59-65.
- Hölscher, C., Schnee, A., Dahmen, H., Setia, I., & Mallot, H. A. (2005). Rats are able to navigate in virtual environments. *Journal of Experimental Biology* 208, 561-569.
- Jacobs, W. J., Laurance, H. E., & Thomas, K. G. F. (1997). Place learning in virtual space I: acquisition, overshadowing, and transfer. *Learning and Motivation*, 28, 521-541.
- Jacobs, W. J., Thomas, K. G. F., Laurance, H. E., & Nadel, L. (1998). Place learning in virtual space II: Topographical relations as one dimension of stimulus control. *Learning and Motivation*, 29, 288-308.
- Kállai, J., Kőczán, G., Szabó, I., Molnár, P., & Varga, J. (1995). An experimental study to operationally define and measure spatial orientation in panic agoraphobia subjects, generalized anxiety and healthy control groups. *Behavioural and Cognitive Psychology*, 23, 145-152.
- Kanit, L., Taskiran D., Furedy, J. J., Kulai, B., McDonald, R., Pogan, S. (1998). Nicotine interacts with sex in affecting rat choice between "lookout" and "navigational" cognitive styles in the Morris water maze place learning task. *Brain Research Bulletin*, 46, 441-445.
- Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationships to spatial ability and spatial anxiety. *Sex Roles*, 30, 765-779.
- Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, 12, 239-260.
- Nadel, L., Thomas, K. G. F., Laurance, H. E., Skelton, R., Tal, T., and Jacobs, W. J. (1998). Human Place Learning in a Computer Generated Arena. In: (Eds). C. Freksa, C. Habel, K. Wender, Spatial Cognition. An Interdisciplinary Approach to Representing and Processing Spatial Knowledge, Springer, Berlin.
- O'Keefe, J., & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*, Oxford: Clarendon Press.
- Overman, W. H., Pate, B. J., Moore, K., & Peuster, A. (1996). Ontogeny of place learning in children as measured in the radial arm maze, Morris search task, and open field task. *Behavioral Neuroscience*, 110, 1205-1228.
- Perrot-Sinal, T. S., Kostenuik, M. A., Ossenkopp, K. P., & Kavaliers, M. (1996). Sex differences in performance in the Morris water maze and the effects of initial nonstationary hidden platform training. *Behavioral Neuroscience*, 110, 1309-1320.
- Roof, R. L. (1993). Neonatal exogenous testosterone modifies sex differences in radial arm and Morris water maze performance in prepubescent and adult rats. *Behavioural Brain Research*, 53, 1-10.
- Sandstrom, N.J., Kaufman, J., & Huettel, S. A. (1998). Differential cue use by males and females 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, 403-10.
- Shore, D. I., Stanford, L., Klein, R. M., & Brown, R. E. (2001). Of mice and men: Virtual Hebb-Williams mazes permit comparison of spatial learning across species. *Cognitive, Affective & Behavioral Neuroscience*, 1, 83-89.
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Eds. J. H. Barkow, L. Comides, & J. Tooby. Oxford University Press: Oxford.
- Toga, A. W., & Thompson, P. M. (2003). Mapping Brain Asymmetry. *Nature Reviews: Neuroscience*, 4, 37-48.
- Tapley, S. M., & Briden, M. P. (1977). An investigation of sex differences in spatial ability: mental rotation of three-dimensional objects. *Canadian Journal of Psychology*, 31, 122-130.
- Tottenham, L. S., Saucier, D., Elias, L., Gutwin, C. (2003). Female advantage for spatial location memory in both static and dynamic environments.
- Waller, D., Knapp, D., & Hunt, E. (2001). Spatial representations of virtual mazes: The role of visual fidelity and individual differences. *Human Factors*, 43, 147 - 158.
- Ward, S. L., Newcome, N., & Overton, W. F. (1986). Turn left at the church, or three miles north: A study of direction giving and sex differences. *Environment and Behavior*, 18, 192-266.
- Williams, C. L., & Meck, W. H. (1991). The organizational effects of gonadal steroids on sexually dimorphic spatial ability. *Psychoneuroendocrinology*, 16, 155-176.

### Acknowledgements

We wish to thank Ute Kreitz, Jens Kunkemueller, Jiayong Liu, Frank Schumann, Saskia Nagel, Nicolas Neubauer, Oleksandr Kolomiyets and Stan James for help with data collection and useful discussions. Furthermore we would like to thank Derek A. Hamilton for his ideas regarding the experiment.