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Chapter 15

QUALITATIVE SEX DIFFERENCES IN SPATIAL LEARNING

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ABSTRACT

A sex or gender difference in spatial learning is a controversial topic with uncertain results. A selection of studies [25, 26, 37, 41] in the standard rat and also in humans is reviewed. These studies show different strategies used by the two sexes to solve navigation tasks, as well as a marked distinction between what the participants learn and what they prefer (i.e., learning vs. performance), which reveals new insights in this literature. The measure used being a critical factor. Both the origins of these differences and some possible implications are discussed.

INTRODUCTION

There is evidence that male and female rats can use different types of spatial cues when navigating. Female rats tend to focus on landmarks (which are often near to a goal objects), while males prefer geometry, as a source of information. The same claim is consistent in the human literature (for reviews see [1, 2, 3]). These results are consistent with the predictions of the range size hypothesis described in several species of mammals. The crucial idea is that sex differences in task performance have arisen from a process of natural selection: a difference in range expansion between males and females is associated with a difference in spatial cognition [4]. In people that difference arises largely because men hunted and women gathered; in other animals it arises from the fact of polygyny (see Section 7 for more details).

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A Background Story: The Proposal by Cheng (1986)

Cheng [5] (see also Gallistel [6]) was the first author to present evidence that rats can use geometric information to locate a hidden goal. He trained male rats in a rectangular arena, where the two short walls of the box and one of the long walls were black, while the other long wall was white. In addition, distinctive visual patterns were placed in each of the box's corners (as well as other non-geometric cues). Food was buried in one corner of the box, and the rats had to search for it. Although rats learned to search in the correct location for the food, they made frequent rotational errors searching in the corner diagonally across from the one where the food was hidden.

The only characteristic that the target corner and the corner diagonal from it shared in common was having one long wall to the left and one short wall to the right, which implies that the information provided by the non-geometric sources of information to find the food location did not seem to be important. Cheng concluded that the rats used the geometric framework of the box itself. Similar results have been found not only with rats but also with other species (for reviews, see [7, 8]).

According to Cheng and Gallistel, learning about geometric information (i.e., like the metric relations of distances and angles between a target place and the shape of an apparatus) occurs in a specialized module, which is impenetrable to non-geometric information (although see [9]). Features such as landmarks are considered to be related to this featureless metric frame by means of address labels [5]. If this is the case, an important question to answer is: Does shape or geometry learning consist of the conditioning of approach responses to a goal that is defined in terms of the spatial relationship that it maintains regarding a particular geometry, like the shape of an apparatus (i.e., an associative point of view) or alternatively, is this a kind of learning different and independent of the traditional ways of learning (like classical and instrumental conditioning), as Cheng claims? In other words, is knowledge about shape or geometry location acquired in the same way as knowledge about other relations between events? (for a related question see [10]).

Two main predictions should be considered in this controversial topic. If geometry and landmark learning represent quite independent modes of solution [5, 6], one might not expect to see any interaction or competition between them. Consequently, no evidence of cue competition effects (like blocking and overshadowing) should be found between geometric and non-geometric information. However, Miller and Shettleworth [11] have claimed that changes in the associative properties of the geometric cues are governed by the same principles that apply to more traditional stimuli. Consequently, one might expect to see interactions or competition between geometric and non-geometric information. Although the evidence is not yet clear, the more common outcome is that landmark learning does not interfere with, overshadow, or block the learning of geometry (in favor of this result with rats see [12, 13, 14, 15,]; with humans [16]. For the opposite result with rats see [17, 18, 19]; with humans [20, 21]. But neither Cheng nor any of the studies mentioned in this paragraph examined sex differences when using rats. What would have happened if they had also considered female rats?

Shape and Landmark Cues: Differential Preference or Salience for Males and Females

When solving maze tasks, it has been suggested [22, 23] that male rodents tend to use geometric information, such as the shape and dimension of the experimental room, while females rely more on landmarks, such as specific objects near the maze. In the study by Williams, Barnett, and Meck [22], with rats and a radial-maze, after acquisition, two manipulations were conducted. The two manipulations were alteration of the geometry of the testing room and rearrangement of the landmark cues. The results revealed that alteration of the geometry of the testing room clearly affected normal males (as well as females treated with estradiol benzoate), but these changes did not affect normal females (or neonatal castrated males). Normal male rat performance was not impaired when landmark cues were rearranged, while normal female performance was impaired (for a similar result in a circular pool, see [24]).

One problem with the study by Williams et al. [22] is the lack of description of the experimental room. Theoretically, the room's geometry determined the males' superior performance when learning the geometric relations between food caches and the overall shape of the environment (i.e., global shape learning). However, a salient and distant landmark (like a bright light or a window) could have been present in the room, guiding the males' performance so that geometry would not be implicated. The aim of the study by Rodríguez, Torres, Mackintosh, and Chamizo [25], with rats and a pool, was to evaluate whether there are qualitative sex differences in the acquisition of a spatial task when two sources of information (i.e., the geometry of the apparatus and one landmark) simultaneously indicate the goal's position (i.e., a hidden platform) by means of a simple but highly controlled situation. In the two experiments of the study, circular black curtains surrounded the pool, half of which could be triangular. Moreover, five pretraining trials were conducted in the circular pool without the landmark but with the platform present. During the training phase, rats were given eight trials per day over five days (a total of 40 trials). In Experiment 1, at the point of the triangular part of the pool, one salient landmark, a beach ball hanging from a false black ceiling, was presented so that the two sources of information (i.e., the landmark and the shape) indicated the position of the hidden platform. The rats could learn that the hidden platform was at a certain distance from both the landmark and the point of the triangle with a straight wall both to the right and to the left. No other room cues could provide additional information to find the platform. The shape of the pool and the landmark were rotated from trial to trial, and the position of the platform also changed for each trial, thus preserving a constant relation between the platform, the shape, and the landmark. All rats improved their performance as the experiment progressed, and spatial learning took place equally in males and in females. Then, on a test trial without the platform, the two sources of information (i.e., the landmark and the shape) were put into conflict by presenting them 180° apart. The amount of time that the rats searched in two different areas (one in front of the landmark, although at the incorrect shape, and the other in front of the triangular shape, although without the landmark) was recorded. Following Williams et al. [22] and Roof and Stein [24], the test trial prediction was that males would spend more time searching for the platform in the shape area than in the landmark area, while the reverse was predicted for the females. The results revealed a clear preference in females for the landmark area over the shape area, while males' performance did not show any clear preference between the two areas. In addition, males spent more time searching for the platform in the shape area than females, while males and females did not differ in the landmark area. In Experiment 1, it was also examined the possibility that the estrous cycle of females could have had an influence on their performance; it did not.

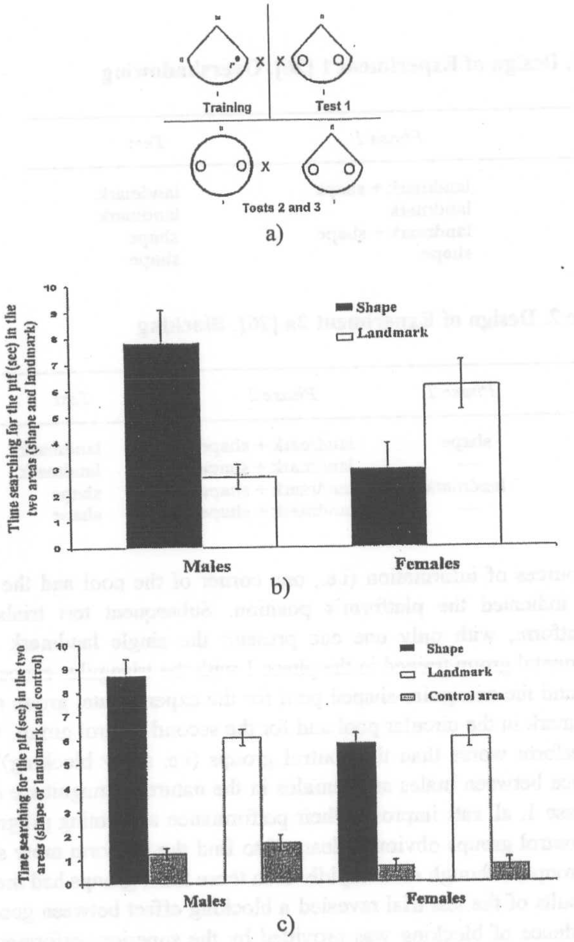

Figure 1. Experiment 2 [25]: A schematic representation of the pool and the position of the landmark, X, as well as the hidden platform (P) A (Top): Left panel, for acquisition; right panel, for test 1. (Bottom): for tests 2 and 3. B: Mean time spent in the two recording areas (shape and landmark) by the subjects during test trial 1. C: Mean time spent in the two recording areas (shape or landmark and control) by the subjects during test trials 2 and 3 (shape and landmark, respectively). Error bars denote standard error of means.

Would the males have shown a significant preference for the shape with a new set of "stimuli" (i.e., shape and landmark)?

The aim of Experiment 2 [25] was to test such a possibility (see Figure 1). The landmark used was a small ninepin instead of the big beach ball as in Experiment 1. The solution based on the shape of the pool was such that now the target point had a straight wall to the left and a circular wall to the right instead of two straight walls on both sides as in Experiment 1. Therefore, the rats could learn that the hidden platform was at a certain distance from both the new landmark and the new shape. All rats improved their performance as the experiment progressed, and spatial learning took place equally in males and in females. After training, in a test trial without the platform, the two sources of information (i.e., the landmark and the shape) were put into conflict by presenting them 180º apart. A second purpose of this experiment was to measure what males and females had learned about the two sources of information independently of their preferences. For this purpose, two additional test trials (tests 2 and 3) were also conducted and counterbalanced. In one trial, the landmark was present in the circular pool (i.e., in the absence of the triangular shape), and in the other trial, the triangular shape was present in the absence of the landmark. According to Williams et al. [22], male rats are predisposed to attend to a single aspect of the environment (global shape), while female rats use multiple environmental cues (global shape and landmarks). The results of the preference test (i.e., test trial 1) revealed that while female rats spent more time in the landmark area than in the shape area, the reverse was true for males. These results, as well as Experiment 1, clearly agreed with the claim that males and females can use different types of spatial information when solving maze tasks [22, 24]. In addition, males spent more time searching for the platform in the shape area than females, while females spent more time searching for the platform in the landmark area than males.

Experiment 2 [25] (i.e., tests 2 and 3) also revealed that males and females had learned to find the platform using the two sources of information. When the landmark and the shape were tested one by one, the results showed that males had learned about the landmark (i.e., the less preferred source of information) and females had learned about the shape of the pool (i.e., the less preferred source of information). These last results seem to contradict the claim of Williams et al. [22], suggesting that while male rats are predisposed to attend to a single aspect of the environment (global shape), female rats use multiple environmental cues (global shape and landmarks). According to these authors, when multiple sources of information are presented together, male rats learn the geometric relations between food caches and the overall shape of the environment such that those sources of information overshadow all others and prevent them from becoming associated with the food caches. In contrast, female rats appear to process and use both geometric and non-geometric sources of information when they are presented together.

The results of tests 2 and 3 of Experiment 2 [25] show that males and females process and use both geometric and non-geometric sources of information when they are presented together. It is true that the different measures of the three test trials gave quite different results, showing a clear distinction between learning and performance. On test trial 1, female rats did not seem to know much about shape, while males did not seem to know much about the landmark. Then, test trials 2 and 3 clearly revealed that such was not the case. Using a variety of tests was crucial to know what the rats had learned. The present experiments also show a clear male advantage on geometry or shape learning.

Overshadowing and Blocking between Shape and Landmark Learning: The Importance of Sex Differences

If male and female rats rely on landmark and geometry cues to different degrees, then a natural progression of the Rodríguez et al. study [25] was to see whether this would affect the extent to which competition could be seen between these cues. That was the aim of the study by Rodríguez, Chamizo, and Mackintosh [26]. Experiment 1 was designed to check for overshadowing. The term overshadowing refers to the finding that the presence of a second relevant cue will cause animals to learn less about a first than they would have done if trained on the first cue in isolation (Pavlov [27]). Because overshadowing depends on the relative salience of both overshadowing and overshadowed stimuli (Mackintosh [28]), one might reasonably expect that if overshadowing is observed, it would be asymmetrical, with shape learning overshadowing landmark learning more than landmark learning overshadowing shape learning in males (as McGregor, Horne, Esber, and Pearce [13] have already shown), and precisely the opposite effect in females, where landmark learning should overshadow shape learning to a greater degree than shape learning should overshadow landmark learning. Experiment 1 [26], with four groups of rats, had a classical overshadowing design (see Table 1) in which two experimental groups (Compound cue groups) were trained in a compound cue learning task (i.e., learning was with the single landmark and one corner of the pool both predicting the platform's position), while two corresponding control groups (Single cue groups) were trained with a single cue. For one control group the position of the hidden platform was predicted by a single landmark presented in a circular pool, while for the other control group it was predicted by one corner of the triangular-shaped pool in the absence of the landmark. A subsequent test trial was conducted, without the platform, in the presence of a single cue. For both one experimental group and the control group trained with the single landmark, the tested cue was the single landmark; and the other experimental group and the control group trained in the triangular-shaped pool, were tested in the triangular-shaped pool with no landmark. Would the experimental groups perform worse than the control groups and would there be any sex difference in any such overshadowing effect? Although all rats improved their performance as training progressed, on day 1 the rats learning with the two cues, the compound groups (Compound-S and Compound-L), were faster than the rats learning with a single cue (Landmark and Shape); moreover, males were faster than females. The results of the test trial revealed an overshadowing effect between geometry and landmark learning. Evidence of overshadowing was provided by the superior performance of single groups by comparison with compound groups. More importantly, overshadowing was asymmetrical, both in males and in females. Specifically, in males, shape learning overshadowed landmark learning, but not vice-versa; while in females, landmark learning overshadowed shape learning, but not vice-versa. These effects were not influenced by the females' estrus cycle.

Experiment 2 of the study by Rodríguez et al. [26] (2a and 2b) examined whether prior training with either geometry or landmark cues would block learning about the other cue when, in a second phase of the experiment, both sources of information simultaneously signalled the location of the platform (see Table 2). Traditionally, blocking is observed when prior establishment of one element of a compound cue as a signal for reinforcement reduces or blocks the amount learned about the other cue (Kamin, [29]). Experiment 2a had a classical blocking design in which two experimental groups were trained in phase 1 with a single cue. For one group the position of the hidden platform was predicted by a single landmark presented in a circular pool, while for the other group it was predicted by one corner of a triangular-shaped pool in the absence of the landmark. In the second phase of the experiment, the two experimental groups and two new groups, control groups, were trained in a compound cue learning task.

Table 1. Design of Experiment 1 [26]. Overshadowing

Group	*Phase 1*	*Test*
Compound-L	landmark + shape	landmark
Landmark	landmark	landmark
Compound-S	landmark + shape	shape
Shape	shape	shape

Table 2. Design of Experiment 2a [26]. Blocking

Group	*Phase 1*	*Phase 2*	*Test*
Experimental-L	shape	landmark + shape	landmark
Control-L	---	landmark + shape	landmark
Experimental-S	landmark	landmark + shape	shape
Control-S	---	landmark + shape	shape

For all animals both sources of information (i.e., one corner of the pool and the single landmark) simultaneously indicated the platform's position. Subsequent test trials were conducted, without the platform, with only one cue present: the single landmark in the circular pool for the experimental group trained in the phase 1 with the triangular-shaped pool and for one control group; and the triangular-shaped pool for the experimental group trained in the phase 1 with the landmark in the circular pool and for the second control group. Would the experimental groups perform worse than the control groups (i.e. show blocking)? And would there be any difference between males and females in the nature or magnitude of any such blocking effect? In phase 1, all rats improved their performance as training progressed. Then, in phase 2, the two control groups obviously learned to find the platform more slowly than the two experimental groups, although more rapidly than these latter groups had made on days 1-3 in phase 1. The results of the test trial revealed a blocking effect between geometry and landmark learning. Evidence of blocking was provided by the superior performance of control groups by comparison with the pretrained groups. Most importantly, it was also found that the variable sex played a significant role in this effect because blocking was asymmetrical. Specifically, in males, shape learning blocked landmark learning, but not vice-versa; while a reciprocal blocking effect was obtained in females (shape learning blocked landmark learning and landmark learning blocked shape learning). These effects were not influenced by the females' estrus cycle.

Then, in Experiment 2b, only with male rats, it was attempted to increase the chance that landmark learning could block shape learning by giving extended initial training with the landmark. (i.e., 80 trials instead of 40 trials, as in Experiment 2a). The experiment was conducted with two groups of rats only. For one group the position of the hidden platform was initially predicted by the single landmark presented in the circular pool. In the second phase of the experiment, the single cue group and one new group were both trained in a compound cue learning task; for all animals both sources of information (i.e., the single landmark and one corner of the triangular-shaped pool) simultaneously indicated the platform's position. Subsequent test trials were conducted, without the platform, with only the triangular-shaped pool present (i.e., in the absence of the landmark). After such an extended single training with the landmark, on the test trial single cue rats showed a worse performance than the rats without the single training (i.e., landmark learning could block shape learning).

The results of the study by Rodríguez et al. [26] are inconsistent with the suggestion that learning about the shape of an environment takes place in a special module that is impenetrable to non-geometric information [5, 6]. Two main conclusions can be drawn from this study [26]. The first is that cue competition effects such as overshadowing and blocking can be found between shape learning and landmark learning; the second is that the competition between shape learning and landmark learning is influenced by the sex of the subjects, implying that the outcome of such experiments depends on the relative salience of landmark and shape information. The clear general implication of the overshadowing and blocking experiments that we have just reviewed is that the mechanism responsible for shape or geometry learning seems to be clearly associative, since it interacts with landmark learning in the same way as the conditioning of a light interacts with the conditioning of a tone [29]. A second straightforward implication of this study (see also Rodríguez et al. [25]) is that the model proposed by Miller and Shettleworth [11] should incorporate a flexible term to explain sex differences.

Does the Estrus Cycle Influence Hippocampal-Dependent Navigation Tasks in Rats?

Many studies have shown a profound impairment on a variety of spatial tasks after lesions in the hippocampus [30, 31, 32]. The study by Morris, Garrud, Rawlins, and O'Keefe [30] revealed that hippocampal lesion rats showed a profound impairment in a place navigation task (i.e., with a circular pool and a hidden platform); and this effect disappeared when a visible platform was used. Both control rats (i.e., sham operated) and rats with a different lesion (i.e., a superficial cortical lesion) learned to escape rapidly from the water in the two kinds of tasks (i.e., with the hidden platform and with the visible platform). Morris et al. [30] concluded that the performance of the task in which the rats had to learn about the location of a hidden platform in relation to distal cues is hippocampal-dependent but not the other kind of task in which the platform is visible, thus supporting the idea that the ability of navigation, which is essential for the survival of animals, depends critically on the integrity of this limbic structure.

Spatial tasks have been considered hormonally dependent (for a demonstration in the radial maze, see Williams el al. [22]). The hormonal and reproductive cycle of female rats, called estrus cycle, lasts about four-five days and consists of four distinct phases: proestrus, estrus, metaestrus and diestrus. These different phases of the estrus cycle correlate with different levels of the sex hormone estradiol circulating. According to Woolley and McEwen [33], during the phase of the estrus cycle in which occurs the peak level of estradiol (i.e., the proestrus phase), the hippocampus shows an increase in synaptic density in the apical cells of the pyramidal cells of the CA1 area of up to 30%. These changes have been suggested to affect spatial performance. But the literature is inconsistent in the direction of these changes (for three different results see [34, 35, 36]). For example, Warren and Juraska [34] trained two groups of female rats (one with high hormonal levels and the other with low hormonal levels) in a similar place navigation task like the one used by Morris et al. [30]. The results of a test trial, without the platform, at the end of acquisition showed that female rats with low hormonal levels outperformed females with high hormonal levels. However, Healy, Braham, and Braithwaite [36], who trained and tested two groups of female rats (one with high hormonal levels and the other with low hormonal levels) but in a different way to Warren and Juraska [34], also found differences in the performance of the two groups, but exactly in the opposite direction: unexpectedly, females with high hormonal levels performed the task significantly better than females with low hormonal levels. Finally, Berry, McMahan, and Gallagher [35] did not find any effect when they trained and tested two groups of female rats also differing in their hormonal levels, neither in the acquisition nor in a final test trial. How could this be? Of particular note, these studies have used different procedures and measures.

The main aim of the next study reviewed (Rodríguez, Aguilar, and Chamizo [37]) was to conduct experiments in a highly controlled situation, using the Morris pool, to specifically see whether landmark learning is affected by the female's estrus cycle. Circular black curtains surrounded the pool, with two external three-dimensional landmarks inside this enclosure, so that no other room cues (like the shape of the room) could provide additional information to find the platform. The landmarks were hung from a false ceiling and rotated from trial to trial with the platform, thus preserving a constant relation between the platform and the landmarks (i.e., eliminating olfactory and auditory cues outside the curtains). Four starting points were used. During acquisition, the rats were required to escape from the pool by swimming to an invisible platform that was located in the same place relative to one configuration formed by the two landmarks which were placed relatively far and equidistant from the hidden platform (D and A in Figure 2). After training the rats were tested, without the platform, in the presence of the landmarks, with the pool surface spatially divided into four quadrants: where the platform should have been, right to it, left to it and opposite to it. The time the rats spent in all the quadrants was measured.

The test trials revealed a preference for searching in the correct quadrant of the pool. In Experiment 1 such a test performance was identical in two groups of females, one tested with high hormonal levels (i.e., in the proestrus phase) and the second one tested with low hormonal levels (i.e., either in the estrus, metaestrus or diestrus phase); in addition, these two groups differed from a third group of male rats (i.e., males had a better performance than females). Experiment 2 replicated the females' previous results with a better procedure. The experiment compared the performance of two groups of female rats which were both trained and tested always in the same estrus phase (i.e., every four days only), one group in the proestrus phase, and the second group in the estrus phase. The implication of these results is that the estrus cycle seems to have little impact on the performance of female rats when landmark learning in a navigation task. The previous sex difference found in Experiment 1 disappears (unpublished results) if the two landmarks are trained and tested relatively near from the hidden platform position (B and C in Figure 2).

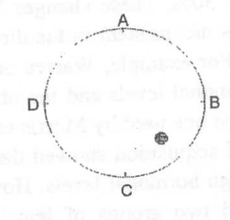

Figure 2. A schematic representation of a pool and the position of four landmarks (A, B, C, and D), as well as the hidden platform (*black circle inside the pool*).

Relatively Near vs. Relatively Far Landmarks: Human Participants

A model of hippocampal function proposed by Jacobs and Schenk [38] predicts a dissociation between proximal and distal cues between males and females. Some authors (i.e., Chai and Jacobs [39], Barkley and Gabriel [40] have claimed that their work provide support for this model. Following Jacobs and Schenk [38] sex differences arise from preferences for cues that provide either direction (i.e., far cues, most preferred by males) or position (i.e., near cues, most preferred by females). Directional cues are distant objects that appear to remain stationary with respect to each other as an organism wanders about a specific terrain or virtual arena (e.g., stars and mountains). This kind of information is difficult to use to pinpoint a location. In contrast, positional cues are close or local objects that are often used to pinpoint a location.

Chai and Jacobs [39] used virtual navigation to explore two types of landscapes. Their participants were trained to collect a visible target (e.g., a blue spike-like crystal) that was located either in a landscape containing only directional (i.e., graded, gradient) cues or positional (i.e., pinpoint) cues (Experiments 1 and 2, respectively). After training, the participants underwent test trials without the crystal. In these trials, they were told to go back to the crystal's location from the previous phase and stay there until the end of the trial. At the conclusion of the trial, the researchers calculated the distance between the participant's position and the target position. The test results showed that the men got closer to the target position under both conditions but that the men's advantage was larger when the directional cues were available. The participants' self-reported information corroborated these results. Chai and Jacobs suggested that an often reported male advantage in the presence of distant objects and geometric cues is derived from these objects' functions as directional cues, as males rely more heavily on directional cues than females.

If the results reported by Chai and Jacobs [39], represent a more general manifestation of the response patterns from men and women to proximal- and distal-space visual objects, then similar results should also be found with respect to other tasks. The purpose of the study by Chamizo, Artigas, Sansa and Banterla [41] was to determine whether sex differences in a virtual navigation task can be observed in the absence of directional cues. Specifically, four pinpoint landmarks (i.e., proximal cues) were used. If the aforementioned differences exist, then other factors in addition to directional cues may underlie the sex differences that often accompany spatial learning tasks. The aim of Experiment 1 was to study sex differences that occur when the participants use virtual navigation while learning with pinpoint landmarks: two relatively near and two relatively distant landmarks in relation to a hidden platform. To that end, there were four landmarks present at each training trial (i.e., A, B, C, and D in Figure 2), arranged symmetrically around the circumference of the pool, and two groups of participants (i.e., men and women). At the end of the training (24 trials in total), one test trial was administered in the presence of either one or two of the distant landmarks, without the platform. The amount of time that the students had spent in the platform quadrant was recorded. All participants improved their performance as the trials progressed, and spatial learning took place equally in men and in women. When the two landmarks located relatively distant from the platform during training were tested both men and women showed a preference for the platform quadrant, indicating that these landmarks were sufficient for determining the location of the platform. Thus, the landmarks relatively near the platform did not prevent learning about the landmarks relatively distant away from it. However, when only a single distant landmark was present, neither group showed a preference for the platform quadrant in the test. A relatively distant landmark could not unambiguously define the location of the platform. This pattern of results clearly indicates configural learning. Most importantly, Experiment 1 found a clear gender difference when the two distant landmarks were simultaneously present in the test. In this case, the men outperformed the women when searching for the platform.

Experiment 2 (Chamizo et al. [41]) replicated the previous results by showing that the men outperformed the women at the test trial when both of the distant landmarks were present. However, when the distant landmarks were presented individually instead of together, this difference disappeared, and the performance clearly declined to chance level. Experiment 2 also revealed that no sex differences existed when the landmarks near the platform were present. In the near conditions, the participants' performances in the platform quadrant were the best and always above the level of chance. Thus, proximity to the goal was the main determinant of landmark control for all the participants. This pattern of data favors elemental learning, a type of learning which is based on individual landmarks instead of multiple landmarks (i.e., configural learning).

Overall, the results of the study by Chamizo et al. [41] confirm, if only partially, the male advantage shown in previous studies on virtual navigation [42, 39, 43, 44, 45, 46]. Moreover, Chai and Jacobs's [39] study showed with pinpoint cues that the men outperform the women. This result was replicated only with the relatively distant landmarks, not the relatively near landmarks in which men and women did not differ. Of particular note, the two studies have used different procedures and measures. The experiments by Chamizo et al. [41] do show a clear male advantage when searching is based on relatively distant landmarks in the absence of directional cues, which clearly suggests that other factors, in addition to making use of directional cues, can underlie the sex differences in spatial learning processes.

Sex Differences in Spatial Cognition: One Biological Explanation

As Mackintosh suggests [2 □see also 47], there can be little doubt that males and females do differ in particular cognitive skills and that the precise nature of these differences is still an open question; for example, a test battery that emphasizes spatial and mathematical items will favor males, but one that emphasizes some aspects of language, perceptual speed, and memory will favor females. An important question to answer is can these differences be changed with experience? Recent research shows that this is the case [48].

Previous authors have claimed (Coluccia and Louse [3]) that sex differences tend to appear only when the task is difficult. In other words, spatial tasks high in cognitive demands are accompanied by sex differences, whereas spatial tasks low in cognitive demands are not. The results by Chamizo et al. [41] support this suggestion. The tests with the near landmarks would count as easy tasks, but the test with the two distant landmarks would be considered difficult, as the test with only one distant landmark is the most difficult overall. Both the human and the rat data are consistent with the hypothesis that a sex difference in spatial cognition arises only when there is a difference between the sexes in range size [4,2]. When males occupy a larger home range than females, they also show evidence of superior spatial ability. In most monogamous species, males and females share the same territory. That is not the case in polygynous or promiscuous species (polygynous males mate with more than one female in a single breeding season, and therefore have larger ranges). In ancient times, men hunted while women gathered [49]. Ancient hunting, like persistence hunting, implies exhausting the pray over a long distance and then killing it as the animal collapses. Later ways of hunting, using missile weapons, also implied hunters covering long distances. But both, humans and rodents, have the same consequence –a difference in range size, which is the more proximal cause of the difference in spatial cognition (although see [50] for a different account).

In rodents, the data that support the range size hypothesis tend to be consistent with the fertility and parental care hypothesis, which states that female reproductive success, is enhanced by reduced mobility during reproductive periods [for a review see 4].

IN CONCLUSION: IMPORTANT IMPLICATIONS

When scholars have made the effort to analyse the variable sex or gender from a qualitative point of view, sometimes important and unexpected results have been found. For example, Nardi, Newcombe, and Shipley [51] have shown that terrain slope can be used as a cue to find a goal. When that is the case, women rely less than men on slope cues, preferring to solve the task using other strategies, even if they are less effective. The causes of this sex difference are still unknown.

For many years in our western culture it has been assumed that men and women do not differ in cognitive skills or abilities. To question this assumption was considered 'politically incorrect'. But such an idea is an error that could have important practical consequences. For example, the perceptual strategies which are responsible for visuospatial disorientation in several mental illnesses could be different in the two genders. Consequently, an implication would be to consider alternative treatment strategies and behavioral therapies for men than for women when dealing with disorientation problems in old age and in several mental illnesses. In line with these arguments, it has been claimed (Beinhoff, Tumani, Brettschneider, Bittner, and Riepe [52]) that gender-specificity of neuropsychological performance needs to be accounted for in clinical diagnosis of Alzheimer's disease. According to Beinhoff et al. [52], gender is a factor explaining variance in the pattern of cognitive decline where, in relation to visuospatial memory, men seem to show an advantage. In conclusion, basic research is certainly needed to clarify all these challenging issues.

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