S

Spatial Orientation

Victoria D. Chamizo[1] and Teresa Rodrigo[2]
[1]Department of Cognition, Development and Educational Psychology, Institute of Neurosciences, Universitat de Barcelona, Barcelona, Spain
[2]CCiTUB, Animal Research Unit of Psychology, Universitat de Barcelona, Barcelona, Spain

Synonyms

Navigation; Spatial abilities; Spatial learning and memory; Visuospatial memory

Definition

Spatial orientation refers to the ability of organisms to navigate. It is essential for their survival.

Background

While navigating, we become familiar with an environment and acquire knowledge about it, thereby extracting information from it and storing this information in our memory so that we can recall it later for a variety of purposes (Ekstrom et al. 2018). Examples concerning rodents and humans will be presented since there is an important parallelism between them when dealing with spatial tasks. However, most of the examples will focus on how males and females differ when solving these tasks – on something that has recently been referred to as "qualitative" sex differences – thus counteracting the unjustified practice of ignoring females for so many years in psychological and biomedical research (for a review see Beery and Zucker 2011). To understand the sexually dimorphic spatial abilities between males and females – which are so influenced by sex hormones – a specific explanation, the range size hypothesis, will be discussed. For different reasons, this hypothesis applies to both rodents and humans. A brief description of the role of the hippocampus while navigating and of the evolutionary origins of the human species is also presented. For navigational strategies and mechanisms used by rats see "► Rodentia Navigation" in the present issue (for the same in humans, see Ekstrom et al. 2018).

Although historically it has been assumed that sex differences do not exist or are not important beyond the reproductive system, this view has changed drastically in the last two decades. As it is widely recognized today a critical problem of ignoring females for so long has been the inability to understand the potential magnitude of the effect of sex on the outcome being measured, with the consequence of important problems in the reproducibility of basic research (Cahill 2006). No doubt research conclusions are needed that can be applicable to all. This requires sex as a biological variable "from womb to tomb."

J. Vonk, T. K. Shackelford (eds.), *Encyclopedia of Animal Cognition and Behavior*,
https://doi.org/10.1007/978-3-319-47829-6_1416-1

Sex Differences While Solving Spatial Problems

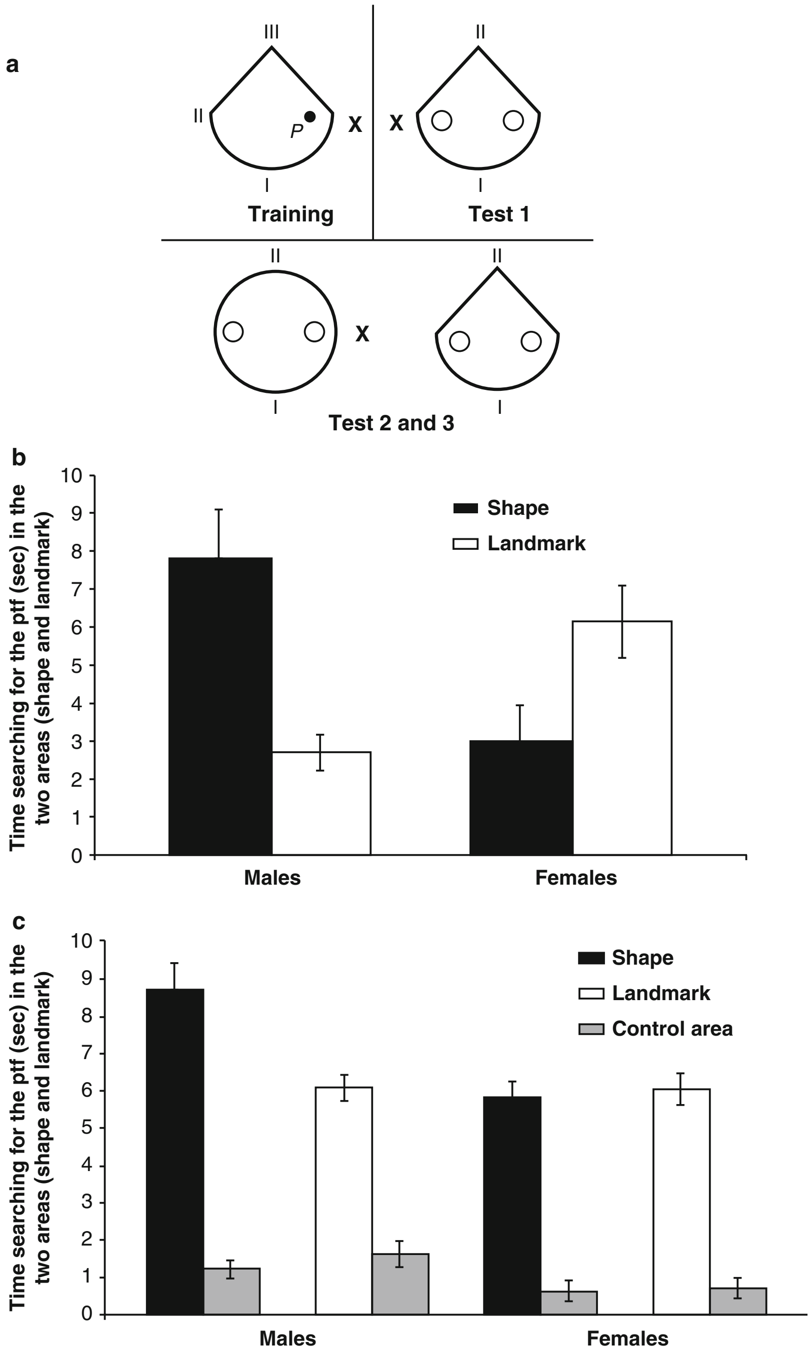
Experiments on spatial learning and memory have shown that males and females of many mammalian species, including humans, often differ in their use of cues for spatial navigation (for reviews see Halpern 2012; Kimura 2000; Mackintosh 2011). It is not just that males tend to learn to solve a spatial problem faster than females, but that males and females can use different strategies to solve the same problem (i.e., this is what is considered a "qualitative" sex difference). In both rats and humans, males seem more likely to rely on geometrical information to reach a goal, while females are more likely to use landmarks.

Williams et al. (1990) showed that female rats have a clear tendency to use landmarks, such as specific objects and pictures on the walls, when solving spatial tasks, while male rats prefer geometric cues or sources of information, such as the shape of the testing room. Moreover Williams et al. found that if there were no landmarks available, the females used the geometric cues; however, males preferred to use the geometric cues, practically ignoring the landmarks. A similar difference in the preferred mode of solution has been obtained with human participants, while using different navigational tasks (Sandstrom et al. 1998; Ward et al. 1986). For example, Ward et al. (1986) study how college students, males and females, give directions from maps – either perceptually available or committed to memory. Different aspects of direction giving were recorded. The results clearly revealed that when giving directions, women tend to use landmarks as points of reference, while men tend to use distance or cardinal directions (like North, South, East, and West). In the study by Sandstrom et al. (1998), male and female participants navigated through a virtual water maze where both landmarks and room geometry were available as distal cues. Manipulation of environmental characteristics revealed that females relied predominantly on landmark information, while males more readily used both landmark and geometric information.

Due to the important parallelisms between rats and people, recent research by Rodríguez et al. (2010) explored these "qualitative" sex differences in rats. The aim of the study by Rodríguez et al. (2010) was to evaluate whether there are differences in the way that males and females solve a simple but highly controlled spatial task in a modified Morris pool. In their Experiment 2, rats were trained in an unusual triangular-shaped pool to find a hidden platform, whose location was defined in terms of two sources of information: one landmark next to the platform, outside the pool, and one particular corner of the pool (see Fig. 1a, top-left). Three subsequent test trials without the platform were conducted. The first test trial pitted the two sources of information – landmark versus pool-shape – against one another (i.e., a preference test – see Fig. 1a, top-right). The results revealed that females spent more time searching the platform in an area of the pool next to the landmark, while males spent more time in the corner of the pool where the platform had originally been located (see Fig. 1b). In the following two tests the two sources of information were presented individually (i.e., learning tests – see Fig. 1a, bottom) and the results showed that both sexes had learned about both cues: males performed significantly better on the shape than the landmark test, while females performed equally well on both. In addition, males spent more time searching for the platform in the target area on the shape test than females (see Fig. 1c). In conclusion, despite having clearly differentiated preferences, males and females process and can use both geometric and nongeometric sources of information when they were presented together in the acquisition phase. Thus, this study shows a clear distinction between learning and performance, which was possible to gauge due to the different measures used in the three test trials.

A subsequent study by Rodríguez et al. (2011), where cue competition designs were used, confirmed the previous conclusion that shape (i.e., geometry) is clearly more salient for males, and landmarks somewhat more salient for females. Employing the same apparatus and general procedure as Rodríguez et al. (2010), this new study

Spatial Orientation, Fig. 1 Experiment 2: 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 (right, testing the shape cue; left, testing the landmark cue). (**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. (After Rodríguez et al. 2010 – with permission)



showed an asymmetrical overshadowing effect in both sexes. In males, shape overshadowed landmark learning, but landmark learning did not overshadow learning about shape; while in females, landmark learning overshadowed learning about shape, but shape learning did not overshadow landmark learning. It was the more discriminable, salient, or preferred source of information (shape or pool-geometry for males and landmark for females, as shown by Rodríguez et al. 2010) that overshadowed the less discriminable, salient, or preferred cue. The study by

Rodríguez et al. (2011) helps to explain a frequently reported failure in the literature of landmarks to overshadow or block learning about geometry in male rats.

Importantly, in both studies (Rodríguez et al. 2010, Experiment 1; Rodríguez et al. 2011, Experiments 1 and 2a) the possibility that the estrus cycle of females could influence their performance was examined. It did not. There is one difference between the procedures used by Rodríguez et al. (2010, 2011) and those employed by Williams et al. (1990) that should be noted: in the experiments by Rodríguez et al. the landmark and the correct corner of the pool could be regarded as beacons which the rats learned to approach, whereas in the Williams et al. experiment the landmarks and shape of the room can hardly have acted as beacons. It is an open question whether this difference is important: but the parallel between these studies suggests that it may not be.

Taken together, all the data in the present section show that in the two species, rats and humans, adult males and females clearly differed in their preferred cues to solve navigation tasks. Importantly, a further study in rats by Rodríguez et al. (2013) with the same apparatus and general procedure as Rodríguez et al. (2010) revealed a different result when the rats were prepubertal. Specifically, juvenile female rats behaved like males (both adult and juvenile), but unlike adult females, when searching for the platform in the preference test trial. This result reveals a change in the behavior of female rats as they grow older. Why is this? Based on the observation that ovariectomized females behaved like younger rather than older rats, Rodríguez et al. (2013) suggested that the obvious answer was that the hormonal changes associated with the onset of puberty changed the females' preference. That young female rats behave like males on a spatial task, while a sex difference appears only after puberty is consistent with the suggestion that sex differences in spatial cognition in humans appears due to the hormonal and cognitive changes associated with puberty (for a meta-analysis on this issue see Voyer et al. 1995).

One Biological Explanation That Strengthens Over Time

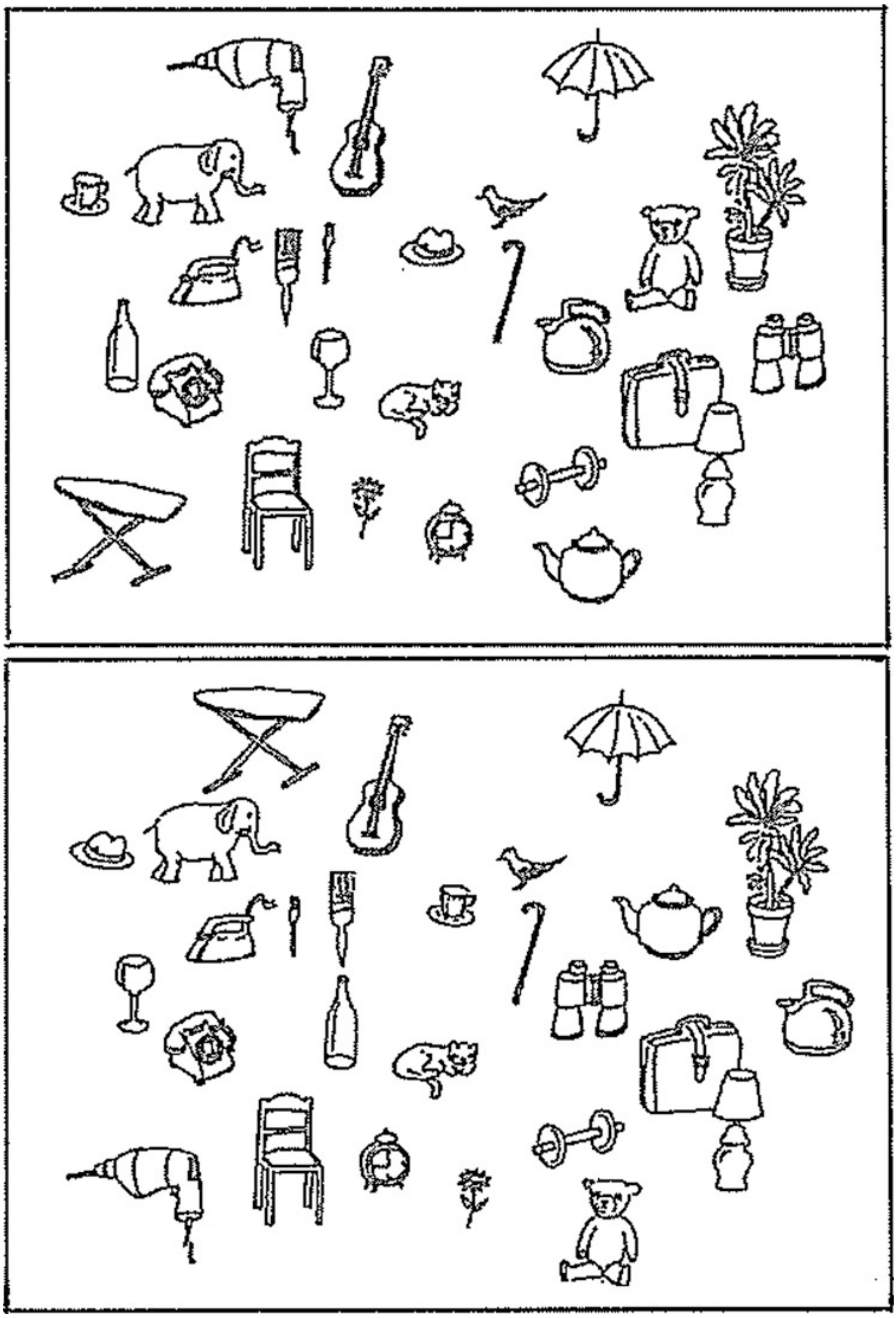
A large number of hypotheses have been proposed to explain the qualitative, as well as other quantitative, sex differences often found in the spatial domain (for a review see Jones et al. 2003). Jones et al. (2003) concluded that the best predictor of the sex difference was range size, a biological hypothesis. This hypothesis is consistent with the argument that the differences found in males and females of many mammalian species are the result of some form of *natural selection*. Specifically, that both sexes have developed different strategies for spatial navigation and search due to a selective pressure of the environment, giving rise to different skills. In humans, the critical reason being that for a long time men hunted and women gathered. In other animals the most frequent explanation refers to polygyny, a mating system in which one male mates with several females in a single breeding season.

In agreement with the previous claim favoring males, in rats it has been found that different species of vole have a different range size between males and females depending on their mating system: males occupy a larger home range than females only if they are promiscuous, and not if they are monogamous. When males occupy a larger home range than females, they also show superior spatial ability. The promiscuous male meadow vole is better than the female at several maze learning tasks (Gaulin et al. 1989), but in monogamous prairie and pine voles, there is no sex difference in maze tasks. The sex difference in meadow voles has also been observed in the Morris pool, which suggests that the result is strong in spite of using different tasks. Polygynous male deer mice are better than females at spatial learning, but again there is no sex difference in monogamous kangaroo rats (Jones et al. 2003).

Let's consider a pioneering study by Silverman and Eals (1992), which has expanded in humans the previous hypothesis, range size. According to these authors, the critical reason to explain the range size hypothesis is the division of labor that occurred in our earliest ancestors, where males were primarily hunters of mobile prey and females gatherers of immobile plant foods. Consequently, spatial abilities associated with hunting were naturally selected in males (and some typical tests that are currently used to measure these abilities include mental rotations, map reading, and different forms of maze learning); while spatial abilities related to gathering were naturally selected in females (and the measures suggested by Silverman and Eals include recognition and recall of spatial configurations of objects, as well as incidental learning for objects and their locations). They claim that our evolutionary history is thus responsible for different attributes in men and women when dealing with spatial tasks. A bias favoring men should be expected in those tasks reflecting abilities appropriated to hunting; while a bias favoring women should be expected in those tasks reflecting abilities appropriated to gathering. Therefore, sex differences in the spatial domain are expected to be task dependent. In their surprising work (Silverman and Eals 1992), they present a series of four studies that explore the hypothesized female spatial specializations by means of foraging scenarios. Briefly, in Study 1 – a pencil and paper test – university students of both sexes were asked to memorize the position of 27 objects which were drawn on a sheet of paper. They had a minute to study the array. Following this, the sheet of paper was hidden and a new sheet of paper with some new items added was presented to the participants. They were asked to identify the new items in the second sheet of paper. The results showed that females were better at this task than males. Most importantly was the demonstration, in a third sheet of paper presented to the students, that females were also better when, instead of adding some new items to the initial array, the experimenters moved some of the items in the first sheet of paper to a different location – as shown in Fig. 2 – and the main task was to identify the moved items (i.e., a test of spatial or location memory). This better spatial memory score by females was not found if the participants were prepubertal (Study 4). Silverman and Eals (1992) emphasized that their results give clear support to the hypothesis that sex differences in the spatial domain are task dependent.

Two experimental field studies (Pacheco-Cobos et al. 2010; Vashro and Cashdan 2015) support the expanded range size hypothesis in humans. The work by Pacheco-Cobos et al. (2010) addresses the hypothesized female spatial specializations predicted by Silverman and Eals (1992). Specifically, the study focuses on the foraging techniques and success rate of Mexican men and women from a small village, San Isidro Buensuceso, as they searched for edible mushrooms on the slopes of La Malinche volcano, a region whose inhabitants have a long tradition of collecting mushrooms. The authors GPS tracked the foraging pathways of pairs of men and women from San Isidro Buensuceso while searching for mushrooms. Measures of costs, benefits and general search efficiency were analyzed and related to differences between the two sexes in foraging patterns. Although men and women collected similar quantities of mushrooms, men did so at significantly higher cost. They travelled further, to greater altitudes, and had higher mean heart rates and energy expenditure (kcal). They also collected fewer species and visited fewer collection sites. The authors conclude that in terms of search strategies developed for gathering wild mushrooms, and presumably other wild plants, women outperform men. The women proved to be more efficient foragers than men in energy efficiency terms since they collected significantly more mushrooms while expending significantly less energy in doing so. These results provide the first support from a field study for the idea of a domain-specific spatiotemporal advantage for women in the type of foraging context that has probably been important for ancestral human females, as predicted by Silverman and Eals (1992). In agreement with the authors, similar studies are needed for other cultural groups, and for the gathering of different resources, such as firewood.

The study by Vashro and Cashdan (2015) focuses on the relationship between spatial-cognitive ability and range size in a population (the Twe and Tjimba of northwestern Namibia) that faces navigational challenges similar to those



Spatial Orientation, Fig. 2 Silverman and Eals' (1992) Object Location Memory task. Top: sheet of paper 1. Bottom: sheet of paper 3. (Reproduced with permission) that faced many of our earliest ancestors, and tests the hypothesis that increased range size and better spatial ability confers fitness benefits (more mates and more children) for men. Data on range size, spatial ability, and reproductive success are combined in this study, in which the tasks employed were: mental rotation, water-level, object location memory task, pointing, range size measures, and reproductive history. The main results showed that Twe and Tjimba men have larger visiting ranges than women and are more accurate in both spatial (mental rotations) and navigational (accuracy pointing to distant locations) tasks. Men who performed better on the spatial task not only travelled farther than other men, but also had children with more women. Vashro and Cashdan (2015) argued that these findings offer strong support for the relationship between sex differences in spatial ability and ranging behavior, and identify male mating competition as a possible selective pressure shaping this pattern. The authors concluded that the benefits of increased mating range, increased hunting range, increased raiding ability, and women's preference to limit their range size may all have added to the selective pressure favoring sex differences in range size, navigation, and spatial cognition.

Taken together the main implication of the research in this section is that males and females in the two species, rats and humans, have a very long evolutionary history which seems to be responsible, at least partly, of naturally "selecting" those traits of individuals that enhance their survival, giving rise to differential spatial abilities in the two sexes.

The Role of the Hippocampus in Spatial Learning and Memory

The hippocampus plays a critical role in spatial learning and memory (Ekstrom et al. 2018; O'Keefe and Nadel 1978). Although hippocampal lesions do not impair rats' ability to swim to a visible platform in a Morris pool, such lesions have a drastic effect on their ability to swim to an invisible platform (Morris et al. 1982; Pearce et al. 1998). Morris et al. (1982) 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. The following question has been repeatedly asked for many years. Is hippocampal volume different in the two sexes? The hippocampal complex (i.e., hippocampus and entorhinal cortex) is larger in male than in female rats, kangaroo rats, and polygynous species of voles (Kimura 2000). The importance of a sex difference in human hippocampal size is more controversial (McCarthy 2016). As Cahill (2006) has suggested, males and females of many mammalian species evolved under some similar, and some very different pressures. Thus, their brain organization would be expected to be both similar in some respects, and very different in others. This is precisely the situation found in the sex difference literature when dealing with spatial tasks.

There have been few studies that have used both sexes to understand the functional role of the hippocampal complex. For one exception see Roof et al. (1993). The Roof et al. (1993) study addressed working spatial memory in a Morris pool. They found that unilateral lesions of the entorhinal cortex resulted in a differential performance in male and female rats. Specifically, males' performance was drastically impaired whereas females showed only a slight impairment, independently of the size of the lesion. These results already suggested that the role of both the hippocampus and entorhinal cortex in spatial learning seems to be different in males and females. Roof et al. (1993) ended their work by claiming that "Whatever the mechanism underlying the recovery or lack of impairment in females, it is clear from these results that more attention must be paid to the study of gender differences in determining or specifying structure-function relationships in the central nervous system. It is also clear that the issue of gender must be given more weight in planning and developing treatment and rehabilitation strategies for brain-damaged patients" (p. 50). Unfortunately, at present, most basic research in neuroscience is still conducted with males only.

In humans, a frequent way to understand the importance of the hippocampus while navigating has been to study London taxi drivers. Drivers of Black Cabs are not allowed to have satnavs, therefore they can only use their memory in order to navigate between more than 25,000 streets and thousands of places of interest. The exam to obtain permission to drive one of London's iconic *black cabs* is considered one of the most difficult in the world. It is known as "The Knowledge." At present, there are approximately 21,000 black cabs operating in London, although only around 2% of them are women. In a classic study conducted by Maguire et al. (2000), the relationship between spatial memory and grey matter in the hippocampus was studied in London taxi drivers. Maguire et al. (2000) found that grey matter in the hippocampus positively correlated with years of driving experience. Subsequent work by the same authors where more sophisticated techniques were used (such as functional magnetic resonance imaging – fMRI) replicated and expanded the previous results. Together these studies show that the hippocampus has an enormous flexibility and that the daily experiences we engage in can have an impact on it. This is also true when virtual tasks are used. For example, a recent study by West et al. (2018) has provided the first evidence that activities such as action video games can reduce grey matter in the hippocampus and that this impact is mediated by a person's learning strategy. This is most important because low grey matter in the hippocampus is a risk factor for developing many neuropsychiatric illnesses. No doubt more work is needed in this fascinating line of research (West et al. 2018).

In conclusion, although currently it is well known that the hippocampus can be crucial when considering spatial tasks, recent research has revealed that other parts of the brain are also involved in these tasks, so that the main role of the hippocampus could be as an integrator "hub" in the brain (Ekstrom et al. 2018). Future work will have to deal with the many unanswered questions, including those related to sex differences.

Our Earliest Ancestors: Hunter-Gatherers Societies and Human Evolution

Nomadism and the absence of private property are the two most important characteristics of the *hunter-gatherers* societies, in which men and women collaborated for subsistence. The understanding of the way of acting of those men and women is fundamental to understand the origin of humanity itself. Paleolithic societies are defined as nonproducers, acquiring their plant resources through harvesting, and animals through fishing, scavenging and hunting. This last one developed enormously during the Paleolithic, from being an opportunistic and indiscriminate hunting it become more specialized and the acquisition of resources, more diversified. Human hunting differs qualitatively from hunting by other animals. Unlike most animals, which either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters used a wealth of information to make context-specific decisions, both during the search phase of hunting and when the prey has been caught (Clottes 2008; Fernández Martínez 2007; Kaplan et al. 2000). Hunter-gatherer societies lasted for over one hundred thousand years. This is much longer than all of recorded history. Undoubtedly, our present predispositions must be a result of such a long period. Currently only a few such societies remain (such as the San Nyae Nyae Pam of Namibia, the Twe and Tjimba of Northwestern Namibia, or the Hadzabe in Northern Tanzania). These societies often constitute an authentic window to the past (like the study by Vashro and Cashdan 2015), thus complementing the information found at archaeological sites – the only direct testimonies that have reached us until today.

Since our split form the chimpanzee lineage, the human evolutionary branch underwent many great changes, like an increase in brain size with respect to the rest of the body, smaller teeth, bipedalism, great manual dexterity, the ability to make and use tools, satnavs, etc. Our evolutionary story is not linear. Rather, like other animals, the human family tree is much more like a bush made up of a variety of "adaptive radiations" in response to changing environmental circumstances (Fernández Martínez 2007). A frequently asked question in the literature among anthropologists is how was the labor collaboration between men and women done? Here are two opinions of experts. In his beautiful book addressed to his grandchildren Clottes (2008) says “the men, physically stronger, were engaged in hunting. While the women, who took care of the children and accompanied the older members of the family clan, had the mission of collecting all kinds of edible wild fruits and locating dead animals from which meat could be used” (pp. 43–44). According to Kaplan et al. (2000), “human pair bonding and male parental investment is the result of complementarity between males and females. The commitment to caring for and carrying vulnerable young, common to primate females in general, together with the long period required to learn human hunting strategies, renders hunting unprofitable for women” (p. 173). Several reasons have been used to explain this division of labor. Men are, in general, taller than women and they are also more muscular. Thus, women tend to have less physical strength than men, and a lot of physical power is required to throw spears and missile weapons at large-game. In addition, women are more valuable than men because they have children. The group survival depended on women and, therefore, it was important for the group to avoid their implication in situations of great danger. The differences between men and women are largely due to different hormonal actions during development (i.e., testosterone production in men and estrogen production in women). Contrary to what was believed for a long time (Kaplan et al. 2000) recent research has shown that collecting mushrooms, wild fruits, and edible plants (activities that women and children mainly did) constituted up to 60–70% of the food. Nowadays it is considered that these activities were more important in the long term than that of large-game hunters for the survival of the group (Clottes 2008; Fernández Martínez 2007; Mackintosh 2011). From the perspective of human evolution, the gender-specific tasks (i.e., men primarily hunters, while women primarily gatherers) are an excellent example of cooperation between men and women due to a selective pressure of the environment to solve adaptative problems, ultimately to ensure the perpetuation of the human species.

In conclusion, as we saw in section “One Biological Explanation That Strengthens Over Time,” evolution by natural selection seems to have been the process of adapting human males and females attributes to best function in their environment. The spatial domain is not an exception. A sensible view would be to consider that males should not be regarded as more highly spatially specialized than females, but differently specialized, as claimed by Silverman and Eals (1992). If we refer to the ability to navigate in large spaces, men tend to have a better performance than women. On the contrary, if we refer to the ability to navigate in small spaces, the opposite is usually frequent and women tend to have a better performance than men.

Final Conclusions

At present, it is well known that the brain has a great plasticity and that activities we engage in during our daily lives have a direct impact on it. For example it has been shown (West et al. 2018) that 90 h of action video games can shrink the hippocampus. Considering this evidence, what could we expect after ten millennia of the division of labor? This is an open question waiting for clear answers. At least different predispositions to attend to various sources of spatial information could be expected due to our evolutionary history. No doubt, cognitive intervention programs at schools (for example, different types of games – geometric for girls and spatial memory ones for boys) could help to reduce the sex differences observed in adulthood. Furthermore, it is quite remarkable that young baby boys and baby girls differ when mental rotation tasks with 3D objects are used (Lauer et al. 2015; Moore and Johnson 2008). These results reveal clear sex differences in the spatial domain long before puberty which are difficult to explain, thus weakening the apparent parallel between rats and humans. Future research will have to deal with the very many unanswered questions.

A final thought refers to technology. Is it really good for us? Are not we atrophying our grey matter in the hippocampus with so much dependence on satnavs or GPS for example? Following GPS indications resembles a route following task, where a specific part of the striatum, the caudate nucleus, can be very active. Recent research has shown (for a review see Ekstrom et al. 2018) that the caudate nucleus shares an inverse relationship with the hippocampus, in both humans and rodents (i.e., increased grey matter in one structure is correlated with decreased grey matter in the other). Consequently, with so much dependence on technology, we could be impoverishing ourselves as a species. This worrisome situation should be taken more into account in the new spatial habits we are acquiring.

Cross-References

- ▶ Charles Darwin
- ▶ Cognitive Map
- ▶ Evolution
- ▶ Geometric Module
- ▶ Hippocampus and Caudate Nucleus
- ▶ *Homo sapiens*
- ▶ Natural Selection
- ▶ Puberty
- ▶ Rodentia Navigation
- ▶ Sex Hormones
- ▶ Sexual Dimorphism
- ▶ Visuospatial Memory

References

Beery, A. K., & Zucker, I. (2011). Sex bias in neuroscience and biomedical research. *Neuroscience & Biobehavioral Reviews, 35*, 565–572.

Cahill, L. (2006). Why sex matters in neuroscience. *Nature Reviews Neuroscience, 7*, 477–484.

Clottes, J. (2008). *La prehistoria explicada a los jóvenes.* Barcelona: Paidós (Translation of the French original *La Préhistoire expliquée à mes petits enfants* of 2002. Paris: Éditions du Seuil.).

Ekstrom, A. D., Spiers, H. J., Bohbot, V. D., & Rosenbaum, R. S. (2018). *Human spatial navigation*. Princeton: Princeton University Press.

Fernández Martínez, V. M. (2007). *Prehistoria. El largo camino de la humanidad* [Prehistory. The long road of humanity]. Madrid: Alianza Editorial.

Gaulin, S. J. C., Fitzgerald, R. W., & Wartell, M. S. (1989). Sex differences in spatial ability and activity in two vole species. *Journal of Comparative Psychology, 104*, 88–93.

Halpern, D. F. (2012). *Sex differences in cognitive abilities* (4th ed.). New York: Psychology Press.

Jones, C. M., Braithwaite, V. A., & Healy, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience, 117*, 403–411.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*, 156–184.

Kimura, D. (2000). *Sex and cognition*. Cambridge, MA: MIT Press.

Lauer, J. E., Udelson, H. B., Jeon, S. O., & Lourenco, S. F. (2015). An early sex difference in the relation between mental rotation and object preference. *Frontiers in Psychology, 6*, 558.

Mackintosh, N. J. (2011). *IQ and human intelligence* (2nd ed.). New York: Oxford University Press.

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, R. S., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America, 97*, 4398–4403.

McCarthy, M. M. (2016). Multifaceted origins of sex differences in the brain. *Philosophical Transactions of the Royal Society B, 371*, 20150106.

Moore, D. S., & Johnson, S. P. (2008). Mental rotation in human infants. A sex difference. *Psychological Science, 19*, 1063–1066.

Morris, R. G. M., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature, 297*, 681–683.

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

Pacheco-Cobos, L., Rosetti, M., Cuatianquiz, C., & Hudson, R. (2010). Sex differences in mushroom gathering: Men expend more energy to obtain equivalent benefits. *Evolution and Human Behavior, 31*, 289–297.

Pearce, J., Roberts, A. D. L., & Good, M. (1998). Hippocampal lesions disrupt a cognitive map but not vector encoding. *Nature, 996*, 75–77.

Rodríguez, C. A., Torres, A. A., Mackintosh, N. J., & Chamizo, V. D. (2010). Sex differences in the strategies used by rats to solve a navigation task. *Journal of Experimental Psychology: Animal Behavior Processes, 36*, 395–401.

Rodríguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2011). Overshadowing and blocking between

landmark learning and shape learning: The importance of sex differences. *Learning & Behavior, 39*, 324–335.
Rodríguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2013). Do hormonal changes that appear at the onset of puberty determine the strategies used by female rats when solving a navigation task? *Hormones and Behavior, 64*, 122–135.
Roof, R. L., Zhang, Q., Glasier, M. M., & Stein, D. G. (1993). Gender-specific impairment on Morris water maze task after entorhinal cortex lesion. *Behavioural Brain Research, 57*, 47–51.
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.
Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 531–549). New York: Oxford Press.
Vashro, L., & Cashdan, E. (2015). Spatial cognition, mobility, and reproductive success in northwestern Namibia. *Evolution and Human Behavior, 36*, 123–129.
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.
Ward, S. L., Newcombe, 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*, 192–213.
West, G. L., Konishi, K., Diarra, M., Benady-Chorney, J., Drisdelle, B. L., Dahmani, L., Sodums, D. J., Lepore, F., Jolicoeur, P., & Bohbot, V. D. (2018). Impact of video games on plasticity of the hippocampus. *Molecular Psychiatry, 23*, 1566–1574.
Williams, C. L., Barnett, A. M., & Meck, W. H. (1990). Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience, 104*, 84–97.