



Research report

Mental imagery skills and topographical orientation in humans: A correlation study

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ABSTRACT

Several studies provide evidence that mental imagery is critical for human navigation. However, the contribution of different mental imagery abilities to the individuals' skill of using specific orientation strategies remains unclear. In the present study we assessed a variety of mental imagery skills and investigated their contribution in relationship with the selective individuals' ability of forming and using a mental representation of the environment, namely a cognitive map. Indeed, despite the use of alternative strategies that individuals may adopt while moving along the same well-known route, cognitive maps are critical for orientation since they allow individuals to reach any target location from any place in the environment. We found that the ability to form a cognitive map was related to the specific ability of performing mental rotations of simple geometrical shapes, and the ability to imaging ourselves moving on a map. Other imagery skills such as the ability to generate mental images from memory or the ability of mentally manipulate objects were not correlated with the individuals' performance in forming the cognitive map. Moreover, we revealed gender differences in forming a cognitive map, as well as in performing some of the mental imagery tests. We discuss these findings in order to shed more light on the specific role of mental imagery in human topographical orientation.

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1. Introduction

Topographical orientation is generally defined as the individuals' ability to become familiar and orient in the environment [1]. This complex phenomenon requires the integrity of several cognitive functions such as visual perception, attention, memory, and decision-making skills [2,3], which all contribute to successful navigation in both familiar and unfamiliar surroundings. Among these cognitive functions, mental imagery skills have been suggested to be critical for orientating within the environment [2,4–6].

In human navigation, mental imagery refers to the individuals' ability to mentally represent the information available within the environment such as landmarks and routes, and use them for the purpose of orientation [2,4,5]. For example, in order to reach different locations, individuals are required to create a mental image (or representation) of the environment in which they are moving, and manipulate and rotate it in order to update their current position with respect to the target location they are aiming to

reach. Evidence that imagery skills are critical for orientation is provided by several neuropsychological studies showing that brain-damaged patients impaired in topographical orientation usually report difficulties in "revisualisation" and create internal representation of pathways and landmarks encountered while navigating [7,8]. Similar imagery defects have been reported in a patient with a congenital brain malformation that resulted in a selective impairment in topographical orientation [9]. Finally, patients with selective mental imagery defects such as representational neglect (i.e. the inability to mentally represent the contralesional part of the environment) are generally reported having navigational and orientation impairments as well [10]. Altogether, these findings are consistent with the critical role of mental imagery in human navigation and orientation.

In the last years, several studies in healthy individuals aimed at investigating the relationship between navigational skills and specific mental imagery abilities, such as the ability to mentally rotate objects and geometrical figures. For instance, Moffat et al. [11] used a virtual maze test to investigate gender differences in navigational abilities and the correlations with the individuals' performances in solving spatial mental rotation tasks including the *Vandenberg Mental Rotations Test* [12], the *Guilford-Zimmerman Spatial Orientation Test* [13] and the *Money Road Map Test of Direction Sense* [14]. In this

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study, participants were required to navigate within a virtual environment appearing as a monochrome layout interconnecting halls and doorways, and were asked to find the exit of the maze as quick as possible. The authors reported that men were better than women in solving the task, and that their performances were positively correlated with their ability to solve the mental imagery tasks. Similar findings have been recently provided by other studies [15,16] in which participants were required to solve a virtual version of the *Morris Water Maze Test* [17], consisting of finding a hidden location within the environment. The results of these studies show that men were better than women in solving the navigational task and that such a better performance was significantly correlated with the individuals' mental rotation abilities.

Studies performed in ecological surroundings are consistent with the findings reported in virtual environments [18–21]. For instance, Montello et al. [21] found that men outperform women on tests in which they are required learning from direct experiences in new surroundings, as well as in mental rotation and geographic knowledge tests (i.e. to locate 15 cities on a world map). In a different study, Dabbs et al. [19] reported gender differences related to the strategies that individuals adopt while navigating within the environment: while giving directions, men prefer using metric-distances (miles) and north–south–east–west directions, whereas women show a bias in using landmark available within the environment. Importantly, the authors reported that men perform better than women in both mental rotation and geographic knowledge tests.

Although the findings described above provide useful information regarding the relationship between mental imagery skills and the ability to navigate within the environment, it should be noticed that (1) mental imagery skills include different abilities that can be specifically related to navigational environmental information or not and (2) despite the use of alternative strategies, topographical orientation mainly rely on the formation, first, and use, then, of a mental representation of the environment, namely a cognitive map [22,23]. Indeed, the use of environmental cognitive maps is critical for orienting since it allows individuals to reach any target location starting from any place and by following any route available within the environment. The contribution of different imagery skills to the formation and use of cognitive maps has never been investigated in previous studies.

Here, we aimed at verifying the hypothesis that the ability to form and use environmental cognitive maps is differently related to the mental imagery skills according with the nature of the information that individuals are required to mentally manipulate. First, we made use of a virtual environment in order to assess the individuals' ability to both form and use a cognitive map of the environment, namely the *Cognitive Map Test* (CMT) [24]. Then, we assessed the specific contribution of different mental imagery skills related to the individuals' ability of forming and using an environmental cognitive map, respectively. Finally, in order to shed more light on the findings previously reported in the literature, individuals' gender differences were investigated while performing both the *Cognitive Map Test* and the mental imagery tasks.

2. Methods

2.1. Participants

Thirty-two healthy subjects with no history of neurological or psychiatric disorders participated in this study. The sample included 15 women (mean age, S.D. = 23.3 years, 3.24; mean education, S.D. = 14.5 years, 1.96) and 17 men (mean age, S.D. = 23.9 years, 4.11; mean education, S.D. = 14.6 years, 2.32). The study was approved by the local Ethics Committee, and all participants gave written informed consent.

2.2. Experimental protocol and procedure

Participants performed two experimental sessions. During the first session, they were required to perform a navigational test in a virtual environment, namely the *Cognitive Map Test* [24]. In the second session, subjects were administered several table-tests in order to assess different components of the complex mental imagery skill. Hereafter we provide a description of the tests performed in both sessions.

2.2.1. The Cognitive Map Test (CMT)

The experimental paradigm consisted of a virtual city, which was created by using the editor of a three-dimensional game software (Game Studio A6, La Mesa, CA, USA). The virtual city, which was composed of several buildings of different size and shape but the same texture, included six clearly identifiable landmarks: a cinema, a restaurant, a bar, a hotel, a pharmacy and a flower shop. Participants navigated in the city by using a three-button keypad, each button corresponding to movement in one of three directions: left, forward and right. See Fig. 1 for a schematic view of the environment and examples of landmarks available within it.

Before testing, in order to practise the motor aspects of the tasks and familiarize themselves with the virtual environment, participants underwent a *practise phase* in which they navigated freely for 10 min in a virtual city similar to the experimental one (no landmarks were present in this environment). After this *practise phase*, subjects were asked to perform three *control trials* in which they were required to navigate as quickly as possible a route defined by arrow signs present within the environment. These *control trials* were performed to ensure that all subjects were comfortable moving within the environment in a similar way. The experimental tasks started only when participants ended the three *control trials* without stopping along the designed pathways.

The experimental test consisted of two tasks, namely the *Learning and Retrieval* tasks. During the *Learning Task*, the participants were instructed to freely explore the environment in order to create a mental representation of the city including the landmarks' locations. Subjects were asked to report when they felt that they had completed that mental representation, and were told that at that "terminal moment" the examiner would ask them to report the locations of the landmarks on a schematic map representing the city from a top-view perspective. In addition to this terminal assessment, participants were also aware that during their exploration the examiner would stop them occasionally (every minute after the six landmarks have been found) to ask them to report the locations of the landmarks on similar maps. The learning task was considered completed as soon as the participant was able to indicate the correct locations of all six landmarks, either during one of the every-minute interrogations of the examiner or at the terminal moment when the participant felt that s/he had formed the mental map. The time spent to reach this point was taken to be the time required to form the cognitive map.

Immediately after learning, participants were administered the *Retrieval Task*. This task consisted of 18 trials in which the subjects were asked to use the mental representation that they had formed in order to reach the location of specific landmarks. On each trial, the subjects started by facing a landmark and a sign indicating the target location they needed to reach as quickly as possible by following the shortest pathway. The duration of each trial was recorded as a measure of behavioural performance. Since all participants were able to follow the shortest pathway after the cognitive map has been formed, the time in performing the pathway is representative of the ability to make use of such a cognitive map.

2.2.2. Mental imagery skills assessment

This battery of tests aimed at assessing different components of the human mental imagery skill. We administered the *Mental Rotation Test* [25] in order to assess the individuals' ability to make mental rotation of simple geometrical shapes. The test consisted of asking subjects to identify a target stimulus (a pattern of simple connected dots) among four alternatives in which the target was depicted with a rotation of 45°, 90°, 135° or 180°, respectively. The test included 10 test-items and 2 practice-items.

In order to assess a more complex imagery skill not just confined to geometrical shapes, we asked participants to perform a modified form of the *O'Clock Test* [26], which consisted of asking the subjects to image two given different times on two analogical clocks, and make a decision on which one the clock's hands form the wider angle. The task involved two mental imagery skills: the generation of an image and the spatial comparison of the imagined content, which have been shown to rely on different neural systems [27–29]. This test includes sixteen items in which the comparison occurs in the left hemi-face of the clock (i.e., 7.30 and 8.00) and 16 items in which the comparison occurs in the right one (i.e., 3.30 and 2.00).

To investigate the imagery skills involved in representing objects, we asked participants to perform the *Unusual Perspective Test*, which included 16 photographs of objects displayed in an unusual perspective and 16 photographs in which the same objects were presented in a usual perspective. In this task, participants were required to name the objects displayed individually in each photograph. First, we administered the unusual perspective items, which require to match the presented object with the canonical image stored in memory (mentally realigning and rotating it), and then the usual perspective ones, to confirm that participants were actually familiar with the entire set of objects included in the task. The objects presented were common objects such as a book, a coffee machine, a bottle, glasses, etc.

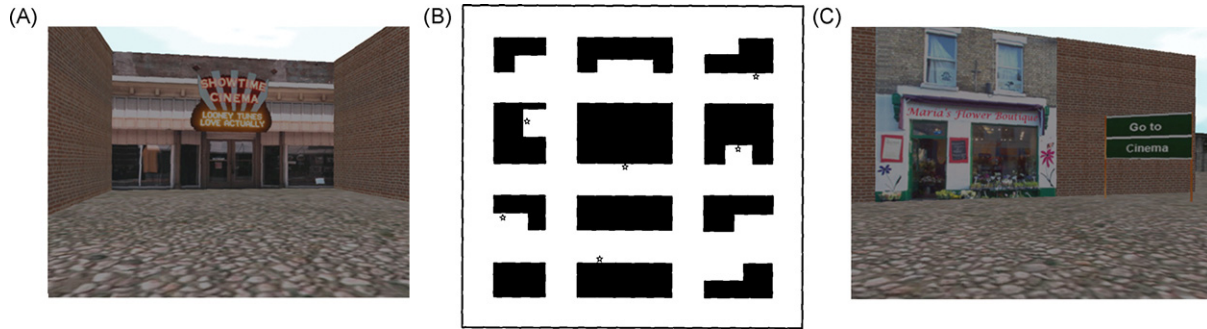


Fig. 1. The structure of the virtual city in which the participants performed both the Learning and the Retrieval tasks (B) including the locations of the landmarks (indicated with *). The figure also shows a view of one of the landmarks available within the environment (A), and a view of the participants' starting position while performing one trial of the Retrieval Task (C).

Three additional tests were administered in order to specifically assess the mental imagery abilities related to a more navigational and environmental context. The *Road Map Test* [14] consisted of an A4-sized paper map on which a pathway is traced. The map is kept still and the subjects are required to imagine themselves moving along the pathway, reporting verbally whether they would make a left or a right turn at each change of direction. The *Familiar Squares' Description Test* [30] requires the subjects to imagine and describe two Roman familiar squares (Piazza del Popolo and Piazza Venezia) from long-term memory as they would appear from two opposite vantage points. Score performances in this test consist in recording the number of elements overall reported as well as the number of elements reported on each side of the square in the two separate descriptions. Finally, participants underwent the *Postcards Test*, in which they were required to recognize landmarks (palaces, monument, etc.) or views (streets, squares, etc.) of known or unknown places in the world. The test consists of 32 postcards of unknown places and 104 postcards of known places. For each postcard, subjects were required to name the landmarks reported on it. Performance was scored as follows: 3 points were assigned for a correct response (the name of the landmark/view), 2 points were given for an appropriate response (for example, the name of the city where is located the landmark or the view), 1 point was assigned to a general response such as the name of the country where the landmarks/view is located, and 0 point was assigned for an incorrect response.

2.3. Data analysis

To investigate the relationship between mental imagery and topographical orientation skills, we performed Pearson correlations between the time that the subjects spent in forming and using the cognitive map (learning and retrieval task, respectively) and their scores at the different mental imagery tests. In addition, we performed a regression analysis aiming at investigating the degree to which each of the mental imagery skills contribute to predict the participants' navigational abilities. Finally, to assess gender differences in both topographical orientation and mental imagery skills, we performed *t*-tests comparing the performances of women and men participants at each test.

3. Results

The multiple matrix correlation's coefficients and their statistical significance values are reported in Table 1. The *Learning Task* resulted to be significant correlated with the *Mental Rotation Test* ($r = -0.37$; $p < 0.05$) (Fig. 2A) and the *Road Map Test* ($r = -0.56$; $p < 0.001$) (B); whereas, the retrieval task was not correlated with

any of the mental imagery test. We also found a statistically significant correlation between the *Learning* and *Retrieval Tasks* ($r = 0.44$; $p < 0.05$) (C). These results reveal that individuals performing better at the *Mental Rotation Test* and the *Road Map Test* spend less time to form a cognitive map of the environment, and that individuals spending less time in forming the cognitive map are more efficient in using it for the purpose of orientation. The regression analysis with *Learning Task* as dependent variable and the other imagery tests as independent variables revealed a statistically significant effect of the *Road Map Test* (B-Weight = 40.02, $p = 0.022$) suggesting that this test is able to predict the individuals' ability in forming a cognitive map of the environment; the remaining imagery tests did not reach statistical significance (*Mental Rotation Test*: B-Weight = 23.28, n.s.; *O'Clock Test*: B-Weight = 5.64, n.s.; *Unusual Perspective Test*: B-Weight = 1.07, n.s.; *Familiar Squares' Description Test*: B-Weight = 0.87, n.s.; *Postcards Test*: B-Weight = 1.53, n.s.). Similar regression analysis with *Retrieval Task* as dependent variable did not reveal any significant effect (*Road Map Test*: B-Weight = 6.31, n.s.; *Mental Rotation Test*: B-Weight = 12.85, n.s.; *O'Clock Test*: B-Weight = 4.8, n.s.; *Unusual Perspective Test*: B-Weight = 21.44, n.s.; *Familiar Squares' Description Test*: B-Weight = 0.44, n.s.; *Postcards Test*: B-Weight = 0.50, n.s.)

With respect to the effect of gender, the participants' performances at the *Cognitive Map Test*, revealed that men (mean, S.D. = 575.29 s, 199.06) were faster than women (mean [S.D.] = 1012 s [509.05]) while performing the *Learning Task* ($t_{(1,30)} = -3.27$, $p = 0.0027$), but not while performing the *Retrieval Task* (women mean [S.D.] = 362.4 s [94.6]; men mean [S.D.] = 298.35 s [112.58]; $t_{(1,30)} = -1.73$, n.s.). At the *Mental Rotation Test*, men's performances (mean [S.D.] = 9.06 [1.3]) were significantly better than the female ones (mean [S.D.] = 8 [1.25]) ($t_{(1,30)} = 2.34$, $p = 0.026$). Similar findings were found at the *Road Map Test* ($t_{(1,30)} = 4.14$, $p = 0.0026$), where men (mean [S.D.] = 30.47 [2.58]) showed a better performance than women (mean [S.D.] = 24.33 [5.47]). No statistical difference between

Table 1
The Pearson correlations among the tests

Tests	Unusual perspectives	Mental Rotation Test	Road Map Test	O'Clock Test	Familiar Squares' Description Test	Postcards Test	CMT-learning condition	CMT-retrieval condition
Unusual perspectives	1	0.13	0.20	0.35	0.12	0.08	-0.10	0.13
Mental Rotation Test	0.13	1	0.52**	0.34	0.2	0.35	-0.37*	-0.07
Road Map Test	0.20	0.52**	1	0.21	0.26	0.28	-0.56***	-0.26
O'Clock Test	0.35	0.34	0.21	1	0.07	0.24	-0.14	-0.07
Familiar Squares' Description Test	0.12	0.2	0.26	0.07	1	0.52**	-0.24	-0.19
Postcards Test	0.08	0.35	0.28	0.24	0.52**	1	-0.31	-0.25
CMT-learning condition	-0.10	-0.37*	-0.56***	-0.14	-0.24	-0.31	1	0.44*
CMT-retrieval condition	0.13	-0.07	-0.26	-0.07	-0.19	-0.25	0.44*	1

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

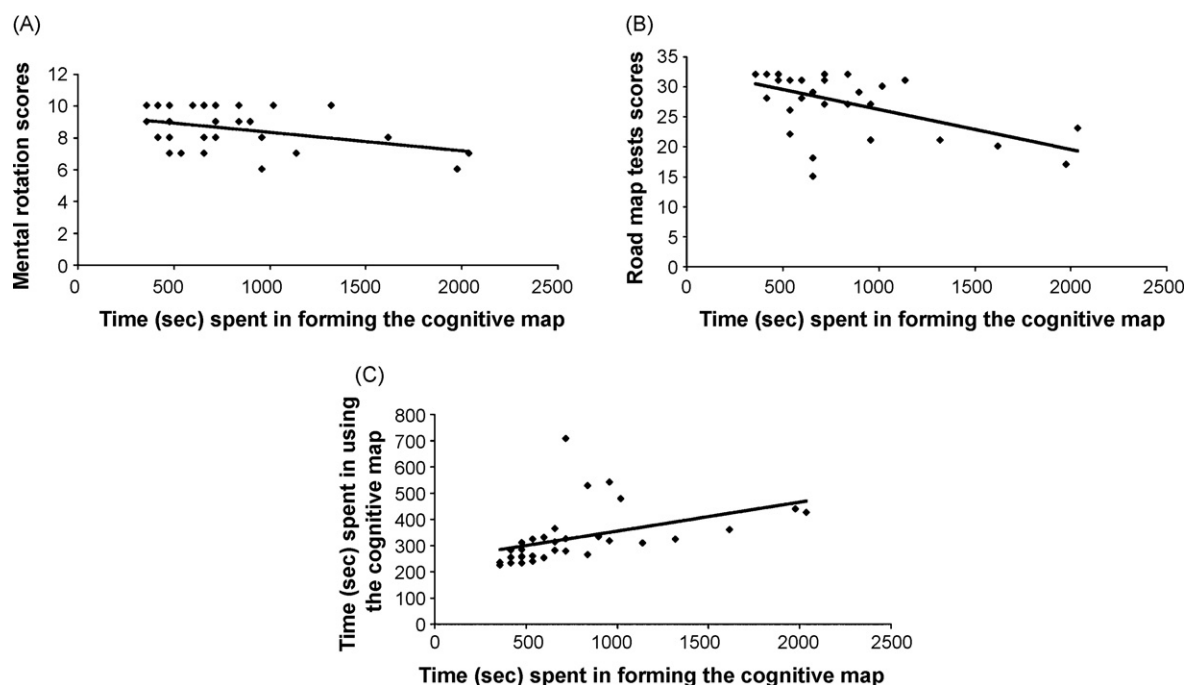


Fig. 2. The statistically significant correlations found between the Learning Task (formation of the cognitive map) and the individual's performances at the Mental Rotation Test (A), the Road Map Test (B) and the Retrieval Task (use of the cognitive map) (C).

men and women were found at the *O'Clock Test* (women mean [S.D.] = 29.87 [2.45]; men mean [S.D.] = 30.18 [1.78]; $t_{(1,30)} = 0.41$, n.s.), the *Unusual Perspective Test* (women mean [S.D.] = 13.4 [1.05]; men mean [S.D.] = 13.47 [1.23]; $t_{(1,30)} = 0.17$, n.s.), the *Familiar Squares' Description Test* (women mean [S.D.] = 29.67 [13.6]; men mean [S.D.] = 32.71 [17.87]; $t_{(1,30)} = -0.54$; n.s.), and the *Postcards Test* (women mean [S.D.] = 164.66 [37.5]; men mean [S.D.] = 187.88 [40]; $t_{(1,30)} = 1.69$, n.s.).

4. Discussion

In the present study we investigated the relationship between individuals' topographical orientation skills and mental imagery abilities. More specifically, we assessed the ability of forming and using a cognitive map, which is critical for orienting [22], and the contribution of different mental imagery skills to these abilities. We found that the ability to form a cognitive map of the environment is significantly correlated with the ability to perform mental rotations of simple geometric shapes (i.e. *Mental Rotation Test*) and the ability to imagine ourselves moving within the environment (*Road Map Test*). Less time spent in forming a cognitive map significantly correlated with a better performance in these two imagery tasks. No correlation was found with other mental imagery skills such as the ability to generate images from memory, or the ability to mentally manipulate objects and make spatial comparison between them. Interestingly, although both the ability to form and use cognitive maps were significantly correlated (better ability in forming a map results in a better ability in using it), the use of a previously formed cognitive map resulted to be not correlated with any of the imagery skills assessed in the pool of participants.

The results we presented in this study are consistent with previous studies showing a correlation between navigational skills, *Mental Rotation Test* [15,16] and the *Road Map Test* [11], suggesting that these specific mental imagery skills are critical for orientation. Our study, however, extends previous findings in that (1) we assessed the specific ability to form and use environmental cognitive maps (rather than assessing the so generally termed nav-

igational skill which may rely on the use of different strategies for orientation), and (2) we showed that other mental imagery abilities, not directed related to navigational information, are not critical for such a topographical orientation skill.

The specific contribution of the mental rotation (*Mental Rotation Test*) and the mental representation of ourselves within the environment (*Road Map Test*) during the formation of the cognitive map may be interpreted as following. While becoming familiar with the environment individuals create spatial relationships between the landmarks encountered while navigating [31,32], which later on will allow the formation of the cognitive map [33]. The formation of spatial relationship between landmarks requires the subjects to continuously perform mental rotations of those landmarks according to the structural properties of the buildings available in the environment. This specific cognitive demand may rely on a very basic mental rotation skill such as the one assessed in the *Mental Rotation Test*. In addition to this cognitive demand, however, individuals are required to continuously updating their location and position according with the mental environmental representation that they are engaged in forming (i.e. keeping track of where they are according to the landmarks previously found) [24]. This specific ability to update the individuals' actual location on a cognitive map is similar to the ability to imagine ourselves moving on a map printed on a paper, which is what the *Road Map Test* is actually assessing. In sum, simple mental rotations and mental images of ourselves moving on a map, seems to be related to the different skills of creating spatial relationships between landmarks and the updating of the individuals' actual location within the cognitive map. Studies in both humans [24,34–36] and animal [37,38] provide evidence that these distinctive demands while forming a cognitive map involve different brain structures such as the hippocampus and the retrosplenial cortex, respectively. Thus, it is reasonable to hypothesize that these different brain regions may be distinctively involved in different mental imagery skills as well. On the other hand, the lack of correlations between mental imagery skills and the use of a cognitive map seems to suggest that as soon as the cognitive map has been formed, individuals may rely on

mental imagery skills that are different from the ones we assessed here, such as the ability to represent environmental layouts.

The regression analyses performed on the participants' navigational abilities confirmed the findings reported in the correlation analysis, showing that the individuals' performances at the *Road Map Test* predicts their ability to form a cognitive map of the environment. However, the subjects' performances at the *Mental Rotation Test* did not result a statistically significant predictor of the same ability to form environmental cognitive maps (as found to be related in the correlation analyses). This may be due to several reasons including a possible issue with the statistical power of the analyses due to the relatively limited number of subjects included in the present study. Consistent with this possibility, in fact, one may note that although the correlations findings resulted to be statistically significant, the magnitude of these effects were moderate, especially for the *Mental Rotation Test*, which suggest caution in the statement any definitive conclusion before similar findings are replicated in a larger sample of participants.

With respect to the gender differences, we found that men were better than women in the *Mental Rotation Test* and in the *Road Map Test*. These findings are consistent with previous studies [11,39–42] suggesting an advantage of male subjects in performing these specific mental imagery tasks. No other differences were found between women and men in performing the other mental imagery tasks, suggesting that gender differences in mental imagery may depend on the nature of the material participants are required to mentally operate on, to which women and men may have different degrees of familiarity.

Differences between women and men were revealed also in the *Cognitive Map Test*. We found that men were faster than women in forming an environmental cognitive map, but no differences were detected when individuals were required to make use of it for the purpose of orientation. This difference across individuals in forming the environmental cognitive map cannot be explained by men being more familiar with videogames [43], since if this was the case then we would have found a better performance of the male participants in the use of the cognitive map as well. Thus, the gender difference in learning should be interpreted as due to different abilities in generate mental maps per se, which may be strictly linked to gender differences in mental rotation skill. Indeed, the absence of gender differences in the retrieval task (i.e. the use of cognitive map) suggests that women are only slower in generating the cognitive map, but once this has been formed and stored in long-term memory then their ability to use it is equivalent to the ability of men. This is in line with a recent report showing that women are slower in learning a sequence of steps in a walked version of the *Corsi Block Test*, whereas they did not differ from men in retrieval the sequences previously learned [44]. The better performance of men compared to women's ones in forming a cognitive map may explain why gender differences have been detected in some studies but not in others [45–47]. In studies in which a gender difference has not been reported, in fact, the subjects usually were tested after learning occurred [45], or tested in familiar environments where by definition learning has already occurred [46,47]. In addition, the formation and use of a cognitive map are two different aspects of the complex topographical orientation ability, which involve different neural substrates [24], and thus may develop differently in men and women.

In summary, the findings we reported in the present study suggest that some mental imagery abilities are critical for forming a cognitive map of the environment, therefore crucial for topographical orientation, whereas others are not. Gender differences may occur in the formation of a cognitive map and reflect gender differences occurring in mental imagery as well. Importantly, such

differences in navigational skills are specifically confined to the learning phase, and seem to disappear as soon as a cognitive map of the environment has successfully formed.

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References

- [1] Maguire EA, Burke T, Phillips J, Staunton H. Topographical disorientation following unilateral temporal lobe lesions in humans. *Neuropsychologia* 1996;34:993–1001.
- [2] Brunson R, Nickels L, Coltheart M. Topographical disorientation: towards an integrated framework for assessment. *Neuropsychol Rehabil* 2007;17:34–52.
- [3] Redish AD. *Beyond the cognitive map. From place cells to episodic memory*. London: MIT Press; 1999.
- [4] Davis SJC, Coltheart M. Rehabilitation of topographical disorientation: an experimental single case study. *Neuropsychol Rehabil* 1999;9:1–30.
- [5] Farah MJ. In: Boller F, Grafman J, editors. *The handbook of neuropsychology. Disorders of visual behavior*. Amsterdam: Elsevier; 1989. p. 395–413.
- [6] Riddoch M, Humphreys G. In: Brown JW, editor. *Neuropsychology of visual perception*. Hillsdale: Lawrence Erlbaum Associates; 1989. p. 79–103.
- [7] Aguirre GK, D'Esposito M. Topographical disorientation: a synthesis and taxonomy. *Brain* 1999;122(Pt 9):1613–28.
- [8] De Renzi E. *Disorders of space exploration and cognition*. Chichester: Wiley; 1982.
- [9] Iaria G, Inccoccia C, Piccardi L, Nico D, Sabatini U, Guariglia C. Lack of orientation due to a congenital brain malformation: a case study. *Neurocase* 2005;11:463–74.
- [10] Guariglia C, Piccardi L, Iaria G, Nico D, Pizzamiglio L. Representational neglect and navigation in real space. *Neuropsychologia* 2005;43:1138–43.
- [11] Moffat S, Hampson E, Hatzipantelis M. Navigation in a virtual maze: sex differences and correlation with psychometric measures of spatial ability in humans. *Evol Human Behav* 1998;19:73–87.
- [12] Peters M, et al. A redrawn Vandenberg and Kuse mental rotations test: different versions and factors that affect performance. *Brain Cogn* 1995;28:39–58.
- [13] Guilford JP, Zimmerman WS. *Guilford–Zimmerman aptitude survey*. Beverly Hills: Sheridan Supply Company; 1956.
- [14] Money J, Alexander D, Walker HT. *A standardized road map test of direction sense*. Baltimore: The Johns Hopkins Press; 1965.
- [15] Astur RS, Tropp J, Sava S, Constable RT, Markus EJ. Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behav Brain Res* 2004;151:103–15.
- [16] Driscoll II, Hamilton DA, Yeo RA, Brooks WM, Sutherland RJ. Virtual navigation in humans: the impact of age, sex, and hormones on place learning. *Horm Behav* 2005;47:326–35.
- [17] Morris RG. Spatial localization does not require the presence of local cues. *Learn Motiv* 1981;12:239–60.
- [18] Coluccia E, Martello A. Il Ruolo Della Memoria Di Lavoro Visuo-Spaziale Nell'Orientamento Geografico: Uno Studio Correlazionale (The role of VSWM in geographical orientation: a correlational study). *Giornale Italiano di Psicologia* 2004;3:523–52.
- [19] Dabbs JM, Chang EL, Strong RA, Milun R. Spatial ability, navigation strategy, and geographic knowledge among men and women. *Evol Human Behav* 1998;19:89–98.
- [20] Malinowski JC, Gillespie WT. Individual differences in performance on a large scale, real word wayfinding task. *J Environ Psychol* 2001;21:73–82.
- [21] Montello DR, Lovelace KL, Golledge RG, Self CM. Sex-related differences and similarities in geographic and environmental spatial abilities. *Ann Assoc Am Geogr* 1999;515–34.
- [22] O'Keefe J, Nadel L. *The hippocampus as a cognitive map*. Oxford: Clarendon Press; 1978.
- [23] Tolman EC. Cognitive maps in rats and men. *Psych Rev* 1948;55:189–208.
- [24] Iaria G, Chen JK, Guariglia C, Pito A, Petrides M. Retrosplenial and hippocampal brain regions in human navigation: complementary functional contributions to the formation and use of cognitive maps. *Eur J Neurosci* 2007;25:890–9.
- [25] Grossi D. *La riabilitazione dei disordini della cognizione spaziale*. Milano: Masson; 1991.
- [26] Grossi D, Modafferi A, Pelosi L, Trojano L. On the different roles of the cerebral hemispheres in mental imagery: the "o'Clock Test" in two clinical cases. *Brain Cogn* 1989;10:18–27.
- [27] Formisano E, et al. Tracking the mind's image in the brain. I. Time-resolved fMRI during visuospatial mental imagery. *Neuron* 2002;35:185–94.
- [28] Sack AT, Camprodon JA, Pascual-Leone A, Goebel R. The dynamics of inter-hemispheric compensatory processes in mental imagery. *Science* 2005;308:702–4.

- [29] Sack AT, et al. Tracking the mind's image in the brain. II. Transcranial magnetic stimulation reveals parietal asymmetry in visuospatial imagery. *Neuron* 2002;35:195–204.
- [30] Bisiach E, Luzzatti C. Unilateral neglect of representational space. *Cortex* 1978;14:129–33.
- [31] Davachi L, Wagner AD. Hippocampal contributions to episodic encoding: insights from relational and item-based learning. *J Neurophysiol* 2002;88:982–90.
- [32] Schacter DL, Wagner AD. Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus* 1999;9:7–24.
- [33] O'Keefe J, Dostrovsky J. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res* 1971;34:171–5.
- [34] Burgess N, Maguire EA, O'Keefe J. The human hippocampus and spatial and episodic memory. *Neuron* 2002;35:625–41.
- [35] Iaria G, Lanyon LJ, Fox CJ, Giaschi D, Barton JJ. Navigational skills correlate with hippocampal fractional anisotropy in humans. *Hippocampus* 2008;18:335–9.
- [36] Maguire EA. The retrosplenial contribution to human navigation: a review of lesion and neuroimaging findings. *Scand J Psychol* 2001;42:225–38.
- [37] Cho J, Sharp PE. Head direction, place, and movement correlates for cells in the rat retrosplenial cortex. *Behav Neurosci* 2001;115:3–25.
- [38] Taube JS. Head direction cells and the neurophysiological basis for a sense of direction. *Prog Neurobiol* 1998;55:225–56.
- [39] Collins DW, Kimura D. A large sex difference on a two-dimensional mental rotation task. *Behav Neurosci* 1997;111:845–9.
- [40] Linn MC, Petersen AC. Emergence and characterization of sex differences in spatial ability: a meta-analysis. *Child Dev* 1985;56:1479–98.
- [41] Sanders B, Soares MP, D'Aquila JM. The sex difference on one test of spatial visualization: a nontrivial difference. *Child Dev* 1982;53:1106–10.
- [42] Voyer D, Voyer S, Bryden MP. Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychol Bull* 1995;117:250–70.
- [43] Barnett MA, et al. Late adolescents' experiences with hand attitudes toward videogames. *J Appl Soc Psychol* 1997;27:1316–34.
- [44] Piccardi L, et al. Walking in the Corsi test: Which type of memory do you need? *Neurosci Lett* 2008;432:127–31.
- [45] Bosco A, Longoni AM, Vecchi T. Gender effects in spatial orientation: cognitive profiles and mental strategies. *Appl Cogn Psychol* 2004;18:519–32.
- [46] Montello DR, Pick HL. Integrating knowledge of vertically aligned large-scale spaces. *Environ Behav* 1993;25:457–84.
- [47] Sadalla EK, Montello DR. Remembering changes in direction. *Environ Behav* 1989;21:346–63.