



Research report

Effect of reference frames and number of cues available on the spatial orientation of males and females in a virtual memory task

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ABSTRACT

The aim of this study was to examine the influence of the number of cues and cue location in human spatial learning. To assess their importance, subjects performed variants of a virtual task called “The Boxes Room”. Participants were trained to locate, in a computer-generated environment with 16 boxes, the rewarded boxes through 8 trials. In experiment I, the number of distal cues available was zero, one, two or the standard arrangement (seven cues). In experiment II, place navigation was compared based on distal landmarks (extra-maze cues placed on the walls) and proximal landmarks (proximal cues placed between the boxes). The results of experiment I demonstrated that one cue in the room is enough to obtain a good performance in the task. Experiment II showed that groups using proximal cues were slower and less accurate than groups using distal cues. In addition, our data suggest that men are better navigators than women, as they found the rewarded boxes sooner and committed fewer errors in both studies. These results indicate that performance can change depending on the number and location of available cues.

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1. Introduction

Navigation through both novel and familiar environments is one of the most important activities for survival of all mobile organisms. In the last 10 years, there has been an increasing interest in understanding human spatial memory by using virtual reality technologies [1,4]. The development of virtual reality-based tasks like the Morris water maze or the radial maze provided tools for understanding human behaviour and made also possible the comparison of different species under similar spatial problems [1]. However, this approximation opens new questions.

There is a wealth of data showing that not only individual landmarks but also their relationships are processed and, therefore, learning a goal position in a visually rich environment may involve a complex spatial representation [7,27,36]. However, it is not clear the minimum amount of cues necessary for an accurate orientation. Hence, Prados and Trobalon [28] and Rodrigo et al. [30] trained rats to find a hidden platform in the Morris water maze with four landmarks available. On the probe trial they removed some of these landmarks and reported that rats succeeded in finding the platform with two cues but they had great difficulties when only one cue was available. It is unknown how many cues are necessary in a virtual environment.

On the other hand, although most spatial navigation experiments have been undertaken using distal cues [11,14], several studies have also demonstrated that proximal landmarks can also support mapping strategies [2,21]. It is often reported that it is easier and faster to train animals in spatial navigation based on distal cues than on proximal cues [9,33]. Is this applicable to virtual reality tasks?

The aim of the present paper was to study how human beings navigate and understand space by manipulating various types of spatial information in a virtual spatial task called “The Boxes Room” [4] which reproduces holeboard demands, a spatial task previously used in rodents [17,20,37]. We conducted two experiments. Experiment I was aimed at manipulating the number of distal cues in the room and their effect on the performance of males and females. Experiment II was aimed at comparing two different sets of cues – distal and proximal cues – and their influence on the performance displayed by males and females. In experiment II, the difficulty of the task, i.e. number of rewards, was also modified in different groups.

2. Materials and method

2.1. Participants

One hundred male (mean age = 22.53; SD = 5.04) and one hundred female (mean age = 20.67; SD = 3.3) undergraduate students from the University of Almería were recruited to participate in this study. Those subjects with impaired vision, neurological disorders or under any medication that could potentially affect their cognitive

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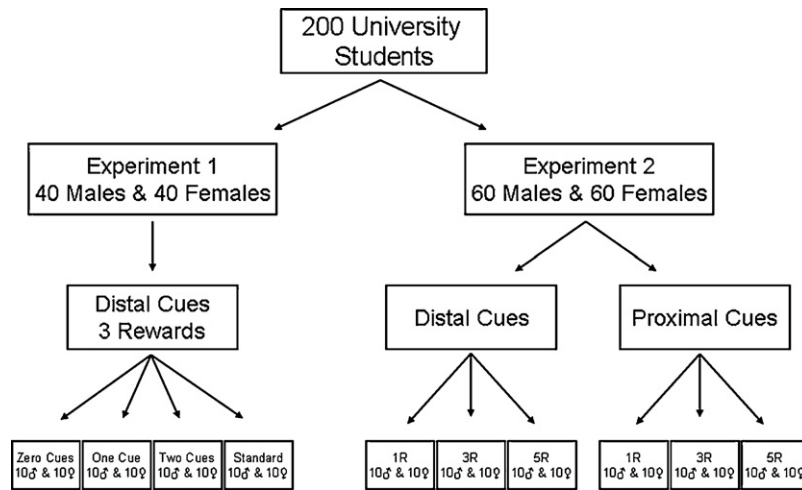


Fig. 1. Diagram of the participants' distribution in experiments I and II. R shows the number of rewards.

performance were excluded. They were randomly assigned to the experimental conditions (Fig. 1).

The participants were informed in advance about the aims and procedures of the experiment. All subjects gave written informed consent and were fully free to leave the experiment at any time. The study was conducted in accordance with the European Communities Council Directive 2001/20/EC and Helsinki Declaration for biomedical research involving humans.

2.2. Apparatus

A Hewlett Packard 2600-MHz portable computer equipped with 3 GB of RAM and a 15.4 XGA TFT color monitor (1920 × 1200) was used for testing. Participants navigated through the maze by manipulating a Logitech joystick. The computer speaker was used to provide auditory feedback to the participants.

2.3. Procedure

Subjects received written instructions on how to proceed with the task. They were asked to find, in a computer-generated environment with 16 boxes, the position occupied by the rewarded boxes, which was constant during the whole experiment. Subjects had to open the lowest number of boxes necessary to discover all the rewarded positions as quickly as possible. The starting position changed from one trial to the next and they began the same number of times from every side of the room. No information regarding useful strategies, the location of the rewarded boxes or any other features of the experiment was provided.

Participants received direct feedback during the experiment. Hence, when they opened a rewarded box it turned green and a pleasant melody sounded. When a wrong box was opened it turned red and an aversive, discordant tone sounded and this was considered an error. The already opened boxes remained green or red during the trial to help the participants to remember their position, whereas non-opened boxes remained brown. As soon as all rewarded boxes were located or 150 s elapsed, the maximum trial duration, a written message appeared on the display congratulating the participant and stating that the next trial would proceed. When a new trial began all the boxes turned back to their original brown color. The inter-trial interval was 5 s. A session consisted of 8 trials.

Experiment I was aimed to determine how distal cues control subjects' behaviour, by reducing the number of cues available in the room. All participants had to discover 3 rewarded boxes, but the number of cues was manipulated to be

zero (bare and identical walls with no marks), one (only a door on a wall), two (one picture and a door in adjacent walls) or standard configuration (a door and a window on one wall, tins and Egyptian pictures in the second wall, three pictures covering the third wall and the fourth wall was bare).

Experiment II was designed to compare how distal and proximal cues can inform during navigation. In the distal cues version, room walls had various marks that disambiguated spatial locations including a door, a window, tins and several pictures (Fig. 2A) (see also [4]). In the proximal cues version, room walls were bare, did not have any pictures or decorations hanging on them and were identical. However, three columns were placed between the boxes (red, blue and yellow, respectively) (Fig. 2B). The number of rewarded boxes on each procedure was manipulated as an independent variable to be 1, 3 or 5.

Upon completion of the experiment, participants filled a questionnaire that queried their age, sex, and experience playing 3D computer games. Specifically, participants marked on a 4-point Likert scale the frequency with which they played such games (0, never; 1, rarely; 2, occasionally; 3, frequently). Joystick handling was assessed by asking participants: Have you ever used a joystick? (Yes/No). In addition, participants were asked about any neurological problem, medical treatments and drug-taking as well. The duration of the entire experiment was approximately 15 min.

3. Results

3.1. Experiment I: Effect of number of cues on spatial orientation

Latency and distance to discover the rewarded boxes as well as the number of errors (visiting a non-rewarded box) in each trial were statistically analyzed in an ANOVA, with Sex and Number of Cues as the between-subjects factor and Trial as the repeated measure factor, followed by post hoc Newman-Keuls test when necessary. Significant differences were reported for $p < 0.05$.

Analysis of the latency to discover the rewarded boxes showed a main effect of Trial ($F_{7,504} = 59.50$, $p < 0.001$) and Gender ($F_{1,72} = 6.41$, $p < 0.05$), but there were neither significant differences

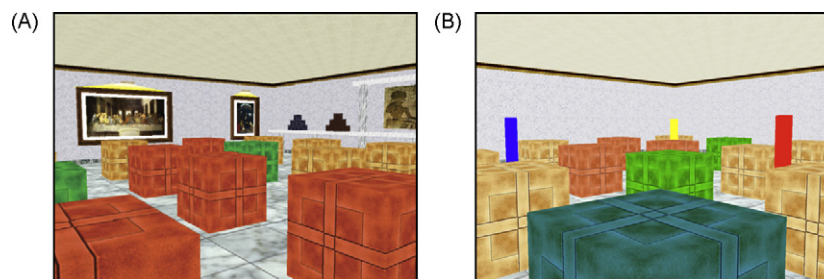


Fig. 2. Representative views of the environments from a participant's perspective. (A) Boxes Room: Distal Cues. The position of the hidden goals was determined relative to extra-maze landmarks. (B) Boxes Room: Proximal Cues. The position of the hidden goals was determined relative to intra-maze landmarks.

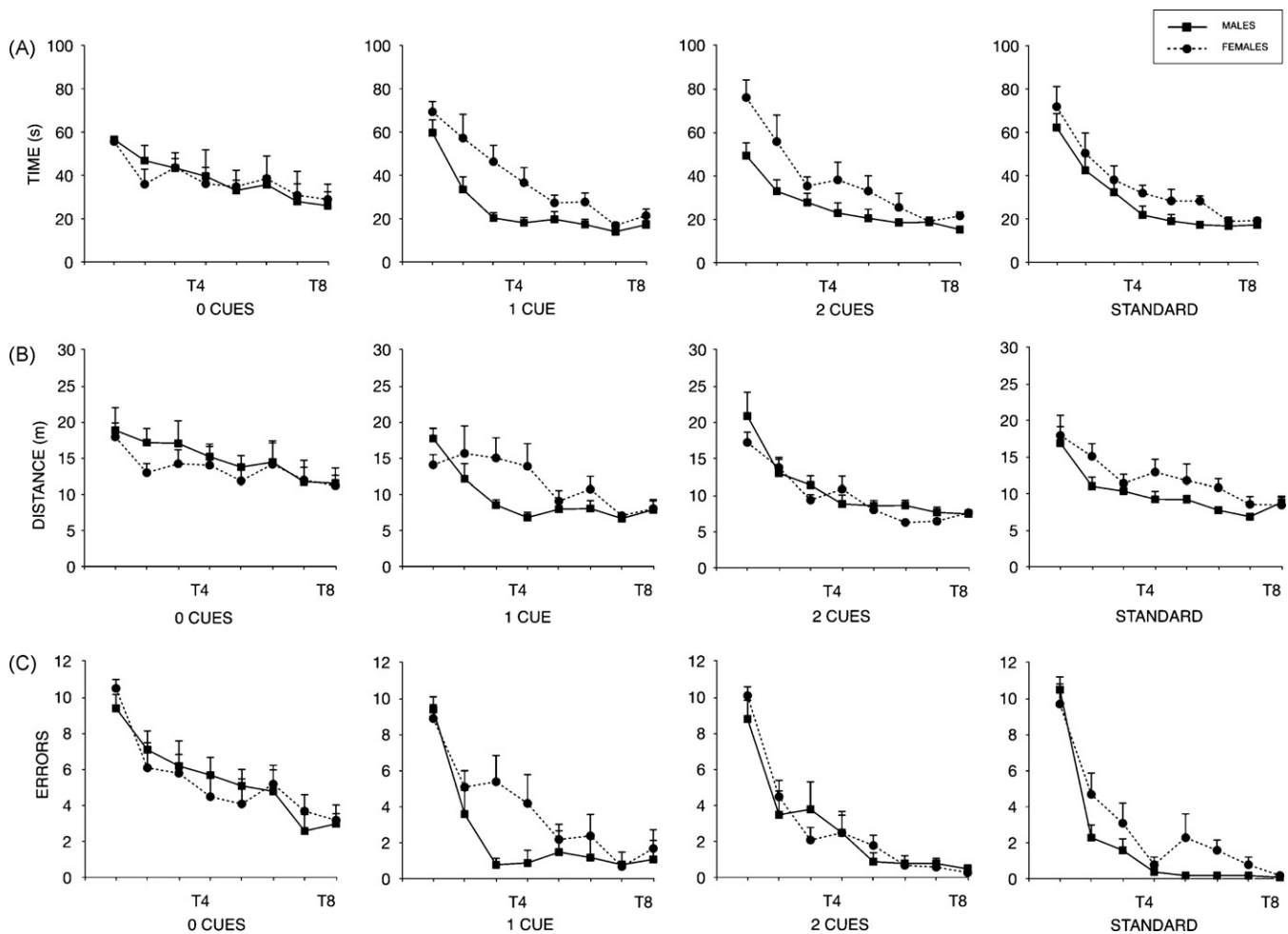


Fig. 3. Latency (A), distance (B) and errors (C) to locate 3 rewards by males and females with zero, one, two and standard cue-configuration. Note that participants using zero cues traveled longer distances to find the rewards than the groups with cues and still committed 2–4 mistakes by the end of the experiment. X axes show the number of trial. Mean + S.E.M.

of Number of Cues ($F_{3,72} = 1.09, p > 0.05$) nor significant interactions. Newman–Keuls test indicated that participants solved the maze faster in the last 2 trials compared to the 4 initial ones ($p < 0.05$), but males found the rewards significantly sooner than females ($p < 0.05$) (Fig. 3A).

Regarding distance covered, there was a main effect of Trial ($F_{7,504} = 26.59, p < 0.001$) and Number of Cues ($F_{3,72} = 4.53, p < 0.05$), but there were neither significant differences of Gender ($F_{1,72} = 0.55, p > 0.05$) nor significant interactions. Newman–Keuls showed that participants travelled shorter distances in the last 2 trials compared to the 4 initial ones ($p < 0.05$), but the group with zero cues travelled longer distances to find the rewards than the groups with one or more cues available ($p < 0.05$) (Fig. 3B).

Analysis of the number of errors disclosed a significant main effect of Trial ($F_{7,504} = 101.01, p < 0.001$) and Number of Cues ($F_{3,72} = 8.95, p < 0.001$), but there were neither significant differences of Gender ($F_{1,72} = 1.73, p > 0.05$) nor significant interactions. Post hoc analysis revealed that participants made significantly fewer errors on each subsequent trial ($p < 0.05$), but the group with zero cues committed more errors to find the rewards than the groups with one or more cues available ($p < 0.05$) (Fig. 3C). Besides, an independent analysis of the number of errors in males and females revealed significant differences in males ($F_{3,36} = 6.54, p < 0.05$) and females performance ($F_{3,36} = 3.22, p < 0.05$). Newman–Keuls test showed that males committed significantly more errors to find the rewards under the null-cue condition than under the three groups with cues ($p < 0.05$), whereas females

committed significantly more errors to find the rewards under the null- and one-cue conditions than under the two- and standard-cues conditions ($p < 0.05$).

Males and females did not differ in their experience playing videogames ($t_{78} = 1.07, p > 0.05$).

3.2. Experiment II: Distal vs proximal cues

Latency and distance to discover the rewarded boxes as well as the number of errors (visiting a non-rewarded box) in each trial were statistically analyzed using an analysis of variance (ANOVA), with Gender, Number of Rewards and Type of Reference Frame as the between-subjects factor and Trial as the repeated measure factor, followed by post hoc Newman–Keuls tests. Significant differences were reported for $p < 0.05$.

Analysis of the latency to discover the rewarded boxes showed a main effect of Trial ($F_{7,756} = 99.91, p < 0.001$), Number of Rewards ($F_{2,108} = 74.5, p < 0.001$), Gender ($F_{1,108} = 19.86, p < 0.001$) and Reference Frame ($F_{1,108} = 9.22, p < 0.05$). There were also significant interactions between Trial \times Number of Rewards ($F_{14,756} = 3.33, p < 0.001$), Trial \times Gender ($F_{7,756} = 2.1, p < 0.05$), Trial \times Reference Frame ($F_{7,756} = 3.01, p < 0.05$) and Reference Frame \times Number of Rewards ($F_{2,108} = 5.54, p < 0.05$). Post hoc Newman–Keuls test of the interaction term indicated that as the number of rewards increased, participants needed more trials to reach their asymptotical level of performance ($p < 0.05$), although males reached their asymptotical level sooner than females ($p < 0.05$). Besides, only when participants

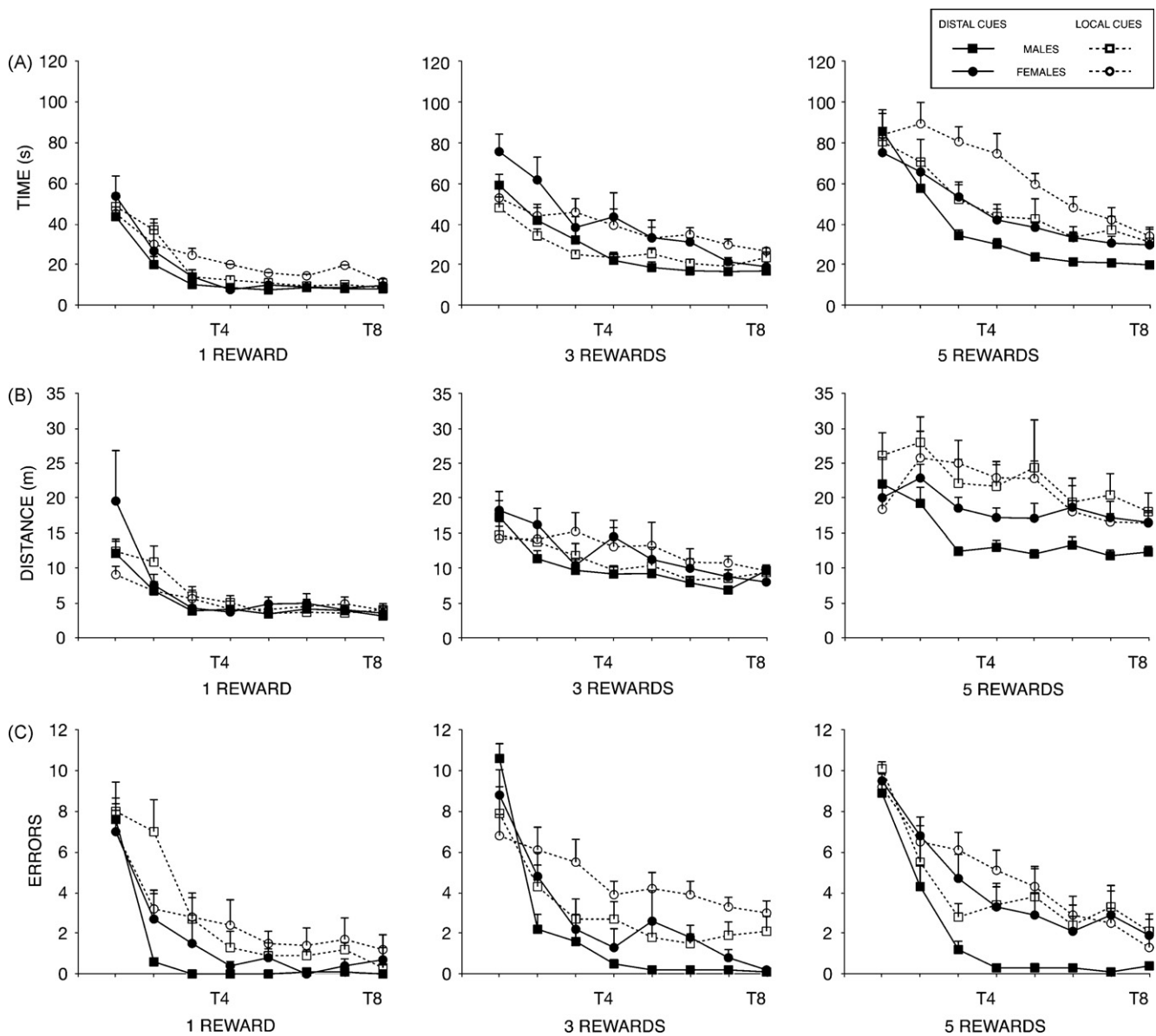


Fig. 4. Latency, distance and errors to locate 1, 3 or 5 rewards by males and females in a distal and proximal cue procedures. Note that as the number of rewarded boxes increased, males found the rewards sooner than females and groups using distal outperformed proximal cues groups (A). Regarding the distance covered, significant differences appeared only in the 5 rewards condition (B). The number of errors is higher with more rewards to discover and for groups using proximal cues (C). Males using distal cues were the most efficient group. X axes show the number of trial. Mean + S.E.M.

had to discover 5 rewards, the distal-cue group outperformed the proximal-cue one ($p < 0.05$). There were not differences between distal and proximal-cue groups for 1 and 3 rewarded conditions ($p > 0.05$) (Fig. 4A).

Regarding distance covered, there was a main effect of Trial ($F_{7,756} = 25.84$, $p < 0.001$), Number of Rewards ($F_{2,108} = 84.91$, $p < 0.001$) and Reference Frame ($F_{1,108} = 4.96$, $p < 0.05$), but there was not a main effect of Gender ($F_{1,108} = 1.78$, $p > 0.05$). There were also significant interactions between Trial \times Number of Rewards ($F_{14,756} = 1.95$, $p < 0.05$), Trial \times Reference Frame ($F_{7,756} = 3.74$, $p < 0.001$) and Reference Frame \times Number of Rewards ($F_{3,87} = 5.54$, $p < 0.05$). Post hoc analysis of the interaction term showed that as the number of rewards increased, participants needed more trials to reach their asymptotical level ($p < 0.05$). The distal-cue group required shorter distances than the proximal-cue group if 5 rewards had to be discovered ($p < 0.05$). There were not significant differences in the distance covered between groups using distal and proximal cues for 1 and 3 rewards conditions ($p < 0.05$) (Fig. 4B).

Finally, analysis of the number of errors disclosed a significant main effect of Trial ($F_{7,756} = 129.08$, $p < 0.001$), Number of Rewards ($F_{2,108} = 10.59$, $p < 0.001$), Gender ($F_{1,108} = 9.23$, $p < 0.05$) and Reference Frame ($F_{1,108} = 19.71$, $p < 0.001$). There were also significant interactions between Trial \times Gender ($F_{7,756} = 3.71$, $p < 0.05$), Trial \times Reference Frame ($F_{7,756} = 3.89$, $p < 0.05$) and Trial \times Reference Frame \times Number of Rewards ($F_{14,756} = 1.84$, $p < 0.05$). Post hoc analysis of the interactions indicated that participants made significantly fewer errors on each subsequent trial, but males reduced their number of errors sooner than females ($p < 0.05$). As the number of rewards increased, participants committed more errors and needed more trials to achieve their asymptotical level ($p < 0.05$). Moreover, groups using distal cues committed fewer errors under the three levels of difficulty (1, 3 and 5 rewards) and they reached their asymptotical level sooner than the groups using proximal cues ($p < 0.05$) (Fig. 4C).

Males and females did not differ in their experience playing videogames ($t_{118} = 1.81$, $p > 0.05$).

4. Discussion

Our experiments showed that the available number of cues as well as their location (distal vs proximal) are important attributes to consider during the spatial memory training in a virtual navigation task.

Results of experiment I showed that participants only need one cue for an accurate performance in the task. They were able to learn about the surrounding environment and its relationship to the rewards. This finding contrasts with those from the animal research, where rodents need at least two cues to orientate themselves [28,30]. It may be that human rate of learning or even human spatial representation is more accurate. Hence, when comparing the performance displayed by rodents and humans in some mazes, several studies have found that rodents need more prolonged trainings than humans to reach their asymptotic learning level [1,3,35]. Nevertheless, it is also important to note methodological differences between our work and those by Prados and Trolalon [28] and Rodrigo et al. [30]. We used a square room containing several boxes that marked the potential locations of the goals, whereas Prados and Trolalon [28] and Rodrigo et al. [30] trained their rodents in a circular pool with a submerged invisible platform, which constitutes a geometrical uniform environment. Hence, our subjects could have profited from geometrical information of the room by using the boxes and their arrangement to improve orientation. This is consistent with the behavior we observed in the null condition. Although the room was deliberately devoid of either internal or external cues; there was a reduction in the number of errors in the last trials, which demonstrates that our subjects were using any source of information to improve their performance, although they still had important difficulties in finding the rewards. Moreover, the existence of significant differences in the learning rates depending on the presence or absence of cues supports a large body of research that has emphasized the importance of distal cues to create the cognitive map that permits orientation using allocentric information [11,14].

In experiment II, the performance of the participants was compared under two different sets of cues: distal and proximal cues. Distal and proximal cues provide different information for navigation and place learning. Distal cues are visual cues located beyond the animals' route, so do not change their relative positions as the animal moves in the environment. In contrast, proximal cues are objects that can be directly approached and left behind, so they change their relative position during navigation. Participants in the distal-cue groups demonstrated a more proficient use of the cues by spending less time, covering less distance and committing fewer errors in finding the rewards than the proximal-cue groups. Visual examination of the trajectories showed that participants in the distal-cue groups reached the rewards by using fairly straight paths from any of the four starting points. In contrast, participants in the proximal-cue groups adopted a less accurate strategy, by moving around the proximal cues until they found the rewards (see Fig. 5). These results are in agreement with other studies demonstrating that proximal landmarks are more difficult to use for accurate task-solving than distal landmarks [9,33]. Nevertheless, we should be careful in interpreting these results since the number of cues available as well as their features were different in the distal and proximal cues versions of the task. Hence, in the distal-cue version, the landmarks consisted in several real objects (a door, a window, tins and pictures), whereas, in the proximal-cue version, the landmarks were three columns that differed in color (red, blue and yellow, respectively).

In addition to this, several studies have attended to the brain structures involved in processing these two kinds of landmarks during navigation. Save and Poucet [33] and Save et al. [34] demonstrated that hippocampal lesions produced an impairment in using

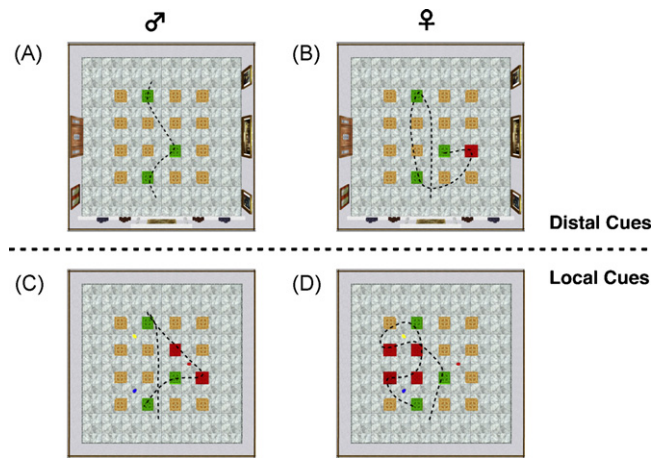


Fig. 5. Representative paths during the final trials by males (A, C) and females (B, D) in the distal and proximal conditions. Note that males were more accurate.

both proximal and distal landmarks whereas parietal lesions produced a deficit only when navigation relied on proximal landmarks. Electrophysiological studies have also showed that the activity of place cells is differently influenced by extra-maze distal and intra-maze proximal cues. Specifically, intra-maze proximal cues seem to be related to spatial tuning of place cells whereas extra-maze distal cues might set the orientation of the place fields of place cells [15,16].

On the other hand, we manipulated the difficulty level by increasing the number of rewarded boxes. Latencies, distances and errors varied according to the number of places to remember as demonstrated in previous studies [4,5]. Hence, when the number of rewards increases, latencies and distances were longer and participants needed more trials to solve the task accurately. It is important to stress that the type of cue, distal vs proximal, interacted with the number of rewarded locations. In the 1 reward condition, all participants were able to finish the task almost without errors. The 3 rewards and 5 rewards conditions were difficult for the proximal-cue group since they err in the last trials. This fact provides additional support for the statement that navigation using proximal cues involves higher cognitive demands [9,33].

Our data suggest that men are better navigators than women, as they found the rewarded boxes sooner and committed fewer errors in both studies. In experiment I, men committed more errors to find the rewards under the null-cue condition than under the three conditions with cues, indicating that one cue is enough for them to locate the rewards. However, women were slower than men under all testing conditions and they did not show significant differences between the null and one-cue conditions. This suggests the existence of sex-related differences in spatial ability; specifically, it seems to be easier to discriminate the reward locations in a poorer environment for men than for women (see Fig. 3C).

In experiment II, women were slower and less accurate than men under the 3 and 5 rewards conditions. Sex-related differences appeared in using both the distal and proximal cues under the 3 reward condition, whereas for the 5 rewards condition there was an advantage for men only in using distal cues. The lack of sex differences with 5 rewards in the proximal cues group could be explained by the higher cognitive demands of this condition, creating difficulties for both sexes.

These findings are in line with previous research on both humans [1,29] and rodents [6,23] showing sex-dimorphism during navigation, with males outperforming females in allocentric orientation tasks. Male advantage was also demonstrated using object location memory paradigms, which require remember the position of objects in a space and therefore share many aspects with

the “Boxes Room” and other spatial navigation tasks. Specifically, clear evidence for more accurate male performance was obtained for metric estimations of the spatial relationships [12,25,26]. In contrast, an absence or even reversed pattern of differences have been reported when the task required objects recognition or binding objects to their locations [8,38]. These results could suggest the existence of gender-related preferences for spatial strategies: males could have a better route knowledge and prefer metric estimations, whereas females could use mainly landmark information [32].

In our experiments, both landmark- and Euclidian-based information were available, however we found that females needed more prolonged training to reach the asymptotic level. This gender-related rate of learning was also reported in previous studies [22,24], with men forming an environmental cognitive map faster than women and reaching sooner the learning criterion in the Corsi Block Test.

Moreover, it has been demonstrated that spatial orientation in humans depends on the integrity of the hippocampus, the right hippocampal activity being associated to accurate navigation [13,19]. However, males and females show additional activations in different structures during navigation [10]. Men exhibit stronger activation in the left hippocampal region, whereas women engage the right parietal and prefrontal areas [18,31,32].

Overall, the experiments presented here demonstrated that the number and location of available cues represent critical factors to be taken into consideration in human spatial navigation, as well as the fact that these attributes affect men and women differentially.

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