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CORRELATIONS BETWEEN SPATIAL SKILLS: A TEST OF THE HUNTER-GATHERER HYPOTHESIS

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Abstract. The hunter-gatherer hypothesis of SILVERMAN and EALS (1992) is the best-supported evolutionary explanation for sex differences in human spatial cognitive skills. It proposes that the sex differences in performance on a range of spatial task are a consequence of males (who hunted much more than did females) being better adapted to encode space allocentrically, and to rely on Euclidian navigational strategies employing distant landmarks, whereas females (who gathered much more than did males) are better adapted to encode space more egocentrically, navigating based more on local landmarks, and to be better able to precisely encode the position of particular objects. We tested this hypothesis by comparing the performance of male and female participants in a virtual navigation task (in which we could manipulate the landmark information available), a virtual dead-reckoning task and an object location memory task. The patterns of sex differences in the spatial tasks were strongly supportive of the hunter-gatherer hypothesis, but the sex-specific correlations between tasks thought to be underpinned by the same spatial-cognitive ability were not always supportive of the hypothesis, suggesting that the hunter-gatherer hypothesis requires some revisions or extensions.

Keywords: spatial cognition, sex-differences, hunter-gatherer hypothesis

INTRODUCTION

One of the largest human psychological sex differences is in spatial ability (LINN and PETERSEN 1985; VOYER, VOYER and BRYDEN 1995). Traditional approaches to these differences have treated them as a consequence of socialization pressures, and while experience clearly matters, more recent evidence illustrating the impact of hormonal effects on brain organization and activation, points to a more basic, biological basis for the differences (CHOI and SILVERMAN 2002; PHILLIPS and SILVERMAN 1997; POSTMA et al. 2004; POSTMA et al. 1999; RAHMAN, ANDERSSON and GOVIER 2005; GRÖN et al. 2000; HALPERN 1996; HAUSMANN et al. 2002; RILEA, ROSKOS-EWOLDSENB and BOLES 2004). Probably the most successful explanation for how a basic, biological sex difference in spatial ability may have

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evolved is the hunter-gatherer (HG) hypothesis put forward by SILVERMAN and EALS (1992). They proposed that the sexual division of labor practiced by our ancestors, in which males predominantly hunted and females predominantly gathered (BIRD 1999; ECUYER-DAB and ROBERT 2004a), could have resulted in differing spatial specializations, since hunting presents different types of spatial challenges from foraging, and strong selection for efficiency in 'both' foraging strategies could result in different spatial specializations in the two sexes.

Males, when hunting, would have ranged further from the home than females in order to track animals and prey. They would have been led into unfamiliar terrain by this prey and then have had to find their way home quickly (COLUCCIA and LOUSE 2004; DABBS et al. 1998; SHERRY and HAMPSON 1997; SILVERMAN et al. 2000). They would have been more likely to use direct routes using distance and directional cues, rather than following the same path home. Remembering starting positions by learning global coordinates would be more reliable than learning local landmarks for this type of task (DABBS et al. 1998; JAMES and KIMURA 1997).

Females, when gathering, would have been more likely to stay nearer to the home, collecting small and immobile food such as plants, locating these resources in complex arrays of vegetation and need to find them at a later time (DABBS et al. 1998; EALS and SILVERMAN 1994; GALEA and KIMURA 1992; JAMES and KIMURA 1997; SILVERMAN and EALS 1992). They probably would have encountered fewer new items than the hunters, and therefore been able to encode detailed information about the objects around them, and thus would be better able to navigate using local landmarks (COLUCCIA and LOUSE 2004; DABBS et al. 1998; ECUYER-DAB and ROBERT 2004a; JAMES and KIMURA 1997).

SILVERMAN and EALS (1992) suggested that traditional spatial tasks, such as mental rotation, that typically find a male advantage, are reflective of attributes such as an allocentric encoding of space, which would have aided efficient hunting. Females, on the other hand were predicted to have developed a system that is better able to recognize and recall spatial relationships and configurations of different objects, and to associate certain locations with particular objects. In line with this reasoning, SILVERMAN and EALS (1992) predicted and found a female advantage on tasks examining memory for the locations of objects.

The HG hypothesis is not the only evolutionary theory of sex differences in human spatial cognition, but it is the theory that explains the greatest proportion of the data and so is the one we sought to probe further. Indeed, in a review of such theories, JONES, BRAITHWAITE and HEALY (2003) outlined seven different evolutionary accounts of sex differences in spatial ability (although the HG hypothesis is counted twice in this scheme – once as male foraging and once as female foraging). JONES et al. actually recommended that the HG hypotheses (among others) be discarded because they apply only to human sex differences, a situation that they regard as rendering them untestable, and conclude that the best-supported theory is that sex differences in spatial ability are a consequence of different home range sizes. This theory does an excellent job of explaining sex and seasonal differences in spatial ability in a range of rodent species (eg. GAULIN and FITZGERALD 1986, 1989; GALEA et al. 1994; GALEA, KAVALIERS and OSSENKOPP 1996), and it seems very likely that this is the ecological factor that selected for superior male spatial abilities in those species in which males range further, making it a clear candidate for explaining sex differences in other groups. However, given that within the rodents there are monogamous species that show no sex differences in spatial ability, suggesting rodent-specific adaptations, human sex differences (even if they are due to range size differences), are likely to be a consequence of an independent evolutionary event, and so the rodent data are not directly relevant to evaluating any specific hypothesis about the origin of human sex differences.

ECUYER-DAB and ROBERT (2004b) directly tested the possibility that human home range size predicted spatial abilities, and found evidence for greater ranging in males, even in a modern, industrialized society (Montreal), and for males outperforming females on all tasks except object location memory. Home range size predicted performance on most tasks for males, including object location memory, but only predicted performance on an embedded figures test for females. These results are most obviously consistent with the possibility that greater navigational *experience*, driven by larger home ranges, improves spatial abilities. The effect may have been harder to detect in females because there was much less variance in home range size to correlate with performance. In any case, a significant positive correlation between home range size and object location memory in males, and no significant negative correlation between these two measures in females, render this hypothesis unlikely to be a good explanation of better performance by females on tests of object location memory. ECUYER-DAB and ROBERT (2004b) conclude, in fact, that the HG hypothesis is "still relevant" to understanding the superior female object location memory originally discovered by SILVERMAN and EALS (1992).

A number of studies have directly reexamined the female advantage for remembering object locations reported by SILVERMAN and EALS (1992) and EALS and SILVERMAN (1994). POSTMA, IZENDOORN and DE HAAN (1998) and POSTMA et al. (2004) failed to find the reported female advantage, but in one case used fewer objects than in the original studies (and so the task may have been too easy for males), and in the other used a different retention interval (3 minutes rather than immediate) and only asked participants to mark objects that had moved. JAMES and KIMURA (1997) did replicate SILVERMAN and EALS (1992) findings, however, this female advantage was only seen when objects were not moved to previously unoccupied locations. They suggest that when objects are moved to previously unoccupied positions, object identity information is deemphasized and location can also be determined by unfilled and filled space, meaning that 'both' sexes use different but equally adaptive strategies.

MCBURNEY et al. (1997) also found a female advantage on the commercial concentration game "Memory", in which participants are required to match pairs of objects on cards that are face down in an array in front of them. No more than two cards are turned over at any time, and if there is no match they are replaced in their respective positions. This female advantage was replicated using a dynamic condition on a computerized version of the game (TOTTENHAM et al. 2003).

Since the HG hypothesis predicts that females are better able to use nearby information and males better able to use more distal information, SANDERS, SINCLAIR and WALSH (2007) predicted and found an interaction between participant sex and the perceived location of the to-be-solved task in a range of visuo-spatial tests. When the task was presented in near space (in which the objects are directly manipulable), females outperformed males, but when the task was projected into far space (outside extra-personal space) males outperformed females. This is another example of a successful prediction about performing spatial tasks based on the HG hypothesis.

The most straightforward way to test the hypothesis that the sex differences in spatial abilities are a consequence of different evolved navigational systems is to compare males and females on tasks that actually require navigation, and a number of investigators have done so. SAUCIER et al. (2002) asked participants to navigate to four unknown destinations on a university campus. They provided the participants with either Euclidean instructions, which included cardinal directions and metric distances, or landmark instructions, which included salient landmarks and relational (left/right) turn directions. As predicted by the HG model, females following the Euclidean instructions were slower and made more errors than males, and than other females who had been given landmark instructions. In contrast with the model's predictions, males performed about as well as females using landmark instructions. In a similar vein, PACHECO-COBOS et al. (2010) showed that women gathered mushrooms more efficiently than men in a real-world foraging setting in Mexico.

Male advantages have been found in 'both' a virtual labyrinth maze, containing no local landmarks (MOFFAT et al. 1998) and a virtual analog of the Morris Water Maze, when local landmarks were rendered useless (SANDSTROM et al. 1998). The male advantage persists even after controlling for computer game experience (ASTUR et al. 1998, 2004). Females perform best in the virtual Morris Water Maze when landmarks are useful, although, again, not better than males (SANDSTROM et al. 1998). Performance on the virtual Morris Water Maze also correlates with performance on another male advantage task, mental rotation (ASTUR et al. 2004; DRISCOLL et al. 2005), which is consistent with HG hypothesis' prediction that spatial tasks showing male advantages are those that share elements with hunting-based, geometric, Euclidean or allocentric navigation. No previous study has found better female performance on a navigation task, even when the use of landmarks is encouraged. One of the aims of the current study (as explained later) was to design a task in which local landmarks are needed to successfully navigate, and so in which females might outperform males.

Greater aptitude for using allocentric cues should also make males better at dead-reckoning – indicating which direction they have come from after traveling along a winding path. SILVERMAN et al. (2000) designed a dead-reckoning task that replicated the navigational aspects of hunting. Following an experimenter through a moderately dense wooded area, participants stopped at designated points along the way and indicated the direction of the starting point. At the end of the course, participants were asked to return to the starting point by the most direct route. Males indicated more accurate directions and found more direct routes to the starting point than females. A significant correlation was found between scores from this task and 3D mental rotation performance when data from both sexes was included, but there was only a non-significant trend in the expected direction when the male data were analyzed separately. Differences in pointing accuracy are also found in 3D computer-simulated environments (LAWTON and MORRIN 1999; WALLER et al. 2004), suggesting that differences occur regardless of whether or not there is vestibular and kinaesthetic input.

If the HG theory of spatial sex differences is correct, and this is the cause of males' and females' different navigation strategies, then, in addition to sex differences in the predicted direction on particular spatial tasks, there should be correlations between navigation skills and tasks that are thought to replicate the spatial demands of hunting and gathering. Few studies have looked at correlations between spatial tasks that reflect these demands, and actual navigation performance. In the studies that have, the findings are variable. Correlations are sometimes found between navigation tasks and memory/concentration tasks (MCBURNEY et al. 1997), while at other times no correlations are found (GALEA and KIMURA 1992). Some correlations have been found between traditional spatial tasks and navigation performance (ASTUR et al. 2004; MOFFAT et al. 1998), though some studies suggest these tasks explain more variance in male navigation (BOSCO, LONGONI and VECCHI 2004), whilst other studies have found significant correlations for females but not males (SILVERMAN et al. 2000). Mental rotation performance was found to correlate with errors when following Euclidean navigation instructions, but not landmark instructions (SAUCIER et al. 2002).

In the current study, we used three tasks to investigate the HG theory's predictions that sex differences in both navigation and other spatial cognition tasks are due to males and females having evolved different aptitudes for using either allocentric, distal navigational cues or local, landmark-based navigational cues. The *navigation task* involved participants navigating through a virtual environment in three different conditions where environmental cues were manipulated, to test the HG theory prediction that males and females navigate by different cues. A unique feature of this task is that all participants learned to navigate through the maze in the presence of both distal and local landmarks, and were then tested on their ability to navigate with only one set of cues available. Previous evidence for a sex-difference in navigational style (reviewed earlier) has come from either self-reports of information used or navigation tasks in which participants are forced to use one or other kind of information form the beginning. Our task was designed to enable participants to learn the route as naturally as is possible in a virtual task, and then to probe the information upon which that navigation was based. A *pointing task* was designed to replicate hunting-type navigation and to assess dead-reckoning ability. In a virtual environment, participants had to follow a novel winding path, designed to be analogous to tracking an animal through unknown terrain, and to stop at set points and indicate the direction of the starting position. An *object location task* was also included. Unlike most object location tasks, however, this task involved a picture of a real scene and participants had to *place* some of the objects back in their respective positions in a subsequently empty scene, in order to maximize the demands placed on being able to remember what was where. The decision to only include some of the objects was based on the observation by JAMES and KIMURA (1997) that when all objects are included, males may be able to use information about filled and unfilled space to determine an object's location, and thus may cause confusion in interpretation of results.

Correlations between these tasks were then examined to test the extent to which the sex differences in traditional spatial tasks predicted (and found) by the HG theory do actually depend on differences in navigational ability/style. We were particularly interested to examine whether the unique prediction of the HG theory – superior female performance on object location memory tasks – is, in fact, based on a navigation style that focuses on local landmarks.

MATERIALS AND METHODS

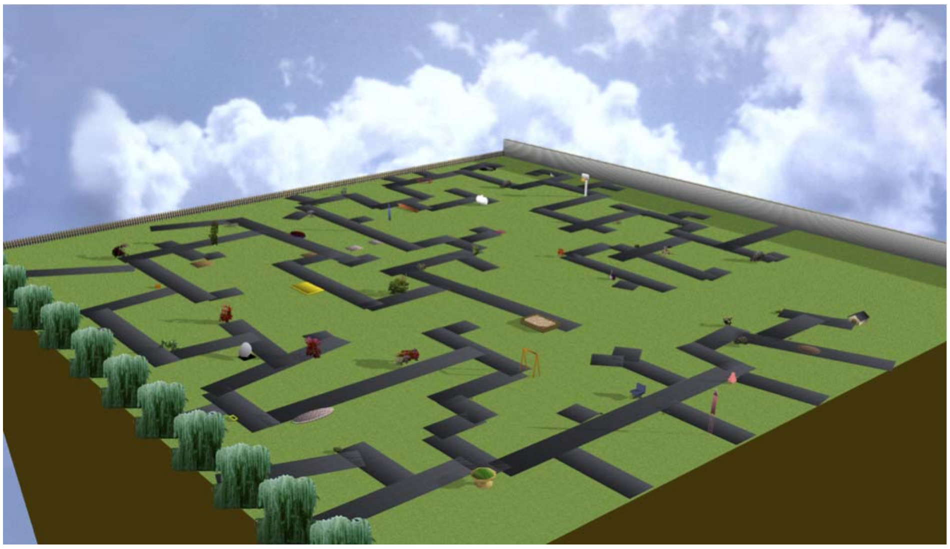
Participants

A total of 65 undergraduate students of Macquarie University participated in the study for nominal course credit. The mean age of participants was 23.38 (males 22.15, and females 24.66). Two participants did not complete the route-learning task because they went over the 1 hour time limit for the experiment. The photograph for one of the participant's gathering task did not save, and therefore positional errors could not be analyzed. The data from the other tasks completed by these participants was included.

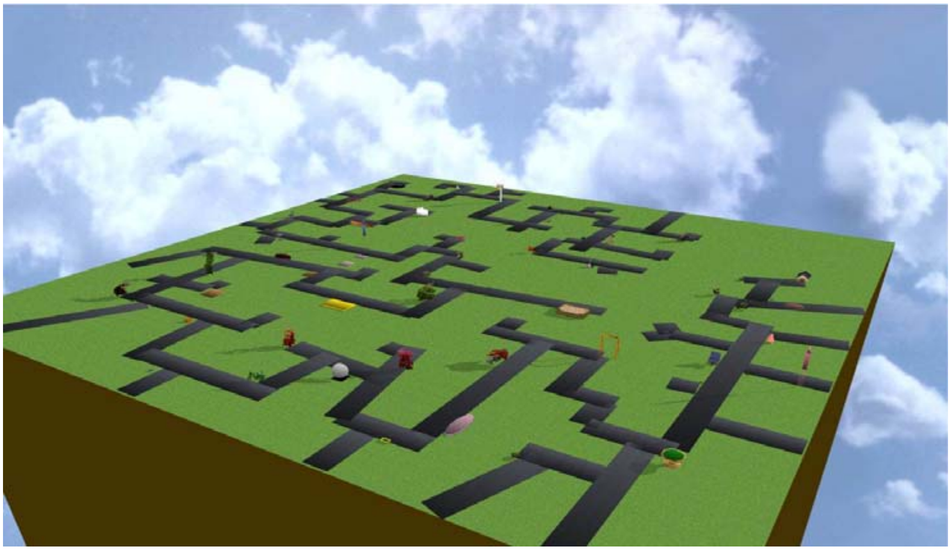
MATERIALS

Navigation task

A 3D environment was created using Professional Home Design Platinum® version 8 by Punch! Software®. The course was in an outdoor environment which had 4 distinct distal views (a tall wall, a picket fence, a row of tall trees, and clouds in a blue sky) surrounding the course in a square (see *Figure 1*). There were also common objects along the paths at random positions. There was only one correct way through the course, which the participant was required to find and navigate through

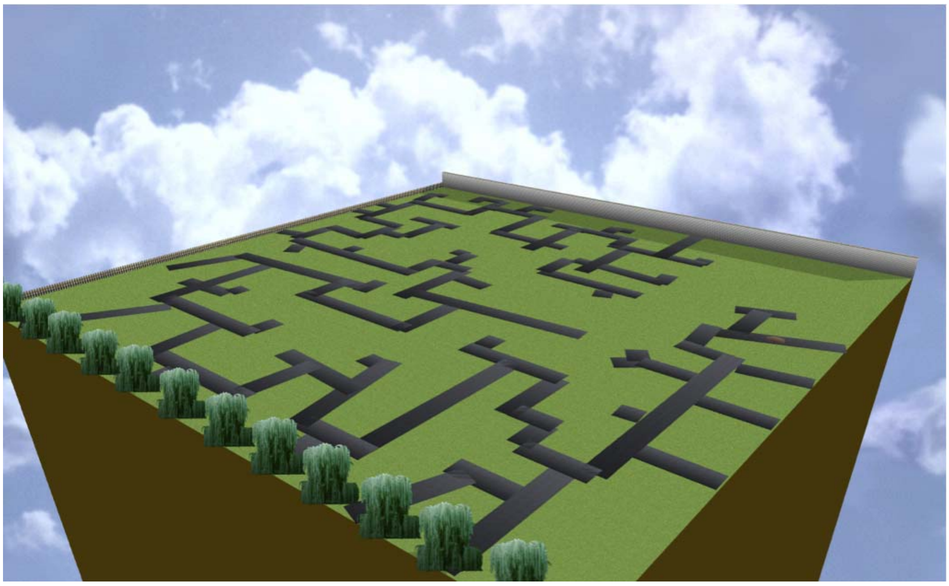


a)

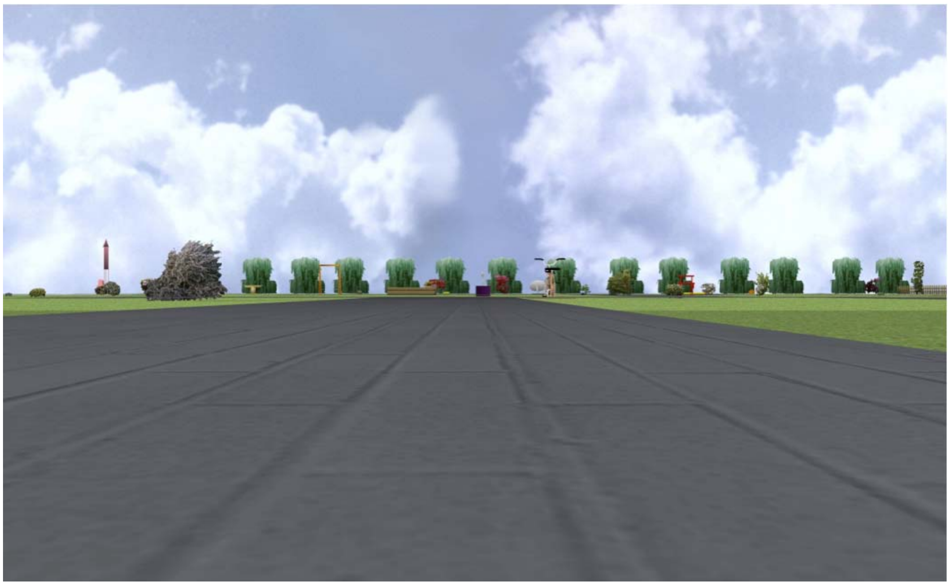


b)

Figure 1. Navigation course: *a)* shows a perspective view of the 'both' condition, *b)* shows a perspective view of the 'object-only' condition

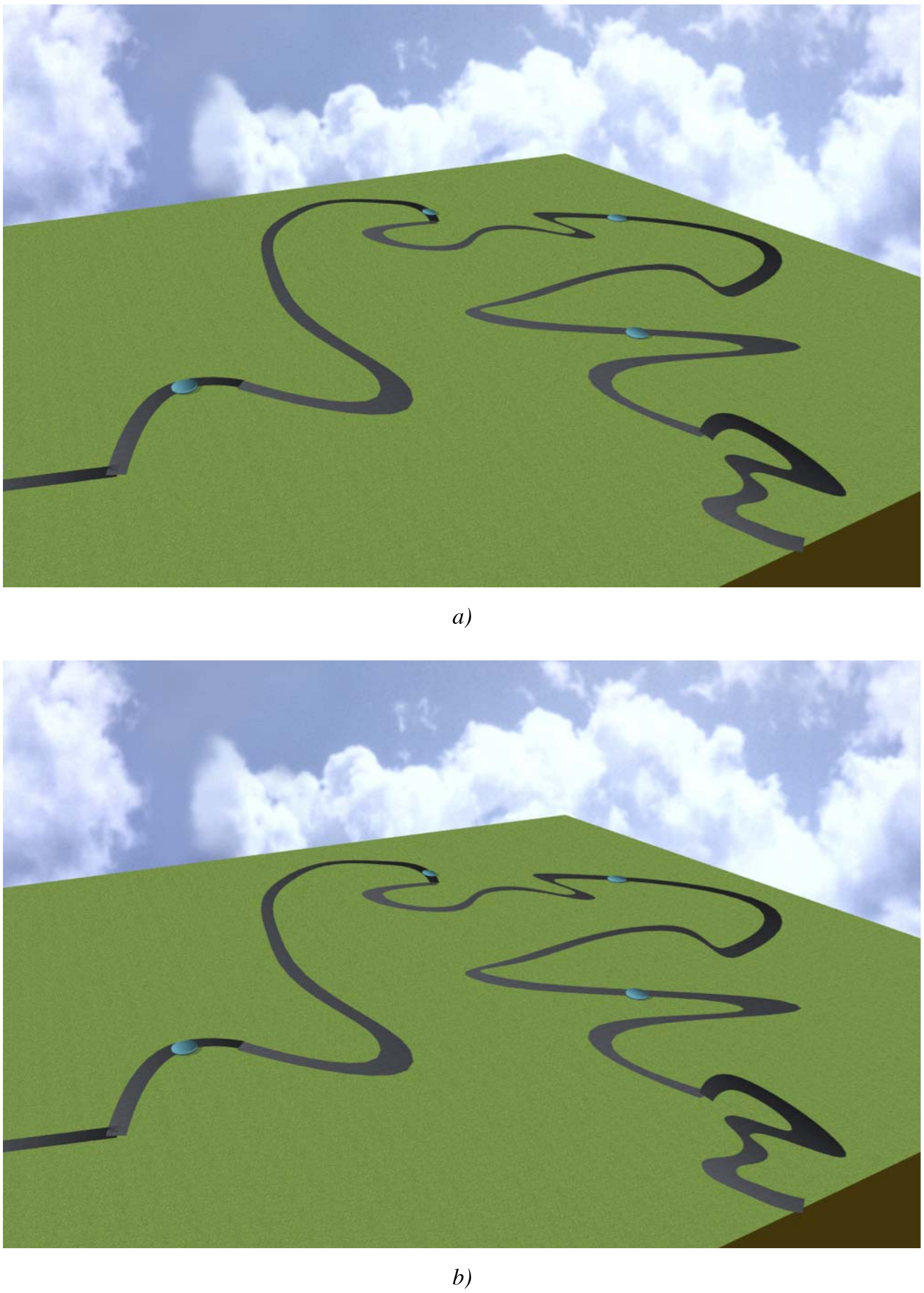


c)



d)

Figure 1. Navigation course: *c)* shows the distal-only condition,
d) shows the participant’s view of the course



a)

b)

Figure 2. *a)* aerial and *b)* ground view of the pointing task

using a mouse. At the end of the course there was a flat brown circle and the participant was informed they had reached the end. The task was run on a Pentium 4 computer with 2GB RAM running windows XP. A Sony 19-inch SDM-X93 LCD monitor (1280 × 1024 resolution) was used with the participant sitting approximately 50cm away.

There were three different courses designed for this task: the ‘both’ condition described above and the two other courses were the object-only and distal-only conditions, which either had just the distal landmarks removed or just the proximal landmarks removed respectively. *Figure 1* displays the different conditions. The course was quite long and difficult in order to maximize the possibility of finding differences.

Pointing task

The pointing task was constructed using the same software and methods as in the navigation task. There were 4 stopping points along the path, which contained only grass, sky, and raised blue circle stopping points. A ‘compass’ was created with a circular piece of cardboard with marks on the outer edge ten degrees apart and a pointer attached to the centre of the circle. *Figure 2* shows an aerial and ground view of the course.

Object location task

Based on the SILVERMAN and EALS (1992) stimulus room and object array experiments, a digital photograph of a picnic scene containing 27 different objects was taken and printed on an A4 page. In the test phase, a picture of an empty scene with just a picnic rug was viewed and 18 cut-out images of the original objects were placed beside the picture. *Figure 3* displays the learning and test picture scenes used.

General procedure

Participants first completed the navigation task, with the object-only and distal-only conditions being counterbalanced in order to reduce any possible effects of order and practice. This was followed by the pointing task and finally the object location task.

a)

b)

Figure 3. *a)* learning and *b)* test scenes in the object location task. See text for details

Navigation task

Instructions and player controls

Participants were asked to keep their ‘player’, which was a small yellow figure, at the bottom centre of the screen, and informed that this was the player they had to move along the path until the end. Participants had complete control over movement for this task. To move the player, the participant was required to hold down the button while pushing the mouse in the direction they wished to travel.

Speed was determined by pressure on the mouse. Participants had to learn to control the mouse by gently nudging it, and pausing in order to control speed of movement and to remain on the path. Participants were instructed to stay on the path and to follow it until they reached the end.

Navigation procedure

Participants navigated their way around the course four times. The first time was the learning trial, in which the participant became familiar with the course and confident in their ability to control movement. The learning trial was the same as the ‘both’ condition where ‘both’ sets of landmarks were visible.

It was explained that the aim was to reach the brown circle at the end of the course. Participants were told that there was only one correct route through the course, and wrong turns along the way. They were told that time and speed were not recorded, and so to go as slowly as was comfortable in order to stay in control. Participants were not explicitly told that wrong turns were being recorded, but that their ability to get to the end was being examined. A wrong turn was recorded as an error if the participant turned and started to travel down the wrong path, but not if they only turned and “looked” in the wrong direction.

In the learning trial, if a participant was heading back in the direction of the starting point, they were informed after approximately three turns that they had already been down that path. As speed of movement was primarily determined by the skill with which the participant controlled the mouse, time taken to reach the end was not a reliable measure of navigation knowledge and so was not recorded.

After completing the learning trial, the participant completed the ‘both’ condition followed by object-only and distal-only conditions in a counterbalanced order. While the program was loading the object- and distal-only conditions, the participant was informed that the course would be the same except that the objects or distal cues would be removed respectively.

Pointing task

Participants were required to follow the single winding path. Participants were instructed to go as slowly as necessary to stay on the path and not lose their sense of direction. When participants reached one of the four blue circles on the path, they were given the 'compass' set on 0 degrees facing straight ahead, and asked to move the central arrow to indicate the direction of the original starting position. The pointing position was recorded and error was measured as deviation (in degrees) from the correct position at each blue circle.

Object location task

Based on the SILVERMAN and EALS's (1992) stimulus room task, the picture of a scene was placed in front of participants. After two minutes the picture was taken away, and participants were immediately given another picture of the empty scene with just a picnic rug, and cut-outs of 18 of the 27 original objects. Participants were given two minutes to place these objects back in their original positions. A photograph was then taken for later scoring, and to make further observations regarding positions of objects.

Photographs were displayed on a computer monitor with a grid overlaid in order to more precisely measure positional errors. The grid divided the photograph into 11 × 8 segments. Participant ID, but not participant sex, was known when scoring. Objects were recorded as correct if they were within a one square grid radius of where the object was in the original scene.

RESULTS

Navigation task

A mixed 2 × 3 (sex x landmark condition) repeated measures ANOVA was carried out. Condition was found to be significant (Wilks' Lambda = .809, $F(2, 62) = 7.303$, $p = .001$). There was also a significant interaction between condition and sex (Wilks Lambda = .312, $F(2,62) = 68.413$, $p < .0005$). The pattern of differences for the three conditions is shown in *Figure 4*.

To investigate where the differences occurred for each sex, tests of simple effects for condition and sex were carried out. Bonferroni adjustments were made at $.05/6 = p = .008$. For females, there was a significant difference in errors made between the 'both' condition ($M = 6.688$, $SD = .407$) and the object-only condition ($M = 4.313$, $SD = .528$) ($p < .0005$) and the object-only and distal-only conditions ($M = 7.000$, $SD = .493$) ($p < .0005$). Females made significantly fewer errors in the object-only condition compared to the 'both' and distal-only conditions. There was no significant difference between the 'both' and distal-only conditions. For males, there was a significant difference in the number of errors made in the 'both' condition ($M = 4.909$, $SD = .404$) compared to the object-only ($M = 6.394$, $SD = .527$) ($p = .002$) and distal-only ($M = 2.061$, $SD = .488$) ($p < .0005$) as well as between the object-only and distal-only conditions ($p < .0005$). Males made significantly fewer errors in the distal-only condition compared to the 'both' and object-only conditions, and significantly fewer errors on the 'both' condition compared to the object-only condition.

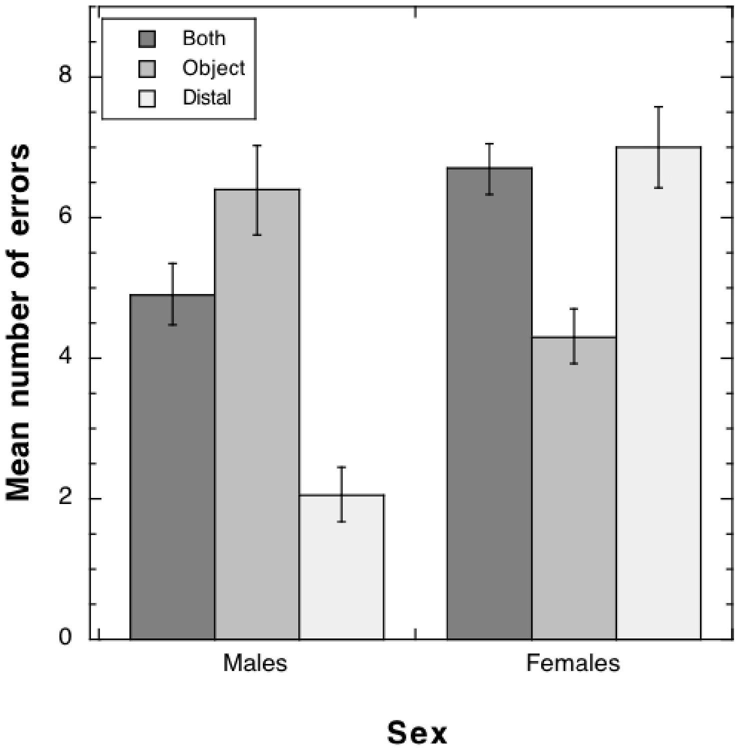


Figure 4. Mean errors (wrong turns) in the 3 conditions by females and males in the navigation task. Error bars represent 95% CI

For the simple effect of sex, Bonferroni adjustments were made at *p* .05/3 = .016. The difference between sexes was significant in the 'both' (*p* = .003), object-only (*p* = .007) and distal-only conditions (*p* < .0005). Females made significantly fewer errors than males in the object-only condition but significantly more errors than males in the distal-only and 'both' conditions.

Pointing task

As in the navigation task a mixed 2 × 4 (sex x circle position) repeated measures ANOVA was used. The main effect of pointing position was significant (Wilks

Lambda = .473 $F(3, 61) = 22.642$, $p < .0005$) as was the interaction between sex and pointing position (Wilks Lambda = .770 $F(3, 61) = 6.077$, $p = .001$). The pattern of differences for the 4 pointing positions is shown in *Figure 5*.

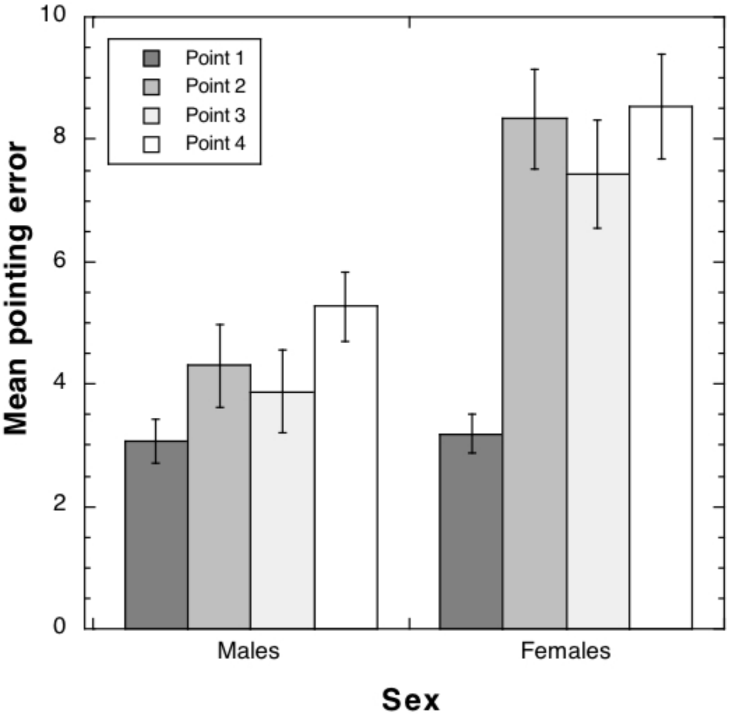


Figure 5. Mean accuracy deviations from correct direction by females and males. Error bars represent 95% CI

Interaction contrasts indicated that the pattern of differences between Point 1 and Point 2 ($p = .002$) and Point 4 ($p = .002$) were significantly different between the sexes. The difference between Point 1 and Point 3 was not significant at the $p = .008$ level ($p = .016$).

For the simple effect of pointing position Bonferroni adjustments were made at $.05/12 = p = .004$. For females, there was a significant difference in the number of errors made at Point 1 ($M = 3.188$, $SD = .338$) compared to Point 2 ($M = 8.344$, SD = .747) ($p < .0005$), 3 ($M = 7.438$, $SD = .790$) ($p < .0005$) and 4 ($M = 8.531$, $SD = .732$) ($p < .0005$). Females made significantly fewer errors in Point 1 compared to the other three points. Males had only one difference close to significance at the $p =$

.004 level, between Point 1 (*M* = 3.061, *SD* = .333) and Point 4 (*M* = 5.273, *SD* = .721) (p = .005). Males made fewer errors at point 1 compared to Point 4.

For the simple effect of sex, Bonferroni adjustments were made at p = .05/4 = .012. There was no significant difference between the sexes at point 1. There were significant differences between the sexes at point 2 (p = .001), Point 3 (p = .008), and Point 4 (p = .003). Males made significantly fewer pointing errors than females at all of these points.

Object location

For this task a univariate ANOVA was carried out. A significant sex difference was found for correct score ($F_{1,\,63}$ = 70.421, p < .0005). Females placed significantly more objects in their correct location than did males, as is shown in *Figure 6*.

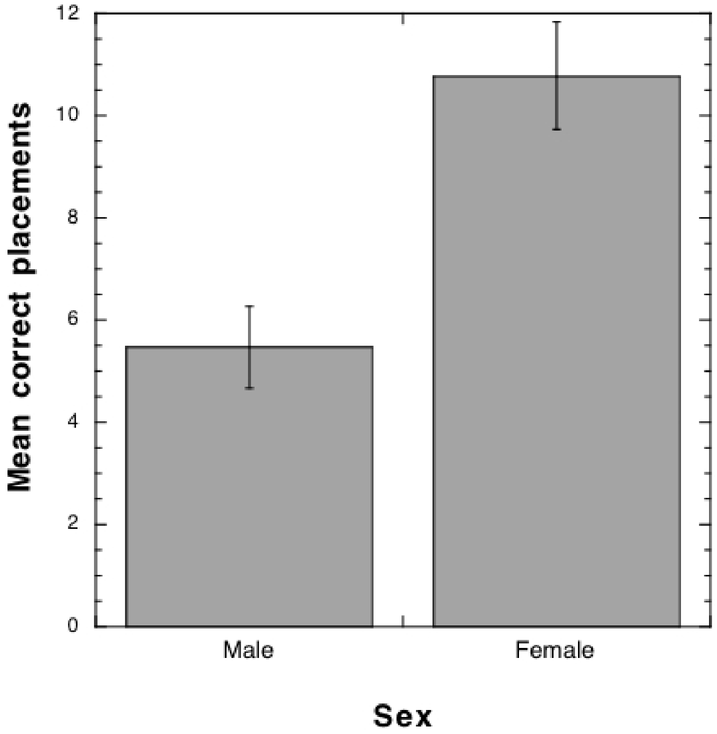


Figure 6. Mean correct placements in the object location task by females and males. Error bars represent 95% CI

Correlations

Correlations between the tasks were calculated for the data from ‘both’ sexes combined (shown in *Table 1*) and for males and females separately (shown in *Table 2*). We used the score from trial 4 in the pointing task in these correlations since it was the trial on which male and female performance were predicted to be the most divergent. Since we examined 10 correlations per data set we adjusted the α rate to 0.005. Significant correlations under these criteria are in bold, and those approaching significance are in italics. The patterns of correlations will be discussed later.

Table 1. Correlations between tasks collapsed across sex

	Object	Distal	Point 4	Object location
Both	**r =.355**	**.541**	.196	.132
	p =.004	**.000**	.117	.293
Object	1	.234	–.126	**–.364**
		.061	.838	**.003**
Distal		1	*.306*	**.397**
			.013	**.001**
Point 4			1	**.373**
				.002

Significant correlations are in bold, those approaching significance are in italics. Both, Object and Distal are errors made on the three navigation task conditions, Point 4 is errors made in the pointing task judgments at Point 4, Object location is the number of correct placements made in the object location task.

Table 2. Correlations between tasks for males and females analyzed separately

	Both	Object	Distal	Point 4	Object location
Both	1	.299	.293	–.245	*–.390*
		.096	.104	.176	*.027*
Object	**.647**	1	**.655**	–.163	.098
	.000		**.000**	.371	.595
Distal	**.637**	**.783**	1	.004	–.065
	.000	**.000**		.983	.725
Point 4	**.459**	*.369*	.255	1	.170
	.007	*.035*	.152		.353
Object location	–.040	–.265	*–.364*	.151	1
	.824	.136	*.037*	.400	

Correlations for female participants are in red, male participants in green. Significant correlations are in bold, those approaching significance in italics. Both, Object and Distal are errors made on the three navigation task conditions, Point 4 is errors made in the pointing task judgments at Point 4, Object location is the number of correct placements made in the object location task.

DISCUSSION

The aim of this study was to investigate predictions based on SILVERMAN and EALS's (1992) HG theory of sex differences in spatial cognition. Of most interest was the relationship between navigational skills and forms of spatial tasks that replicate cognitive demands used for hunting and gathering. Most of the hypotheses were supported.

Navigation task

On the basis of SILVERMAN and EALS's (1992) HG theory, which suggests that males and females navigate using different environmental cues, it was predicted that after learning a novel route through a 3D virtual environment, males and females would be differentially affected by the removal of either local or distal landmarks.

Males were more affected by the removal of distal cues than the removal of proximal cues, and were more affected than females. This was demonstrated as males made significantly more errors in the object-only condition than the distal-only condition, and significantly more errors than females. There was also a significant difference between errors made in the 'both' and the distal-only conditions with males making fewer errors in the distal condition. This finding may demonstrate learning across trials as the distal condition was completed after the 'both' condition, or alternatively it could mean that males are distracted by local objects. Males did make significantly more errors in the object-only condition compared to the 'both' condition, suggesting that if learning occurred, distal cues were involved, or if objects were a distraction and males also had no distal cues, they would find it much harder to navigate.

Male performance scores in this task support the HG hypothesis. It appears that males perform significantly better on navigation tasks that include global information, and perform better when proximal cues are not present.

Females were affected more by the removal of proximal cues than distal cues, and were affected more by the removal of proximal cues than males. Females made significantly more errors in the distal-only condition than the object-only condition, and compared to males. There was a significant difference in number of errors made between the 'both' condition and the object condition. This demonstrates learning occurred as fewer errors were made in the object condition. No such learning appeared to occur for the distal-only condition. Females were unable to improve their scores in the distal condition. Females performed significantly better when proximal cues were present than when they were not, and did not appear to be disrupted by the removal of distal cues. They also did not appear to be as disadvantaged by the removal of proximal cues as scores in the distal condition were not significantly lower than in the 'both' condition.

On the basis of these findings it may be concluded that male navigation is significantly affected by removal of distal cues, while female navigation is more affected by removal of proximal cues. These findings are supported by other studies demonstrating that males and females use different information for navigation (LAWTON 1994; SANDSTROM et al. 1998; SAUCIER et al. 2002). They are also in line with the HG theory's prediction that males rely on global and distal information, while females rely on local landmarks (SILVERMAN et al. 2000). The fact that males were more affected by the removal of distal cues than females were by the removal of proximal cues, suggests females may use some distal information. This is also the first navigation task to show a female advantage – as predicted by the HG theory, females outperformed males when navigating with local, object-based cues alone.

Pointing task

The HG theory proposes that because males hunted more frequently they are more likely to use a global orientation strategy to maintain a bird's eye view. It is useful for hunters to ignore much of the detail of local objects and take the most direct path home, and thus males evolved cognitive adaptations to facilitate this (DABBS et al. 1998).

There were no significant differences between males and females at point 1, but males showed significantly greater accuracy over the 2nd, 3rd and 4th points, suggesting males were better at dead-reckoning, whilst females were not able to update direction as the difficulty of the task increased.

These findings are consistent with previous data showing that males are more accurate at pointing to unseen landmarks in both the real environment (LAWTON 1996; SILVERMAN et al. 2000) and in a virtual environment (LAWTON and MORRIN 1999).

Object location task

The object location task was designed to be more similar to the spatial cognitive demands used for gathering than tasks typically used. It was predicted that as ancestral women were gatherers, women would have evolved superior object memory and location compared to males.

Females were significantly more accurate in placing objects back in their location in a real world scene, thus demonstrating their proficiency in remembering objects and their locations. This is in line with previous research findings showing that females are better at object location and memory in paper-and-pencil location exchange tasks, and real-world object arrays (JAMES and KIMURA 1997; SILVERMAN and EALS 1992). As previously mentioned, only 18 of the original objects were used in the test phase, preventing participants relying on information about filled and unfilled space, thus ensuring it was testing their skills in object memory and location.

Correlations

The HG theory proposes that the cause of spatial sex differences *and* dimorphic navigation strategies is the differential spatial demands of hunting and gathering. If this is so, then there should be relationships between tasks employing the cognitive spatial demands of hunting and navigation conditions that would be advantageous to a hunter, and relationships between a task employing the cognitive spatial demands of gathering and navigation conditions congruent with gathering.

As might be expected, in the data collapsed across sex, there were significant correlations on the navigation task between performance in the 'both' condition and the distal and object conditions. This is likely to be a consequence of the reliance of overlapping navigational cues in such conditions. For example, individuals who navigate well using distal landmarks will do well in the distal condition and the 'both' condition, since such landmarks are available in each case. As predicted by the HG hypothesis, there is a negative correlation between performance on the object location task (scored as number correct) and performance on the object-only navigation condition (scored as errors). These two tasks are thought to tap similar spatial cognitive mechanisms – those useful for gathering – and so they should be related. The HG hypothesis is also consistent with the fact that performance on hunting-based spatial tasks, like navigation in the distal condition and performance in the pointing task, are significantly negatively related to performance in the object location task (the negative relationship produces positive correlation coefficients since navigation performance is measured as errors and object location performance measured as number correct). The HG hypothesis also predicts a relationship between performance in the distal navigation condition and on the pointing task, since these are both hunting-based cognitive skills, and that relationship approached significance in the current data set. The data from both sexes analyzed together, then, provides further evidence in support of the HG hypothesis, but the difficulty with interpreting correlations from the collapsed data is that males and females differed in the predicted directions on the individual tasks, and so the correlations may well be being driven by good male performance and poor female performance on the "hunting" tasks and good female performance and poor male performance on the "gathering" tasks. In order to avoid this difficulty it is important to consider the correlations within sexes.

In the male data there are strong correlations between all of the conditions in the navigation task, suggesting the use of a common navigational ability, but performance on the pointing task only significantly correlates with performance on the 'both' navigation condition (the relationship to the object-only condition approaches significance). The conditions in which the HG hypothesis predicts a relationship – between distal-only navigation and the pointing task – is not significant, but this could potentially be due to a lack of variation caused by a ceiling effect, since males only made an average of 2 errors on the distal navigation condition. Such a possibility is not entirely consistent with the significant correlations between performance in the distal condition and in the 'both' and object conditions. Even more problematic for such a possibility, and for the predictions of the HG hypothesis, is that the correlation between distal navigation condition and the object location task approached significance. The HG hypothesis would predict male performance on these two tasks to be unrelated or even negatively related, since one taps hunting-related abilities and the other gathering-related abilities.

The only significant correlation in the female data is between the 'both' and object conditions in the navigation task, the *least* likely of the navigation conditions to correlate from the perspective of the HG hypothesis. The correlation between navigation in the presence of 'both' kinds of landmarks and performance in the object location task approaches significance, but perhaps the most straightforward prediction of the HG theory is that performance in the object location task should correlate with navigation in the presence of objects-only, and there is no evidence of this in the data.

The current study found strong support for the HG hypothesis in the patterns of sex differences in the individual spatial tasks, including a demonstration, for the first time, of superior female navigation in the presence of only local landmarks. The patterns of correlations are less obviously supportive of the theory, since there are a few tasks that ought to correlate but which did not. Most problematic for the theory is the dissociation between female performance on the object location task and their performance in the object-only navigation condition. There is no evidence at all of a relationship between these tasks in the current data set, which suggests that female superiority in object location memory, the original female-advantage task designed by SILVERMAN and EALS (1992), is not a consequence of gathering involving *navigating* by local landmarks. *Figure 7* is the scatterplot of scores on these two tasks and it is clear that the low, non-significant correlation is due to a genuine lack of relationship between the variables, rather than to a restricted range of scores or a non-linear relationship. There are at least two possible reasons for the lack of relationships, neither of which is necessarily fatal for the theory in general.

The first possible explanation for failing to find a correlation between two tasks hypothesized to depend on evolved gathering capacities is that at least one of the tasks failed to properly engage the evolved mechanism. Failure to engage the evolved mechanism raises the general problem in all lab-based studies of ecological validity. Inconclusive and sometimes contradictory findings reported in the literature may reflect weakness of laboratory tasks. Evidence that indirectly supports this possibility comes from a study by NEW et al. (2007), in which they led participants around a farmers' market, and then asked them to point to the location of particular foods. They found a female advantage on the pointing task, despite such tasks typically favoring males. Remarkably, they also found a significant correlation between pointing accuracy and the calorific content of the food. They argue that together these results are strong evidence of a gathering adaptation that is engaged by moving around *for* food (perhaps particularly plant food). This study raises the possibility that fully engaging evolved foraging mechanisms depends on the foraging context. There is evidence from omnivorous birds, for example, that different spatial memory systems are engaged when foraging for nectar, which has a predictable spatio-temporal distribution, as opposed to invertebrates, which do not (SULIKOWSKI and BURKE 2007). In the current study, if one of the "gathering" tasks better activated the hypothesized evolved gathering mechanism, then a correlation might not be expected. Of course, such a possibility leaves unanswered the question of why both "gathering" tasks nevertheless evidenced female advantages.

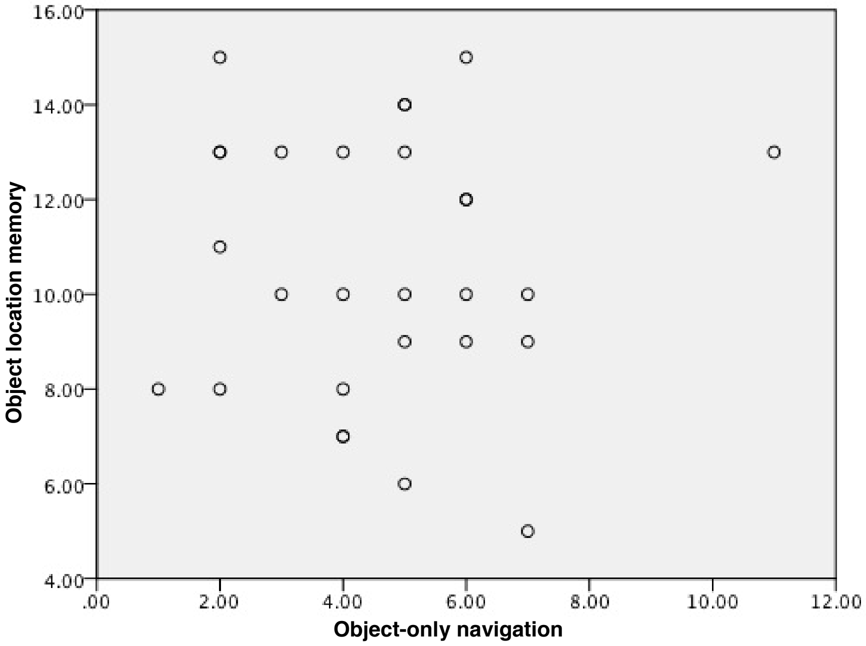


Figure 7. Scatterplot showing the relationship between performance on the object location task and the object-only condition in the navigation task for female particpants

An alternative possibility, which is consistent with a female advantage in both tasks (as we found), is that performance on an object location memory test and on a navigational task using local landmarks depends on different mechanisms, both of which favor females. In support of this possibility, SAUCIER et al. (2008) found some evidence for superior object location memory in female rats. As argued earlier, this need not be seen as evidence that superior female object location memory is general to all mammals, particularly in light of other evidence from HERMAN and

WALLEN (2007) that in rhesus macaques males rely more heavily on local landmarks than do females, but it does raise the possibility that selection pressures other than the spatial demands of gathering can produce a female advantage in object location memory. It is possible that superior female navigation using local landmarks is reflective of past selection for gathering ability, and that superior female object location memory (in both humans and rats) is actually a consequence of some other selective force. Alternatively, superior human female object location memory performance could be a consequence of past selection for gathering, as SILVERMAN and EALS (1992) originally proposed, and the superior female navigation using local landmarks that we have discovered may be due to different selective forces, or to experiential factors. Sex differences in home range size (ECUYER-DABB and ROBERT (2004b) is a plausible candidate for driving either an evolved or an experienced-based female advantage in navigation using local landmarks, and since it is an independent causal factor from hypothesized gathering adaptations, such performance would not be expected to correlate with object location memory. It is even possible (and perhaps likely) that doing well on an object location memory task and navigating better using local landmarks depend on *independent* adaptations to gathering, a foraging task that places selection pressure *both* on navigating to particular locations through familiar terrain, *and* on remembering exactly what kind of food is where (and when).

The current study found some strong evidence to support the HG hypothesis. In each task significant sex differences in the predicted directions were found. The patterns of correlations between the tasks, however, revealed some important inconsistencies. Tasks that should have correlated did not. This raises the interesting possibility that the female advantage in object location memory and females' greater aptitude for using local landmarks when navigating depend on different underlying mechanisms, albeit possibly *different* evolved adaptations to gathering. Usage of different mechanisms supports the idea of unique facets of spatial ability, found by VOYER et al. (1995)'s metaanalyses. Further research will be needed to fully flesh out the diversity of mechanisms that contribute to sex differences in spatial cognitive tasks, possibly incorporating the roles played by hormonal factors (which we did not measure) and the context in which spatial cognition is assessed, but it seems likely that hypotheses derived from evolutionary considerations will be central to our ultimate understanding.

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