

Differences in cue use and spatial memory in men and women

Catherine M. Jones and Susan D. Healy*

Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, Kings Buildings, Edinburgh EH9 3JT, UK

Men and women differ in their ability to solve spatial problems. There are two possible proximate explanations for this: (i) men and women differ in the kind (and value) of information they use and/or (ii) their cognitive abilities differ with respect to spatial problems. Using a simple computerized task which could be solved either by choosing an object based on what it looked like, or by its location, we found that the women relied on the object's visual features to solve the task, while the men used both visual and location information. There were no differences between the sexes in memory for the visual features of the objects, but women were poorer than men at remembering the locations of objects.

Keywords: sex differences; spatial cognition; humans

1. INTRODUCTION

Probably the most consistent cognitive difference between men and women is their ability to solve spatial problems. Indeed, in several mammalian species, males typically outperform females on navigational tasks (e.g. humans, Dabbs *et al.* 1998; deer mice *Peromyscus maniculatus*, Galea *et al.* 1994; meadow voles *Microtus pennsylvanicus*, Gaulin & FitzGerald 1986; mice, Mishima *et al.* 1986; rats, Seymoure *et al.* 1996). Males and females appear to use different cues to solve spatial tasks. Females rely on landmark or feature cues, while males use more abstract cues, such as Euclidean properties of the environment (geometry) and cardinal (compass) directions. In humans, sex differences in cue use have been found across a wide range of spatial tasks, such as drawing maps (Spencer & Weetman 1981), giving verbal directions (Dabbs *et al.* 1998), moving around a computer-generated virtual maze (Sandstrom *et al.* 1998) and performing real-world or map-based tasks (Galea & Kimura 1993; Montello *et al.* 1999; Gron *et al.* 2000; Saucier *et al.* 2002). A similar sex difference is apparent in laboratory rats (e.g. Williams *et al.* 1990; Kanit *et al.* 1998, 2000a,b; Roof & Stein 1999; Tropp & Markus 2001). It is likely that the difference between the sexes in which cues they use to orient underlies the sex difference in performance on spatial tasks, as these tend to be most effectively solved using global, rather than landmark, cues.

A number of evolutionary hypotheses have been proposed to explain sex differences in spatial ability (reviewed in Ecuier-Dab & Robert 2004; Sherry 1997; Jones *et al.* 2003). To date, the most strongly supported in non-human animals is the Range Size Hypothesis. This hypothesis leads to the prediction that in species where males have larger home ranges than females, males will be better at navigation (Gaulin & FitzGerald 1986; Gray & Buffery 1971). While at least one study provides evidence that human males also have larger home ranges than do females (Ecuier-Dab & Robert 2004), there are several

other hypotheses that have also been proposed explicitly to explain sex differences in spatial ability in humans: the Male and Female Foraging Hypotheses (Silverman & Eals 1992; Eals & Silverman 1994), the Female Choice Hypothesis (Sherry 1997), the Male Warfare Hypothesis (Geary 1995) and the Female Fertility Hypothesis (Sherry 1997). Under all of these, with the exceptions of the Female Fertility and Female Foraging Hypotheses, it is assumed that natural selection has favoured enhanced spatial ability in males. Under the Female Fertility Hypothesis, however, the suggestion is that selection has acted on females to reduce their spatial ability at certain reproductive stages when it is beneficial for females not to move far from their dependent offspring. Under the Female Foraging Hypothesis, the suggestion is that females will do better than males at very specific 'object-location' spatial tasks.

One of the problems with this list of possible evolutionary scenarios is that it is difficult to determine which of them is the most plausible explanation for the observed sex differences. This is because they all broadly predict the observed differences, while the specific predictions of more than one hypothesis are rarely tested with the same set of data. The one exception to the broad predictions of a male advantage is the Female Foraging Hypothesis, which predicts the observed female advantage on a small subset of tasks that require some degree of spatial ability for accurate solution. One of the early tests of the Female Foraging Hypothesis involved subjects being shown an array of pictures of familiar objects for 1 min (Silverman & Eals 1992). The array was then replaced with another that contained the same objects as the original array, but the locations of some had been switched. Subjects were asked to mark the exchanged items and women were better at doing so than were the men. Women have since been found to score higher than men on several other object-location tasks. For instance, women remember the locations of common objects, such as chalk and shoes, in a real room more accurately than men (Montello *et al.* 1999). They are also better than men

* Author for correspondence (s.healy@ed.ac.uk).

at the commercial game memory in which players try to match pairs of pictures on cards laid out face-down on the table by turning over no more than two cards at a time (McBurney *et al.* 1997; Tottenham *et al.* 2003).

These task-dependent sex differences make it even more difficult to distinguish between the proposed evolutionary hypotheses. Indeed, the data from one species alone is rarely a compelling way of demonstrating an evolutionary route. Here, we use a task that has previously been used to demonstrate species differences in spatial cognition in birds, to compare spatial abilities of men and women. Food-storing birds, birds that are presumed to process a greater amount of spatial information than non-storers, have been shown to outperform non-storing species on a computer-controlled, delayed-non-match-to-sample (DNMTS) task in which their ability to remember either the location or the colour of an object was tested (Hampton & Shettleworth 1996; Biegler *et al.* 2001). Food storers only outperform the non-storers on the spatial task. The same kind of task can also be used to determine which cues are used to solve a task, as well as the memory abilities *per se*. Food-storing birds have a greater preference for using spatial cues than do non-storers (Shettleworth & Westwood 2002). The advantage of this kind of task is that one can examine a variety of aspects of spatial cognition as well as non-spatial cognitive abilities using a single task.

In the experiments described here, we utilized a slightly modified version of the DNMTS task used to test birds. In Experiment 1 we tested the ability of men and women to remember either the visual features or the location of objects. To do this, we used two similar tasks, which differed only in what information could be used to solve the task: in one, only the object's features provided useful information and in the other, only the object's location. In Experiment 2, we investigated whether men or women had a preference for the type of cue they used to solve a task, where either cue would result in the correct outcome. The data from the bird experiments would lead to the following predictions: (i) if men have a better memory for spatial information they would do better than the women on the location task, but there would be no sex differences on the feature task; (ii) if men were better at remembering spatial information, they would also rely more heavily on spatial cues than would women to solve a task where more than one cue type could be used.

2. EXPERIMENT 1

(a) Method

(i) Subjects

Subjects were 21 male (mean age, 22.14 years; range, 20–24) and 26 female (mean age, 21.54 years; range, 20–24) student volunteers.

(ii) Procedure

Each subject was presented with two DNMTS tasks, which were the same in all aspects except that the feature task could only be solved using feature cues, while the location task could only be solved with location cues (figure 1). A single trial of each task consisted of a sample phase followed by a retention interval and a choice phase. Each subject was given both tasks in a pseudorandom order so that approximately half of the men (11 out of 21)

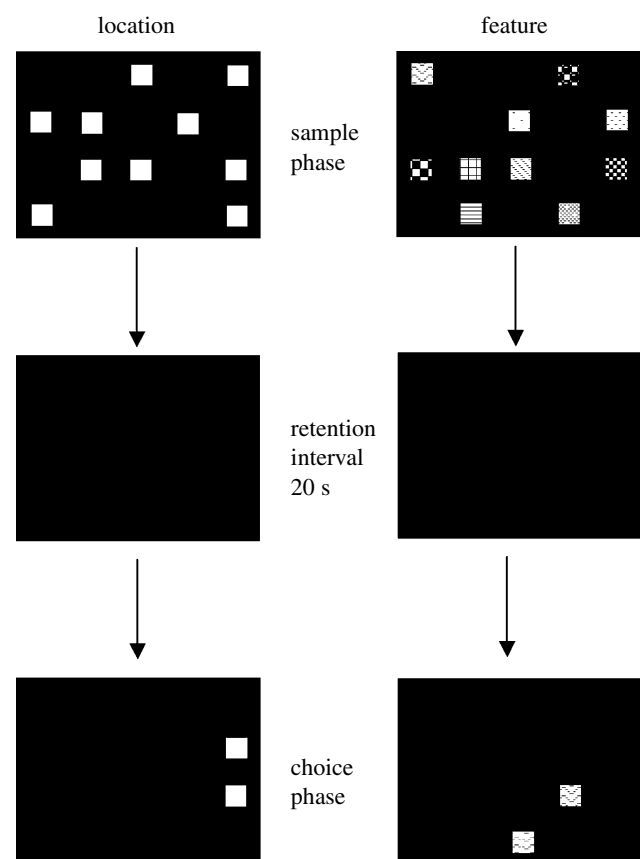


Figure 1. A single trial of each of the tasks used in Experiment 1. The patterned squares in the feature task represent coloured photographs. After an inter-trial interval of 5 s the trial was repeated using randomly chosen locations and pictures. Each subject was given 20 trials of each task.

and half of the women (12 out of 26) received the feature task first. Each task consisted of 20 trials.

The sample phase of both tasks consisted of ten objects (2×2 cm) displayed in random locations in a 5×4 grid on the computer screen. The coloured pictures (for the feature task only) and locations were chosen at random for each trial within a task, but these choices were then remembered and used again each time the task was run such that each trial was the same for each subject. The subjects used the mouse to click on each object, which then disappeared. When all of the objects had disappeared a retention interval of 20 s began. During the retention interval, the screen was blank except for the letters 'RI' and the trial number in the top left corner. After the retention interval had elapsed there was a choice phase in which the subject was presented with two objects, one of which had appeared in the sample phase. If the subject chose the new object the word 'correct' was briefly displayed on the screen. There was then a 5 s inter-trial interval, during which the screen was blank except for the phrase 'next trial is' followed by the number of the next trial displayed in the top left corner. If the subject chose the incorrect object, the inter-trial interval began immediately.

The pictures in the feature task were chosen from a selection of 40 colour photographs of man-made and natural objects (e.g. flower, motorbike, starfish, hot-air balloon). The pictures were divided into two sets of 20 and paired so that each pair consisted of two different objects

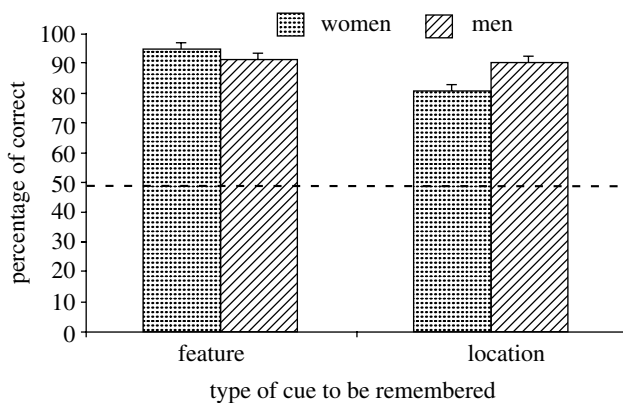


Figure 2. Mean scores (\pm s.e.m.) on the feature and location tasks during Experiment 1.

of the same type. Ten images from one of the sets of 20 (i.e. half of each pair) were used for each sample phase, randomly chosen by the computer. In the choice phase, only two pictures were presented, one that had been presented in the sample phase and its pair from the other set (i.e. a different picture of a similar object). During the choice phase both pictures appeared in locations not used in the sample phase, so that location cues were irrelevant to making a correct choice.

All of the objects in the location task were plain white squares. In the sample phase, 10 white squares were presented (see figure 1), each in one of the possible 20 locations in the 5×4 grid. Two objects appeared in the choice phase, one in a location used in the sample phase and the other in an adjacent, but previously unoccupied, location.

All subjects received instructions on the task immediately prior to testing and were individually tested between 11.00 and 18.00 h. In the location task subjects were told to choose the new square in the choice phase and in the object task, the new picture. The subjects took approximately 40 min to complete both tasks.

Two experimenters, each working in a different room, tested a total of 47 subjects. Experimenter A tested 18 subjects (nine men and nine women) and Experimenter B tested 29 subjects (12 men and 17 women). Subjects were all given exactly the same instructions.

(iii) Statistical analyses

A significance level of 0.05 was used in all analyses. The number of correct choices made on each of the two tasks was analysed using a repeated-measures analysis of variance (ANOVA) with three between-subjects factors (sex, order and experimenter) and one within-subject factor (task). Non-significant interactions were excluded from the final model. The data were square-root transformed in order to meet parametric test assumptions.

(b) Results

There was a significant sex by task interaction ($F_{1,44} = 14.37$, $p < 0.001$; figure 2). As predicted, men scored significantly higher on the location task than did the women (Tukey simultaneous test: $t = 4.16$, $p = 0.001$). There was no sex difference in performance on the feature task (Tukey simultaneous test: $t = -1.11$, $p = 0.69$). There was no difference in performance on the two tasks by the men (Tukey simultaneous test: $t = -0.21$, $p = 0.99$).

However, the women scored significantly higher on the feature task than they did on the location task (Tukey simultaneous test: $t = -5.77$, $p < 0.001$).

Although the men tested tended to be older than the women (one-way ANOVA: $F_{1,45} = 2.94$, $p = 0.09$) and the two experimenters tested subjects of significantly different ages ($F_{1,45} = 9.24$, $p = 0.004$; experimenter A's subjects: mean, 22.44 years; range, 21–24; experimenter B's subjects: mean, 21.41 years; range, 20–24), age was not correlated with performance on either task (controlling for sex and experimenter; feature: $F_{1,43} = 1.36$, $p = 0.25$; location: $F_{1,43} = 0.45$, $p = 0.50$). Therefore, the observed differences in performance between the men and women on the location task is unlikely to have been due to differences in their ages.

There was also a significant experimenter by task interaction ($F_{1,44} = 7.31$, $p = 0.01$). The subjects tested by experimenter B scored significantly higher on the feature task than those tested by experimenter A (Tukey simultaneous test: $t = 3.41$, $p = 0.007$). There was no significant difference between the location scores of the subjects tested by the two experimenters (Tukey simultaneous test: $t = -0.39$, $p = 0.98$). As the experimenter by task interaction was included in the final model, this effect does not explain the significant sex by task interaction.

3. EXPERIMENT 2

(a) Method

(i) Subjects

Subjects were 20 male (mean age, 21.75 years; range, 21–24) and 20 female (mean age, 21.55 years; range, 21–23) volunteers. All were undergraduates at the University of Edinburgh. None of the subjects had taken part in Experiment 1.

(ii) Procedure

Each subject was given 30 trials of a DNMTS object-location task, which could be solved using either feature or location cues, and included a probe trial on every fifth trial. Thus a session consisted of 24 control trials and six probe trials. The same experimenter tested all subjects individually, but testing took place in one of two rooms.

The task was similar to that used in the first experiment in that each trial consisted of two parts, a sample phase, followed by a retention interval and then a choice phase. There was a 5 s inter-trial interval between trials. In the sample phase, the subject was presented with 10 objects, each consisting of a colour picture. The pictures were the same as those used in Experiment 1.

Each picture was displayed in a square, chosen at random, of a 5×4 grid on the computer screen. The grid lines were visible on the screen. The subjects used the computer's mouse to click on each object, which then disappeared. When all of the objects had disappeared the retention interval started. This retention interval lasted 15 s and was counted down in large green numbers on the screen. After the retention interval the subject was given a choice of two pictures presented in adjacent locations on the screen.

On control trials the choice phase consisted of a choice between a sample picture in a sample location (incorrect choice), and a new, similar picture (the pair of the sample picture) in a new location adjacent to that occupied by

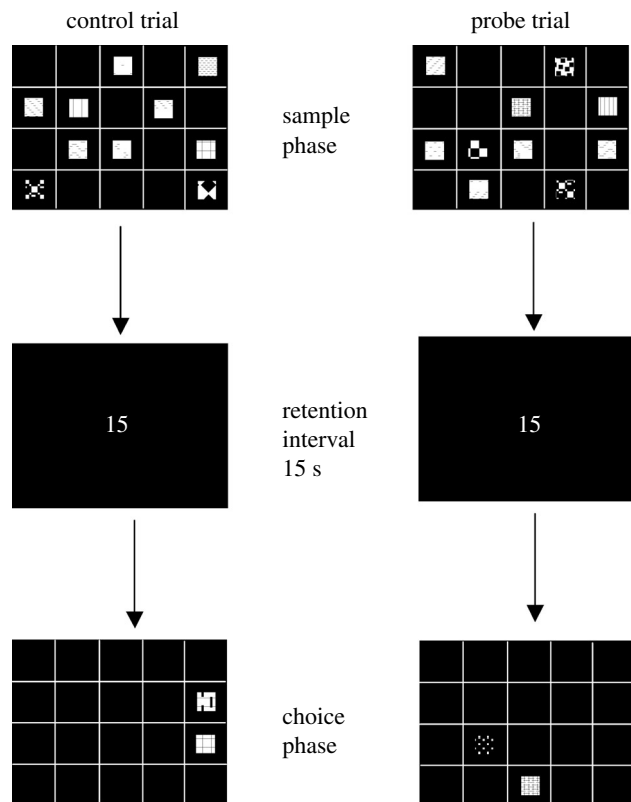


Figure 3. The two types of trials used in Experiment 2. The patterned squares represent photographs. After an inter-trial interval of 5 s the trial was repeated using randomly chosen locations and pictures. Each subject was given a total of 30 trials consisting of four control trials followed by one probe trial repeated six times.

the other object (correct choice). A correct choice was followed by a brief presentation of the word 'correct' on the screen, while the inter-trial interval began immediately following an incorrect choice. During the inter-trial interval the screen was blank except for the phrase 'next trial is' next to the number of the next trial, displayed in the top left corner. On probe trials the choice was between a sample picture in a new but adjacent location, and a new but similar picture in a sample location (figure 3). The word 'correct' was displayed after the choice was made irrespective of which picture was chosen.

Prior to starting the experiment the task was explained to the subject using laminated printouts of a sample and choice phase from a control trial (these particular sample and choice phases were not used in the experiment). The experimenter emphasized that both an object's features and its location were important and that the subject should choose the new picture in the new location. Subjects were instructed to complete the trials as quickly as possible and were timed using a stopwatch.

The general method used differed from that of the first experiment in three ways—the grid lines were made visible, the retention interval was reduced and counted down on-screen, and visual aids were used to explain the experiment to the subject beforehand. This was because in a pilot study using the same conditions as Experiment 1 it was found that the subjects tended to solve the experiment using feature memory regardless of sex, and rarely made errors on the control trials. The visible gridlines and visual explanation were introduced to help to emphasize

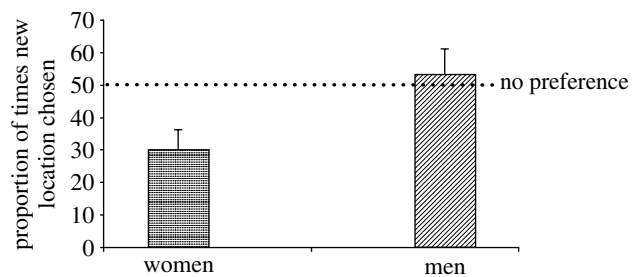


Figure 4. Mean number (\pm s.e.m.) of times that the men and women chose the new location on the probe trials during Experiment 2 (out of a possible six). The dashed line represents random choice.

the location element of the experiment, while the on-screen countdown of the retention interval was introduced to make it more difficult to remember the objects from the sample phase.

The subjects each took approximately 20 min to complete the task. All testing took place between 14.00 and 17.00 h. 26 subjects (14 men and 12 women) were tested in one room and 14 (eight men and six women) in the other.

(iii) Statistical analyses

Two-way ANOVAs were used to test for effects of sex and room on the total number of correct choices made by each subject on the control trials (out of a possible 24), the number of times that each subject chose the new location on the probe trials (out of a possible 6) and the time taken to complete the task. The control trial data were cube transformed in order to meet parametric test assumptions. The probe trial and time taken data did not need to be transformed (Dytham 1999). The interaction term was not significant for any of the analyses and so was excluded from the final model.

(b) Results

There was no effect of either sex or room on the number of correct choices made during the control trials (two-way ANOVA: sex $F_{1,37}=0.06$, $p=0.81$; room $F_{1,37}<0.01$, $p=0.99$). There was also no effect of either sex or room on the time taken to complete the task (two-way ANOVA: sex $F_{1,37}<0.01$, $p=0.99$; room $F_{1,37}=1.71$, $p=0.20$). During the probe trials, however, the women chose the new location significantly less often than did the men ($F_{1,37}=5.29$, $p=0.03$; figure 4). There was no effect of test room on the number of trials in which location was chosen ($F_{1,37}<0.01$, $p=0.95$).

One-sample *t*-tests were used to determine whether the number of times that the men and women chose the new location on the probe trials differed from random (i.e. a score of three). The choices of the men did not differ from random ($n=20$, $t=0.42$, $p=0.68$), but those of the women did ($n=20$, $t=-3.33$, $p=0.004$). Women chose the new location significantly less often than would be expected if they were making choices at random.

4. DISCUSSION

In this task, the men were better at remembering spatial locations than were the women. There were no differences between the sexes in memory for the visual features of an

object. Women preferred to use the visual features of an object over its location when there was a choice of cues, while the men showed no preference. Thus, there appear to be sex differences in memory for spatial information and in cue preference, but not in memory for featural information.

Most of the tasks used to assess cognitive abilities in humans compare which cues the sexes use or examine a specific cognitive skill (e.g. mental rotation). The results from our second experiment are consistent with the large body of literature on cue use in women: they prefer to use cues associated with the visual aspects of an object (e.g. landmark cues). We had predicted, however, that the men tested in our preference task would have preferred to use the spatial cues. They did not show this preference and, indeed, showed no cue preference. This may have been because the spatial cues provided were not geometric cues. This result is, however, also consistent with data from other experiments that have examined cue use. In one such experiment, for example, subjects were trained to find a target within a computer-generated virtual environment where initially both landmark and geometrical cues were available. The males and females performed equally well when the geometrical cues were removed, but when the landmark cues were removed the females took much longer than the males to find the target (Sandstrom *et al.* 1998). Likewise, when men and women were provided with either Euclidean- or landmark-based instructions for navigational tasks, men did not make more errors when using landmark-based instructions (Saucier *et al.* 2002).

Unlike the majority of the literature, in Experiment 1 we explicitly compared memory for spatial location and for features, separately, within the same subjects on two very similar tasks. As we predicted, the men made more correct choices than did the women on the spatial task, while the sexes did not differ on the feature task. Although it is possible that women may compensate for poorer spatial ability by enhancing their ability to remember featural information, these data would suggest that this is not the case. They were not better than the men on the featural task and were poorer at remembering spatial information, even when this was the only way to perform correctly. It is possible that the two tasks in Experiment 1 were not equivalent in the amount of information available in the sample phase, as the feature task included irrelevant location cues as well as the feature cues that were needed to complete the task, while the location task did not contain any irrelevant feature cues. However, we would, then, expect the feature task to have been more difficult than the location task, thus it is all the more surprising that the women performed more poorly on the (relatively simple) location task.

The results from Experiment 1 provide evidence that women are relatively poor at remembering spatial information, which may be why they then prefer to use feature cues to solve tasks, both like that used in Experiment 2 as well as those used by other labs. Men, on the other hand, did not prefer to use either cue to solve the object-location task, perhaps because they remember both locations and features equally well. These findings could explain the observed sex differences in human spatial ability if the male-typical use of both sets of cues is the most effective way to solve spatial tasks while

the female-typical use of feature cues is the most efficient way to solve object-location tasks. Women may rely on feature cues to solve spatial tasks because they can remember feature information more easily than they can remember the spatial cues, even though such tasks may be more effectively solved using spatial information.

One explanation as to why women sometimes excel at object-location tasks may be due to a difference in attention and not in memory. If feature cues are more salient to women than they are to men, this may explain female superiority on tasks in which there are changes to features and not to locations (as in Silverman & Eals' 1992 task). If the men were dividing their attention equally between the feature and spatial information, then in the same time provided for viewing the array, the men will necessarily encode less of the more important, feature information than they need to complete the task successfully. In tasks such as that used by James & Kimura (1997), who did not find sex differences in performance, the subjects are required to remember both spatial and feature information. In such tasks, the preference of women to pay more attention to feature than to spatial cues coupled with their poorer spatial memory would lead either to no sex differences or one in which males outperformed females.

Although we did not set out to differentiate among the evolutionary hypotheses that have been proposed to explain sex differences in spatial ability, we find we can do so as a result of these experiments. Our data are superficially consistent with the predictions from the Range Size, Male Warfare, Female Choice and Male Foraging Hypotheses, as men performed better than did women on a spatial memory task but they did not differ on a task requiring memory for object features. However, the men were no better at the spatial task than they were at the feature task, an outcome that is not consistent with the predictions from these hypotheses. Our data are also consistent with one of the predictions of the Female Fertility Hypothesis in which it is assumed that natural selection has acted on female, rather than male, spatial ability due to the costs of a female being too mobile from late pregnancy through to weaning (Sherry 1997). One of the predictions from this hypothesis is that there should be variation in spatial ability among females, dependent on their reproductive status or the stage in their oestrous/menstrual cycle. At some of these periods, females will perform as well as males while at others they will perform more poorly. On average, then, female performance on spatial tasks will be poorer than that of males. The results from our first experiment are thus consistent with this prediction. We would need to test women across their menstrual cycle, or at different reproductive stages, to confirm that our data offer support for this hypothesis.

A final possibility is that our results are due to problems with the experimental design. Most experiments investigating cognitive abilities in humans involve verbal or written instructions regarding what the subjects are expected to do in the task or, perhaps, providing an expectation of the correction solution. We gave our subjects minimal verbal instructions. In Experiment 1, we made it clear that the subject was to choose the new object (either square or picture). As the 'new' could only refer to its feature cues in one set of trials and to its location cues in the other set of trials, it seems unlikely

that the subjects could have misinterpreted what we were asking them to do. In Experiment 2, on the other hand, we purposively told them only to choose the new object although we made it explicit that they should try to use both feature and spatial cues. We chose to provide minimal instructions (and training) so that we could assess untrained preferences for cue type. It is possible that the women misconstrued what it was that they were expected to do in this task and thus we saw a preference for feature cues in females and no preference in males. However, we think it unlikely that the women should have misinterpreted the instructions any more than the men did.

In conclusion, we have demonstrated that women prefer to use feature cues to solve tasks when given the option of choosing between feature and spatial cues. Our data suggest that this preference might be because women have poorer spatial memory than do men. This may, then, explain why women tend to not to be as good as men at solving spatial problems such as map reading and giving directions.

We thank the Biotechnology and Biological Sciences Research Council, UK for funding C.M.J.; Robert Biegler for writing the original program; Andy Koppe for help with modifying the program; and Catriona Greig, Matthew Bloxham, Mikey Hartley, Paul Wright, Moheet Verma and Olivia Ashman for help with data collection. We also thank Robert Biegler, Victoria Braithwaite, David Shuker and three anonymous reviewers for their helpful comments on an earlier version of the manuscript.

REFERENCES

- Biegler, R., McGregor, A., Krebs, J. R. & Healy, S. D. 2001 A larger hippocampus is associated with longer-lasting spatial memory. *Proc. Natl Acad. Sci. USA* **98**, 6941–6944. (doi:10.1073/pnas.121034798)
- Dabbs, J. M., Chang, E. L., Strong, R. A. & Milun, R. 1998 Spatial ability, navigation strategy, and geographic knowledge among men and women. *Evol. Hum. Behav.* **19**, 89–98. (doi:10.1016/S1090-5138(97)00107-4)
- Dytham, C. 1999. *Choosing and using statistics: a biologist's guide*. Oxford, UK: Blackwell Science.
- Eals, M. & Silverman, I. 1994 The hunter–gatherer theory of spatial sex-differences—proximate factors mediating the female advantage in recall of object arrays. *Ethol. Sociobiol.* **15**, 95–105. (doi:10.1016/0162-3095(94)90020-5)
- Ecuyer-Dab, I. & Robert, M. 2004 Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition* **91**, 221–257. (doi:10.1016/j.cognition.2003.09.007)
- Galea, L. A. M. & Kimura, D. 1993 Sex-differences in route-learning. *Pers. Individ. Diff.* **14**, 53–65. (doi:10.1016/0191-8869(93)90174-2)
- Galea, L. A. M., Kavaliers, M., Ossenkopp, K.-P., Innes, D. & Hargreaves, E. L. 1994 Sexually dimorphic spatial learning varies seasonally in two populations of deer mice. *Brain Res.* **635**, 18–26. (doi:10.1016/0006-8993(94)91419-2)
- Gaulin, S. J. C. & FitzGerald, R. W. 1986 Sex differences in spatial ability: an evolutionary hypothesis and test. *Am. Nat.* **127**, 74–88. (doi:10.1086/284468)
- Geary, D. C. 1995 Sexual selection and sex-differences in spatial cognition. *Learn. Individ. Diff.* **7**, 289–301. (doi:10.1016/1041-6080(95)90003-9)
- Gray, J. A. & Buffery, A. W. H. 1971 Sex differences in emotional and cognitive behaviour in mammals including man—adaptive and neural bases. *Acta Psychol.* **35**, 89–111. (doi:10.1016/0001-6918(71)90014-X)
- Gron, G., Wunderlich, A. P., Spitzer, M., Tomczak, R. & Riepe, M. W. 2000 Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nat. Neurosci.* **3**, 404–408. (doi:10.1038/73980)
- Hampton, R. R. & Shettleworth, S. J. 1996 Hippocampal lesions impair memory for location but not color in passerine birds. *Behav. Neurosci.* **110**, 831–835. (doi:10.1037/0735-7044.110.4.831)
- James, T. W. & Kimura, D. 1997 Sex differences in remembering the locations of objects in an array: location-shifts versus location-exchanges. *Evol. Hum. Behav.* **18**, 155–163. (doi:10.1016/S1090-5138(97)00004-4)
- Jones, C. M., Braithwaite, V. A. & Healy, S. D. 2003 The evolution of sex differences in spatial ability. *Behav. Neurosci.* **117**, 403–411. (doi:10.1037/0735-7044.117.3.403)
- Kanit, L., Taskiran, D., Furedy, J. J., Kulali, B., McDonald, R. & Pogun, S. 1998 Nicotine interacts with sex in affecting rat choice between “look-out” and “navigational” cognitive styles in the Morris water maze place learning task. *Brain Res. Bull.* **46**, 441–445. (doi:10.1016/S0361-9230(98)00008-2)
- Kanit, L., Taskiran, D., Yilmaz, O. A., Balkan, B., Demiregoren, S., Furedy, J. J. & Pogun, S. 2000a Sexually dimorphic cognitive style in rats emerges after puberty. *Brain Res. Bull.* **52**, 243–248. (doi:10.1016/S0361-9230(00)00232-X)
- Kanit, L., Yilmaz, O., Taskiran, D., Kulali, B., Furedy, J. J., Demiregoren, S. & Pogun, S. 2000b Sexually dimorphic cognitive style, female sex hormones, and cortical nitric oxide. *Physiol. Behav.* **71**, 277–287. (doi:10.1016/S0031-9384(00)00327-9)
- McBurney, D. H., Gaulin, S. J. C., Devineni, T. & Adams, C. 1997 Superior spatial memory of women: stronger evidence for the gathering hypothesis. *Evol. Hum. Behav.* **18**, 165–174. (doi:10.1016/S1090-5138(97)00001-9)
- Mishima, N., Higashitani, F., Teraoka, K. & Yoshioka, R. 1986 Sex-differences in appetitive learning of mice. *Physiol. Behav.* **37**, 263–268. (doi:10.1016/0031-9384(86)90230-1)
- Montello, D. R., Lovelace, K. L., Gollidge, R. G. & Self, C. M. 1999 Sex-related differences and similarities in geographic and environmental spatial abilities. *Ann. Assoc. Am. Geogr.* **89**, 515–534. (doi:10.1111/0004-5608.00160)
- Roof, R. L. & Stein, D. G. 1999 Gender differences in Morris water maze performance depend on task parameters. *Physiol. Behav.* **68**, 81–86. (doi:10.1016/S0031-9384(99)00162-6)
- Sandstrom, N. J., Kaufman, J. & Huettel, S. A. 1998 Males and females use different distal cues in a virtual environment navigation task. *Cogn. Brain Res.* **6**, 351–360. (doi:10.1016/S0926-6410(98)00002-0)
- Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., Bell, S. & Elias, L. J. 2002 Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behav. Neurosci.* **116**, 403–410. (doi:10.1037/0735-7044.116.3.403)
- Seymour, P., Dou, H. & Juraska, J. M. 1996 Sex differences in radial maze performance: influence of rearing environment and room cues. *Psychobiology* **24**, 33–37.
- Sherry, D. G. H. E. 1997 Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends Cogn. Sci.* **1**, 50–56. (doi:10.1016/S1364-6613(97)01015-2)
- Shettleworth, S. J. & Westwood, R. P. 2002 Divided attention, memory, and spatial discrimination in food-storing and non-storing birds, black-capped chickadees

- (*Poecile atricapilla*) and dark-eyed juncos (*Junco hyemalis*). *J. Exp. Psychol.: Anim. Behav. Process.* **28**, 227–241. (doi:10.1037/0097-7403.28.3.227)
- Silverman, I. & Eals, M. 1992 Sex differences in spatial abilities: evolutionary theory and data. In *The adapted mind: evolutionary psychology and the generation of culture* (ed. J. Barkow, L. Cosmides & J. Tooby). Oxford, UK: Oxford University Press.
- Spencer, C. & Weetman, M. 1981 The microgenesis of cognitive maps—a longitudinal-study of new residents of an urban area. *Trans. Inst. Br. Geogr.* **6**, 375–384.
- Tottenham, L. S., Saucier, D., Elias, L. & Gutwin, C. 2003 Female advantage for spatial location memory in both static and dynamic environments. *Brain Cogn.* **53**, 381–383. (doi:10.1016/S0278-2626(03)00149-0)
- Tropp, J. & Markus, E. J. 2001 Effects of mild food deprivation on the estrous cycle of rats. *Physiol. Behav.* **73**, 553–559. (doi:10.1016/S0031-9384(01)00487-5)
- Williams, C. L., Barnett, A. M. & Meck, W. H. 1990 Organizational effects of gonadal secretions on sexual differentiation in spatial memory. *Behav. Neurosci.* **104**, 84–97. (doi:10.1037/0735-7044.104.1.84)