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Sex differences in spatial ability

A.N. Other
Contents
Preface

The work contained within this thesis is my own and has not been done in collaboration, except where otherwise stated. No part of this thesis has been submitted to any other university in application for a higher degree.
Acknowledgements

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Abstract

Males outperform females on spatial tasks in a number of mammalian species. However, sex differences are not consistently found in laboratory rats and I investigated possible reasons for this. I found no significant effect of the female oestrous cycle, landmark cues, and different types of spatial task on sex differences in spatial ability. I then hypothesised that the performance of male and female rats on spatial tasks could be due to sex differences in response to stress or food restriction. I tested groups of male and female rats in the radial arm maze under high and low stress conditions and high and low food restriction. The results were not clear-cut, but female, and not male, rats’ spatial performance may have been adversely affected by high levels of food restriction. If food restricted female rats perform worse than food restricted males on spatial tasks, this could result in sex differences on appetitively-motivated spatial tasks.

In a separate experiment I predicted that male Mongolian gerbils (Merionesunguiculatus) would have better spatial ability than conspecific females because they have larger ranges and larger hippocampal volumes. Both range size and hippocampal volume is positively correlated with spatial ability. I did not find a sex difference in spatial ability in gerbils. There were also no sex differences in hippocampal volume in these subjects.

To conclude, I found that high levels of food restriction adversely affect female rats’ spatial performance and could cause sex differences in spatial ability on appetitively-motivated tasks. I did not find any sex differences in either hippocampal morphology or spatial ability in gerbils. I found evidence to suggest that women’s superior performance on object-location tasks is due to better feature memory rather than spatial memory, as was previously thought.
Chapter 1  Spatial ability introduction and literature review

1.1  Introduction and overview

Many species show morphological and physiological differences between the sexes and there is also evidence for sex differences in cognitive abilities. One of the best-studied cognitive sex differences is an apparent male advantage in spatial cognition. There are a number of evolutionary hypotheses that have been proposed to explain this difference, and there are also endocrinological and neurophysiological data providing the mechanistic basis for such a difference between the sexes.

1.1.1  What is spatial ability?

Spatial ability is not a unitary ability; rather the concept is likely to encompass several different cognitive abilities. See Figure 1-2 on page 2.

In humans spatial ability has been defined as:

“The ability to imagine what an irregular figure would look like if it were rotated in space or the ability to discern the relationship among shapes and objects.”¹

However, Linn and Peterson’s (1985) meta-analysis of studies on sex differences in spatial abilities found that the studies tested three distinct types of spatial abilities: spatial perception, the ability to ignore distracting information in order to determine spatial relations; mental rotation, the ability to use the imagination to quickly and accurately rotate figures; and spatial visualization, being able to manipulate complex spatial information through several stages to reach the correct solution.

Spatial ability tests

In both rodents and humans many different tests of spatial ability are used and different types of test may measure different cognitive abilities. Spatial ability tests in rodents usually involve the subjects learning to complete a maze. However,

¹ Other definitions can be found in Halpern, 1991
Sex differences in spatial ability

even within maze tests different protocols may measure different things. For example, the memory involved may be either working or reference memory. Working memory can be defined as retaining trial-specific information, which is usually only useful for a short period of time, while reference memory involves information that remains constant over time (task-specific information) and is usually of a longer duration (Bimonte et al., 2000).

Mental rotation test: which of the figures on the right are the same as the one on the left, except for orientation?

![Mental rotation test](image)

*Figure 1-1: Mental rotation test*

Embedded figures test: trace the outline of the shape on the left within the figure on the right.

![Embedded figure test](image)

*Figure 1-2: Embedded figure test*

1.1.2 Which species show sex differences in spatial ability?

Although the male advantage in spatial cognition is sometimes considered to be universal, to my knowledge only 11 species have actually been tested for sex differences in spatial ability (table 1.1). Of these, only six species, all of which are primates or rodents, show a male advantage in spatial ability. Five other species (more rodents and a single bird species) have been tested but no differences have been found.
There is variation, both within and between species, in sex differences in spatial ability that needs to be explained.

1.2 Mechanistic explanations

The mechanism of why the males and females of certain species have different spatial abilities can be described in several different ways: the ways in which their brains differ, the effects of sex hormones, possible effects of differential experience, and sex-specific cognitive styles.

1.3 Alternative explanations

The evolutionary hypotheses all assume that sex differences in spatial ability are adaptive products of natural selection. However, it is also possible that the observed sex differences in spatial ability are a by-product of selection for another feature (Gould & Lewontin, 1979). The way that spatial ability is tested, especially in rodents, means that spatial ability could be confounded with another feature that shows variation between the sexes, i.e. the tests might not be testing differences in spatial ability, but rather differences in another trait.

These separate lines of evidence consistently point to two ways of solving spatial problems:

The ‘male-typical’ cognitive style may activate the hippocampus to use distant navigational or geometric cues.

The ‘female-typical’ cognitive style may use the parietal and prefrontal cortex to learn and recall more local, landmark cues.

Table 1-1: A summary of the evolutionary hypotheses

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Species</th>
<th>Prediction</th>
<th>Selective pressure</th>
</tr>
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<tbody>
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<td>Any</td>
<td>Dispersing sex better</td>
<td>Natal dispersal distance</td>
</tr>
<tr>
<td>Fertility and parental</td>
<td>Any</td>
<td>Female&lt;male</td>
<td>Females reduce mobility to decrease</td>
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</table>
Sex differences in spatial ability

care

<table>
<thead>
<tr>
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</tbody>
</table>

*Table 1-2: Reference memory errors data table*
Chapter 2  Learning differences

2.1 Introduction

Although laboratory rats are often used in studies of sex differences in spatial ability, sex differences are not consistently found in un-manipulated (control) rats even within the same laboratory (e.g. Roof, 1993b; Luine & Rodriguez, 1994; Kolb & Cioe, 1996; Van Haaren et al., 1987; Kanit et al., 1998a, 1998b). The evolutionary hypotheses discussed in chapter 1 do not provide any strong predictions about sex differences in spatial ability in laboratory rats. There is some evidence that male rats may have larger home ranges, which would result in a prediction of superior male spatial ability from the ‘range size’ hypothesis, but these data have not been confirmed (Taylor, 1978; Macdonald & Fenn, 1995). There is also the problem of rats’ long history of domestication - most of the strains used today were developed in the early twentieth century (Koolhaas, 1999). Artificial selection may have altered characteristics created by natural selection in the laboratory rats’ wild ancestors in unpredictable ways.

Therefore, it seems possible that there are no sex differences in spatial ability in laboratory rats. The inconsistent study results might be due to differences in experimental methods between laboratories, such as having more or fewer landmarks, using different strains, using rats that are used to being handled to a greater or lesser extent, or differences in food restriction regime (Williams et al., 1990; Andrews, 1996; Miller & Dess, 1996; Perrot-Sinal et al., 1996). Van Haaren et al. (1987) suggested this possibility more than 15 years ago, but little research has been done to test it. I decided to test whether some of these possibilities could result in sex differences in spatial ability in laboratory rats.

When they are found, sex differences in spatial ability in laboratory rats are often only present during the initial stages of a maze task. Females tend to take longer than males to reach an asymptotic performance, but, once reached, there is no significant difference between the sexes. This is apparent in both RAM and Morris water maze (MWM) studies (section 1.4; e.g. Juraska et al., 1984; Williams et al.,
There are several possible explanations as to why sex differences are only apparent during the acquisition phase of a test. First, it may be that the tasks are too easy and have a ceiling level of performance below both sexes’ maximum performance. However this seems unlikely, as acquisition-only sex differences have been found on a mixture of tasks of varying difficulty. Second, there may be sex differences in the rate of learning a spatial task, but not in memory once the task is learnt. There are several aspects that the subject has to learn during the early stages of maze training including the maze procedure (i.e. what is involved and how to solve the task), the landmarks in the room, and the position of the rewards within the maze. It is possible that females may take longer to learn some or all of these features (Williams et al., 1990; Kanit et al., 1998a). Third, there could be sex differences, not in spatial ability, but in the subject's response to the novel environment provided by the maze. This could affect apparent spatial ability in the initial stages, but not once the subject has become habituated to the task. There is some evidence that the sexes might respond differently to stress caused by the maze procedure.

2.2 Radial arm maze experiment

2.2.1 Maze
The RAM used in this experiment was locally made. It consisted of eight arms measuring 800mm long by 80mm wide with 200mm high sides, which could be slotted into an octagon-shaped central compartment (figure 2.1). The floor of each arm was opaque green plastic, while the sides of the arms were made from clear plastic and so prevented escape whilst allowing the subject a clear view of the room. The octagonal central compartment was made from opaque green plastic, it was a maximum of 315mm wide. Each side of the central compartment was 130mm long by 200mm high and had a door measuring 70mm by 150mm cut into it to allow the subject entry to the attached arm. When assembled the overall diameter of the maze was 1.91m.
2.3 Results and analysis

The data were analysed using Minitab. The first and second patterns were analysed separately. The assumptions of normality of error (Anderson-Darling normality test of the residuals) and homogeneity of residuals (plot of fitted values against residuals) were tested and appropriate transformations applied to the data. Repeated-measures analyses of variance (ANOVAs) were carried out using ‘sex’ as the between-subjects effect and ‘block’ (where each block was the mean of five trials) as the within-subject effect. It is usual to analyse blocked data in RAM studies (e.g. Williams et al, 1990; Roof, 1993b; Seymoure et al, 1996). Although blocking did not change the significance of the sex effect, it did affect the within-subject effect by reducing variation. The following general linear model (GLM) was fitted to the data:

\[ \text{Response} = \text{sex} + \text{rat(sex)} + \text{block} + \text{sex} \times \text{block} \]

The F-ratio for the effect of sex was calculated by dividing the sex mean square (MS) by ‘rat(sex)’ MS in order to use an appropriate error term for the between subjects factor. When the interaction term was non-significant it was excluded from the final analysis. Working memory errors were square-root transformed for all of the analyses, neither of the other measures needed to be transformed.
Chapter 3  Oestrous cycle stage

3.1 Introduction

Activational levels of the hormones oestrogen and progesterone are known to affect female spatial ability (section 1.3.2.2). Much of the evidence for these effects has come from studies of the natural fluctuations in female hormones during fertility (menstrual and oestrous) cycles. The majority of studies in humans, rats and rhesus monkeys (*Macaca mulatta*) have found that poor performance on spatial tasks is correlated with high oestrogen and progesterone cycle phases (e.g. Hampson & Kimura, 1988; Hampson, 1990; Frye, 1994; Moody, 1997; Phillips & Silverman, 1997; Warren & Juraska, 1997; Hausmann et al., 2000; Lacreuse et al., 2001; McCormick & Teillon, 2001; but see Gordon & Lee, 1993; Berry et al., 1997; Stackman et al., 1997; Epting & Overman, 1998; Healy et al., 1999; Postma et al., 1999; Frick & Berger-Sweeney, 2001; Halpern & Tan, 2001; Mumenthaler et al., 2001). Similarly, when ovariectomised rats are given hormones to mimic oestrous cycle phases, those given hormones that mimic the levels present during the high progesterone and oestrogen phase (pro-oestrus, figure 1.5) perform worse on a spatial task than those given lower levels of progesterone and oestrogen to mimic di-oestrus (Frye, 1994).

3.2 Pilot study

3.2.1 Materials and methods

A pilot study was carried out during May-June 2001 in order to familiarise myself with the techniques involved. Subjects were six male and six female Sprague-Dawley rats, previously used for the experiment described in chapter 4. They were approximately 20 weeks old at the start of the pilot study and were housed in the animal house under the conditions described in section 2.2.2. Food was available *ad libitum* in their home cages throughout the study. All of the female rats had vaginal smears taken for 14 days prior to, and throughout, the study.

The methods used were similar to those described in section 2.3.2. The subjects had no pretraining in the MWM. A single platform location was used. The order in
which the subjects went into the maze and the release position used for each session were fully randomised. The subjects were given three trials per day in the MWM for five days. Each trial consisted of the subject being released into the water from the designated release position and being allowed to swim until the platform was found. If the subject did not find the platform within 2 min the experimenter guided it to it. The subject was left on the platform for 30 sec before being removed from the maze, dried, and returned to its home cage. On the sixth day they were given a probe trial, which consisted of a 60 sec swim in the maze from which the platform had been removed.

![Figure 3-1: Time spent in the correct quadrant](image)

**Figure 3-1: Time spent in the correct quadrant**