

# Sex Differences in Spatial Abilities: Evolutionary Theory and Data

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Cognitive sex differences have remained a prominent topic in psychology for several decades, and one of the most consistent findings has been superior performance for males on tests of spatial abilities. Earlier attempts to account for this difference dealt mainly with socialization practices (Maccoby & Jacklin, 1974), but the generality of the phenomenon across populations and situations led to a shift in emphasis to genetic determinants. Relationships have been found for both sexes between spatial performance and hormonal variables, measured or manipulated directly or inferred from correlates such as pubertal status, physical characteristics, menstrual cycle phase, and atypical androgen levels associated with medical disorders. Additionally, similar spatial sex differences have been found in infrahuman species. (See Gaulin & Hoffman, 1988; Harris, 1978; Kimura & Hampson, 1990; Linn & Peterson, 1985; and McGee, 1979, for reviews.)

## SELECTION PRESSURES FOR SPATIAL SEX DIFFERENCES

The near universality of sex differences in spatial abilities across human cultures and their occurrence in other species indicate the feasibility of an evolutionary approach, but it was not until 1986 that the first systematic attempt of this nature was reported by Gaulin and Fitzgerald. These investigators theorized that spatial abilities in males would have been selected for in polygynous species because polygynous males require navigational skills to maintain large home ranges in which to seek potential mates and/or resources to attract mates. To test these notions they compared sex differences in range size and spatial ability between meadow voles, which are polygynous, and pine voles, which are monogamous. As predicted, male biases for both variables occurred in meadow voles, whereas pine voles showed no disparities between sexes. A follow-up study (Jacobs, Gaulin, Sherry, & Hoffman, 1990) revealed that in meadow voles, but not pine voles, males had proportionally larger hippocampi than females, which had been anticipated based on the role of the hippocampus in mediating spatial functions.

There is another measure of animal mobility, however, termed *natal dispersal* by Greenwood (1980), which is defined as the distance an animal travels from its natal site to its first breeding place. As with range size, sex differences in natal dispersal have been related to mating practices (Greenwood, 1980, 1983), but in his analysis, mating

systems are dichotomized in terms of resource defense versus mate defense rather than monogamy versus polygyny.

Greenwood's theory is that in most resource defense systems, males compete for and hold territories in which they attract females; consequently, females disperse more. In mate defense, males usually locate and defend females; thus they are the greater dispersing sex. In support of these notions, Greenwood noted that birds, who tend to use resource defense, show a female bias in natal dispersion, while mammals, who mainly employ mate defense, show a male bias.

An alternative to Gaulin and Fitzgerald's model of spatial sex differences can be derived from Greenwood's concepts. It may be posited that species that employ mate defense strategies, with greater male dispersal, will show male superiority in spatial abilities; species using resource defense, with greater female dispersal, will show female superiority; and species showing neither of these patterns in typical form, and nil dispersal differences between sexes, will show no spatial sex bias.

Regarding meadow and pine voles, the former show a characteristic mate defense strategy with males dispersing more (Madison, 1980). Pine voles, on the other hand, fall into the third category above, in that they cannot be precisely designated as mate defense or resource defense. They possess a unique social structure for microtine rodents, living in highly cohesive groups comprising reproductively active members of both sexes (Fitzgerald & Madison, 1983). Thus, Gaulin and Fitzgerald's data can be explained by this extension of Greenwood's model as well as by their own theory.

On the other hand, these two theories lead to discrepant predictions regarding human spatial sex differences. By most accounts, humans are moderately polygynous (Symons, 1979), and there are cross-cultural data showing a tendency from early childhood for males to maintain larger home ranges (Gaulin & Hoffman, 1988). On the other hand, humans are resource defenders (Chagnon, 1979), with greater natal dispersal on the part of females (Koenig, 1989). Inasmuch as sex differences in spatial performance favor males, Gaulin and Fitzgerald's theory would appear to prevail in the human case.

Our own work with humans, however, was based on an alternative theory to both Gaulin and Fitzgerald's and Greenwood's. This may be a violation of parsimony inasmuch as our explanation does not extend across species as handily as the other two. On the other hand, it takes account of a particular aspect of human evolution that appears on logical grounds to be highly relevant to spatial sex differences, and it has enabled predictions that would not have emanated from the others.

We hold that the critical factor in selection for spatial dimorphism in humans was sexual division of labor between hunting and gathering during hominid evolution. Although there has, undoubtedly, been overlap between sexes in these functions, archaeological and paleontological data show that across evolutionary time, males predominantly hunted and females predominantly foraged (Tooby & DeVore, 1987).

Tracking and killing animals entail different kinds of spatial problems than does foraging for edible plants; thus, adaptation would have favored diverse spatial skills between sexes throughout much of their evolutionary history. The cognitive mechanisms of contemporary *Homo sapiens* appear to reflect these differences, insofar as the various spatial measures showing male bias (e.g., mental rotations, map reading, maze learning) correspond to attributes that would enable successful hunting. Essentially, these attributes comprise the abilities to orient oneself in relation to objects or places, in view or conceptualized across distances, and to perform the mental transformations

necessary to maintain accurate orientations during movement. This would enable the pursuit of prey animals across unfamiliar territory and, also, accurate placement of projectiles to kill or stun the quarry. In fact, there have been studies based on the same evolutionary notions, demonstrating direct relationships between standardized spatial test scores and throwing accuracy (Jardine & Martin, 1983; Kolakowski & Molina, 1974).

In the present paper, we have extended the premise to propose that if these attributes evolved in males in conjunction with hunting, spatial specializations associated with foraging should have, correspondingly, evolved in females. Food plants are immobile, but they are embedded within complex arrays of vegetation. Successful foraging, then, would require locating food sources within such arrays and finding them in ensuing growing seasons. These abilities entail the recognition and recall of spatial configurations of objects; that is, the capacity to rapidly learn and remember the contents of object arrays and the spatial relationships of the objects to one another. Foraging success would also be increased by peripheral perception and incidental memory for objects and their locations, inasmuch as this would allow one to assimilate such information nonpurposively, while walking about or carrying out other tasks.

In the following sections, we describe a series of studies exploring these hypothesized female spatial specializations, using student subjects from York University in Toronto.

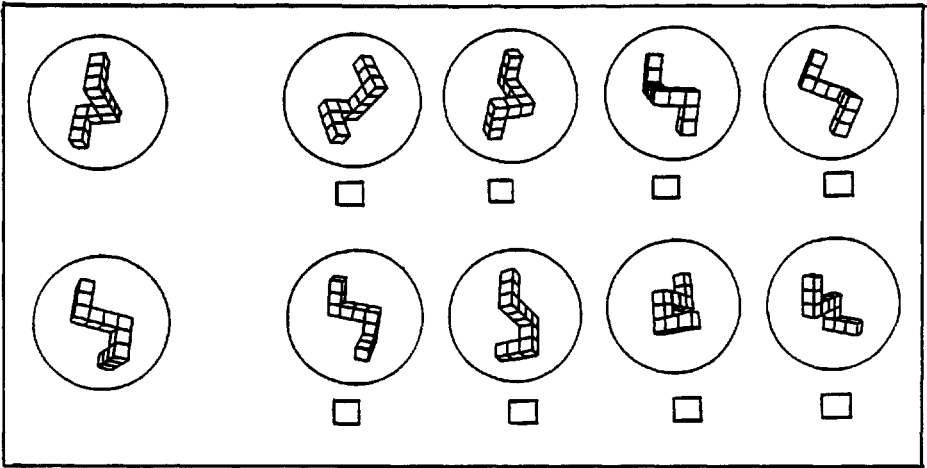
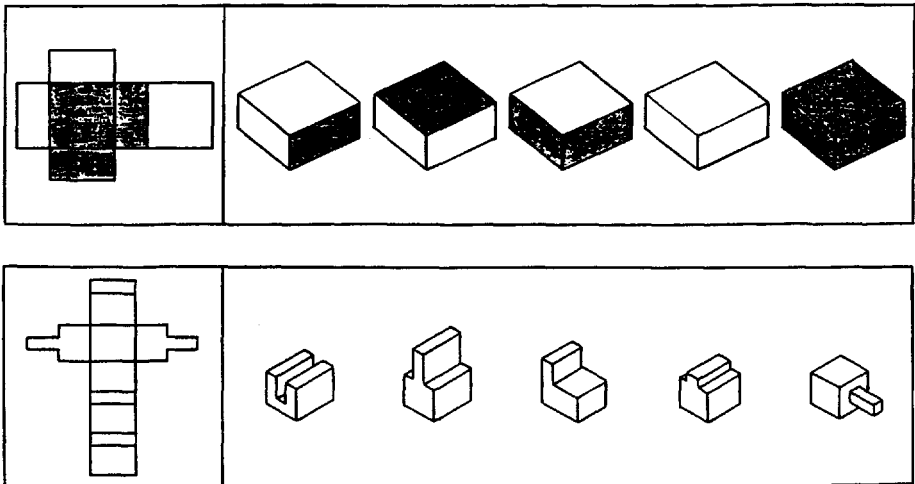
First, however, data will be presented from other ongoing studies with the York student population in order to demonstrate that it is comparable to the population in general in regard to male biases on traditional spatial tests.

## STUDIES OF MALE SPATIAL SPECIALIZATIONS

Figure 14.1 contains sample items from two widely used group-administered spatial tests that customarily show male bias: Mental Rotations (Vandenberg & Kuse, 1978) and Space Relations (Bennett, Seashore, & Wesman, 1947). The Mental Rotations test requires subjects to designate which two of the series of four drawings on the right represent the target object on the left in alternative positions. The task for Space Relations is to indicate, for each item, all of the figures on the right that could be constructed from the pattern on the left. For both tests, subjects were told they could give as many responses, per item, as they wished, but would score a point for each correct response and would have a point subtracted for each incorrect response. For each test, 20 items were used, and seven minutes were allowed.

The two tests were given to separate York samples. Space Relations was administered in individual sessions or in groups of two or three and was included in a test battery. Mental Rotations was the sole test given and was administered in larger groups. Most subjects were volunteers, recruited in classrooms or elsewhere on campus, though some Mental Rotations subjects took the test as part of a course demonstration. Findings were equivalent across all conditions.

Table 14.1 shows the results. As expected, there were significant differences favoring males for both tests. Further, sex differences on both measures appeared exceptionally large in our samples compared with extant published data (e.g., Vandenberg & Kuse, 1978), though statistical comparisons were not feasible because of differences in item composition and/or procedure.

**Mental Rotations****Space Relations**

**Figure 14.1** Sample Items from the Mental Rotations and Space Relations Tests.

**FEMALE SPATIAL SPECIALIZATIONS****Study One: A Group Test**

As in the studies just described, our initial study of foraging-related spatial abilities was administered both in individual sessions and in groups of various sizes and comprised both volunteers and students taking part in course demonstrations. Again, results were similar across all conditions.

**Table 14.1** Mean Space Relations and Mental Rotations Scores, by Sex, for York University Student Samples

	Space relations			Mental rotations			
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>	
Males	18	46.60	13.72	Males	105	15.57	9.43
Females	20	30.89	12.40	Females	98	8.66	7.48
	$t = 3.69$	$p < .001$		$t = 5.80$	$p < .001$		

Subjects in this study were presented first with copies of the object array (called the stimulus array) depicted in Figure 14.2 and asked to “examine the objects” for one minute.

They were then instructed to fold their copies and put them aside and were presented with copies of the array in Figure 14.3. This was identical to the stimulus array, except that a number of additional items were interspersed. Subjects were told to put a cross through all of the items that were not in the original array and that they would be allowed one minute, would be given a point for each item correctly crossed, and would have a point subtracted for each item incorrectly crossed. This served as a measure of memory for objects in an array, independent of location (*object memory*).

Finally, subjects were shown the array in Figure 14.4. This contained the same items as the stimulus array, but some were in the same location and others were not. Subjects were asked to circle the objects that were in the same place and put a cross through those that had been moved and were scored a point for each correct response.

**Figure 14.2** The stimulus array used for tests of object and location memory.



**Figure 14.3** The stimulus array with added items for the object memory test.



**Figure 14.4** The stimulus array with item locations changed for the object memory test.

**Table 14.2** Mean Object Memory and Location Memory Scores, by Sex, for Study One

	Object Memory			Location Memory			
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>	
Males	63	12.25	4.27	Males	83	18.45	3.58
Females	115	14.15	3.90	Females	134	20.14	4.11
	$t = 2.92$	$p < .01$		$t = 3.20$	$p < .01$		

This was a measure of memory for the locations of objects in an array (*location memory*).

Table 14.2 shows the results.<sup>1</sup> Females scored significantly higher on both tasks; they more accurately recalled which items were in the array and where they were located.

### Study Two: A Naturalistic Setting

In the following study, we attempted to replicate the findings above using an actual object array rather than a drawing, and an array presented in a naturalistic setting as opposed to an experimental context. Our criterion for naturalistic setting, following Silverman (1977), was that subjects were unaware during their exposure to the object array that it was part of a study.

We recruited volunteers for an ambiguously labeled experiment. Subjects were scheduled individually and were seen by either a male or female examiner, with the examiner's and subject's sex counterbalanced. The examiner met the subject at the

**Figure 14.5** The stimulus room for the naturalistic tests of object and location memory.

**Table 14.3** Mean Location Scores, by Sex, for Study Two

	Location memory		
	<i>N</i>	Mean	<i>SD</i>
Males	21	6.80	4.34
Females	20	11.55	5.23
<i>t</i> = 4.04	<i>p</i> < .001		

laboratory, then led him to a cubicle-type office nearby (the stimulus room), and asked him to wait there several minutes while she completed preparations in the laboratory. Subjects were encouraged to leave books or other materials they were carrying in the laboratory, in order to prevent them from reading or studying while waiting.

Figure 14.5 is a photograph from the entrance to the stimulus room. It was outfitted as a typical graduate student office, containing a variety of work-related and personal items, and was located in an aisle of such offices. Subjects occupied the chair shown in the photograph, which was the only place to comfortably wait. The examiner returned in precisely two minutes and escorted the subject back to the laboratory.

In the laboratory subjects were told that the purpose of the study was to assess how people naturally process their environments. They were asked to name as many objects in the stimulus room as they could and, as precisely as possible, the location of each object. The examiners used prearranged probes if locations were not forthcoming or vague. In response to exit interviews, two subjects, a male and a female, indicated that they had been suspicious in the stimulus room that it was part of the study. Their scores were not atypical, however, and were kept in the data.

Subjects' full responses were tape recorded, with their permissions, and scored from written transcripts by two independent raters. Raters were unaware of which protocols were male or female. Subjects were credited if they approximated the correct location of an object; for example, "the right side of the small desk." Scoring discrepancies between raters were few and were resolved by the second rater.

Table 14.3 shows these results. Females correctly recalled significantly more items by location. Their mean score, in fact, was a robust 70% higher.

There was no measure of object memory, irrespective of location, that could be culled from these data. When subjects reported an item, they tended, with rare exceptions, to know where it was. This may reflect the manner by which people assimilate object arrays, or it may have been an artifact of the emphases on locations in the instructions and the probes.

There were, also, no sex-of-examiner effects or interactions of sex of examiner and subject.

### Study Three: Incidental and Directed Learning

We then undertook a further study, using the same general procedure as Study Two, for two purposes: One was to eliminate systematic biasing of responses by examiners that may have attended the use of open-ended questions and probes in Study Two. (The examiners were not informed of the hypotheses, but were close enough to the investigator's research program to develop accurate suspicions.)

The other was to assess whether sex differences in object and location memory



would be obtained in a directed learning paradigm, whereby subjects were specifically instructed to try to learn objects and their locations. In Study Two, subjects were kept unaware that the room in which they waited was part of the experiment; hence, recall was based wholly on incidental learning. In Study One, subjects were instructed to “examine the objects” in the array, and though they probably surmised that they would be tested for frequency of items remembered, it is uncertain whether they would have attempted to learn locations. Consequently, location memory in this study may have also reflected incidental learning.

In Study Three, the same laboratory and stimulus room were used as in Study Two, but the number of items in the stimulus room was doubled to bring the total to 70. The reason for this was that the dependent measures for this study were based on recognition rather than recall, which was expected to yield higher scores, and we wished to avoid a ceiling effect.

The female examiner from Study Two conducted all sessions. As in Study Two, she met subjects in the laboratory, took their books and other materials, then led them to the stimulus room. For half the subjects of each sex, determined by a prearranged, randomized order of assignment, the procedure continued exactly as previously: subjects were asked to wait in the room while the examiner completed preparations in the laboratory and were left there for two minutes. This was the incidental learning condition.

The other half of subjects were instructed when they were brought into the stimulus room to “try to memorize as many objects in the room as possible, and their approximate locations” and informed that the examiner would return to test them in two minutes. This comprised the directed learning condition.

Testing was the same in both conditions. Subjects were presented first with a list of 35 objects, 25 of which had been in the stimulus room, and were asked to indicate for each whether or not it was there. They were given a point for each correct response, including items identified as in the room and items identified as not, which comprised the measure of object memory.

Following this task, subjects were shown a schematic drawing of the room, divided into seven numbered areas, and were asked to note the area in which each item in the room was located. The number of correct responses for this task served as the measure of location memory.

Table 14.4 presents mean object and location memory scores by sex and incidental versus directed learning conditions.

The data for object memory showed a significant main effect of sex, based on higher female scores across learning conditions, and no significant interaction of sex and condition. In the analyses of simple effects, however, the sex difference for the incidental learning condition reached significance ( $t = 2.25, p < .05$ ), but this difference for the directed learning condition did not ( $t = 1.37, p = .18$ ). Thus, support was obtained for a female bias in incidental learning of objects, but the findings were equivocal for directed learning. The trend for the latter sex difference, however, was in the expected direction, and a larger  $N$  may bring it to a significant level.

For location memory, there was also a significant main effect of sex favoring females and no interaction of sex and condition. Analyses of simple effects revealed significant sex differences for both incidental and directed conditions ( $t = 3.44$  and  $4.45$ , respectively;  $p < .001$  for both). As in Study Two, females' location memory scores based on incidental learning were more than 60% higher than males'.

**Table 14.4** Mean Object Memory and Location Memory Scores, by Sex and Incidental vs. Directed Learning Conditions, for Study Three

Object memory				
Condition	Males		Females	
	Mean	SD	Mean	SD
Incidental	19.45	(3.61)	22.20	(4.12)
Directed	25.50	(3.55)	27.05	(3.59)
F tests				
Sex	6.67	$p < .01$		
Condition	42.83	$p < .001$		
Interaction	.52	ns		
Location memory				
Condition	Males		Females	
	Mean	SD	Mean	SD
Incidental	6.30	(3.23)	10.25	(4.00)
Directed	12.05	(2.86)	16.50	(3.44)
F tests				
Sex	30.40	$p < .001$		
Condition	62.30	$p < .001$		
Interaction	.11	ns		

( $N = 20$  for each sex in each condition: Total = 80)

### Separating Location Learning From Object Learning

In our studies, object memory and location memory were measured separately whenever possible, eschewing the possibility that these may not be independent of each other. Females may have learned more locations by virtue of their greater capacity to learn objects, or they may have learned more objects as a function of their greater capacity to learn locations. The data of Study 3 afforded an opportunity to assess sex differences in location learning with object learning controlled.

First we compared sexes on the number of objects correctly identified as *not* having been in the room in the object memory task. Means were equivalent; 7.80 ( $SD = 2.14$ ) for males and 7.97 ( $SD = 1.86$  for females). This confirmed that there were not differential tendencies between sexes to give "yes" responses, indicating that the object was in the room, when guessing. (If there had been, this would have confounded the proportional measure described next.)

Then, we took the subject's score for number of objects correctly identified as *being* in the room and divided that into the number of locations of these objects correctly identified. This proportion comprised a measure of location memory corrected for object memory.

The results are in Table 14.5. The female bias remained, as indicated by the significant main effect of sex, and simple effects tests showed that the sex difference was significant in both incidental and directed learning conditions ( $t = 3.15, p < .01; t = 4.17, p < .001$ , respectively).

**Table 14.5** Mean Scores by Sex and Learning Condition for Locations Correctly Identified Proportional to Objects Correctly Identified (Location Memory Corrected for Object Memory)

Condition	Males			Females		
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>
Incidental	20	.53	.21	20	.71	.15
Directed	20	.71	.12	20	.87	.12
F tests						
Sex	24.33	$p < .001$				
Condition	23.99	$p < .001$				
Interaction	.09	ns				

#### Study Four: Hormonal Status

Are female spatial specializations related to hormonal status? One indication of the hormonal basis of the spatial abilities for which males excel is that sex differences tend to emerge most strongly after puberty (see Harris, 1978, for a review). Thus, we compared sex differences in object and location memory among school children from grades 4 through 9 (ages 8½ through 13½) to ascertain whether the female advantage would increase with grade level, as more children came into puberty.

The group test developed for Study One was used, with the same procedure described in that section. Subjects came from three junior high schools in the Toronto area and were tested in their classrooms as part of their daily routines.

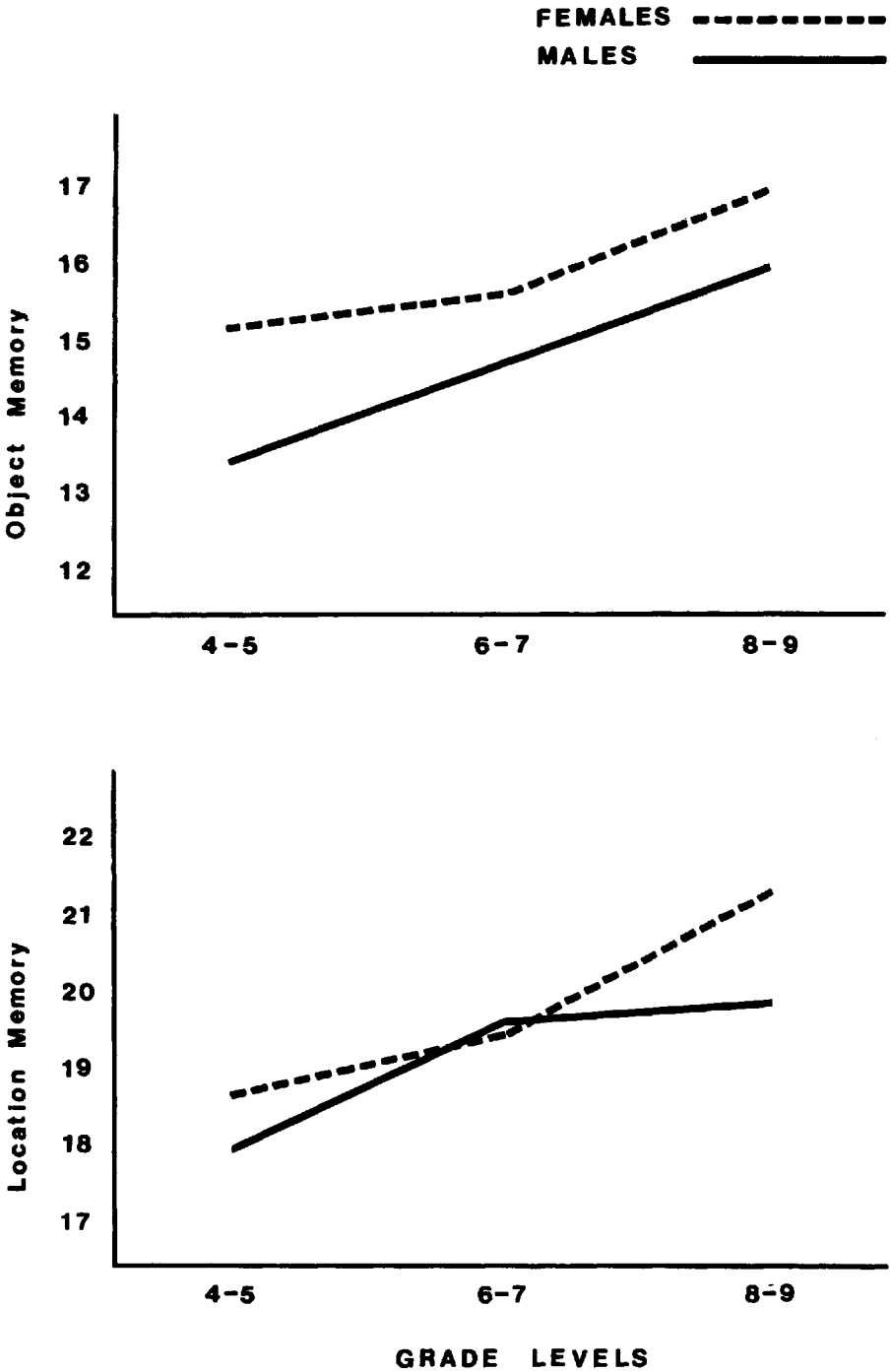
Grade levels were paired in the data analysis to balance subject frequencies across conditions. This resulted in *N*s of 56 versus 66, 83 versus 78, and 81 versus 86 for, respectively, males and females in grades 4–5, 6–7, and 8–9.

Results for both object and location memory scores are shown in Figure 14.6. A multiple ANOVA was performed for sex and grade level across both dependent variables.

For object memory, there were significant main effects of grade level and sex ( $F = 13.13$  and  $12.45$ , respectively;  $p < .001$  for both) and nil interaction effect between these. In terms of simple effects, sex differences favoring females for grades 4–5 and 8–9 were significant ( $t = 2.41$  and  $2.08$ , respectively;  $p < .05$  for both). Thus, a female bias in object memory was replicated with child and early adolescent subjects, but, contrary to expectations, it did not begin or increase with pubertal status.

For location memory, there was a significant main effect of grade level ( $F = 8.83$ ,  $p < .001$ ), and the main effect for sex approached significance ( $F = 2.66$ ,  $p = .10$ ). The interaction effect between sex and grade level was in the predicted direction, but did not approach significance. The sole, significant simple effect for sex difference, however, was for the higher female mean in grades 8–9 ( $t = 2.24$ ,  $p < .05$ ). The sex difference took a similar direction for grades 4–5 but did not approach significance, and the female mean for grades 6–7 was, in fact, slightly lower than the male.

Thus, despite the absence of a significant interaction effect, the data provide a strong suggestion that female superiority in location memory begins with puberty. Considering that some adolescents do not reach puberty by age 13½, the addition of data for grades 10 and upward would be expected to augment this trend.



**Figure 14.6** Mean object and location memory scores by sex and grade level.

Though unanticipated by our hypotheses, the finding that a female bias among prepubertal subjects occurred for object memory, but not location memory, is congruent to the data of Kail and Siegel (1977). They presented letters of the alphabet in various locations in a  $4 \times 4$  matrix to males and females in third grade, sixth grade, and college, and independently measured frequencies of letters and locations recalled. For the third and sixth grades, females remembered more letters, but not more locations, than males. Similar to our first three studies, Kail and Siegel's college age females surpassed their male counterparts in locations recalled.

The discrepancy in the age at which sex differences in object and location memory become manifest is also consistent with our findings, reported in the prior section, that these are separate abilities, although there is no apparent reason for the earlier emergence of sex differences in object memory.

## GENERAL CONCLUSIONS

The data of all of our studies corresponded closely to predictions from the hunter-gatherer model of spatial sex differences and consistently demonstrated a greater capacity by females to remember spatial configurations of objects. Females outperformed males in memory for both frequencies and locations of objects, in both incidental and directed learning paradigms. Sex differences for incidental learning of locations in a naturalistic setting were most striking, however; females' mean scores exceeded males' by 60 to 70%, for measures of both recognition and recall.

The findings of a female bias for both directed and incidental learning supported the specific deduction of our theory that sexes differ in perceptual style as well as learning ability. Studies with the waiting room ploy revealed that females are generally more alert than males to objects in the environment and their locations, whether or not these are perceived as relevant to a task at hand. It is often a topic of humor that the male partner is dependent on the female for locating items in the household, which is ascribed in the conventional wisdom to the greater role of the female in domestic matters. It appears, however, that this capacity is a manifestation of a global, female perceptual trait. Further, our developmental data suggested that the emergence of this trait coincides with puberty, when hormonal differentiation between sexes and male spatial specializations become pronounced.

## DIRECTIONS FOR FURTHER RESEARCH

The question arises of whether the present results can be attributed to superior memory, in general, for females. The tendency, however, has been for memory tasks to show nil sex differences (Maccoby & Jacklin, 1974). Among the exceptions are several studies that reported a male bias for "spatial memory," in seeming contradiction to the present data, but the dependent variables for these were similar to traditional spatial abilities tests rather than the measures developed here.

Nevertheless, it may be informative to assess whether female superiority obtains solely for holistic learning of spatial configurations, or whether it occurs, as well, with serial presentations of objects and locations. If female spatial specializations were selected for because of their contribution to foraging, then they evolved in a holistic

context. Assuming that holistic and serial learning involve different cognitive mechanisms, we may expect sex differences only for the former.

In a related question, we are exploring the suggestion in the present data that males and females employ different modes of processing the environment, which may apply both to specific learning tasks and to daily routines. The open-ended responses of Study Two were scrutinized for indications that males and females undertook the task of trying to recall the stimulus room differently. A number of strategies were detected; for example, subjects reported a distinctive object and then attempted to remember objects nearby, or focused initially on a particular location. Individuals tended to use multiple strategies, and there were no apparent sex differences, although the emphases on locations in the instructions and probes may have induced similar approaches among subjects to the task.

We are also planning follow-up studies using uncommon objects, for which subjects would not possess verbal labels. Another well-documented finding in the area of cognitive sex differences is that females excel on measures of verbal ability (Maccoby & Jacklin, 1974). The female advantage in object and location memory observed here may represent a rudimentary manifestation of superior verbal skills; specifically, a greater capacity to recall object names. If so, the female bias may not occur with uncommon objects, and if it does, we will want to investigate whether it is attributable to a greater adeptness of females at inventing verbal labels for unfamiliar stimuli.

If object and location memory are enhanced by verbal facilities in this manner, it may suggest that female verbal superiority at least its initial form, also evolved as part of division of labor. Similar to spatial differences, verbal sex differences are near universal and show hormonal correlates (Burstien, Bank, & Jarvick, 1980). Nevertheless, there has been no prior attempt to explore their ultimate causation.

### **Evolutionary Explanations and Proximate Mechanisms**

These conjectures about spatial/verbal interactions may bear on a long-standing theory of the neuropsychology of spatial sex differences. They may also illustrate the nature of the relationship between evolutionary and proximate explanations. Evolutionary explanations are not intended to supplant proximate theories; they function, rather, to give these direction. They attempt to go beyond the question of how specific psychological, psychophysiological, or cultural mechanisms operate to elicit behavior and try to explain how these mechanisms, as opposed to all other possible mechanisms, came to exist.

The neuropsychological theory in question is based on findings that suggest that males' brains are functionally lateralized to a greater degree than females'. On this basis, it has been assumed that spatial abilities, which are primarily the province of the right hemisphere, have a larger and more homogeneous area in which to develop in the male (see McGlone, 1980, for a review).

Stated as such, without benefit of an ultimate-level causal perspective, the reasoning seems to be that male and female brains became differentially lateralized by happenstance or some circumstance unrelated to spatial processes, and spatial sex differences developed as an incidental effect of this divergence. These kinds of causal gaps necessarily pervade pure proximate theories.

Our concept of the evolution of spatial sex differences can serve to fill the gaps. The tenet of evolutionary theory is that form follows function, in regard to anatomical,

physiological, behavioral, and cognitive variables. If spatial sex differences were selected for because they maximized the effectiveness of division of labor, then it would follow that sex differences in lateralization emerged as a consequence—the psychophysiological mechanism to which the selection pressures gave rise.

Our model may also bear on a problematic aspect of the lateralization theory, pointed out by Gaulin and Hoffman (1988, pp. 36–37). The theory assumes that greater specialization occurs with greater lateralization. It begs the question, however, of why the more highly lateralized brain functions of males do not render them superior to females in verbal as well as spatial abilities, inasmuch as verbal abilities are mediated mainly by the left hemisphere.

A solution to the problem may reside in the present model, in that males are not regarded as more highly spatially specialized than females, but differently specialized. Further, as contended in the prior section, the theory suggests that females' spatial specializations may interact with verbal processes and have evolved in conjunction with these, which could underlie both their enhanced verbal abilities and more heterogeneous hemispheric functions.

### **Relationships Among Evolutionary Models**

Finally, we consider the relationships among the Gaulin and Fitzgerald model, the Greenwood model, and the present model.

To the extent that these are competing theories, there are opportunities for tests between them. Wherever polygynous species employ resource defense systems or monogamous species show mate defense, the Gaulin and Fitzgerald theory and the theory derived from Greenwood potentially lead to opposite predictions about spatial sex differences. There is also at least one case that could generate a test between our division of labor model and the two mating system theories. Lions are polygynous and possess a resource defense system in which, atypically, females hold territories and males disperse. Thus, both the Gaulin and Fitzgerald model and the Greenwood model would predict a male bias in spatial abilities. On the other hand, females do most of the hunting, which, from the concept we have presented here, would lead to the prediction of female superiority.

Such studies, however, may not render one theory prepotent. There will probably always remain cases that best fit one or another model or do not fit any. An alternative approach would eschew the concept of general spatial abilities in favor of an attempt to delineate specific spatial functions on which various species show differentiation by sex. From this standpoint, the ecological circumstances associated with these differences may be explored on a species-by-species basis. This approach may ultimately provide the most productive path to a unified theory of spatial sex differences.

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Angeles, CA, in August, 1990, and the European Sociobiological Society in Prague in August, 1991.

## NOTE

1. Table 14.2 shows smaller *N*s (numbers) for object memory than location memory. In the early trials, fewer items were added to the original array for the object memory task than are depicted in Figure 14.3. Because there was an apparent ceiling effect in the scores, additional items were inserted, and the object memory data of the early trials excluded.

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