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Evolved mechanisms underlying wayfinding: further studies on the hunter-gatherer theory of spatial sex differences

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Abstract

Based on Silverman and Eals' hunter-gatherer theory of the origin of sex-specific spatial attributes, the present research sought to identify the evolved mechanisms involved in hunting that contribute to the dimorphism. The focus of these studies was the relationship between three-dimensional mental rotations, the spatial test showing the largest and most reliable sex difference favoring males, and wayfinding in the woods. Space constancy was presumed to be the evolved mechanism fundamental to both of these abilities. Measures of wayfinding were derived by leading subjects individually on a circuitous route through a wooded area, during which they were stopped at prescribed places and required to set an arrow pointing in the direction the walk began. As well, subjects were eventually required to lead the experimenters back to the starting point by the most direct route. In support of the hypotheses, males excelled on the various measures of wayfinding, and wayfinding was significantly related across sexes to mental rotations scores but not to nonrotational spatial abilities or general intelligence.

Keywords: Evolution; Wayfinding; Space constancy; Hunter-gatherer; Sex differences; Spatial abilities; Mental rotations; Allocentric perception

Based on the theory that sex differences in spatial abilities originated in human evolution as a function of division of labor between sexes as hunters and gatherers, Silverman and Eals (1992) demonstrated in a series of studies that females outperformed males on original spatial tests mimicking foraging-related attributes. These findings have been replicated and, in some cases, extended to incorporate the question of specific evolved cognitive and neural mechanisms underlying these attributes (Choi and Silverman, 1996; Dabbs et al., 1998; Eals and Sil-

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verman, 1994; James and Kimura, 1997; McBurney et al., 1997; McGivern et al., 1997; Silverman and Phillips, 1998.) There have been few studies, however, of the corollary relationship emanating from the hunter-gatherer theory, that is, the link between hunting abilities and spatial tests favoring males. These have been limited to several investigations of the relationships between spatial test scores and throwing accuracy (Jardine and Martin, 1983; Kolakowski and Malina, 1974; Watson and Kimura, 1991), with inconsistent findings between reports.

The present studies dealt further with the association of male-biased spatial abilities and hunting, specifically in regard to the navigational aspects of the latter, that is, the ability to pursue an animal through unfamiliar terrain and then expeditiously find the way home. The spatial attribute on which these studies focused was three-dimensional mental rotations. The initial reason for this was that mental rotations tests have yielded the largest and most consistent male bias and sex hormone effects (Halpern, 1992; Silverman and Phillips, 1993, 1998; Phillips and Silverman, 1997). Subsequently, based on observations of the pilot study, we were able to formulate a more precise rationale in terms of the cognitive mechanisms common to both mental rotations and wayfinding.

1. Pilot study

A pilot study attempted to determine whether men and women differ in wayfinding in a naturalistic setting and if this capacity relates to three-dimensional mental rotations ability.

1.1. Methods

1.1.1. Subjects

Subjects were volunteer undergraduate students from York University who received either bonus course credits as part of York's Introductory Psychology subject pool procedures or cash payments for their participation. There were 105 females and 81 males, with respective mean ages of 21.58 ($SEM = 0.40$) and 22.24 ($SEM = 0.54$).

1.1.2. Procedures

To assess wayfinding, a winding path of approximately 250 meters was charted through a labyrinth of passageways comprising two floors of one of York University's buildings. Subjects followed the experimenter along the path, individually, with the knowledge that they would have to lead her back to the starting point as quickly as possible by the precise same route. Three measures of wayfinding were taken.

1. *Time to return.* When embarking on the return, subjects were instructed to proceed as quickly as they could but not to walk faster than did the experimenter when she led them, which was a brisk normal pace. The experimenter did not exceed this pace when following subjects from the turnaround point, and in the few instances whereby subjects did, they were told immediately to slow down until the experimenter caught up.
2. *Frequency of deviations from the route.* A deviation was counted when subjects strayed from the path in any way while leading the experimenter. When this occurred, the experimenter immediately brought the subject back to the correct route.
3. *Frequency of hesitations.* A hesitation was scored when the subject came to a complete stop at any point when leading the experimenter.

The measure of three-dimensional mental rotations was administered following the wayfinding task and consisted of the adaptation used by Vandenberg and Kuse (1978) of the test reported by Shepard and Metzler (1971) (Fig. 1).

1.1.3. Data analyses

There were some unanticipated factors that complicated the data analyses. First, experimenters changed during midstudy and, although both were female, there were significant wayfinding differences between groups attributable to pace differences between experimenters. Further, the first experimenter recruited subjects from both the regular academic year session and the following summer session, and found that the latter group scored significantly lower in both the mental rotations and wayfinding measures. Finally, during the tenure of the second experimenter, one of the corridors used in the study underwent renovations, which required that the route be altered slightly. Thus, the sample was divided into four groups for data analyses: experimenter 1 with regular and summer session subjects and experimenter 2 before and after the revision of the route. Data for the mental rotations test and each of the three wayfinding measures were converted into standardized *Z* scores separately for the four groups, with the mean scores for each group weighted for sex. The *Z* scores for the four groups were then combined for the final measures. Partial correlations, controlling for sex, showed that the three wayfinding measures were significantly related to each other ($r(180) = .45$, $p < .001$ for time and deviations; $r(180) = .45$, $p < .001$ for time and hesitations; $r(180) = .16$, $p < .05$ for deviations and hesitations). Thus, the three were averaged to comprise an overall wayfinding score used in all further analyses.

1.2. Results and conclusions

Sex differences for mental rotations favored males at a significant level ($M = .33$, $SEM = .10$ compared to $M = -.51$, $SEM = .09$; $F(1,184) = 39.37$, $p < .001$). Male scores also were significantly lower than females scores for wayfinding, indicating superior male perfor-

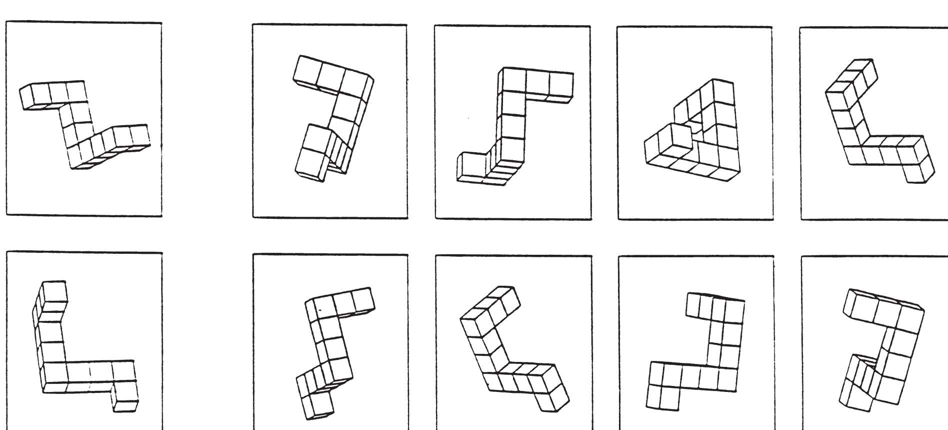

Fig. 1. Two sample items from the mental rotation test. The task is to designate which two of the four figures on the right depict the figure on the left in alternative positions.

mance ($M = -.28$, $SEM = .24$ compared to $M = .43$, $SEM = .23$; $F(1,184) = 4.47$, $p < .05$). The relationship between mental rotations and wayfinding, using a partial correlation to control for sex, was significant as well ($r(180) = -.26$, $p < .001$), with the negative correlation coefficient denoting superior rotations scores associated with superior wayfinding performance. Correlations by sex were as follows: $r(81) = -.15$, $p = .19$, for males; $r(105) = -.36$, $p < .001$, for females.

These results were generally consistent with expectations and with results of a study by Moffat et al. (1998), using a computer-generated virtual hallway maze, in which similar sex differences and a similar relationship between wayfinding and mental rotations was found. The present study demonstrated that these findings can be generalized to a naturalistic setting.

The present experimenters, however, made a further informal observation, which was that most subjects did not appear to memorize turning points and landmarks in order to retrace their paths, as expected. Instead, subjects' orienting movements during the return suggested that they were trying to keep themselves continuously aligned to the starting point and find their way back on this basis. Regrettably, no records were kept of individual differences in the use of this strategy; thus, we could not explore possible associations with sex or wayfinding success. These observations and their correspondence to the literature described later, however, provided a potential explanation for the association of wayfinding and mental rotations and the conceptual basis for the principal study.

2. Principal study

Consistent with the observations noted earlier, Lawton (1994, 1996) described two wayfinding strategies: the "route strategy," which focuses on information such as turns and landmarks; and the "orientation strategy," which makes use of global reference points. Lawton provided various examples of global reference points for outdoor routes, such as position of the sun, and cited configuration of the structure as a possible frame of reference for indoor routes. She also presented self-report data suggesting that males tend to use the orientation strategy more than females in both outdoor and indoor routes. In the same vein, Dabbs et al. (1998) contended on the basis of personal reports that experienced hunters "ignore much of the detail of what they pass." Instead, they sustain "a bird's-eye view of their position," which enables them to take the most direct path home.

These findings, together with the observations of our pilot study, led to the conjecture that the orientation strategy may be the superior strategy for wayfinding during hunting. The orientation strategy has two advantages for the hunter. First, it eliminates the distractions of noting turns and landmarks while searching and following tracks or prey; and second, it provides the most direct route home. Thus, the cognitive capacity underlying this strategy may have been subject to stronger selection pressures in the hunter male than his foraging female counterpart. Foraging would be presumed to occur within a more limited area, close to the home base, and the forager would not be required to keep pace with an animal on the move, which would allow her to maintain her own pace and direction, and enable her to use landmarks more effectively.

Furthermore, the nature of this capacity may be reflected in the association between wayfinding and mental rotations, in that both require that the individual maintain the integrity of a space while exploring its boundaries from various perspectives. Relative to other spatial tests, three-dimensional mental rotations is least accessible to solution by verbal or logical means (Vandenberg and Kuse, 1978). The sole method for solving mental rotations problems with any degree of efficacy, demonstrated in a number of studies, is by visualizing the rotation in three-dimensional space of the test objects and noting whether they can or cannot match the target object (Cocharan and Wheatley, 1989; Freedman and Rovegno, 1981; Schultz, 1991). This essentially requires perusal of the periphery of an object while maintaining a mental representation of its whole, which appears analogous to walking about in the woods while maintaining a mental representation of the space within the periphery of one's route. In fact, from a purely perceptual standpoint, the process of mental rotations is equivalent to walking around the object.

Thus, it is this capacity to maintain a mental representation of a space, a "bird's-eye view," that enables an individual both to solve mental rotations problems and to turn toward the starting point from any location or perspective during hunting. By this explanation, the evolved mechanism at the core of the relationship between mental rotations and wayfinding would appear to involve some form of perceptual constancy, whereby "the properties of objects tend to remain constant in consciousness although our perception of viewing conditions may change" (Coren and Ward, 1989: 406). The most commonly cited constancies, such as size, shape, and color, refer to adjustments in the perception of singular properties of specific objects. There is a less frequently discussed constancy, however, which appears most applicable to wayfinding by orientation. Referred to as space constancy, it encompasses all of the processes involved in maintaining the stability of the surrounding environment while in locomotion (Bisiach et al., 1997; Niemann and Hoffmann, 1997; Probst et al., 1986).

These notions provided the conceptual basis for the principal study, which again focused on sex differences in wayfinding and the relationship of these differences to three-dimensional mental rotations abilities. This study, however, used an outdoor route in a wooded area, and the measures of wayfinding required that the subjects use an orientation strategy. Hypotheses were that males would surpass females in wayfinding by orientation and that this ability, across sexes, would relate to mental rotations performance.

Further, we wished to establish that the relationship between mental rotations and wayfinding was primarily a function of the capacity for space constancy rather than general spatial ability or intelligence. Thus, measures of nonrotational spatial abilities and general intelligence were administered as well. Assuming that these tests may nevertheless show some relationships to wayfinding by virtue of common elements, that is, a *g* factor in spatial abilities and/or intelligence, the hypothesis was that mental rotations would bear the strongest, if not the sole, significant correlation with wayfinding.

2.1. Methods

2.1.1. Subjects

Subjects were volunteer undergraduate students from York University, each of whom elected to receive as remuneration either bonus course credits as part of the Introductory Psychology course subject pool procedures, or cash payments, or some combination thereof. There were 65 females and 46 males, with respective mean ages of 21.93 ($SEM = .77$) and 21.88 ($SEM = .71$).

2.1.2. Wayfinding tests

To measure wayfinding, a route of approximately 410 meters was constructed and covertly marked in a moderately dense wooded area of approximately 2.5 hectares on the York University campus (Fig. 2). The university is located in a low-rise industrial area; hence, there were no visible landmarks above the tree line that could serve as a guide. The route was plotted so that adjoining buildings or other landmarks were kept out of view, although at various times of the day, the sun was visible at some points. The great majority of subjects were first-year students who had recently arrived on campus and were not aware of the woods. Of those who were aware, none had previously been inside.

Five experimenters, one male and four females, conducted the tests with two experimenters assigned to each subject. In order to maintain a constant experimenter sex ratio, the male experimenter was present for all subjects, and the four female experimenters alternated as his partner. The starting point was an open area approximately 25 meters inside the perimeter of the woods. The subject was asked to pretend that the group was tracking an animal and his or her main task would be to lead them back to the starting point by the most direct route. Subjects walked between the two experimenters, with the lead experimenter walking at a normal pace.

At four places along the route (shown in Fig. 2) the group halted and the subject was asked to place a wooden arrow in the direction of the starting point. Experimenters took compass

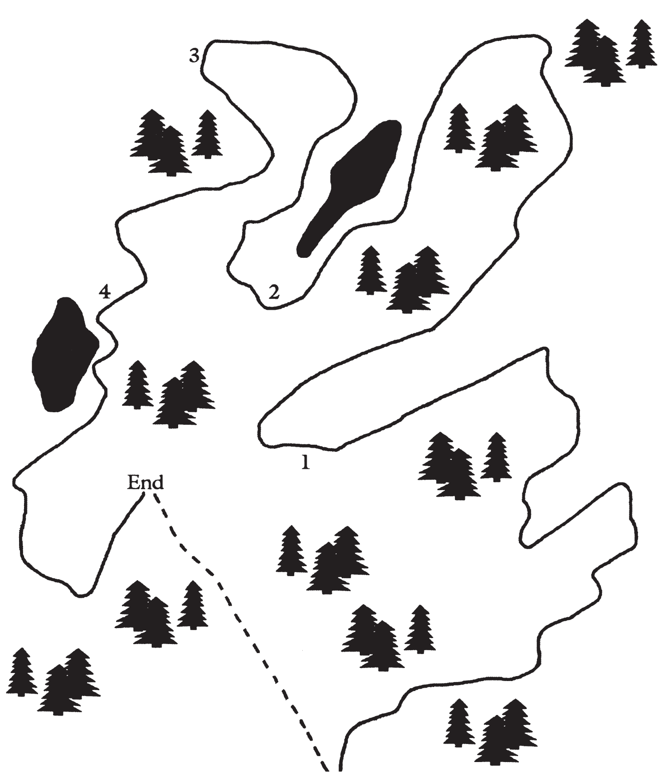

Fig. 2. Schematic layout of the wayfinding route.

readings of each of the placements in terms of degrees of deviation from magnetic north, and these readings comprised one of the wayfinding measures.

For a second measure, subjects were halted at an end point (also shown in Fig. 2) and were asked to take the lead and return to the starting point by the most direct route. Subjects were informed that their times would not be scored and were asked to walk at their normal pace and circumvent dense brush. In the few cases of noncompliance with the latter request, the subject was stopped immediately and asked to go around the brush. Subjects also were instructed not to leave the woods during their search.

The experimenter following directly behind the subject used a hidden, silent counter to tabulate the number of steps taken by the subject. As well, both experimenters independently rated subjects on their competence in finding the most direct route back. A four-point scale was used, ranging from (1) "Good performance with occasional minor deviations at most" to (4) "Subject did not locate the starting point within the ten minutes allowed."

Individual differences in stride were not expected to affect number of steps taken insomuch as the route consisted mostly of underbrush requiring careful treading. To assure that this was the case, however, and to provide a means of control if it was not, the subject's stride was measured before the group departed for the woods. The subject was asked to walk at a normal pace along a 6-meter hallway and the number of steps taken was recorded.

2.1.3. Cognitive tests

The three-dimensional mental rotations test was the same used in the pilot study. Nonrotational spatial measures were the Group Embedded Figures test (Oltman et al., 1971) and a Piagetian water-line test, adapted from Akiyama et al. (1985) (Fig. 3). The measure of general intelligence was Raven's Progressive Matrices (Raven, 1983). The present version consisted of the abbreviated 12-item form combined with items 13 through 25 of the Standard Form A. Prior use of the test by the researchers with the York University student population showed that this combination of items yielded an acceptable level of interindividual variation, whereas one or the other resulted in either a ceiling or floor effect.

2.1.4. Procedures

The first session of the study comprised the test of wayfinding. Subjects were scheduled individually and requested to wear shoes and other clothing suitable for trekking in moder-

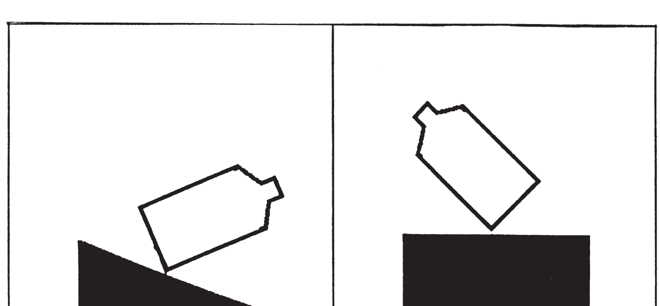

Fig. 3. Two sample items from the water-line test. The task is to imagine that each bottle is half filled with water and draw the top of the water line.

ately dense woods. The second session consisted of the spatial tests and Raven's Matrices, administered in same-sex groups of 4 to 7 subjects. Wayfinding sessions were conducted between mid-September to mid-November to take advantage of full foliage, and the pencil and paper test sessions were scheduled during the following 4 weeks. For both sessions, sex of subject was systematically varied across time, with one sex scheduled in the morning and the other in the afternoon; the order was switched on alternate days. The paper and pencil test sessions were conducted individually by two of the four female experimenters used for the wayfinding tests.

The order of tests in the second session was water-line, mental rotations, Embedded Figures, and Progressive Matrices. Subjects were given 3 minutes to complete the 12 items of the water-line test; 10 minutes to complete the 24 items of the mental rotations test; 12 minutes to complete the 25 items of the Embedded Figures test; and 15 minutes to complete the 25 items of the Progressive Matrices. In keeping with standard practice, scores were calculated in terms of the number of correct responses for all tests except for mental rotations, for which a point was added for each correct answer and subtracted for each incorrect response. Subjects were informed of scoring methods and time allowances prior to each test.

2.2. Results

2.2.1. Wayfinding

2.2.1.1. Arrow placement. Table 1 shows mean scores and standard errors of arrow placements, separately for sex and for each of the four stopping points, in terms of deviations in degrees in either direction from true compass readings. True compass readings were taken by visual sightings in the spring when the woods were bare. A multivariate analysis of variance (MANOVA) of the four placements with sex as a factor was significant (F (4,101) = 2.44, $p <$ .05). Males, as predicted, demonstrated more accurate placements, as indicated by lower deviation scores. Univariate analyses reached significance solely for the second placement, although the analysis for the first placement approached significance (p = .08).

Table 2 shows partial correlations, controlling for sex, among scores for the four placements. All were positive, and all but one, between the first and last placements, were significant. There was a general trend for stronger relationships between placements closer in the series to each other. The coefficient of reliability across the four placements was acceptable at $\alpha = .69$, and the four scores were averaged for each subject to constitute a combined placement score. Males showed a significantly lower average deviation than females on this combined measure (M = 30.46, SEM = 3.04 compared to M = 39.46, SEM = 3.06; F(1,104) = 4.39; $p <$ .05).

Table 1
Mean deviations (SEM) from true compass readings of the four arrow placements by sex

	Males	Females	*F* Test
Point 1	20.83 (3.01)	29.52 (3.68)	3.07
Point 2	20.65 (2.80)	36.88 (4.03)	9.70*
Point 3	45.91 (5.91)	54.07 (6.06)	0.89
Point 4	33.02 (5.12)	41.17 (5.75)	1.05

*$p < .01$.

Table 2
Partial correlations, controlling for sex, between the four arrow placements

	Point 2	Point 3	Point 4
Point 1	0.53*	$0.22^{\dagger}$	0.11
Point 2		0.46*	0.38*
Point 3			0.51*

*$p < .001$; $^{\dagger}p < .05$.

2.2.1.2. Return to point of origin. As anticipated, females required more strides than males to traverse the test corridor ($M = 9.77$, $SEM = .12$ compared to $M = 8.63$, $SEM = .13$; F (1,104) = 40.91, $p < .001$). As also anticipated, the partial correlation, controlling for sex, between normal stride and steps taken on the route back was negligible ($r(103) = .001$, $p > .05$); hence, controls for normal stride were not applied to the steps data. Consistent with predictions, the mean number of steps taken by male subjects on the route back was significantly less than for females ($M = 238$, $SEM = 22.25$ compared to $M = 333$, $SEM = 28.59$; $F(1,104) = 6.19$, $p < .05$).

Regarding the experimenters' assessments of competence in finding the most direct route back, the correlation between the two experimenters' ratings for each subject was significant ($r(103) = .95$, $p < .001$) and indicated robust scale reliability. Subjects' scores on this measure were calculated in terms of the average of the two ratings. As predicted, males showed better ratings in terms of lower scores ($M = 1.87$, $SEM = .12$ compared to $M = 2.25$, $SEM = .14$; $F(1,104) = 4.06$, $p < .05$).

The partial correlation, controlling for sex, between steps and ratings scores was significant ($r(103) = .84$, $p < .001$). Thus, the two measures were converted to standard (Z) scores based on their respective means and averaged. Sex differences on this combined score favored males at a significant level ($M = -.26$, $SEM = .11$ compared to $M = .16$, $SEM = .13$; $F(1,104) = 4.63$; $p < .05$).

2.2.1.3. Overall wayfinding score. The partial correlation, controlling for sex, between combined placement scores and combined scores for return to point of origin was significant (r(103) = .42; $p < .001$). Thus, placement scores also were converted into standard (Z) scores and averaged with return to point of origin scores for an overall wayfinding measure, used in further analyses. Sex differences on this overall score were significant favoring males ($M = -.23$, $SEM = .09$ compared to $M = .17$, $SEM = .12$; $F(1,104) = 6.66$, $p < .01$).

2.2.2. Cognitive tests

Table 3 shows mean scores by sex for the paper and pencil tests. Male spatial test scores were all higher than female scores, as expected, but this difference was significant only for mental rotations and the water-line test. Unexpectedly, males showed significantly higher scores than females on the Raven's test as well.

As a matter of incidental interest, partial correlations controlling for sex were assessed across all four paper and pencil tests. All were positive and significant ($p < .001$, r range from .37 to .57).

Table 4 shows the correlations between each of the tests and wayfinding scores, separately by sex and for the total sample, with a partial correlation controlling for the sex for the latter.

Table 3
Mean performances (SEM) on cognitive tests by sex

	Males	Females	*F* Test
Mental rotations	25.07 (1.58)	16.50 (1.38)	16.72*
Water line task	9.91 (0.46)	7.68 (0.40)	13.51*
Embedded figures	19.54 (0.73)	18.23 (0.64)	1.83
Raven's matrices	16.57 (0.55)	14.77 (0.48)	5.99†

*$p < .001$; †$p < .05$.

Consistent with the hypothesis, the sole significant correlation for the analyses across the total sample was a direct relationship with mental rotations.

Finally, a stepwise multiple regression analysis was performed on the overall wayfinding score with sex and the four tests as independent variables. The sole variable that contributed significantly to wayfinding was the mental rotations score ($\beta = -.26$, $p < .05$).

2.3. Discussion

The main hypotheses of this study were generally supported. For the analyses across sexes, males outperformed females on all measures of wayfinding by orientation and three-dimensional mental rotations performance related directly and exclusively with wayfinding. Mental rotations scores also emerged as the sole significant predictor in a multiple regression analysis, suggesting further that sex differences in wayfinding were specifically a function of differences in this capacity.

This study provided additional support for the hunter-gatherer theory of spatial sex differences in two ways. For one, it demonstrated that sex differences favoring males occur in a naturalistic setting designed to depict a hunter's navigational tasks. For another, confirmation of the hypothesis that mental rotations and wayfinding by orientation were related supported the investigators' concept of space constancy as the evolved mechanism underlying sexually dimorphic navigational abilities.

The question arises, however, as to the extent to which space constancy operates as a domain-specific mechanism or as part of the larger domain of allocentric perception. The latter position provides a rationale, beyond simply noting the existence of a *g* factor for spatial abilities, for males performing better than females on nonrotational spatial tests. These generally entail some degree of allocentricity; that is, they require perceivers to detach themselves from their ingrained egocentric perceptual modes. In the water-line test described

Table 4
Correlations between wayfinding and cognitive tests by sex and for the total sample

	Mental rotations	Embedded figures	Water-line test	Raven's matrices
Males ($n = 46$)	−.09	.08	−.16	−.002
Females ($n = 60$)	−.29*	−.26*	−.11	−.12
Total sample ($N = 106$)	−.22*	−.15	−.13	−.08

Note. Partial correlations, controlling for sex, were used for analyses with the total sample
*$p < .05$.

here, for example, subjects must resist perceiving the water line as parallel to the base of its container, which is the way it is customarily seen in daily life.

On the other hand, the domain-specific interpretation of space constancy is implied in the factor analytic study of Linn and Petersen (1985), which found that, in terms of cognitive processes involved, three-dimensional mental rotations tests occupied their own separate factor. Silverman and Phillips (1998) also concluded that, "the capacity for three-dimensional mental rotations seems to be no more part of a general domain of spatial reasoning than the capacity of an infant to avoid crawling over precipices or a squirrel to leap between branches" (p. 606).

Ultimately, these questions may be resolved at the neural level. Recent research using electrophysiological, lesion, and functional imaging techniques with human and animal subjects have begun to identify separate brain regions and mechanisms underlying various manifestations of allocentric and egocentric perception (Bures et al., 1998; Maguire et al., 1998; Steckler et al., 1999; Taube, 1998).

Another implication of the notion of space constancy as the evolved mechanism underlying both mental rotations and wayfinding is that both of these abilities should emerge at virtually full capacity at a relatively young age. In two separate studies, Cornell et al. (1992, 1994) found that wayfinding measures did not differentiate between 12-year-olds and adults in their twenties, although 8-year-olds were notably inferior. Similar studies for three-dimensional mental rotations were not found, however, and comparisons across studies using different age groups were confounded by differences in test items, scoring procedures, or other conditions. It would be an apt test of the present theory to determine whether the emergence of effective wayfinding abilities between the years of 8 and 12 coincides with the appearance of the capacity for three-dimensional mental rotations.

An alternative interpretation of the ontogeny of wayfinding and sex differences therein emanates from classic studies suggesting that early experience with lines and angles are instrumental in the development of shape constancy (Allport and Pettigrew, 1957). It is reasonable to assume that comparable early experiences may similarly affect the development of space constancy. In this vein, the universal tendency from childhood for males to occupy larger home ranges (Gaulin and Hoffman, 1988) may be noteworthy, inasmuch as their early experiences in developing and cultivating larger ranges may result in a greater capacity for space constancy or allocentric perception in general. In support of this analysis, Dab and Robert (1997) found significant correlations between several measures of home range size and both three-dimensional mental rotations and cartographic skills.

In two aspects, the present relationships between mental rotations and wayfinding did not meet expectations. For one, although correlation coefficients were significant across sexes both for the indoor route of the pilot study and the outdoor route of the main study, these effects resided mainly in the females' data; in fact, the coefficients for males merely showed nonsignificant trends in the predicted directions. For the other, although statistically significant, the correlations seemed modest in magnitude. The reason for both may reside in the limitations on the size and complexity of the routes, particularly outdoors. This may have readily constricted the variance in the wayfinding measures and, in the case of male scores, which were higher, contributed to somewhat of a ceiling effect. Replications are required in larger woods, which represent the hunters' navigational tasks in a more ecologically valid manner.

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