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The Evolution of Sex Differences in Spatial Ability

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It is widely believed that male mammals have better spatial ability than females. A large number of evolutionary hypotheses have been proposed to explain these differences, but few species have been tested. The authors critically review the proposed evolutionary explanations for sex differences in spatial cognition and conclude that most of the hypotheses are either logically flawed or, as yet, have no substantial support. Few of the data exclusively support or exclude any current hypotheses. The hypothesis with the strongest support proposes that range size was the selection pressure that acted to increase spatial ability. The authors suggest ways in which these hypotheses could be tested by presenting explicit predictions and suggesting suitable test species or conditions.

Males and females differ in their morphology, physiology, and cognitive abilities (Halpern, 1991; Kimura, 1999). One of the most studied examples of sex differences in cognition is the male advantage in spatial ability observed in several mammalian species, including humans (over a wide range of spatial tests; see Table 1).

The proximal causes of sex differences in spatial ability have been well characterized. Both organizational (i.e., in utero) and activational (i.e., throughout postnatal life) levels of testosterone influence spatial ability (organizational: Dawson, Cheung, & Lau, 1973, 1975; Galea, Ossenkopp, & Kavaliers, 1994; Hampson, Rovet, & Altmann, 1998; Isgor & Sengelaub, 1998; Joseph, Hess, & Birecree, 1978; Roof, 1993; Stewart, Skvarenina, & Pottier, 1975; Williams, Barnett, & Meck, 1990; activational: Neave, Menaged, & Weightman, 1999; van Goozen, Cohen-Kettenis, Gooren, Frijda, & van de Poll, 1995). There is an inverted U-shaped relationship between spatial ability and testosterone, with maximal spatial ability in the low normal male range. Spatial ability in females is also related to activational levels of estrogens, with higher levels correlated with poor spatial ability (Frye, 1994; Galea, Ossenkopp, & Kavaliers, 1996; Hampson, 1990; Hampson & Kimura, 1988; Hausmann, Slabbekoorn, van Goozen, Cohen-Kettenis, & Güntürkün, 2000; Lacreuse, Verreault, & Herndon, 2001; McCormick & Teillon, 2001; Moody, 1997; Phillips & Silverman, 1997; Warren & Juraska, 1997).

These reasonably consistent outcomes from studies of, and clear mechanistic causes for, sex differences in spatial ability have resulted in enthusiasm for providing an evolutionary explanation, and a plethora of evolutionary scenarios have been suggested (e.g., Gaulin & Fitzgerald, 1986; Geary, 1995; Gray & Buffery, 1971; Sherry & Hampson, 1997; Silverman & Eals, 1992; Wynn, Tierson, & Palmer, 1996). As new scenarios appear to be added at regular intervals, we believe it timely to assess the value of those already proposed. Here we review the literature from both animals and humans, under the working assumption that there might be a common evolutionary explanation for the observed sex differences. As the evidence stands at the moment, we believe that only the range size hypothesis has any substantial support, and that the others are either untested or difficult to test.

Spatial ability is not a unitary ability and is likely to encompass several different cognitive abilities (Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995). Throughout this review, we equate spatial ability with navigational ability, under the assumption that navigation is likely to have been a major selective force shaping spatial abilities (Dabbs, Chang, Strong, & Milun, 1998; Gaulin, 1995).

Selection for Sex Differences in Spatial Cognition?

At least seven evolutionary hypotheses have been proposed to explain sex differences in spatial ability. Perhaps counterintuitively, one of these proposes selection to have enhanced spatial ability in females, and not males. Most of the theories have undergone little rigorous testing. We shall discuss each in turn, attempting to point out both the weaknesses and the predictions for future testing.

Dispersal

The dispersal hypothesis proposes that in species with sex-biased juvenile dispersal, the sex that disperses further will show superior spatial ability (Silverman & Eals, 1992). There are few species for which data about sex differences in both dispersal and spatial ability are available, and what data are available offer ambivalent support for the hypothesis.

In humans, women tend to disperse further than men, so the dispersal hypothesis predicts that women will have superior spatial ability to men (Koenig, 1989). The data from tests of spatial ability in humans, however, do not support this prediction. Studies involving real navigation problems, such as way-finding in a wood

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Table 1
Examples of Studies That Have Found Sex Differences in Spatial Ability Favoring Males

Study	Species	Spatial task
Kavaliers et al., 1996	Deer mice	Morris water maze
Dabbs et al., 1998	Humans	World map knowledge
Galea & Kimura, 1993	Humans	Route learning
Moffat et al., 1998	Humans	Computer-generated maze
Saucier et al., 2002	Humans	Mental rotation
Silverman et al., 2000	Humans	Way-finding
Gaulin & Fitzgerald, 1986	Meadow voles	Tolman sunburst maze
Gaulin & Fitzgerald, 1989	Meadow voles	Symmetrical maze
Kavaliers et al., 1998	Meadow voles	Morris water maze
Mishima et al., 1986	Mice	8-arm radial maze
Cimadevilla et al., 1999	Rats	Morris water maze
Dawson, 1972	Rats	Tolman sunburst maze
Einon, 1980	Rats	8-arm radial maze
Joseph et al., 1978	Rats	Symmetrical maze
Seymoure et al., 1996	Rats	17-arm radial maze
Lacreuse et al., 1999	Rhesus monkeys	Spatial delayed recognition span test

or learning a route through a computer-generated maze, consistently find that men outperform women (Moffat, Hampson, & Hatzipantelis, 1998; Silverman et al., 2000).

In meadow voles (*Microtus pennsylvanicus*) and prairie voles (*Microtus ochrogaster*), males disperse further than females (Boonstra, Krebs, Gaines, Johnson, & Craine, 1987). Therefore, the prediction is that there should be sex differences in spatial ability favoring males in both of these species. This is supported by the data from meadow voles, as males perform better than females on a symmetrical maze task. However, contrary to the prediction, there are no sex differences in prairie voles tested on the same task (Gaulin & Fitzgerald, 1989).

A correlation between dispersal and spatial ability can also be found in rhesus monkeys and deer mice. Among rhesus monkeys (*Macaca mulatta*), males are the dispersing sex, and they appear to have spatial abilities superior to those of females (Drickamer & Vessey, 1973; Kaplan, Fontenot, Berard, Manuck, & Mann, 1995; Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999). Male deer mice (*Peromyscus maniculatus*) also tend to disperse further than females and perform better on spatial tasks (Dice & Howard, 1951; Galea, Kavaliers, Ossenkopp, Innes, & Hargreaves, 1994; King, 1983).

Data from three out of five species appear to lend support to the dispersal hypothesis. However, we would argue that there is a more serious problem with this hypothesis, which concerns the logic used to construct it. Dispersal is used to describe a single movement away from home. As dispersing animals do not return home, it is not obvious why such an animal would have any greater demand placed on its spatial abilities than a nondisperser. Dispersal could be carried out without a map of the natal area or a compass to maintain a heading; an animal could simply follow a geographical feature that led away from the natal area (e.g., toward a mountain range, or in the direction of river flow). We suggest, therefore, that dispersal is unlikely to have been a strong selective force on spatial ability. However, further data are required.

Comparing species with typical and atypical sex-biased dispersal in both birds and mammals could test whether dispersal is correlated with differences in spatial ability. Variation in the dispersing sex occurs both within and between species of mammals and birds. In many bird species, it is the female that disperses, but several species of duck (Anatidae) display male-biased dispersal. In mammals, on the other hand, males tend to disperse further, although in a few species such as chimpanzees (*Pan troglodytes*) and African wild dogs (*Lycaon pictus*), this pattern is reversed (Greenwood, 1980). If dispersal does select for differences in spatial ability, then we predict that male mammals should normally have superior spatial ability, but not in chimpanzees and wild dogs. We also predict that in birds, females should show greater spatial ability than males, but that there should be exceptions in species such as the ducks. Although the available data are consistent with part of one of the predictions from this hypothesis (i.e., an advantage to male mammals in spatial tests), the data from the appropriate comparison species are not available.

In summary, this hypothesis has not yet been rigorously tested and contains a significant logical flaw. Although there are some supporting data, the outcome of the comparisons between male and female prairie voles and humans would seem to invite rejection of this hypothesis.

Fertility and Parental Care

The fertility and parental care hypothesis states that female reproductive success is enhanced by reduced mobility during reproductive periods, through lower energy expenditure and a reduction in accidents or predation (Sherry & Hampson, 1997). This results in the prediction that there is an accompanying reduction in spatial ability in females during reproductive periods. This hypothesis can potentially explain male superiority in spatial tasks if females tested during a reproductive period perform worse, on average, than do males.

The fertility and parental care hypothesis is the only hypothesis that is able to explain the observed negative correlation between estrogen levels and spatial ability. Estrogen levels are higher during reproductive periods and may mediate the proposed reduction in female spatial ability (Sherry & Hampson, 1997).

The issue of what constitutes a reproductive period is crucial to this hypothesis, especially as it is easily confounded with fertility cycles. Thus, a reproductive period might concern only the period during which a female is actually reproducing (e.g., incubating eggs, pregnant, feeding young), or it may refer to the entire stage of the lifetime during which a female is reproductively active. It is not simply the stage of a fertility cycle when the female is most likely to conceive (Sherry & Hampson, 1997). In female mammals, the period of reproduction that is most likely to correlate with reduced mobility is during late pregnancy and early lactation, whereas in birds (depending on the degree of altriciality) reduced mobility begins with laying the first egg and may extend up until fledging. Most fish and reptiles have almost no time during which the reproducing females reduce their mobility.

There are few studies that have tested the predictions of this hypothesis. An implicit prediction is that sex differences will only be apparent once females are reproductively mature. This seems to be generally upheld in both rats and humans, with sex differences in performance on spatial tasks tending to emerge after puberty (rats, water maze: Kanit et al., 2000; rats, symmetrical maze: Krasnoff & Weston, 1976; humans, mainly pen and paper tests: Voyer et al., 1995). However, three of the other hypotheses also make the same prediction (range size, male warfare, and female choice, see below).

A much more stringent prediction from this hypothesis is that there will be variation in spatial ability among females, depending on their fertility and mobility, rather than between males and females. Galea et al. (2000) found that pregnant rats in the third trimester traveled further to reach the hidden platform in a Morris water maze than nonpregnant rats, suggesting some impairment of their spatial ability. However, pregnant rats in the first and second trimesters tended to be better at the test than nonpregnant rats (using measures of latency and distance traveled to reach the platform). This is in accordance with the fertility and parental care hypothesis, as estrogen levels are higher during the third trimester of pregnancy than during the first and second (Norris, 1997). There were no differences in swim speed between the groups. However, it should be noted that swim speed does not automatically correlate with activity measured on dry land, and neither of these are necessarily related to mobility (Lehmann et al., 2002). These data are, then, equivocal in their support for the hypothesis: The reduced spatial ability during late pregnancy is in accordance with the hypothesis, but the lack of a reduction in swim speed is not.

Data from spatial tests of deer mice support the hypothesis. Female deer mice in the breeding season performed more poorly on a water maze task than did males (although it is not clear in this study whether the females were pregnant or caring for young; Galea, Kavaliers, et al., 1994). Outside the breeding season, there was no sex difference in water maze performance. Swim speed did not differ between the sexes during the breeding season.

Spatial tests of women who were tested when pregnant and following childbirth also provide data that are consistent with the predictions of this hypothesis (Woodfield, 1984, using the embedded figures test, a pen-and-paper test of spatial ability). The women were tested in the 38th–40th week of pregnancy and again while they were breastfeeding 6 weeks after giving birth. Breastfeeding mothers have very low levels of estrogens. They performed better on the test while they were breastfeeding than when they were pregnant, an improvement that was greater than that of a control group of nonpregnant women tested at intervals of similar duration. The women had reduced spatial ability during the late stages of pregnancy, as predicted by the fertility and parental care hypothesis.

There is some evidence that spatial ability is reduced during reproductive periods when estrogen levels are high, as predicted by the fertility and parental care hypothesis. However, it is unclear whether this effect is also associated with the predicted reduction in mobility. Female mobility appears to be reduced during late pregnancy and lactation in mice and humans: Barnett and McEwan (1973) compared the movements of virgin, pregnant and lactating mice in a residential maze. The maze consisted of a nest box with four arms radiating from it. Each arm contained food, water, or balsa wood or was empty. They found that although mice in late pregnancy increased food and water consumption, they made fewer visits to the maze arms and spent less time in them. Similarly, it appears that pregnant women tend to spend more time doing sedentary activities and resting than nonpregnant women (Durnin, 1991; English & Hitchcock, 1968; Prentice et al., 1996). However, variation in the timing and level of mobility has not been well quantified in any species. Birds may make ideal subjects for this test because, not only is there a significant reduction in mobility associated with incubation in many species, but also the sex that incubates varies between species. For example, in jacanas (Jacanidae) the male incubates the eggs alone, whereas in many songbirds the female does most, sometimes all, of the incubating.

The fertility and parental care hypothesis is based, to some degree, on the finding that females' spatial skills vary with hormonal levels through the menstrual cycle. Sherry and Hampson (1997) propose that the fertility cycle fluctuations in spatial ability are a result of selection for a reduction in spatial ability during reproductive periods, and that increased levels of estrogen effect this reduction. The consensus from studies of fertility cycles in humans, rats, and rhesus monkeys is that spatial skills are reduced at the high-estrogen phases relative to the rest of the cycle. These studies use mainly mental rotation tests for humans and water maze tests for rats (Frye, 1994; Hampson & Kimura, 1988; Hausmann et al., 2000; Lacreuse et al. 2001; McCormick & Teillon, 2001; Warren & Juraska, 1997). However, others have found the opposite effect: that spatial ability was enhanced during high-estrogen cycle phases (Frick & Berger-Sweeney, 2001; Healy, Braham, & Braithwaite, 1999; Postma, Winkel, Tuiten, & van Honk, 1999). There are also a number of studies that have found no relationship between fertility cycle and spatial ability. This latter group includes studies that assayed hormone levels to determine cycle stage, so the lack of a relationship between spatial ability and stage of fertility cycle cannot, therefore, be attributed solely to inaccurate methods of cycle phase determination (Berry, McMahan, & Gallagher, 1997; Epting & Overman, 1998; Gordon & Lee, 1993; Stackman, Blasberg, Langan, & Clark, 1997). It is not clear whether the inconsistency in observing the spatial ability fluctuations is due to variation in experimental testing conditions or to the fact that the effect is small and easy to miss.

The fertility and parental care hypothesis is unusual in that it is the only hypothesis to postulate that superior male spatial ability has arisen through selection on female spatial ability. It is the only hypothesis that predicts the observed negative relationship between estrogen levels and spatial ability. However, the correlation between testosterone levels and spatial ability suggests that selection has also acted on male spatial ability (e.g., Isgor & Sengelaub, 1998; Neave et al., 1999; Roof, 1993; Stewart et al., 1975; van

Goozen et al., 1995). It seems, then, that the fertility and parental care hypothesis is an insufficient explanation for the differences in spatial ability between the sexes.

To summarize, there is some evidence that spatial ability is reduced in female humans and rodents during certain stages of their reproductive cycle, results that are consistent with the fertility and parental care hypothesis. In some situations, this may have led to sex differences. However, a major problem is that there is no clear evidence that females are less mobile during this time of reduced spatial ability. It is essential to determine if and when mobility is reduced during reproductive periods and then to test whether spatial ability covaries with the change in mobility.

Female Foraging

This hypothesis has been proposed specifically in relation to humans and is based on a presumed division of labor between the sexes during human evolution, with women gathering food and men hunting for it. It is proposed that the gathering aspect of foraging requires an accurate recollection of the locations of particular food sources (Silverman & Eals, 1992). The main prediction of this hypothesis is that females should be more accurate than males at remembering locations; it has been tested with tasks that involve subjects trying to remember the locations of objects within complex arrays. Women are typically better than men at such object-location tasks, both on paper and in three dimensions (Duff & Hampson, 2001; Eals & Silverman, 1994; James & Kimura, 1997; McBurney, Gaulin, Devineni, & Adams, 1997; Montello, Lovelace, Golledge, & Self, 1999; Silverman & Eals, 1992), although there are some exceptions (Dabbs et al., 1998; Duff & Hampson, 2001; Postma et al., 1999; Postma, Izendoorn, & De Haan, 1999).

The female foraging hypothesis proposes that women should outperform men on object-location tasks because of their superior spatial abilities. However, women have better verbal abilities than men and are thought to perform better than men on object-memory tasks because they use their superior verbal skills to label the objects (Chipman & Kimura, 1998; Galea & Kimura, 1993; Kimura, 1999). It is possible that a similar interpretation could explain women's superiority on object-location tasks, as in these tasks the object identity tends to be confounded with location. For example, in Silverman and Eals' (1992) pen-and-paper location task, subjects were given a sheet of pictures (presentation array) and allowed to examine the objects for 1 min before being given another array (test array) and asked to mark the items that had changed location. Subjects needed to remember both the location and identity of an object in order to solve the task, and women performed better than men. When James and Kimura (1997) decreased the object-memory factor in the task by moving objects to previously empty locations in the presentation array, they found no sex differences in performance. Similarly, there was no sex difference on a task in which the subjects were given the objects and had to replace them in their positions in the original array (Postma et al., 1998, 1999). Both of these results might be explained by female superiority in labeling items, rather than superiority in spatial ability. Consistent with this interpretation is Eals and Silverman's (1994) finding that when uncommon (i.e., difficult to label) objects were used in the test, they found less clear-cut differences favoring women on object-location memory: Women were still better than men at the pencil-and-paper task, but not when real objects were used.

We suggest that the object-location tasks on which women perform better than men are not sufficiently spatial in nature to conclude that women have superior spatial abilities. Rather, this hypothesis may explain women's superior object-memory abilities. Furthermore, none of the data showing sex differences in nonhuman species fit with either the assumption of division of foraging labor between the sexes, or with the experimental finding of female superiority in a spatial task. A hypothesis that can explain an uncommon result on specific tests in humans is not useful as an explanation of the demonstrable sex differences in spatial ability in other species (and, indeed, for the remainder of the human results). We therefore propose that the female foraging hypothesis should no longer be considered a viable explanation for the evolution of sex differences in spatial ability.

Male Foraging

The male foraging hypothesis is also based on the assumption that there was a division of foraging labor in humans (Silverman & Eals, 1992). This hypothesis predicts that men will be better than women at tasks requiring spatial abilities involved in hunting. Support for this prediction comes from the findings that men are more accurate than women at geographic tasks such as giving directions or way-finding in woodlands (Dabbs et al., 1998; Montello et al., 1999; Silverman et al., 2000). Male superiority at motor tasks such as throwing and intercepting a ball have also been used to support this hypothesis (Peters, 1997; Watson & Kimura, 1991; Westergaard, Liv, Haynie, & Suomi, 2000). However, such tasks may be accomplished by having the requisite visual perceptual abilities and do not necessarily tap spatial cognitive abilities.

As yet, there have been no attempts to test the predictions of this hypothesis outside of human subjects. It may be possible to test this hypothesis in nonhuman species in which the male provisions the female while she is rearing young (e.g., hornbills, Bucerotidae: Kinnaird & O'Brien, 1999; Stanback, Richardson, Boix-Hinzen, & Mendelsohn, 2002; wolves, *Canis lupus*: Mech, 1999). The prediction would be that these species would show an enhanced spatial ability in males relative to females, perhaps solely during these periods. Such findings, however, would also be consistent with the predictions of the fertility and parental care hypothesis. To separate the outcomes of the two would require a demonstration that female spatial ability did not vary with parental state.

Range Size

The range size hypothesis links spatial ability to range size and mating system (Gray & Buffery, 1971). It predicts that sex differences in spatial abilities will only be found in species in which males have larger home ranges than do females. In such species, males will show enhanced spatial ability compared to females because they have to cover a larger area in order to father offspring with several females and maximize their reproductive success (Gaulin, 1995).

Data from three species of vole provide some support for this prediction: The promiscuous male meadow vole has a range that is much larger than that of conspecific females, whereas there is no difference in range size between the sexes in the monogamous prairie and pine voles (*Microtus pinetorum*). Male meadow voles outperformed conspecific females on both a Tolman sunburst and a symmetrical maze, but there were no sex differences in performance between the sexes in either the pine or the prairie voles, as predicted by the hypothesis (Gaulin & Fitzgerald, 1986, 1989). The sex difference in meadow voles has also been observed in the water maze, which suggests that the result is robust with regard to changes in task type (Kavaliers, Ossenkopp, Galea, & Kolb, 1998).

Tests on spatial ability in deer mice and desert kangaroo rats (*Dipodomys deserti*) have also produced results that are consistent with the range size hypothesis. Deer mice are polygynous, with males having larger home ranges than females during the breeding season, whereas in the monogamous desert kangaroo rat there are no sex differences in range size. In the breeding season, male deer mice outperformed conspecific females in a Morris water maze task, but there were no sex differences among the kangaroo rats on a task that required them to remember the location of a token buried in a sandbox (Galea, Kavaliers, et al., 1994; Langley, 1994).

The predictions of this hypothesis are also compatible with the observed sex differences in spatial ability in rats and humans, as both species are thought to be somewhat polygynous, with males tending to have larger spatial ranges than females (Gaulin & Hoffman, 1998; Macdonald & Fenn, 1995; Taylor, 1978). Data from mice are similarly supportive: Wild male house mice have larger range sizes than do conspecific females, and male laboratory mice outperform females in a radial arm maze (Chambers, Singleton, & Krebs, 2000; Mishima, Higashitani, Teraoka, & Yoshioka, 1986; Zielinski, vom Saal, & Vandenbergh, 1992).

Comparisons within species also provide support for the range size hypothesis. Deer mice and meadow vole males have larger ranges than females only during the breeding season (Galea, Kavaliers, et al., 1994; Gaulin & Fitzgerald, 1989). Male deer mice perform better than females in the water maze during the breeding season, but not when tested during the nonbreeding season (Galea, Kavaliers, et al., 1994). There are also sex differences in meadow voles in breeding condition, but not between nonbreeding subjects (Galea, Saksida, Kavaliers, & Ossenkopp, 1994; Galea, Kavaliers, Ossenkopp, & Hampson, 1995; Kavaliers et al., 1998).

Despite the agreement with the available data, there are problems with this hypothesis too. The original formulation of the hypothesis was simply that male superiority on spatial tasks is correlated with their larger home ranges (Gray & Buffery, 1971). However, of the species tested to date, mating system is confounded with range size, so that sex differences in range size are always associated with polygynous or promiscuous mating systems. It is necessary, therefore, to test species that do not vary in mating system but which do show sex-dependent range size variation, and species that differ in mating system but in which there is no sex-dependent range size variation. There are more data on both range size and mating system for birds than for mammals, and thus it may be that the predictions from the hypothesis could be usefully tested in birds.

A second possible problem with the hypothesis is that some of the data are equally consistent with the predictions from the fertility and parental care hypothesis. Discriminating between the two would require demonstration of a relationship between range size variation and spatial ability that exists outside the breeding season, or, of female superiority in spatial ability. One potentially suitable group in which to look for the latter are the nest-parasitic cowbirds. Female cowbirds that are nest parasites have larger hippocampal volumes than do their conspecific males (Reboreda, Clayton, & Kacelnik, 1996; Sherry, Forbes, Khurgel, & Ivy, 1993). As the hippocampus in birds is associated with spatial information processing, it may also be the case that these females would outperform their conspecific males on spatial tasks.

Third, determining range size is not always that straightforward. As data for prairie voles show, it is particularly important that range size can be accurately assessed for the animals under test: Although in Gaulin and Fitzgerald's (1989) tests the prairie voles did not differ in range size between the sexes, in other parts of their distribution they do differ (Swihart & Slade, 1989).

Finally, there are data that do not fit with the predictions of the hypothesis. At least one study has failed to find sex differences between male and female meadow voles tested in a water maze (Sawrey, Keith, & Backes, 1994). However, it is not clear whether the subjects were in breeding condition.

To summarize, the mammalian data seem to conform better to the predictions of the range size hypothesis than to any of the others. It must also be noted that in humans, there is still little to distinguish this hypothesis from the male foraging, male warfare, and female choice hypotheses, all of which predict the same correlation between range size and spatial ability. They vary only in the rationale as to why the sexes might differ in range size.

Male Warfare

Sex differences in human spatial ability have been proposed to be due to direct male–male competition, in the form of small-scale warfare (Geary, 1995; Sherry & Hampson, 1997). The male warfare hypothesis proposes that men travel long distances in order to ambush other men (and therefore reduce competition for resources) and capture females (Buss & Shackelford, 1997), rather than to hunt for food.

Small-scale warfare does appear to be related to male mortality and individual differences in number of offspring in extant hunter–gatherer societies (Chagnon, 1983). There is very little other support or evidence for this hypothesis, probably because it has received very little attention in the literature. We would also like to question the relevance of this hypothesis, when compared with the male foraging hypothesis, for example. Men might travel for warfare once every few months but travel to hunt for food every few days. Warfare usually involves attacking acquaintances rather than total strangers; therefore, when men travel for warfare they are usually going to places that they already know through hunting or trading trips (Chagnon, 1983). Therefore, we would argue that warfare is unlikely to have been as strong a selection pressure on male spatial ability as hunting.

It may be possible to test this hypothesis by observing hunter–gatherers to see whether male spatial abilities are more correlated with warfare or hunting ability. This hypothesis is not only logically flawed, but also applies only to humans and thus should be removed from the list of plausible possibilities for the evolution of sex differences in spatial ability.

Female Choice

This hypothesis proposes that females will prefer males who are successful hunters as mates, and that hunters are successful because of their superior spatial ability (Sherry & Hampson, 1997). Like the range size and male warfare hypotheses, this hypothesis predicts that sex differences in spatial ability have evolved through sexual rather than natural selection, and therefore that variation in male spatial ability will correlate with mating success rather than with survival. The female choice hypothesis differs from the other two by proposing that the mechanism is intersexual selection (i.e., the males compete for female attention), rather than intrasexual selection (the males compete between themselves for access to females).

There have been no direct tests of this hypothesis. However, in hunter–gatherer societies such as the Ache tribe of Eastern Paraguay, men share animals that they have killed among the whole tribe, rather than just within their family group (Hawkes, 1991). This public sharing may have a display function, by conspicuously demonstrating foraging success. Whether or not the women of the tribe use this sharing to make subsequent mate-choice decisions is not clear. Bird, Smith, and Bird (2001) observed spear fishing and turtle hunting in the Meriam people of Torres Strait, Australia, and concluded that these hunting practices fulfilled criteria to be costly signals honestly displaying quality. Again, it is unknown whether women use the signals to make mate choices, or whether hunting success is correlated with spatial ability.

Unlike the female foraging and male warfare hypotheses, this hypothesis may plausibly be investigated in nonhuman animals. Courtship feeding, particularly in birds, is often considered a way in which females assess the quality of their males (e.g., Bussiere, 2002; Gonzalez-Solis, Sokolov, & Becker, 2001), although the possibility that the male is thereby specifically demonstrating his spatial ability has not been discussed previously. One way to test this prediction would be to compare courtship gift quality with spatial ability.

Conclusions

The evolutionary hypotheses that have been proposed to explain sex differences in spatial ability are summarized in Table 2. We conclude that the hypothesis that is currently best supported by the data is the range size hypothesis. Of the remainder, the fertility and parental care hypothesis is also supported by data, particularly those showing variation in spatial ability with estrogen levels. However, there is a need to demonstrate that females are less mobile during phases of their reproductive cycle and to show that the reduction in mobility is correlated with the reduction in spatial ability.

None of the remaining hypotheses have much supporting evidence. We propose that three should be dismissed as explanations of sex differences in spatial ability because they are either logically flawed (dispersal), or apply to and are only testable in humans (female foraging and male warfare). Finally, the male foraging and female choice hypotheses remain plausible explanations for sex differences in spatial ability but are, as yet, completely untested.

Most of the hypotheses link spatial ability to space use and differ only in their explanations as to why the sexes differ in their space use. They also make predictions that are remarkably similar; thus, finding evidence that supports one to the detriment of any of the others is difficult. Nonetheless, each makes testable predictions, and if these were all supported it would lead to the exclusion of the opposing hypotheses. We presume that this is a desirable outcome, and one that is preferable to the steady accumulation of hypotheses that is currently occurring.

A caveat to this review is that there are problems with many of the spatial tasks used (and discussed here). These include the fact that certain tasks, such as the pen-and-paper tests for humans, may not necessarily assess navigational ability. In addition, the tasks may affect the motivational or physiological states of the sexes differently. For example, there is evidence that the sexes differ in their response to stress, and this may have a differential effect on their performance on highly stressful tasks such as the water maze (Galea, Saksida, et al., 1994; Hölscher, 1999; Kavaliers et al., 1996; Kimble & Whishaw, 1994; Lawton, 1994; Perrot-Sinal, Kostenuik, Ossenkopp, & Kavaliers, 1996; Shors, 1998; Whishaw & Tomie, 1996). Less stressful test environments may yield more reliable results. There is also evidence that males and females use different cues to solve spatial tasks (rats: Kanit et al., 1998; Kanit et al., 2000; Roof & Stein, 1999; Tropp & Marcus, 2001; Williams & Meck, 1991; humans: Dabbs et al., 1998; Galea & Kimura, 1993; Lawton, 1994; Montello et al., 1999; Sandstrom, Kaufman, & Huettel, 1998; Saucier et al., 2002; kangaroo rats: Langley, 1994). The number and type of landmarks provided in the test setting are likely to vary widely between laboratories and may

Table 2
A Summary of the Evolutionary Hypotheses That Have Been Proposed to Explain Sex Differences in Spatial Ability

Hypothesis	Species	Prediction	Selective pressure
Dispersal	Any	Dispersing sex better	Natal dispersal distance varies between sexes.
Fertility and parental care	Any	Females < males	Females reduce mobility to decrease mortality during reproductive periods.
Female foraging	Humans	Females > males	Division of foraging labor: Women remember locations of food sources.
Male foraging	Humans	Males > females	Division of foraging labor: Men use navigation skills for hunting.
Range size	Any	Males > females	Polygynous males have larger ranges to mate with more females.
Male warfare	Humans	Males > females	Men travel long distances to kill competitors and capture females.
Female choice	Humans	Males > females	Women choose males on the basis of their hunting success.

affect the task difficulty differentially for one or the other of the sexes.

Currently, the range size hypothesis has much greater support than any of the others as an explanation for sex differences in spatial ability, but even this is not very substantial or exclusive and has been gained from tests of only a handful of species. Evolutionary explanations cannot be convincing if only one or a few species are tested. It is especially unhelpful to suggest possible evolutionary explanations each time a difference between the sexes is demonstrated, particularly if the sex difference is observed with a single task. Rather, time and energy should be spent attempting to support or eliminate the current proposed explanations. This is a particular problem with the hypotheses that have been proposed specifically to explain sex differences in spatial abilities in humans, as this makes them especially difficult to test.

In this review of sex differences in spatial ability, we have attempted to focus on the evolutionary hypotheses advanced to explain the observed differences. We chose this approach because we feel that this is the weakest aspect of this exciting interdisciplinary field. We also believe it timely given the recent criticism heaped upon other areas of “neuroecology,” as it would appear that the area of sex differences in spatial ability is a good (perhaps better) example of the problems perpetrated by neuroecologists, as outlined by Bolhuis and Macphail (Bolhuis & Macphail, 2001; Macphail & Bolhuis, 2001). More positively, we hope that our comments and suggestions may provide directions for future testing.

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