

GENDER AND SOCIETY

*Essays Based on Herbert Spencer
Lectures Given in the University
of Oxford*

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Sexual Differentiation and Cognitive Function

LUCIA JACOBS

In 1588, Michel de Montaigne concluded, 'I say that male and female are cast in the same mold: save for education and custom the difference between them is not great' [62]. If Montaigne could be asked about the relative properties of men and women in the area not only of morphology and outward behaviour, but also of cognition I suspect he would give the same answer, perhaps more adamantly. Yet it is an interesting question: how do the sexes differ in their perception and processing of information about their external world? And if such differences exist, do they develop due to 'education and custom', or are cognitive sex differences a consequence of sexual differentiation? And if such differences exist, can we suppose that they are functional (i.e. do they occur in other species and have they arisen through processes of natural selection?).

Questions about sex, gender, and cognitive ability are topics of intrinsic and universal interest, a field of enquiry which has generated tens of thousands of scholarly articles. It is also a field mined with potential political dangers and divisions, and one into which biology ventures at great risk. The firm establishment of the principles and ramifications of

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sexual differences, unrelated to cultural context, is an important goal, but it lies on the far side of treacherous intellectual terrain. But we can, at this juncture of the expedition, find places to set our feet that will not lead to disaster. Generalizations that, presumptuous though they may be, biologists feel will survive their time and their cultural context. For example, I would argue that it is a landscape that must be understood within a historical framework, which, to a biologist, is the framework of evolution by natural selection. Despite the controversy, all would agree that we have at least three good landmarks on which to base our map. These are: first, that in all vertebrate species, male and female cognitive abilities and brains are more alike than different; second, that such differences can arise through the action of hormones on neural development; and third, that the internal environment of the hormonal milieu is influenced both by the genetics of sex determination and by the external environment. Hence, sex differences in the brain and in cognitive abilities can be strongly influenced by the combined actions of the environment and an individual's genetic make-up.

Using these landmarks, each discipline constructs its own map of this terrain, each perhaps with a distinctive distortion, much as Saul Steinberg's 1975 'View of the World from 9th Avenue' is a topologically correct but geometrically distorted representation of the world from the point of view of a New Yorker [73]. My route through this terrain is based on the map of a cognitive psychologist trained in the practice of ethology and the theory of evolution. I begin with the biological underpinnings: the distribution of cognitive sex differences in species other than our own, and the causes and consequences of this pattern in other species.

The puzzle underlying cognitive sex differences is why such a fundamental trait as cognition should differ between the sexes. Yet the same can be said of even more fundamental traits, such as body size. For example, in many polygynous mammals, despite similarities in ecological niche between males and females, males are larger than females [4]. The

functional explanation for this sexual dimorphism is that in polygynous species, males compete amongst themselves for access to females, and therefore require proportionately larger body sizes than females in order to reproduce. In the red deer (*Cervus elaphus*), for example, larger stags are more successful in defending a harem of hinds and hence a stag's body size is directly proportional to his reproductive success [17].

Sexual selection and song

Sexual dimorphisms in body size or antler weight may have little to do with cognition, but illustrate the adaptive significance of sex differences. The boldest and most easily explained example of a cognitive sex difference is also found in the context of males competing for female mates. This is the ability of songbirds, also known as passerine birds, to learn their species-specific song. Passerine birds comprise over half of all bird species in the world, and in many species males must learn to sing [57]. These song-learning species show much variability in the timing and tutoring of song: some species learn only at one time period during development (critical period or age-limited learners) and some learn throughout life (open-ended learners), some learn from a parent and some learn from surrounding adults. Yet across all song learning species, there is a sex difference: males sing more complex songs than females. Although it is true that in some species females and males sing duets, where each part is of equal complexity, in no species do females learn to sing more complex songs than males [76].

The function of this distinct sex difference is clear: males require learned song to attract female mates and to compete against male rivals. The ability to learn song is thus subject to sexual selection, the selective pressure which result from competition among individuals of the same sex [76]. Song learning ability lends an advantage both in territory disputes

and in female preference: in open-ended learners, males with large song repertoires attract more females. A large repertoire is also necessary for effective territory defence, because in many species, the mode of competition among males is their ability to match the songs of their rivals. Neighbouring males mimic each other's repertoire, song for song, apparently an efficient method by which they size up each other's repertoire [8]. Since repertoire often increases with age, this may provide the listening bird with some estimate of the competitive characteristics of his neighbour.

For these and other reasons, birdsong is considered a sexually selected trait, with advantage accruing to those who can learn more complex song than rivals. And since in most species, it is the males who compete more strongly than females for mating opportunities, it is the males who receive the brunt of the sexual selection for song learning. And hence the clear dimorphism in learning ability.

How this dimorphism develops and by what precise mechanism this occurs, is itself a thriving scientific discipline [6]. In brief, however, it is a story of hormonal environments, created by the hormone output of the fetal and perinatal gonad. If the brain tissue of the developing songbird, such as the well-studied canary or zebra finch, experiences high levels of the hormone that normally emanates from the male gonad, during the critical period immediately after hatching, this leads to the structural enhancement of certain nuclei, known as the song nuclei. In the zebra finch, where females do not sing at all, this produces a striking difference in morphology between male and female brains. The male brain contains a series of interconnected nuclei, the song nuclei, which are necessary to learn and produce song and which are smaller or absent in the female brain. The detailed circuitry and functions of these nuclei is outside the province of this essay; the obvious conclusion, however, is that both learning ability and its underlying brain structure are sexually dimorphic [6].

Hence, here is an everyday occurrence of a sexually dimorphic learning ability, with underlying dimorphism in

its neural basis. The different hormonal milieu of males and females produce sex differences throughout the fine structure of these brain areas (e.g. the volume of brain regions, the number of neurons, the size of neuronal cell bodies, the length of dendrites, and the distribution of receptors for steroid hormones). Yet if hatchling females are injected with the steroid hormone oestrogen, the volume of song nuclei areas are increased via reduced neuronal death and such females will both sing and learn song syllables from a tutor. If these females continue to receive male-appropriate steroid hormones as an adult, she will develop further changes in structure, all with the effect of producing a female brain whose song nuclei are increasingly similar to those of males [6].

Although birdsong is a clear example of a cognitive sex difference in vertebrates and an excellent system for the study of their development, it also has the drawback of the special case; no other species, avian or otherwise, learn songs. But in its general outlines, it can be thought of as a template to search for other cases of sex differences, with these attributes: it shows enhanced development in the sex experiencing greater sexual selection, it is shaped by the hormonal environment during a critical perinatal period, and with the degree of neural dimorphism is directly related to the degree of cognitive dimorphism. These attributes are present only in one example of cognitive function in mammals and this is in the realm of spatial cognition.

Sexual selection and space

Spatial cognition is usually defined to include assorted perceptual and mnemonic abilities, such as the ability to perceive and locate visual objects in space and the ability to create map-like internal representations of the environment. Thus 'spatial cognition' includes both simple and complex spatial processing.

Male and female laboratory rats, the domestic strain of the wild Norwegian rat (*Rattus norvegicus*), show striking differences in what they remember from exploring new environments. These differences emerge when the rats are asked to use visual landmarks to return to the food they had found earlier, such as location of bait in a maze [92]. How well males and females are able to find the bait depends on how the visual appearance of the test room has been changed. If the maze is surrounded by a white curtain, so that the shape of the space is changed, males make many more mistakes. It is as if they are using the shape of the room as a compass, to tell them where they are. Thus, if the room is rectangular with a door at one end, the male rat can place himself in this simple map, and remember, for example, that he has already looked for bait at the 'door end'. Or he can use several of these far-off landmarks, such as the door, or the corners of the room, at the same time, to define (or triangulate) a specific point in the room, such as the arm of a maze. Thus, if the male is paying most of his attention to these types of far-off landmarks, he will be badly handicapped if these outer landmarks are suddenly covered by a curtain. This is exactly what happens: he starts looking in the wrong places, revisiting places where he has already eaten the bait, for example, until the curtain is once again removed. Then he can once again solve the maze with almost no errors.

Female rats behave quite differently. They also appear to learn the corners of the room because they also make more mistakes when the curtains are used. But they are not as affected as the males. This is because females have also paid attention to the location of objects that are closer to the maze, such as items on the table or glued to the wall. The females not only use the compass and triangulation technique to define a place in space, but also remember the items that were near that place, such as the box on the table that was behind that arm of the maze. If these objects are rotated, females rotate their search pattern, just as if the whole room had been rotated. A male, however, would continue to use

the far-off landmarks and would therefore not change his search strategy at all. If the objects are not just rotated but are mixed up, so that different objects are exchanged with each other, then females suddenly can no longer find the bait in the maze; she now makes as many mistakes as the males surrounded by the curtain.

What is the mechanism by which this remarkable cognitive sex difference arises? Once again, it is the early hormonal environment [92]. If a rat, regardless of sex, experiences its first week of life in the presence of a certain level of reproductive hormone (oestrogen) in its blood, either produced naturally by male testes or artificially by injection, then that individual, as an adult, will pay attention to the 'compass marks' or distant landmarks, and it will make many more errors in the curtained maze. If a rat does not experience this level of oestrogen, either because its brain produces a certain protein which mops up excess oestrogen, as happens in normally developing females, or because disease or experimental intervention prevent the testes from producing testosterone (which is then converted to oestrogen, the necessary form of hormone), then the rat will pay attention both to distant corners and closer objects, as described for normal females.

This scenario is almost identical to that described for the development of birdsong. This is perhaps surprising that such different learning abilities, song and space, would develop in such similar ways: after birth or hatching, and in response simply to the hormones produced by the neonatal gonad. We can only speculate why this is so; why perhaps sophisticated learning abilities only appear late in brain development, after the staples of sensory perception, motor coordination, learning, and memory of sensory information have already been built. Perhaps, too, it is a good thing to have this tardy development of these structures, so that they develop not as a closed genetic programme, but as one more flexible and responsive to the environment.

Moreover, if spatial learning parallels bird song learning,

then it should also be mediated by a part of the brain that develops during the critical postnatal period and that is responsive to gonadal hormones during this time. These conditions are met by one structure, the hippocampus. The hippocampus is a large forebrain structure with both general and specific cognitive functions. Its general function is the ability to construct and remember conceptual relationships between events [27]. It also has a specialized function to solve problems of spatial representations, such as the ability to map and construct novel routes in the external world [67]. Moreover, like song nuclei, the hippocampus may be sexually dimorphic in size in both birds [78] and mammals [42]. In laboratory rodents, the hippocampus is sexually dimorphic, with a male advantage, in cell number [94], in the volume of fibre tracts [55], and in the volume of the certain dendritic arbors [47]. And, just as in birdsong nuclei, these sex differences can be manipulated by changing the early hormonal environment in which the hippocampus develops; females treated with testosterone at birth show a masculinized pattern of spatial learning and hippocampal structure [72]. Thus, both sex differences in spatial learning in the rodent and sex differences in the hippocampus can be altered with hormones, although the precise mechanism by which hormones change the fate and structure of the hippocampus is not fully understood.

While it is clear that male birds sing so that females will be attracted to them, it is not at all clear why male rats should navigate based on the shape of a room; at least, when the question is stated in that way. So we must instead step back and ask: what is the function of navigation, under natural conditions? Why would males and females differ in how they accomplish this? The answer lies in the observation of space use in nature. Sex differences in maze navigation have been demonstrated in several species of wild rodents. In all of these species, males and females have different patterns of natural space use: males use large, undefended areas which encompass the territories of several females, which live in small,

undefended spaces. This sex difference in space use arises from different mating strategies of males and females: females defend an area large enough to feed themselves and their offspring, while males spend their time searching for females receptive to mating. Under this polygynous system, the difference in natural spatial movements by males and females is reflected in similar differences in spatial learning, such as maze performance. That this difference is related to space use is suggested by the further observation that in monogamous species of rodents, where males and females use territories of the same size, there are no sex differences in the number of errors made learning mazes [32, 33].

Thus, sex differences in behaviour are directly related to learning spatial information in nature. How could this explain why male laboratory rats concentrate on the corners of the room? Perhaps it is because males specialize in learning to find locations quickly, by triangulating their coordinates from distant objects. This is an extremely efficient way to solve a maze which only requires a simple solution, such as learning the location of a few bait locations. But this strategy yields little other information. Females, in contrast, may be learning their territory in much greater detail. Hence, females appear to solve the maze more slowly only because they take in more information than do males. Thus, if females learn two types of spatial information (e.g. both compass direction and the individual features of different landmarks), their progress must be slower; they are learning more and hence learn more slowly [93]. Again, this makes good sense in the real world: female rodents rear litters by their own efforts, and should know their own territory well in order to forage more efficiently. In contrast, for males to increase their success as reproductive citizens, they must travel farther, encounter, and court a greater number of females.

The advantage of spatial navigation ability in males has been best demonstrated in field studies of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). In this species, females are receptive for only one day per year.

Males arrive on a receptive female's territory and follow a queuing convention; the first ones to arrive are also the first ones to mate. A male's ability to find receptive females as soon as possible on their day of oestrus thus has a direct effect on a male's success [75].

Thus, like songbirds, rodents also show cognitive sex differences. The direction of the sex difference is not fixed, but varies predictably with mating system, and these patterns predict sex differences in the hippocampus, a major neural substrate for spatial navigation. Finally, the sex-specific spatial specializations appear to be adaptive solutions to the different spatial problems faced by males and females of these polygamous species in nature.

Yet, compared to the magnitude of cognitive and neural sex differences in songbirds, these differences are not great. In this sense, Montaigne was still correct in saying that even for rodents, males and females are more alike than different.

Of mice and men

For the animal shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth. Henry Beston (1928) [11]

Yet even sovereign nations may obey the same natural laws. We are mammals, after all, and show typical mammalian sex differences in body size. Sexual dimorphisms in structure are common; in fact, whenever one sex cannot maintain exclusive access to another, the tools of competition, such as weapons, body size, even testes size, appear in more exaggerated forms. The degree of sexual selection determines both the trait and the degree to which the trait is sexually dimorphic. For example, highly polygynous male primates

have larger testes and canines than males from species where polygyny is less extreme [4, 18].

Patterns of mate competition also predict the magnitude of sex differences in the brain [43]. The dimorphism of song nuclei, for example, is greater in the zebra finch (*Poephila guttata*), where females do not sing at all, than in the canary (*Serinus canarius*), where females sing a simple song. The sex difference in song nuclei size is even smaller in the bay-breasted wren (*Thryothorus nigricapillus*), where mated pairs sing intricate duets, composed of two equally complex parts. Hence the larger the sex difference in song complexity, the larger the sex difference in song nuclei [16].

Sex differences in hippocampal size also vary with natural patterns of learning ability and space use. In contrast to polygynous vole species, in the monogamous pine vole (*Microtus pinetorum*), where a male, under natural conditions, uses the same size territory as his mate, there is no sex difference in either spatial learning ability or hippocampal size [32, 44]. The same pattern is seen in the space use patterns of birds: in the brood parasitic brown-headed cowbird (*Molothrus ater*), females compete for suitable host nests in which to lay their eggs. Because they must lay their unwelcome egg without being detected by the host, females must remember both the locations of host nests and their hosts' laying schedule to execute a successful foray. In the North American cowbird, this behaviour is correlated with a female advantage in hippocampal size [78]. In Argentinean cowbirds (*M. bonariensis*, *M. rufoaxillaris*, *M. badius*), the degree to which any species relies on brood parasitism determines the size and direction of this female advantage in hippocampal size: species where the male and female search for host nests together show a smaller female advantage [71].

Thus the degree of investment in structures needed to compete for mates is correlated with the level of mate competition. In primates, this can be predicted from the number of females to whom a male is able to maintain exclusive access, and sexual dimorphism in body size in primates is

directly related to the ratio of females per male in a social unit [18]. Because human polygyny is characterized by a relatively small number of women per polygynous group, sex differences in stature and other measures should be correspondingly small, at least in comparison to species where the ratio of available females to available males is much smaller. In accordance with this prediction based on our degree of polygyny, we humans show sex differences in stature that vary between 4 and 10 per cent among cultures [31]; in contrast, the Northern elephant seal (*Mirounga angustirostris*) male, who can maintain exclusive access to a large harem of females, may weigh three times as much as an adult female [4].

Hence, similar body size in men and women already suggests that there are only small socioecological differences between them and that sex differences in cognitive or neural sex differences might also be small or insignificant. Such differences are indeed small [20]. They can also be elusive, varying from study to study. Only too often the conclusion reached by a series of studies on a particular trait is that the magnitude of the difference is slight and sensitive to experimental conditions. Perhaps fuelled both by this uncertainty and the universal interest and importance of the issue, hundreds of researchers have studied the effect of sex on cognitive ability [53, 54]. In recent summaries of this contentious literature, few cognitive measures show a strong effect size (defined as the number of standard deviations between group means). Yet because of the importance of the question (i.e. whether men and women differ in intellectual ability), I concur with Sandra Witelson's conclusion: 'Although they have little, if any, practical significance for any individual, such differences may have major theoretical significance' [95].

Sex differences in human cognition

Sitting in my office in Tolman Hall, I am reminded that before discussing data on humans, I can do no better than to quote

Edward C. Tolman himself, who attempted a similar synthesis on mice and men with his 1948 paper, 'Cognitive Maps in Rats and Men'—'My argument will be brief, cavalier, and dogmatic. For I am not myself a clinician or social psychologist. What I am going to say must be considered, therefore, simply as in the nature of a rat psychologist's ratiocinations offered free' [85]. Keeping in mind, then, that the differences are small, how do men and women differ in cognitive ability?

Women excel in tasks requiring forms of fluency, or what might be described as a rapid deployment of attention and skill. For example, the largest female advantage is seen in 'motoric fluency', where fine motor skills must be used to place pegs into holes, or objects must be constructed by putting things together in a specified order. Verbal fluency, such as the ability to list words beginning with a prescribed letter, also shows a female advantage [20]. Finally, women outperform men on tasks requiring 'attentional fluency': the ability to identify rapidly similarities or differences between objects, match objects by their similarities, or find one symbol amid distractors. Mathematical differences, such as the solutions to algebraic equations, can also be calculated more quickly by women than by men [51].

Perhaps akin to 'attentional fluency' is a woman's ability to unconsciously notice and remember the locations of objects, and to recognize, more quickly than men, that an object has been moved or taken away. When college students are asked to study a drawing of a random array of common or unfamiliar objects, women remember the locations more accurately. Women also remember the locations of objects in a room in which they were asked to wait briefly [26, 80]. It is as if women are keeping a continuous record of the visual images in their environment. This is also seen when they are moving around in space; in either tabletop or full-size spatial mazes, where a route must be traced or walked between two points, women are more likely than men to remember the landmarks en route to the goal [30, 51], similar to the female

laboratory rats, noticing and remembering more details about their environment.

The female advantage is, however, never large. Large cognitive sex differences are found only in spatial tasks with a male advantage. The most consistent task to show this male advantage is the Shepard–Metzgar mental rotation test, where one compares and matches three-dimensional objects by mentally rotating the novel object into the same orientation as the sample [41]. For cognitive sex differences, these are large effects [20]; although, to put these differences into perspective, sex differences in height show effect sizes that are twice as large as those seen on mental rotation, which shows the largest effect size in a human cognitive sex difference [34].

Just as women seem to excel in noticing many things and changing their attention quickly, men seem to excel at tasks with the opposite requirement: those that require the single-minded pursuit of a goal that involves the representation of direction. For example, men throw projectiles much more accurately than women, although there are no sex differences in the ability to block the same projectile [89]. Men learn maze routes more quickly and with fewer errors than women, and can reverse directions on the maze with fewer errors, although they remember fewer details about the route they have taken. This also appears to be a spatial representation based on compass direction, rather than route finding in relation both to landmarks and compass direction as in women [30]. Again, this sex difference in cognitive style is remarkably reminiscent of that observed in male laboratory rats, who prefer to orient to distant cues offering direction information rather than deducing their location from the array of visible landmarks at their current vantage point [92].

Thus, similar to results from rodent studies, men and women differ most consistently in spatial tasks, and do so because they solve the problem in different ways. In the task of mental rotation, the type of strategy used, whether a purely visuospatial strategy or by verbal coding of the objects, can be

detected by imposing an intervening distractor task. Because processing capacity is limited, two tasks that use the same resources interfere with each other, and hence performance on either task declines. On average, a woman's performance declines if she must solve an irrelevant verbal (but not spatial) task and the opposite is true of men, whose performance is affected only by intervening spatial tasks [14].

Development and differentiation

Cognitive systems in birds and rodents are critically tied to the posthatch or postbirth interval; experimental manipulations of the developmental hormonal environment demonstrate that sexual differentiation of song learning and spatial learning are due to the action of steroid hormones, and hence are a consequence of genetic and gonadal sex determination. Thus the development and differentiation of cognitive sex differences suggest that the underlying mechanism is similar in these two types of learning.

The similarities in the use of spatial strategies by male and female mammals (at least, in rats and humans) suggest that spatial ability in humans might also be organized by perinatal hormones. This question has been addressed with data from situations where disease, pathology, or abnormal genotype have produced abnormal hormonal environments in the developing human [20].

For example, in the case of girls with congenital adrenal hyperplasia, the adrenal glands, which normally produce low levels of androgen, produce excessive androgens prenatally. Because aromatase enzymes in the brain can convert androgens to oestrogens, increasing the level of either steroid hormone can masculinize neural substrates; it simply depends on the type of steroid receptor expressed by the structure. Because these androgens masculinize the external genitalia, these girls can be recognized at birth and successfully treated, limiting the excess androgen exposure to periods before and

just after birth. Hence, cognitive abilities that are masculinized in these girls must be due to the effect of excess androgens on neural substrates that differentiate during this period. One consequence of this condition is an increase in performance on spatial tasks such as mental rotation, although there is no effect on verbal intelligence [20].

In contrast, girls with Turner's syndrome have lower than normal oestrogen levels due to a chromosomal abnormality (XO genotype). As adults, they show cognitive deficits both in verbal fluency and in spatial visualization [66]. Because they seem to be handicapped in a diverse group of tasks, it has been suggested that their deficit can be defined as 'processing speed and attention' [20]. In other words, perhaps they lack precisely that attentional and perceptual fluency which characterizes a woman with normal development.

Spatial deficits can also be found in men with pathologically low levels of androgens during development, such as in idiopathic hypogonadotrophic hypogonadism. Here, the testes fail to be sufficiently stimulated to produce normal levels of androgens. It is not clear exactly whether the androgen deficits occur pre- or postnatally, however, males with this condition have significantly impaired spatial ability [37].

It thus appears that in humans, as in the laboratory rodent, it is not the genetic sex of the individual that determines spatial ability, but its hormonal environment during development. However, developmental trajectories in the brain are profoundly influenced by the relative time period spent at each developmental stage [29]. To understand the sexual differentiation of the brain, we must know both which hormones play an active role and when they produce their effects. For example, both congenital adrenal hyperplasia and Turner's syndrome result in increased levels of steroid hormones before and after birth; both show predictable effects on spatial cognition. However, an excess of hormone that is administered before birth only does not appear to affect spatial cognitive abilities. This was concluded from studies of girls whose mothers were treated with a synthetic oestrogen

(diethylstilbestrol or DES) to maintain pregnancy and hence exposure was limited to the prenatal period. Girls exposed to this oestrogen showed normal spatial ability and levels of aggression, two factors which generally show the greatest degree of sexual dimorphism, although they did show a more masculine pattern of language lateralization [20]. Thus, spatial and verbal cognitive traits appear to differentiate at different periods in development. Prenatal hormones may thus influence language lateralization but abnormal hormone levels must continue into postnatal life to influence the differentiation of spatial abilities. This may be similar to the pattern seen in rodents, where spatial learning in females is influenced both by pre- and postnatal oestrogen levels, whereas the male strategy of spatial learning is influenced only by the postnatal hormonal environment [92].

Sex differences in the brain

The evidence for an underlying neural basis for cognitive sex differences in humans is controversial [15, 20]. There must be at least three reasons for this: first, as in cognitive traits, only small or inconsistent differences would be predicted. Second, our species is characterized by plasticity, with an extended period of development; this, too, should affect the development of cognitive abilities. Third, the tasks where men and women differ may call on more generalized cognitive abilities than those described in songbirds and rodents. If we cannot map a cognitive trait to a specialized structure (e.g. a song nucleus) but must map it instead to a constellation of multi-purpose brain structures (and even a seemingly specialized structure such as the hippocampus has more identified functions in humans than the rat [52]), then, once again, we should not expect to find strong sex differences in any one structure.

Thus it should not come as a surprise that men and women appear to differ most not in the size of a particular brain

structure but in a fundamental feature of brain organization: the degree of lateralization. The average adult female brain appears to be more symmetrical and hence less lateralized than the male brain [60]. The consequences of symmetry for brain function are seen in the relative robustness of the female brain in response to stroke; being less lateralized and hence with brain function redundantly represented, women recover speech more quickly after trauma to the left hemisphere [51]. Female brains are less lateralized than male brains even on listening tasks, such as the accuracy with which the time of sound arrival is judged in each ear (the dichotic listening task). Men show hemispheric specialization in this task, with a stronger right ear (i.e. left hemisphere) advantage than do women [39]. More recent examples have used brain imaging techniques to compare the lateralization of language function in men and women. Once again, the female brain is fundamentally more symmetrical, using both frontal cortices to solve a verbal task such as rhyming; the male brain uses predominantly the left hemisphere during the same task [77].

A symmetrical brain requires a greater coordination of effort to process simultaneously information in both hemispheres. Hence, the pathways connecting the cerebral hemispheres should be more extensive in the symmetrical brain. For example, both men and women who represent speech primarily in the right hemisphere have a significantly larger corpus callosum, the main fibre tract connecting the left and right cerebral hemispheres, than people who represent speech in the left hemisphere only [70]. This suggests that bilateral representation of function, whether in males or females, is related to the size of fibre tracts connecting the two sides of the brain.

However, on average, the size of these commissures should be larger in women than in men. There seems to be some evidence for this in three large fibre tracts that connect left to right cerebra in humans. The anterior commissure, a fibre tract connecting left and right temporal neocortices (the area

of neocortex in the vicinity of one's ears) is larger in women than men [1]. Another sex difference is found in the massa intermedia, a tract connecting subcortical areas in the thalamus. This odd structure, present in other primate species but often not found in humans at all, is more likely to be absent in men than in women, and when present, it is smaller in men than in women [1].

However, the most consistent and well-studied sex difference in commissural volume is found in the corpus callosum. Specifically, the difference appears in the posterior callosum. In an area called the splenium, with female splenia having greater maximal length, greater area as a function of brain weight, and greater total callosal area [23]. This result has been controversial; because of the importance of this fibre tract, this result has been replicated by many researchers: those using exactly the same methods as the original study have found the same or a smaller female advantage, although those using other methods have found no difference [20]. The same pattern has also been described in rats: the splenium of the corpus callosum is larger in females than males [46].

The development of lateralized function

How do such sex differences in laterality differentiate? If laterality is associated with differences in cognitive ability, which are themselves strongly influenced by perinatal hormones, then brain laterality may also be hormonally mediated.

Evidence from songbirds and laboratory rodents suggest that steroid hormones do influence the development of sex differences in lateralization of brain structure and function. For example, the male canary's song production is severely disrupted by severing the left, but not the right, nerve which innervates the syrinx [69]. Male gerbils (*Rodentia: Meriones unguiculatus*) show structural asymmetry in the brain nucleus involved in their ultrasonic courtship call, which is larger in

the left than right hemispheres; more important, the development of this lateralization depends on the presence of testosterone [40]. Finally, there are more generalized effects of steroid hormones on lateralization of structure or function: female rats exposed to postnatal androgens show a masculinized pattern of lateralized movements [24, 92].

Similar effects may be found in humans, although the data must be interpreted cautiously. One example is lateralization of function in women with low oestrogen levels: Turner's syndrome women show even less lateralization of function in the dichotic listening test than do normal women [68], suggesting that a certain level of steroid hormone is required for normal lateralization to develop. Other evidence comes from measures of lateralization and cognitive function in male and female homosexuals. Because homosexuals are similar to their opposite sex in sexual orientation, one might expect cognitive similarities as well, if such traits have a common developmental origin. Some studies have found that gay men score lower than heterosexual men on spatial tests [74]. Gay men also show less cerebral lateralization than heterosexual men, since the size of the anterior commissure is larger in gay than heterosexual men [2]. In addition, homosexuals show different patterns of functional laterality on dichotic listening tasks: neither gay men nor lesbians show the widely replicated pattern of perceptual asymmetry with consistent right-handedness. In other words, being right-handed predicts a strong right ear bias in heterosexuals but not homosexuals [58]. All of this is consistent with the idea that hormones, development, and degree of cerebral laterality are somehow inextricably linked.

Laterality and rates of development

The male and female mammal (at least in laboratory rodents and humans) thus appear to differ most dramatically in the domain of spatial cognition. These cognitive sex differences

are related to a general difference in cerebral symmetry: the male brain tends to be more asymmetric than the female brain, which correlates with smaller volume of interhemispheric commissures. Such structural differences are determined not by genetic sex but by the postnatal hormonal environment; experimental manipulations or hormonal abnormalities or perhaps sexual orientation are associated with predictable shifts in the degree of lateralization and spatial ability.

Why should perinatal hormones cause such a shift, increasing or decreasing the degree of symmetry in the developing brain? Perhaps for two reasons: first, the brain does not grow symmetrically; and second, because the brain grows asymmetrically, the length of the developmental period profoundly affects the degree of cerebral asymmetry.

One of the first hypotheses that development is often inherently asymmetric derives from the observation that the left and right sides of a developing embryo responded differently to experimental manipulations, suggesting that some cytoplasmic factor appears to be responsible for the formation of an innate left and right side (described in Morgan [63]). In 1978, Michael Corballis and Michael Morgan proposed a new theory of brain lateralization based on this idea [22, 64]. Arguing that all growth is asymmetrical due to innate properties of the egg's cytoplasm, they proposed that this asymmetry also shows an innate bias for the left side to precede the development of the right side. Eventually, the right side of the brain, given enough developmental time, may catch up with the left and produce a symmetrical structure. But should development continue further, the right may surpass the left and a right bias could eventually develop. Hence, the longer the development, the more potential for asymmetry exists, and the more lopsided a brain might become, as seen in our own species, the 'lopsided ape' [21]. Subsequent researchers have improved on this theory; for example, Ursula Mittwoch has suggested that maturational gradients may start with the left but then switch to the right.

Thus, in any structure the direction of asymmetry should be predictable from its developmental age, relative to other structures. Waves of development proceed down the body, head to toe, and the longer a structure has been differentiated, the greater the probability that its asymmetry will have proceeded from left-biased to right and then back to left, explaining, for example, why arms and legs show different patterns of lateralization [61].

Yet even this model may be too simple. In her 'growth vector' hypothesis, Catherine Best incorporates not only left-right differences, but also anterior-posterior and dorsal-ventral vectors. In the human brain: 'The overall effect on the hemispheres is as though some force had twisted the left hemisphere rearward and dorsal, while twisting the right hemisphere forward and ventral'. The result of these ontogenetic contortions is a different allotment of tissue to the two hemispheres, with a concomitant change in commissural volume to accommodate the coordination of two, more symmetrical and hence more equal hemispheres. And because brain structures develop in a rough phylogenetic order, with 'primitive' areas, such as primary sensory and motor areas developing before areas that associate these inputs, Best hypothesized that such tertiary association areas should develop last in the right hemisphere. Therefore, an increased developmental period should be associated with enhanced higher functions of the right hemisphere, such as visuospatial functions [10].

In accordance with this hypothesis, it appears that the rate of maturation may indeed predict traits associated with symmetry: the degree of cerebral asymmetry, the volume of the cerebral commissures and the level of spatial ability. Once again, there is evidence from humans with chromosomal abnormalities. Turner's syndrome women (XO genotype) show an increased prenatal development rate, and this is associated with greater cerebral symmetry and poorer spatial ability than women with a normal XX genotype. In contrast, men with supernumerary-X syndrome (XXX

or XXY genotype), experience higher than normal steroid hormone levels, develop more slowly than the normal XY genotype men, and have lower verbal abilities relative to spatial abilities [10].

These are the extremes, however. If the growth vector hypothesis is correct, then normal sex differences in spatial ability could be a manifestation of the growth rates of men and women which produce differential growth of the cerebral hemispheres and hence differences in laterality. If so, then an individual's rate of maturation should predict the differentiation of late developing structures and hence their level of spatial cognition.

In 1976, Deborah Waber found that sex differences in spatial ability were a consequence of sex differences in age at puberty; late-maturing girls showed superior spatial ability. Thus, the difference between boys and girls could be ascribed not to sex but to age at puberty and it appeared that cognitive sex differences were a result not of sex but of maturation rate, which, on average, is associated with sex [88]. Her initial finding was based on girls from extremes of the maturation distribution; subsequent attempts at replication failed when such extreme maturation groups were not used. However, a more recent summary of these studies has confirmed this effect, although the effect size is probably much smaller than originally reported [36].

There is a suggestion that this relationship between the rate of maturation and cerebral lateralization can be found in men and women of normal genotype but homosexual orientation. As described earlier, homosexual men appear feminized in regard to measures of laterality and spatial function. They also reach puberty earlier than heterosexual men [56], and are of smaller stature [12]. The pattern of cognitive development in lesbians may be quite different from homosexual men; they show either similar or lower performance on spatial tasks than heterosexual women [59, 86], but it is not clear how this relates to their rate of maturation.

Thus, evidence for a relationship between the rate of maturation, lateralization, and cognitive function may be present in at least three groups who appear to differ in their early hormone exposure: individuals who vary by chromosomal abnormality, who differ by sex, or who differ by sexual orientation. Hence, regardless of the proximate cause, the hormonal environment appears to direct the development of cerebral lateralization. This developmental trajectory then produces subsequent changes in cognitive ability, most noticeably in the realm of spatial cognition, as would be predicted from its late development as a tertiary, right hemisphere association area.

Sexual selection and laterality

Yet such correlations between development and function simply relocate the question of cognitive sex differences to a more proximate level of analysis; they do not address the question of why males and females should mature at different rates. To answer this question, one must leave the realm of cognitive neuroscience and return to that of evolutionary biology.

The most common explanation for sexual bimaturism is that it is a mechanism by which sexual selection can act on the differential allocation to trait size. For example, dimorphism in body size is a common sexual dimorphism. It is also the direct consequence of differential growth patterns between males and females. Because growth for many vertebrate species essentially halts at puberty, individuals that mature more rapidly reach puberty at a smaller adult size. Thus, simply changing development rates produces sex differences in trait size [4].

In humans, sex differences in stature are also correlated with the age at puberty. Girls develop more quickly than boys, reaching the developmental stage where androgens halt

the process of longitudinal bone growth. Most structural growth is reached by late adolescence, though approximately one to two years earlier in girls than boys, at least in westernized societies. This produces a sex difference in stature, since slower maturing individuals will be taller when they reach the stage of skeletal maturation [83].

What is the adaptive significance of such sexual bimaturism? It appears to be an adaptation for polygamy in many species [4], based on the following logic. Small males cannot compete for access to females whereas small females are not handicapped by their body size since the female's slow rate of reproduction assures that they will be the limiting sex. Hence, males will compete for females and hence males, not females, will require a larger body size to compete [19]. In highly polygynous species, where body size dimorphism is most pronounced and male reproductive success is strictly tied to body size, delayed maturation thus functions to increase competitive ability [4].

Therefore, the consequences for the rate of maturation can be subject to sexual selection. Other consequences of maturation rate, such as the differential lateralization of the brain and hence differential cognitive ability, could also be the product or side-product of sexual selection. A simple model could be constructed from the basic biology of cerebral growth vectors and sex difference in the rate of maturation that would explain sex differences in cerebral lateralization and spatial function. If this model is correct, then sex differences in cognitive function would be influenced by any factor that changes the rate of development. The faster the rate of growth or the earlier the date of puberty, the more cerebral symmetry, less right hemisphere development, and hence less specialization of spatial function. If puberty is extremely early, one would predict that left hemisphere function achieves an unnatural dominance; if puberty is extremely late, then right hemisphere function should excel.

Food, sex, and cognitive function

What factors influence the rate of development or age at puberty? One of the best studied examples is the effect of social circumstances, such as social class, westernization, or an urban lifestyle. This is clearly reflected in the patterns of body stature: over the last century, perhaps due to a twentieth-century change in diet, children have become progressively larger at all ages, resulting in an increase of about one inch per generation in added height. As a result, both men and women achieve a greater stature, and attain it in fewer years than they did a century ago. These patterns are strongly influenced, however, by social circumstances: poorer boys are significantly shorter than wealthy boys at all ages [83].

Because stature is related to age at maturity, this suggests that children are maturing at younger ages. Indeed, the age at puberty in girls has changed dramatically over the last century. Using the age at first menstruation as an unambiguous indicator of maturation in girls in six western societies, J. M. Tanner calculated that this age has dropped four years in the last century, a rate of approximately four months per decade, although the trend now appears to have stabilized at an average age of twelve to thirteen years [83].

This pattern also appears in contemporary cultures which differ in their wealth and social class, and thus perhaps in diet. Daughters of unskilled workmen in Britain reach menarche two to three months before daughters of men with managerial jobs [83]. A similar pattern is found between girls living in urban versus rural areas: the average age of puberty in girls living in Warsaw has been almost two years younger than girls living in the surrounding countryside for the past hundred years [82]. Similar patterns can be seen in comparisons of urban and rural populations in Nepal, Bolivia, and the United States [5].

These differences are probably caused by a multitude of factors, including diet, exposure to disease, stress, and even social environment [83]. For example, the rate of maturation

could be a physiological response to social stress, since girls reach puberty earlier in households where the father is absent [81]. However, because diet is directly linked to the reproductive functions, such as hormone levels, ovulation frequency, etc. in humans [28], it may play an extremely important role. Under more natural conditions, such as non-industrial cultures, diet may have an even larger effect on human physiology. In a study of endocrine responses in New Guinea hunters, Carol Worthman reported that testosterone levels were twice as high in rich as in poor men [97].

A consequence of the human's sensitivity to environmental conditions is that rates of maturation may vary dramatically by culture. In New Guinea hunter-gatherer societies, puberty is not only delayed relative to industrial cultures, but is also more protracted; the typical growth spurt seen in the western adolescent is seen as a much more gradual increase in growth rate. As a result, adolescent girls and boys show more similar rates of growth; one might predict an absence of sex differences in brain organization for this reason. However, this effect is mitigated in New Guinea because of differential treatment: boys are valued more highly by parents, and therefore are fed higher quality foods, and hence this potential for developmental equality is not realized [96]. Even so, the sex difference in the age at puberty is smaller in non-industrialized societies. In this sense, the protracted adolescence, with early sexual maturity, found in western societies may be a recent artefact of our urban culture [79].

If growth acceleration exaggerates the sex difference in the age at puberty, when both males and females are developing at their maximum rate, this could theoretically produce a greater difference in cerebral laterality, with a subsequent increase in sex differences on spatial tasks. This model would reconcile two contrary observations: first, that patterns of cognitive sex differences in humans are highly conserved across cultures [34]; and second, that there are equally

striking effects of social environment on the development of cognition in humans.

Research on social effects on cognitive development has concentrated on the tasks which show the largest effect size (i.e. spatial tasks showing a male advantage). Studies of spatial cognition in different societies and cultures suggest that the magnitude of sex differences are highly dependent on environmental conditions and personal history. In short, when individuals are given more freedom to explore their environment, this freedom is correlated with enhanced spatial abilities, both within and between cultures, producing either a male or female advantage, depending on the spatial ecology of the sexes in that culture (reviewed by Mary Van Leeuwen [87]). Thus, the male advantage in spatial cognition is seen in traditional Mexico City households, where girls are kept at home and boys are free to wander, whereas the identical methods, testing a ten-year sample of schoolchildren in Austin, Texas, revealed only small and insignificant differences. In Israel, the pattern of sex difference varied with Jewish subculture: among Sephardic Jews, men outperformed women, but the reverse pattern was seen in Ashkenazy communities. The female advantage seen in the Ashkenazy community might be explained by the atypical social organization of this culture. In a study of Orthodox Jews in New York City, the Sephardic pattern was seen in less traditional households: males scored higher than females on spatial tasks. The reverse was seen in more traditional households, where women obtained the higher spatial scores. The explanation offered by the author is that in strict Orthodox families, women, not men, travel outside the home to obtain goods and services and hence are more mobile than men, who are expected to remain in seclusion for serious intellectual study [87].

Such plasticity can also be distinguished within a culture: in rural Kenyan cultures, regardless of sex, children who wander farther from home, because of duties such as herding livestock, score higher on spatial tasks than children of the

same age with more sedentary duties. On average, this meant that boys scored higher than girls on spatial tests, however in the few cases where girls roamed farther, they also showed superior spatial ability compared to boys of their age [65].

Thus, sex differences in spatial cognition may be enhanced or reversed by the social environment. They may also be completely eliminated. In nomadic cultures, such as the Inuit, where both men and women forage for food over large areas, there are no sex differences on any measure of spatial cognition [9].

Is there an underlying neural basis for these cultural patterns? Would, for example, greater mobility as a child lead to enhanced function in the brain structures mediating spatial learning? For example, early spatial experience could increase hippocampal development and enhance cerebral asymmetries by increasing right hemispheric growth. Although we have no data on humans, in laboratory mammals such as the rat, the hippocampus continues to add new neurons throughout life [3, 7, 50]; this is also found in other mammals (reviewed by M. S. Kaplan [49]). This rate of neurogenesis in the hippocampus appears to be related to learning, as it is linked to a physiological process underlying associative learning, long-term potentiation [98]. The hippocampus also responds to changes in the environment, even in adults. Adult rats moved to complex, semi-natural environments show structural changes in the brain after only four days, including an increase in structure in the hippocampus [45]. Finally, male rats moved to an enriched environment show changes in laterality in the hippocampus: at puberty, the dorsal hippocampus changes from a greater thickness of the right to the left side [25]. These scattered, and not always consistent, lines of evidence suggest that hippocampal plasticity, and perhaps spatial cognition, in the laboratory rat can be influenced by the social and physical environment around the time of puberty. It is perhaps not so far-fetched that in humans, too, social influences have

organizational effects on brain structure, cerebral symmetry, and spatial ability.

In summary, the developmental cascade leading to the sexual differentiation of spatial cognition is determined—but only by the environment. The environment may exert its influence in different ways and at different times, beginning with the prenatal hormonal milieu, affected later by the perinatal influences of diet and other determinants of postnatal endocrinological state, and finally influenced by the culturally determined potential for exploration by the child. Thus, on the one hand, sex differences in cognitive function in humans, like those found in rodents and songbirds, may be the end-product of a long developmental cascade, canalized by the early hormonal milieu, which is in part determined by genetic mechanisms. On the other hand, if such differences are determined by such a general trait as an individual's rate of development then these differences are extremely plastic. Thus, if rate is key, then sex differences are not 'determined' at all—or only in the most minimal sense of the word.

Sexual selection and human ecology

Yet even in the midst of this complex array of environmental influences we can discern faint echoes of the sexually selected pattern seen in other species. Even the diversity of these influences cannot conceal the observation that in most cultures, when there is a sex difference in spatial cognition, it more often shows a male, not a female, advantage. What is the significance of this pattern? Again, the answer must lie in the evolutionary history of sex differences; the magnitude of a sex difference may be explained by an individual's history but the average direction of the difference can only be explained by the history of the species [38].

Just as sexual selection may produce sexual bimaturation because of the advantage of increased body size to one sex

and not the other, so sexual bimaturation of the brain may also be part of a larger adaptation to greater plasticity. Environments change; the social environment changes even more quickly, since conspecifics compete with similar skills and abilities [90]. Our species is characterized by plasticity and adaptability, and perhaps this is also true for patterns of sexual dimorphisms in cognition, as is true in other species. If sexual dimorphism in height varies dramatically according to diet and culture, then perhaps cognitive sexual dimorphisms, small but persistent, reversible according to experience, are simply a subtler example of a sexually selected predilection for a male advantage on certain tasks under average circumstances.

Why would such an advantage exist in *Homo sapiens*? Cognitive sex differences in songbirds and rodents operate in the context of mate choice and mate competition, and have evolved in response to sexual selection for competitive ability. Are sex differences in human spatial abilities also subject to sexual selection? I can only join others in speculating on the possible adaptive significance of our small sex differences and their effect on the course of human evolution [80]. The scenario can be described as follows: man the hunter requires skills in throwing, aiming, and navigation in order to navigate long-distance hunting trips over large or unknown terrain, kill game with projectiles and then return home, often with a heavy meat burden, via the shortest route. Thus, hunter skills tap into the same spatial abilities assessed by laboratory tasks, which would explain the common male advantage on such tasks. Such navigational skills would be adaptive for long-range hunting, but not necessarily for short-range gathering. Here, the ability to remember the location of fruiting plants, notice and remember subtle changes in spatial distribution of food sources, and possess fine motor control for harvesting and processing fruits and seeds, would be advantageous. Thus, the female constellation of cognitive skills would adapt for gathering, which requires tracking the fine-scale spatial distribution of fruiting plants, and also have

the fine motor control to manipulate and clean small food items.

One could thus interpret sex differences in cognitive skills as indications of selection for competitive ability in foraging behaviours such as hunting and gathering women, not competing for mates. This hypothesis, suggested and elaborated by Irwin Silverman and Marian Eals, seemingly reduces the need for sexual selection to act on the evolution of such sex-specific abilities, since natural selection for foraging skills would be sufficient to explain the differences [80]. Yet we can never really know to what extent evolutionary processes such as natural and sexual selection can explain sex differences in spatial ability in our species. Sexual selection could still play a role: even in this Tarzan the Hunter, Jane the Gatherer scenario, hunting prowess may affect the outcome of mate competition. In fact, good hunters are more attractive to women, even if what they hunt is not a necessary or efficient addition to the group's energetic requirements [13]. In the Ache culture of eastern Paraguay, where men must range widely in search of meat and honey, the families of good hunters do produce more surviving offspring, suggesting that women should choose mates by their hunting ability [48].

The peacock's brain

Perhaps Montaigne was right and men and women, save for culture and education, do not differ that much. Perhaps even with 85 per cent of our societies polygynous, we will never be a strongly polygynous species, and hence differences between the sexes will always be subtle. Is this the end of the story? I think there is one more insight to be gained from this discussion and that is the issue of optimization and design. Steven Gaulin and Lee Sailer once argued that among primates, the sexes were not created equal and that females could be considered the 'ecological sex'. Males 'are often

larger, more flamboyant coloured, more aggressive, more mobile, more active in courtship, and more likely to bear structures such as antlers, manes, and large canine teeth that are of little or no use in exploiting nutritional resources' [35]. Thus, it is female, not male body size that is optimized for the species's ecological niche; the larger size of the polygynous male served only to increase his ability to compete with other males, and hence was adaptive but not 'ecological'.

Similarly, a Martian visiting our planet for the first time might note that one-half of the population uses their entire brain to process information, automatically integrates more incidental information, is less aggressive and more cooperative, and overall seems closer to the ideal design for a naked ape. This Martian might view traits such as superior mathematical ability or superior skill in chess as arbitrary skills that have evolved for the same reason as a peacock's tail, representing the 'investment' needed to compete successfully with other males (i.e. the typical solution of the disadvantaged sex). It is usually the male's solution: the ability to compete with other males using traits that serve no other purpose but to compete. This view of things puts a new slant on the old problem of gender and society. Suddenly, the smaller female brain is seen as a miracle of economy and design, destined to survive the turmoils of history, less likely to be disturbed during development or to suffer immune disorders [84], less likely to become involved in unnecessary and damaging acts of aggression and warfare. Thus, it is the female that is the smaller, the 'ecological' sex, best adapted to survive in the ecological niche of the species, and it is the male who carries the heavier burden or handicap [99] of sexual selection, his fitness dependent on arbitrary traits that reduce his competitive ability as a human being, although they are all too necessary for his competitive ability as a man. Thus, if brain structure and function are constrained by the ecology of the species, it may be that sex differences in cognitive traits are no more and no less important than the peacock's tail. This may not be such a bad thing for the species. It has been

argued that sexual selection has served as a forge for rapid evolutionary change, proceeding more rapidly than natural selection and hence arriving more quickly at novel solutions, some of which may benefit both males and females [90]. Far from being a handicap for human evolution, it may be that we should give sexual selection some credit for the rapid evolution of our unique cognitive abilities and complex culture. For to conclude with the words of Oscar Wilde: 'Ethics, like natural selection, make existence possible. Aesthetics, like sexual selection, make life lovely and wonderful' [91].

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