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Sexual selection and the brain

Lucia F. Jacobs

Sexual dimorphisms in the nervous system have been well studied, although largely as models for brain development, and not for their behavioral or evolutionary significance¹. Most studies of sex differences in cognitive mechanisms similarly lack an explicit evolutionary analysis, despite the recent inroads of evolutionary theory into the field of human cognitive neuroscience². Thus, the time is ripe to apply our understanding of sexual selection to the neural bases of behavior and to analyze sexual dimorphisms in the light of sexual selection hypotheses.

The theory of sexual selection was born from Darwin's observations of conspicuous sex differences in morphology and behavior: 'That these characters are the result of sexual and not of ordinary selection is clear, as unarmed, unornamented or unattractive males would succeed equally well in the battle for life and in leaving numerous progeny, if better endowed males were not present'³. It was obvious to Darwin that such conspicuous traits, particularly those displayed only during the breeding season, are involved in mate selection. Not all sexually selected traits are conspicuous,

Sex differences are intrinsically interesting, particularly in the brain. When sexually dimorphic structures mediate learning, and when such learning ability is necessary to compete for mates, then such differences are best understood within the framework of sexual selection. By categorizing recent studies of sex differences in the brain by their role in mate competition, theories of sexual selection can be used to predict and characterize the occurrence of dimorphisms among species with different mating systems.

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however, and when a sex difference consists of an enhancement of a cognitive or perceptual ability, disentangling the separate actions of natural and sexual selection is difficult. Sex differences could, after all, arise from other differences between males and females, such as different feeding habits. However, if such differences arise in the struggle for mates, not merely in the struggle for existence, then we can assume that they are subject to sexual selection. An example of this is the immunocompetence theory of sexual selection: if sexual selection favors the evolution of indicators of good health, then sexual selection will lead to the evolution of indicator structures, such as bright plumage⁴.

Learning ability and its underlying neural plasticity, like immune plasticity, allow an organism to track and respond to a changing environment. Thus the ability to recognize and recall previous encounters is a fundamental property of both immune and neural systems, and such properties may be subject to enhancement by sexual selection as well as natural selection. If females, for example, can assess a male's ability to learn more information, or learn more quickly than

rival males, then the demonstration of enhanced learning ability could be a sign of a superior mate. The rationale for this is based on the idea of limited 'brain space'⁵; learning requires an investment in brain tissue, which is extremely metabolically expensive⁶. Hence, if enhanced learning demands increased allocation to 'brain space', then conspicuous indicators of learning ability (and their underlying brain structures) could be subject to sexual selection.

Learning and mate competition

What types of learning are involved in mate competition? Andersson places precopulatory tactics into four categories of mate competition: active mate choice, scramble polygyny, contest behavior and endurance⁷. Leaving aside endurance, as having no definable neural substrate for learning, we can ask what neural specializations might evolve in response to the other three. Active mate choice by one sex could require that the opposite sex produces signals, and that both sexes recognize and remember encounters. Physical contests could involve the perception and assessment of a rival's strength, and the motor learning needed to fight. Success in scramble competition would be improved with spatial navigation skills to find receptive mates and, once found, with enhanced spatial memory of their locations. If such learning abilities are sexually selected then we would predict that, within a given species, sex differences in the learning ability and its neural basis should be enhanced in the sex that competes more strongly for mates (Box 1).

Learning to advertise

Song production is sexually dimorphic in insects, amphibians and birds⁸, and production of advertisement calls predicts sexual dimorphisms in the underlying neural machinery. Indeed, sex differences in the output, size or neural control of the sound-producing organ have been found in electric fish, frogs and passerine birds (reviewed in Ref. 9). The ability to learn advertisement song, in contrast, has been demonstrated only in birds, where it appears to have evolved independently in three orders: in parrots (Pscittiformes), hummingbirds (Apodiformes) and oscine songbirds (Passeriformes)¹⁰. The cognitive and neural mechanisms of song learning in parrots and hummingbirds are not well understood. But in the well-studied oscines, sexual dimorphism in song production is correlated with sexual dimorphism in the size of forebrain song nuclei¹¹ (for a recent review, see Fig. 1 and accompanying text in Ref. 12). Most importantly, at least one measure of song-learning ability, the size of a male's song repertoire, is correlated with success in competing for mates: in a number of studies, females prefer males with larger repertoires¹³. Comparative studies show a corresponding relationship between the size of the repertoire and the size of a particular forebrain structure (the nucleus HVC, or high vocal center), both within and among species¹⁴. The relationship between repertoire size and sexual selection is not simple, of course, but is further complicated by a species' degree of plasticity in song learning. A female preference for larger repertoires may be expected only in open-ended learners, who continue to add songs to their repertoire. In species where song learning is not open-ended, males may compete by continually rearranging their repertoire in order to match the songs of their rivals¹⁵. In both cases, however, competitive ability is based upon a male's ability to learn or manipulate his song repertoire.

By a number of criteria, song-learning ability and its neural basis appear subject to sexual selection: they are sexually dimorphic in function and structure; the direction and extent of dimorphism are predictable from the type of mate

Box 1. Mechanisms of competition and their neural correlates

Precopulatory tactics, such as advertisement, contests and mate searching, are associated with sex differences in learning ability and in corresponding brain structures. Postcopulatory tactics, such as sperm competition, mate guarding and pair bonding, are associated with species differences in behaviors and corresponding species differences in the brain. For example, the spinal nuclei controlling ejaculation in male mammals are, not surprisingly, larger in males than in females¹. The extent of the dimorphism is much greater in the scramble polygynous laboratory rat than in our own, less promiscuous species⁴⁸, suggesting that sexual selection for sperm competition has produced these species differences not just in the structure involved in sperm production, that is, the testes⁴⁹, but also in the neural structures needed for sperm delivery. Likewise, there are species differences in the pattern of neurotransmitter release that produce mate guarding in rodents; there is greater release and greater guarding in monogamous than polygamous species⁵⁰. Other pair-bonding activities, such as huddling in small mammals, or duetting in monogamous songbirds, also have neural correlates in the size of cortical structures mediating these behaviors^{51,52}. Duetting requires song learning by both sexes, and correlates with increased size of song nuclei in females.

competition; the dimorphism reaches its greatest expression during the period of mate competition; the ability to learn songs is necessary to compete for mates, and competitive ability correlates with enhanced expression. The story is not complete, however, without evidence for individual variation in learning ability, and the impact of such differences on an individual's fitness.

Learning to fight

A successful fighter must be able to assess the opponent and use weapons. Although it seems obvious that males bearing weapons, such as stags with antlers, must develop special motor skills to compete, this idea has not been tested with comparative data. There is, however, evidence for sex differences in weapon control in humans. Men are significantly more accurate than women in throwing and intercepting projectiles, such as darts and ping-pong balls¹⁶. One might speculate that such sex difference in motor learning could be derived from sex differences in the use of projectiles as weapons, although these differences could result from either sexual selection for the fighting ability needed to compete for women or natural selection for hunting ability. More data from other species on sex differences and individual differences in motor learning are

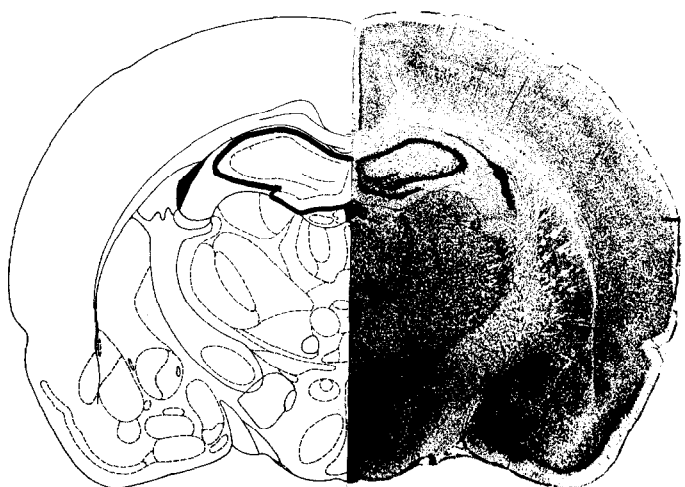


Fig. 1. Diagram of a coronal cross-section of the hippocampal formation (outlined) in the laboratory rat. Adapted, with permission, from Ref. 53.

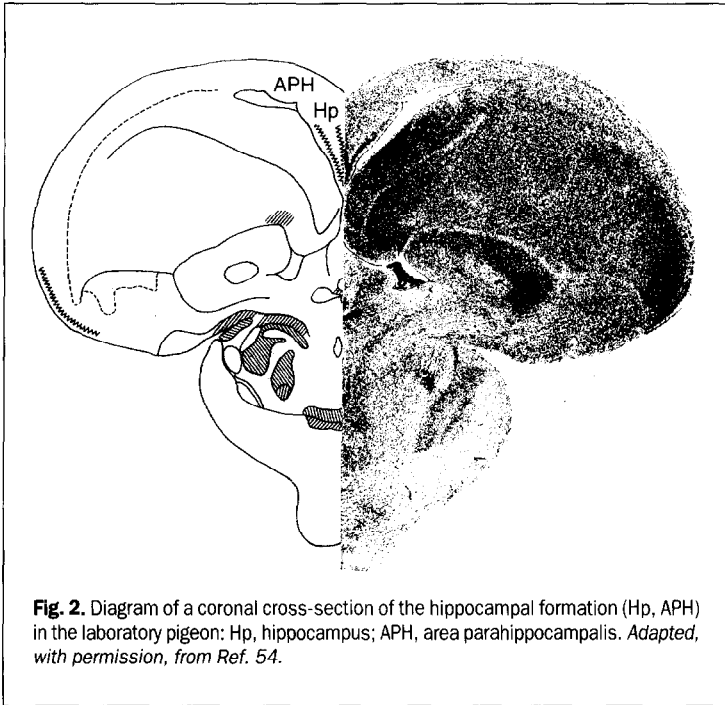


Fig. 2. Diagram of a coronal cross-section of the hippocampal formation (Hp, APH) in the laboratory pigeon: Hp, hippocampus; APH, area parahippocampalis. Adapted, with permission, from Ref. 54.

needed to test the hypothesis that selection for fighting behavior can result in sex differences in motor learning abilities.

Learning to locate

Thus, the cognitive processes involved in scramble competition are both similar to and different from other types of learning in the context of mate competition. Once again, it is generally the male who experiences relatively greater competition for mates and, as in advertisement song, it is usually the male who expends energy 'selling his wares' to potential 'customers' (i.e. females). Yet for many species this form of competition requires a male to be mobile, not sedentary, and to find his customers, not advertise and wait for them to arrive. The cognitive abilities required to locate a receptive mate include spatial navigation, spatial learning of new locations and memory for previously visited sites.

In general, mobile animals use some type of spatial learning to navigate and locate resources; thus, in its various forms, spatial cognition underlies a basic tenet of behavioral ecology – that is, our assumption that the spatial dispersion of resources dictates adaptive patterns of behavior. In the case of mating systems, 'spatial and temporal patterns of resource dispersion' determine the spatial distribution of the limiting sex, usually females, which consequently determines the possible strategies of males and hence the mating system. Where females or resources cannot be defended, males engage in scramble competition¹⁷.

The type of spatial ability that would be subject to sexual selection under these conditions is seen in the competitive tactics of male thirteen-lined ground squirrels. Females are distributed at low density and breeding opportunities are brief: females are receptive only for a few hours and receptive periods are synchronized over short periods. Removal experiments demonstrate that males appear to use their spatial memory of previous encounters to predict the daily distribution of estrous females¹⁸. These social parameters have led to a system of scramble polygyny, with the special convention of orderly queuing. A game theoretic analysis predicts that the males who will do best are those who follow the rule 'first come, first served', and, as predicted, successful males have arrived first at the female's burrow on the

morning of her receptive day¹⁹. Because the length of time a male must search per female strongly influences the operational sex ratio²⁰, the ability to navigate efficient routes should be advantageous to males and subject to sexual selection. This was confirmed in experiments with voles of the genus *Microtus*. In polygynous species, males made fewer errors navigating to the location of a food reward than did females, but there were no such sex differences in monogamous vole species²¹. Thus the pattern of sex-specific spatial ability was correlated with patterns of mate competition.

Spatial navigation thus shows enhanced expression in the sex that competes more strongly for mates. The hippocampal formation is an important forebrain structure in birds and mammals (in mammals, it is defined as both Ammon's horn and dentate gyrus, while in birds it includes both the hippocampus and parahippocampal area; I will refer to these areas in both birds and mammals as the 'hippocampus') (Figs 1 and 2). There are competing models of the exact function of the hippocampus, but its role in mediating spatial learning in birds and mammals has been clearly demonstrated^{22,23}.

The size of the hippocampus is relatively greater in males than in females in three species of polygynous rodents examined thus far (meadow voles, Merriam's and bannertail kangaroo rats), but, as predicted, relative hippocampal volume is not dimorphic in the monogamous pine vole^{24,25}. In addition to volume, other sexual dimorphisms – in cell number and fiber volume – have been described in the hippocampus of laboratory rodents, which are domestic strains of polygynous ancestry^{26,27}.

Sexual dimorphism in hippocampal volume has also been found in birds. In the brown-headed cowbird, a nest parasite where females must find host nests, females have relatively larger hippocampi than males²⁸. In the same study, hippocampal volume was not dimorphic in two harem polygynous species (red-winged blackbird and common grackle), where males and females do not differ in space use. Unexplained dimorphisms have also been found in jackdaws and magpies²⁹.

The hippocampus is the only cortical structure found to be sexually dimorphic in both birds and mammals. If we were designing a brain to compete for mates, perhaps this is exactly what we would expect, given the importance of spatial information for mating success. Yet at first inspection, the hippocampus (and associated cortices) of birds and mammals looks entirely different (cf. Figs 1 and 2); the parallels in function and sexual dimorphism suggest that sexual selection can have striking consequences for brain function and morphology.

Learning and parasites

Sex differences in learning abilities and associated brain structures suggest the action of sexual selection. A stronger case could be made if potential mates or rivals could assess individual differences in learning ability. For example, song learning could be assessed by differences in repertoire size, and motor learning by expertise in fighting. Spatial learning could be indirectly assessed by the order in which males appear at a female's territory or the frequency of visits; for example, the familiarity of a male is a key factor in a female's mate choice in bannertail kangaroo rats³⁰. Increased spatial movement by male kangaroo rats during the breeding season increases their risk of predation³¹. Thus a male's ability to visit a female repeatedly might be seen as an indication of his spatial learning ability and greater allocation to expensive hippocampal tissue.

Spatial learning ability is also condition-dependent. Sub-clinical parasite infestation significantly impairs spatial learning in male mice, particularly during the infective

period of the parasite³². In addition, female mice avoid the odor or presence of infected males³³. Thus, even a small parasite burden in a male rodent could decrease mating opportunities, first by depressing his ability to locate or frequently revisit a female, and second by repelling females with his odor of infection. Females might have to decide which is more attractive, a relatively familiar male or a relatively less infected male. If female rodents choose males who visit frequently or are the first male to arrive, then spatial behavior could serve as a condition-dependent trait that indicates mate quality.

Seasonal modulation of learning

If a learning ability, like a stag's antlers, is subject to sexual selection, then, like the antlers, learning ability might be expected to improve during the season of mate competition and then regress. In fact, changes in learning ability do occur in those abilities associated with mate competition. Birds such as canaries, which are open-ended learners, show a seasonal cycle in song-learning ability, with song learning and production peaking during the breeding season⁵. In polygynous rodents, sex differences in spatial learning are seasonal, being apparent only during the time of mate competition. Males raised under long (breeding) photoperiods show superior maze performance; males caught in the winter, or reared under winter photoperiod, show no enhanced ability relative to females^{21,34}. However, this sex difference in spatial learning can be induced in winter meadow voles if their photoperiod is artificially increased²¹. Spatial learning abilities are also seasonally modulated in other species; spatial learning ability in men is correlated with testosterone level, with spatial prowess peaking in the spring³⁵.

There is also some evidence that hippocampal dimorphisms are present only during the breeding season, when dimorphism in spatial learning is being expressed³⁶. Such plasticity might be expected in the hippocampus, one of the few sites where new neurons are produced in the adult mammalian brain, although adult neurogenesis is also seen in song-control nuclei^{5,37}. Hippocampal plasticity may be important in mammals and in birds: rates of neurogenesis and hippocampal volume undergo seasonal fluctuation in black-capped chickadees, correlating with seasonal changes in space use and foraging behavior^{38,55}. Similarly, certain measures of neural dimorphism in song nuclei are seasonal and modulated by response to photoperiod³⁹.

Why should learning ability and brain structures regress? Again, the argument rests on the metabolic costs. Indeed, the observation that laboratory rats grow larger brains in more intellectually challenging environments⁴⁰ suggests that animals must be economical with their 'brain space'. Seasonal moults, similar to these 'brain moults' (John Kirn's term), are common in other sexually selected traits, such as antlers and nuptial plumage, even if we are not accustomed to thinking of our brains in this way.

A learning ability that is subject to sexual selection could also benefit the bearer in other ways. Laboratory rats raised under summer photoperiods forage more efficiently on an eight-arm radial arm maze⁴¹ and similarly reared deer mice find escape routes more quickly³⁴. Thus the metabolic cost

Table 1. Evidence that song learning and spatial learning are subject to sexual selection^a

	Song learning	High vocal center	Spatial learning	Hippocampus
Sexually dimorphic	11	11	21	24
Mating system predicts direction and extent	11	11	21	24
Development determined by gonadal hormones	44	44	45	46
Plasticity in adults:				
seasonal changes	5	5,47	34	36
adult neurogenesis		5		37

^aThe table lists the references showing that song learning and spatial learning, and their underlying brain structures (the high vocal center and hippocampus, respectively), have characteristics associated with secondary sexual traits.

of building a summer brain may be offset by increases in the efficiency of searching for food and shelter.

Genetics of spatial learning

Genetic analyses of spatial learning in the laboratory mouse have uncovered a strong correlative relationship between learning ability and hippocampal structure⁴². Maze performance, for example, is correlated with differences in the volume of the intra- and infrapyramidal projection of the mossy fiber tract of the hippocampus⁴³. Thus, in the case of spatial learning and the hippocampus, we have evidence that individual variation has a strong genetic component. If this result can be extended to other rodents, then it may be possible to quantify the selective advantage of enhanced spatial learning ability. If these traits are subject to sexual selection, individual differences in mossy fiber structure and spatial learning should, for example, predict a male's use of space, and perhaps his competitive ability and reproductive success. In a polygynous species such as the meadow vole, the sons of the superior navigators should also show enhanced hippocampal structure, learning ability and mating success; if so, this would provide evidence that such processes are subject to sexual selection.

Conclusion

Song learning in birds and spatial learning in small mammals show several remarkable parallels. Table 1 summarizes the evidence that learning associated with two types of mate competition – advertisement and scramble polygyny – and their underlying brain structures are subject to sexual selection. These cognitive specializations fulfill several criteria of sexually selected traits: enhanced function is found in the sex subject to greater sexual selection, and such enhancement is found only during the period of competition for mates. The underlying neural bases are also predictably sexually dimorphic and season-limited. In the case of spatial learning, there is evidence for condition-dependence, and for a genetic basis of individual differences in learning and hippocampal structure.

These parallels suggest a rich future for comparative studies of sex differences in cognitive and neural enhancement. Sex differences can also be studied in the field, using the methods of behavioral neuroendocrinology. Field manipulations of song or spatial learning offer the opportunity to measure the fitness consequences of individual differences in learning. These studies could be important not only to behavioral ecologists but also to developmental neurobiologists interested in the sexual differentiation of the brain in birds, mammals and other vertebrates. Moreover, since the hippocampus plays a critical role in neurobiological models of memory in humans and other animals, the patterns gleaned from comparative studies will no doubt inform the ongoing debates about its function.

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