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Sexual Differentiation of Behavior in Monkeys: Role of Prenatal Hormones

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Abstract

The theoretical debate over the relative contributions of nature and nurture to sexual differentiation of behavior has increasingly moved towards an interactionist explanation requiring both influences. In practice, however, nature and nurture have often been seen as separable, influencing human clinical sex assignment decisions, sometimes with disastrous consequences. Decisions about sex assignment of children born with intersex conditions have been based almost exclusively on the appearance of the genitals and how other's reactions to the gender role of the assigned sex affects individual gender socialization. Effects of the social environment and gender expectations in human cultures are ubiquitous, overshadowing potential underlying biological contributions in favor of the more observable social influences. Recent work in nonhuman primates showing behavioral sex differences paralleling human sex differences, including toy preferences, suggests that less easily observed biological factors also influence behavioral sexual differentiation in both monkeys and humans. We review research, including Robert W. Goy's pioneering work with rhesus monkeys which manipulated prenatal hormones at different gestation times and demonstrated that genital anatomy and specific behaviors are independently sexually differentiated. Such studies demonstrate that for a variety of behaviors, including juvenile mounting and rough play, individuals can have the genitals of one sex but show the behavior more typical of the other sex. We describe another case, infant distress vocalizations, where maternal responsiveness is best accounted for by the mother's response to the genital appearance of her offspring. Together these studies demonstrate that sexual differentiation arises from complex interactions where anatomical and behavioral biases, produced by hormonal and other biological processes, are shaped by social experience into the behavioral sex differences that distinguish males from females.

For many years, one of the defining debates in psychology and biology was centered on the relative contributions of nature and nurture in all aspects of development. In some ways, this argument has been laid to rest and an interactionist view has prevailed. However, in our understanding of sexual differentiation, a curious divide remains. While genital differentiation is attributed to the actions of sex chromosomes and prenatal hormones, behavioral differentiation is most often attributed to the effects of the social environment. Thus, a boy "acts like a boy" because since he was born with a penis and thus his parents and others treat him as a boy. In this view, genital anatomy is the only biological endpoint relevant to determining gender. Such disregard for possible biological contributions to behavior itself is evident in some sex assignment decisions for individuals born with "intersex" conditions. For many years, sex assignment of human infants was based almost exclusively on the appearance of the external genitalia (1): if the individual had a 'viable' penis they were assigned as a male, all else resulted in female assignment. This focus upon genital anatomy made no assumptions

about hormonal effects on neural tissue. The notion that genital masculinization might also be associated with masculinization of the brain was not considered and the possibility that genital and brain effects of androgens were separable phenomena was not entertained, resulting in devastating consequences for some individuals whose psychological sex did not match their sex of rearing (2). One reason for this disconnect is that in humans, gender identity is considered the primary indicator of psychological sexual differentiation, and gender identity and gendered behavior are not always concordant (3,4). There is general agreement that prenatal androgens influence sexually differentiated behavior, but no clear consensus that androgens have the same effect on gender identity. There is some consensus that prenatal androgens may play a smaller role in gender identity development than behavioral development, but this is by no means a resolved issue. Awareness of the importance of biological sexual differentiation on psychology has dramatically increased and practices have been altered (1), but the complexity of the interactions between biology and the social environment are well worth revisiting from basic science perspectives. We here provide a review limited to a subset of behaviors and cognition which illustrate how the interplay between nature and nurture can be addressed in nonhuman primates.

In humans and nonhuman primates, sexual differentiation begins well before birth, and while the effects of genes and hormones on internal reproductive duct structures and on external genitalia are well-understood (5), effects on neural development and subsequent behavior are not as well understood, especially for nonreproductive behavior. Furthermore, the fact that behavioral experience also influences brain development and function (6) suggests that the social environment could contribute to anatomical sexual dimorphisms in the brain, although no data currently address this possibility. As an example, sex differences in preferences for different kinds of toys have long been considered to reflect the strong effect that the social environment has on gendered behavioral development (7,8). Because the social environment can obviously suppress or enhance behavior by changing its form, and because of strong gender socialization in human cultures (9), the influence of socialization on gendered behavior is a more readily acceptable explanation for gendered behavior than are biological factors. What is less often considered, however, is that biological processes produce developmental biases in gendered behavior which are then shaped by socialization processes. In other words, biology proposes and the social environment disposes. For example, biologically determined biases in toy preferences could create a gendered toy market because more boys enjoy playing with the family wheelbarrow and more girls enjoy taking care of infant siblings. Toys are created reflecting these biases, and with each generation, these toys become elaborated and more stereotyped. Some elements of these toys relate to actual biological differences, and others may only symbolize these differences. Thus, by producing differential biases in the brains of males and females, biological processes could indirectly create the social environment that then makes the development of gendered behaviors appear to be the product of socialization without biological input.

As we consider the relationships among physical, neural, behavioral, and psychological sexual differentiation, we must recognize that all behavior occurs within a social context, regardless of the species studied. However, in other species, we are able to manipulate the biological history and environment allowing precise separation of the influences of biology and the social environment on specific outcomes. Rhesus monkeys are an ideal model for their similarities with humans in prenatal development, sex differences in juvenile behavior, and their complex social structure. In this review, we use previous research in rhesus monkeys to examine how prenatal hormones and the social environment interact to produce sexual differentiation., we examine the behavioral and social consequences of having the genital anatomy of one sex and the prenatal hormone profile of another sex. In doing this, we highlight the importance of timing and duration of prenatal hormone exposure for different anatomical, behavioral, and psychological endpoints, resulting in a more nuanced view of sexual differentiation as

reflecting separable processes that produce a range of physical, behavioral, and psychological phenotypes.

In studies of children's toy preferences, one of the most persistent findings is that boys show very strong preferences for masculine types of toys, including vehicles and construction toys, over feminine types of toys, which include dolls, tea sets, and dress-up clothes. Girls, on the other hand, tend to play with these masculine types of toys as well as feminine types of toys (9–13). Thus, the sex difference can be defined in terms of boys showing a strong preference and girls showing only a slight or even no clear preference (14). Evidence for biological contributions to children's toy preferences comes from work with girls who have congenital adrenal hyperplasia or CAH – disorder in which an enzyme deficiency results in, among other things, prenatal androgen exposure comparable to the levels seen in boys. Even when these girls have female genitalia, female gender identity, and feminine parental socialization, they tend to show highly masculinized toy preferences (4,15,16). However, because explicit socialization can never be completely ruled out (the parents know about the disorder and the abnormal androgen exposure), different experimental approaches were necessary to separate socialization from the equation, and one approach has been to study toy preference in other species.

Two studies in two nonhuman primates – vervets (17) and rhesus monkeys (18) – have demonstrated sex differences in interactions with human toys. Only one study allowed assessment of preference by having exemplars of two gender-stereotyped toys available at the same time (19). In our study, we allowed a large social group of rhesus monkeys access to two toys at a time across multiple trials. Each trial simultaneously offered a wheeled toy (e.g. shopping cart, a wagon, and variety of cars and construction vehicles) and a plush toy (e.g. stuffed animals of many shapes and sizes.). Male monkeys, like human boys, showed an overwhelming preference for the wheeled toys, while female monkeys, like human girls, though interacting more with the plush toys did not show a significant preference for one toy type over the other (18; Figure 1).

Our findings show that toy preferences can develop independently of explicit socialization – wheeled and plush objects hold no gendered significance for rhesus monkeys. At first glance, the result seems puzzling: why should rhesus monkeys show any sex differences in interactions with toy types they have never seen before? However, we know from research with children that different kinds of objects are conducive to different kinds of activities (20–22). Boys and girls and juvenile rhesus males and females engage in different kinds of gendered activities, and objects may reflect these differences in activity preference. Rhesus monkeys show sexually differentiated patterns of juvenile and adult behavior (5,23,24), primarily in juvenile mounting and high energy expenditure play (rough play) in juvenile males and higher interest in infants (25) and greater association with adult females in juvenile females (23,24). Human boys, like young rhesus males, engage in more wrestling play (26), and human girls, like young rhesus females, show more interest in young infants (27). These differences in activity preference may drive object preferences. Alternatively, sex differences in object preferences may reflect sex differences in sensory and perceptual processing that are modulated by androgenic influences on sensory gating (14).

Even if rhesus monkeys are not specifically socialized to play with human gendered toys, in some sense they could be socialized to engage in different kinds of activities. For example, rhesus monkey mothers or other adults could discourage males from interacting with young infants or could discourage females from engaging in rough play. Thus, the activities that juvenile males and females prefer could be shaped by the environment. Studies of these behaviors in rhesus monkeys have not found evidence that adult monkeys encourage or discourage particular behaviors (25), but this aspect of socialization has not been investigated

with the detail that it has in studies of children. against such socialization, however, comes from elegant manipulations of prenatal hormones in rhesus monkeys that alter prenatal sexual differentiation (28).

At birth, rhesus monkeys' genitals and internal reproductive anatomy are completely sexually differentiated. During the rhesus monkey's 168 day gestation the testes differentiate between days 38 and 40 (29) and become active, continuing to secrete androgens throughout gestation. Androgen levels peak between gestation days 40–75 and again around day 140 (29). Thus prenatal exposure to testosterone (T) is higher in males than in females, though there are no differences between males and females in exposure to 5 α -dihydrotestosterone (DHT) or androstenedione (29,30). Throughout the prenatal period, the fetal ovaries appear to produce no steroids and the female fetal hypothalamic-pituitary-gonadal axis (HPG axis) is quiescent throughout gestation (31).

Goy and colleagues' early work in rhesus monkeys (28,32) manipulated prenatal testosterone, beginning on or near gestation day 40, the point of gonadal differentiation and active androgen secretion of the testes, and lasted from 55 to 80 gestational days. When testosterone propionate treatments lasting for 55 days or more, the females exposed to such maternal treatments had male external genitalia (penis and scrotum with no vaginal opening) and both male (seminal vesicles, epididymis, prostate) and female (cervix, fallopian tubes, uterus) internal reproductive structures. These genetic females exposed to prenatal androgen were behaviorally masculinized, showing greater rough-and-tumble play and mounting than did their female counterparts, and were no different from control males (28).

While these results suggested a role for prenatal testosterone in sexually differentiated behavior, Goy and colleagues acknowledged (33) that they could not yet separate endogenous influences of steroids from social responses of others in the monkey's environment to the androgenized females' masculine genital sex. Moreover, while it had been shown that neural and behavioral differentiation could be independent from reproductive anatomical differentiation in small mammals, including rats and guinea pigs (34), similar dissociation of these processes had not been demonstrated in any primate species.

To address this issue, Goy and colleagues manipulated prenatal testosterone exposure in rhesus monkey females at two different gestational time points: early, beginning at gestation day 40 (referred to as early androgen females or EAFs); and late, beginning at gestation day 115 (referred to as late androgen females or LAFs). Duration of prenatal exposure was also manipulated with EAFs and LAFs receiving either long (25 day) testosterone treatments or short (15 day) treatments (28).

In this study, genital and behavioral differentiation were very clearly separated. The long and short duration EAFs were physically masculinized with male-like genitalia: a penis, scrotum, and no vaginal opening. In contrast, LAFs, both long and short duration, were not physically masculinized and had normal female genitalia, with a vagina and labia. EAFs did not differ from normal control females in their rough play, but LAFs showed significantly more rough play than did either the EAFs or the control females, though still less than the control males. Thus, although EAFs had male-like genitalia, their play behavior was not masculinized whereas LAFs had female-like genitalia but had masculinized rough play (Figure 2a). While the LAFs showed rough play regardless of treatment duration, another masculine juvenile behavior, foot-clasp mounting, was not affected by the timing of androgen exposure but was affected by treatment duration: both EAFs and LAFs showed increased mounting if they received the long, but not short, duration treatment (28, Figure 2b). Thus, behavioral and physical sexual differentiation occurred independently in a nonhuman primate: long-duration EAFs had masculine genitalia and masculine foot-clasp mounting, but long-duration LAFs did not have

masculine genitalia and still showed masculine foot-clasp mounting. The finding that male-like behaviors occurred even without male-like genitalia suggested that these behaviors emerged because of direct effects of prenatal testosterone on the brain and not because of differential social treatment by group members based on the genitals of the individual. These studies clearly demonstrated that not only were physical and behavioral differentiation separable, but the critical periods for sexual differentiation of behavior varied depending on the specific behavior.

Goy's studies examined rhesus monkeys in small artificial social groups composed of 3–5 mother-young pairs, and used relatively large-dose testosterone treatments (in most studies, 10mg/day for the designated prenatal period). We have used lower androgen doses and the anti-androgen flutamide administered prenatally to further investigate sexual differentiation in both male and female rhesus monkeys living in naturalistic social groups (35). Treatments were done on time-mated pregnant females (36) living as members of 65–125 member social groups containing multiple adult males and females and their offspring. Either early (days 35 or 40 through day 70) or late (day 110 or 115 through day 145) in gestation, pregnant females received either testosterone enanthate (20mg/week, IM in oil vehicle), or flutamide (30 mg/kg twice daily in dimethyl sulfoxide (DMSO) vehicle), or vehicle (twice daily DMSO).

Testosterone treatment resulted in maternal T levels which while well above endogenous T levels were substantially lower than those reported in previous studies that treated mothers with testosterone (37,38) ranging from 2.4ng/ml to 21.7ng/ml at the treatment nadir (35). Thus it seems likely that fetal T levels were substantially lower than those used in previous studies. The EAFs we produced were not genitally masculinized, supporting the idea that our T treatment was substantially lower than previous studies. However EAFs' neonatal gonadotropin secretion was more male-like, suggesting that significant androgen had reached the fetus, but at levels too low to masculinize genitalia (35). In contrast, LAFs showed no clear effects of treatment on genital anatomy or neonatal neuroendocrine function (35). EAFs had penises which were both smaller and less typically masculine than those of control males. LAFs had male typical genitals, but their penises were significantly smaller than those of control males showing that androgen blockade from flutamide had affected genital development at both time points. Females treated with flutamide and males treated with androgen are not discussed here, but details about their development and behaviors are reported elsewhere (25,35,39–42). In contrast to Goy's studies, we found no masculinization of either rough play or foot-clasp mounting in any of our treated female groups, regardless of the timing of the exposure. Thus, while our treatments affected neuroendocrine function (and other behaviors described in the following section) the threshold for masculinizing these juvenile behaviors apparently is greater than the threshold for neuroendocrine effects and other behavioral systems (5).

Adult responses to infant or juvenile behavior are a source of socialization in rhesus monkeys. When males and females consistently engage in different patterns of behavior, maternal response could differentially socialize males and females. Although few infant rhesus monkey behaviors predictably elicit a differential adult response based on infant sex, infant vocalizations are an exception. Rhesus monkeys use vocalizations for many social functions, including threats and aggression, warning calls, and communicating distress and fear (43–45). Vocalizations also indicate emotional distress and infants vocalize intensely when separated from, or are rejected by their mothers, termed separation-rejection vocalizations (41). When housed in a naturalistic social environment, male and female infants vocalized at different frequencies and intensities. Females used a greater variety of discrete call types and had longer separation-rejection vocalization (SRV) bouts than did males. Males used more high energy atonal call types (noisy screams and geckers), while females used more low energy, tonal call types (coos and arched screams) when separated from their mothers (41). In addition

to sex differences in the nature of the calls, males and females differed in the social consequences of their calls, with male infants more likely to be retrieved by their mothers after SRVs than were female infants (41). This may reflect differences in the nature of the calls that males and females employ, or it could reflect an inherent bias of mothers to respond more readily to male than female emotional distress. We examine this possibility by investigating maternal response to SRVs in infants exposed to different prenatal androgen environments.

Prenatal androgen environment influenced the vocalization style used by rhesus infants, with EAFs exhibiting completely masculinized infant SRVs. Androgen exposure late in gestation (LAFs) produced less pronounced masculinization of SRVs in genetic females, but still resulted in masculinization of three of six sexually differentiated vocal characteristics. Early flutamide treated males (EFMs) had the fewest masculine vocal characteristics of all male groups with three of six being completely female-like. Late flutamide males (LFM) were indistinguishable from the control males.

Maternal responses to infant distress vocalizations showed an interaction between genetic sex and prenatal androgen exposure., despite their completely masculinized vocalization characteristics, were retrieved by their mothers at rates comparable to control females. LAFs, who showed less vocal masculinization were also retrieved at rates comparable to control females. Thus even though prenatal androgen masculinized their vocalizations androgen treated females were still treated by their mothers as if they were females.

The picture was different for male infants whose prenatal androgen was blocked by flutamide. whose genitals and SRVs were the least masculinized were treated like females in that their mothers retrieved them at rates comparable to control females. LFMs whose genitals were fully masculinized and who showed decreased masculinization of SRVs, but not to the extent seen in EFMs, were retrieved at rates comparable to control males. Thus in males, timing of androgen blockade and the extent to which masculinization was prevented and not infant genetic sex determined maternal response. These findings raise the possibility that the appearance of the infant's genitals better predicted maternal response than the actual character of the vocalizations made. Since we do not know the basis for the sex difference in maternal response to infant separation vocalizations we cannot rule out that there are aspects of female or male vocalizations that we did not quantify which account for maternal responsiveness. What is clear is that the effects of prenatal hormones on behavioral development reflect a complex interaction between their effects and reproductive anatomy, neural differentiation, and the responsiveness of others in the infant's environment to the characteristics of the infant, both anatomical and behavioral.

From the work reviewed here, it is clear that biological sexual differentiation affects more than simply determining genital anatomy which in turn biases the behavioral responses of others. Behavior can be affected independently of genital anatomy, and specific behaviors are affected independently of one another, with differential dependencies on duration, timing, and level of prenatal androgen exposure. It is likely that future research will reveal additional factors important in determining psychological sexual differentiation. For example, differences in receptor gene expression could determine response to androgens, even when levels of androgen exposure are comparable between individuals. While we do not yet know all of the factors involved in the complex interactions determining sexual differentiation of behavior, we now know that there is little purpose in debating whether nature or nurture is the source of sexual differentiation because it is apparent that such differentiation results from nature interacting with nurture. It is valuable, however, to understand the relative contributions of nature and nurture to the interaction. While there is increasing appreciation, particularly in humans, of this developmental interaction, we still have insufficient information to know which endpoints result from relatively small biological inputs amplified through experience and which reflect

large biological inputs little shaped by experience. For the clinician, the lack of conclusive information makes the process of sex assignment of infants with ambiguous genitalia still a difficult judgment. However, the time has passed when we could believe with confidence that social experience solely determines gender and gender differences.

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Figure 1.

Figure 2.