

Nature Needs Nurture: The Interaction of Hormonal and Social Influences on the Development of Behavioral Sex Differences in Rhesus Monkeys

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Thirty years of research on early social and hormonal environments and their relationship to the expression of behavioral sex differences in rhesus monkeys are reviewed. These studies demonstrate that whether aggressive and submissive behaviors are sexually dimorphic depends primarily on the social and not the hormonal environment. Early rearing environments without mothers or allowing brief periods of peer interaction produced higher levels of male aggression and female submission. Presenting behavior was expressed more by females than males in environments with high male aggressivity and female submissiveness. No sex differences in presenting occurred in low aggressivity environments, unless monkeys were reared isosexually, when males presented more than females. Rough and tumble play and foot-clasp mounting were consistently exhibited more by males than females across all rearing environments studied, but rearing environment affected the degree of the sex difference. When reared isosexually males displayed less, and females more, foot-clasp mounting than when heterosexually reared. No social environment increased the low frequency of female rough and tumble play. Suppressing neonatal androgen in males did not effect any sexually dimorphic behavior. Prenatal androgen administration to genetic females masculinized many aspects of their juvenile behavior, consistently increasing rough and tumble play and foot-clasp mounting across different social environments. Thus the sexually dimorphic behaviors which showed the smallest variability across social contexts were the most profoundly affected by the prenatal hormonal environment. These studies demonstrate that the expression of consistent juvenile behavioral sex differences results from hormonally induced predispositions to engage in specific patterns of juvenile behavior whose expression is shaped by the specific social environment experienced by the developing monkey. © 1996 Academic Press

The relative influence of biological and social factors on the development of human behavioral and cognitive sex differences remains unresolved. One view stresses the social construction of human behavioral sex differences and disputes whether biological sex differences, beyond those directly related to reproduction, contribute to the formation of behavioral sex differences (Bleier, 1984; Fausto-Sterling, 1992). Although no credible researcher argues the contrary, that biological factors solely and completely determine human behavioral sex differences, it is certainly the case that others have emphasized biological processes and focused less often on socialization processes (Barash, 1979; Reinisch, 1974). The more common biologically based view is that biological processes induce predispositions to engage in specific behaviors which can be shaped and modified by specific social experience (Collaer and Hines, 1995). However, this view still leaves unresolved the extent to which either biological processes or socialization influences specific behavioral patterns. One facet of this ongoing debate has been to attempt to relate the results of studies of behavioral sex differences in animals to the development of human sex differences. While animal studies offer a large body of evidence supporting biological influences on the development of sexually dimorphic behavior (Baum, 1979; Adkins-Regan, 1989; Goy and McEwen, 1980; Collaer and Hines, 1995), they have presented less evidence for the effect of social context on the development of behavioral sex differences. One reason for the paucity of evidence of socialization influences is undoubtedly because biological forces more strongly canalize some aspects of behavioral development in nonhumans than is the case for humans. However, there is evidence in animals that even such a clearly biological trait as the number of neurons in

the corpus callosum as well as other areas of the male and female nervous system are exquisitely sensitive to the social context of rearing (Juraska and Kopcik, 1988; Juraska, 1991; Moore, Dou, and Juraska, 1992). Such findings suggest that the lack of evidence for socialization influences on the development of sex differences in animals reflects more the researcher's research emphasis than a fundamental difference between humans and animals. Similarly, the less complete evidence of biological influences on human behavioral sex differences results partly from ethical considerations which preclude the sort of precise physiological manipulations possible with animals. Thus most human evidence results from experiments of nature which alter some aspect of the typical developmental sequence. However, such "accidents of nature" lack the precision and control possible in animal experimentation. Looking at close nonhuman primate relatives offers the opportunity to investigate these issues in species likely to produce information more relevant to the human condition. In this regard the rhesus monkey provides an ideal opportunity to systematically investigate the interaction between biological predispositions and social influences on the development of behavioral sex differences.

Rhesus monkeys in nature live in complex social groups integrated around a complex matrilineal social structure (Lindburg, 1971). Adult patterns of behavior are strongly sexually differentiated in regard to mating behavior, infant care, and patterns of social interaction. In addition, rhesus monkey infant and juvenile development has been studied in a wide range of social contexts ranging from total social isolation to complex age-graded groups of more than 100 animals. This rich data set on the relation between the developmental environment and behavioral sex differences is complemented by 25 years of studies in which the pre- and postnatal hormonal environment has been manipulated in different dosages, through different hormones, and at different developmental times. Integration of these two bodies of developmental data provides insight into the relative contributions of hormonal influences and early social experience on the development of behavioral sex differences. These studies provide a model system for understanding how sex differences develop and demonstrate that neither nature nor nurture determines the developmental trajectory, but, instead, it is the interaction between biological predispositions and the characteristics of the rearing environment which determines the form of behavior displayed during development. In contrast to this view, the first fully developed description of juvenile rhesus monkey behavioral sex differ-

ences argued for constitutional differences between male and female infant rhesus monkeys which led directly to juvenile behavioral sex differences and ultimately shaped adult sexual roles (Harlow, 1965). Harlow's study provides the starting point for this review as it not only attempted to develop a complete description of the development of juvenile behavioral sex differences, but also described their relationship to adult behavior.

Harlow described developmental patterns of male assertiveness and aggressivity as a developmental training ground for adult male rhesus monkey sexual assertiveness. In a complementary manner females were shown to display passivity and accommodation, which would ultimately prepare females for their assumed accommodating role in adult rhesus monkey sexuality. This integrated view of the development and function of behavioral sex differences relied upon several assumptions about rhesus monkey juvenile and adult behavior which have subsequently been shown to be inaccurate. Thus the view of male assertiveness and female accommodation and passivity presented by Harlow, which has substantially influenced thinking on behavioral sex differences in both nonhuman primates and humans, needs reevaluation. This reevaluation requires first reviewing the schema presented by Harlow more than 30 years ago and investigating the assumptions inherent in that view of adult sexual behavior and developmental sex differences.

Our current understanding of adult rhesus monkey sexual behavior has changed substantially from the view 30 years ago and this affects the possible relationship between juvenile behavioral sex differences and adult sexuality. Additionally, as described below, it is apparent that the type and magnitude of behavioral sex differences are functions of the specific conditions of rearing. Finally, the interaction between the developmental social context and the prenatal and early postnatal hormonal environment is considered.

ADULT SEXUAL BEHAVIOR IN RHESUS MONKEYS

Harlow proposed that juvenile sex differences in a variety of social and protosexual behaviors subserved the development of the adult heterosexual affectional system and adult sexual roles (Harlow, 1965). Evaluating this proposition first requires an understanding of adult rhesus monkey sexual behavior as described by Harlow and in comparison to our current understanding.

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