

# Comparative Perspectives on Human Gender Development and Evolution

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**ABSTRACT** Human behavioral sex differences are ubiquitous, but the degree to which these sex differences are evolved or culturally invented is hotly contested across disciplines. A review of the human research yields strong evidence that somatic and social causes are both important in human behavioral sex differentiation, but researchers in this area struggle to agree on the relative importance of each. Understanding the social and somatic determinants of nonhuman primate sex-typed development may shed light on the relative responsibility of social and somatic causes of human behavioral sex differentiation. A review of this research (and related research on the proximate drivers of nonhuman primate

behavioral development more generally) indicates that primate behavioral sex differentiation is rooted in somatic causes, but that these are situated in and cannot be extricated from social influences. Overt gender socialization and phenomena such as gender performance seem to be uniquely human. Primate research using a dynamic systems theoretical approach to behavioral development has the greatest potential to further clarify the workings of human behavioral sex differentiation, and further primate research is indispensable for understanding the evolution of human sex-typed behavior. *Yrbk Phys Anthropol* 000:000–000, 2014. © 2014 Wiley Periodicals, Inc.

Socioecological theory predicts that males and females are likely to maximize their fitness via different behavioral strategies (Emlen and Oring, 1977). This can lead to the evolution of sex-typed behaviors—behaviors that are stably associated with and are more commonly exhibited by one sex or the other (referred to as “sex-related” in Fausto-Sterling et al., 2012a). For example, on average, female spotted hyenas exhibit aggression more often than male spotted hyenas (Drea, 2009), and male chimpanzees exhibit more aggression than female chimpanzees (Watts, 2004). Increased aggression is a female-typed behavior in hyenas and a male-typed behavior in chimpanzees. Although both sexes of both species exhibit aggression, and although male and female distributions of this trait’s expression might overlap, most researchers would agree that increased aggression in female hyenas and male chimpanzees relative to their opposite-sex counterparts has been driven by stronger positive selection for this trait in the more aggressive sex of each species (Clutton-Brock et al., 2006).

Humans exhibit a number of sex-typed behaviors, and these are often thought to be adaptive products of sexual selection. For example, male-typical advantage in three-dimensional spatial skills has been attributed to selection for male hunting prowess (Joseph, 2000) and/or male-male fighting abilities (Geary, 1995), while female-typical advantage in object location memory has been attributed to selection for female foraging efficacy (Eals and Silverman, 1994). However, humans are unique among animals in the degree to which culture directs behavior. Since hypotheses of the evolution versus enculturation of sex-typed behaviors often do not make mutually exclusive predictions, it is often unclear how to reliably distinguish sex-typed behaviors that have evolved from those that have been enculturated.

Because important differences between male and female bodies are maintained by sexual selection (Clut-

ton-Brock et al., 2006), sex-typed behaviors that are causally linked to bodily (somatic) sex differences or that have somatic causes are often interpreted as having evolved (e.g., Thornhill and Gangestad, 1999); those that depend on socialization—the processes by which species-typical and/or sex-typical behaviors are acquired through direct interaction with others (Fragaszy and Perry, 2003)—are often not (e.g., Butler, 1988). Of course, we now know that this sharp delineation between the bodily and social is artificial and that each influences the other. For example, testosterone administration increases aggressive behavior in adult men (Kouri et al., 1995), but men who interact with their children experience reductions in circulating testosterone (Gettler et al., 2011, 2012). We even have evidence that environments individuals did not experience themselves can shape their bodies via environmental effects on the bodies of their progenitors (Drake and Walker, 2004). Indeed, it is widely accepted that behavioral development occurs at the interaction between the soma and the environment (Lewis and Weinraub, 1979; Collaer and Hines, 1995; Maccoby, 2000; Ruble et al., 2006; McCarthy and Arnold, 2011; Fausto-Sterling et al., 2012a). As such, a dynamic systems approach that focuses on understanding how the interactions of social, environmental, somatic, and historical factors work to produce sex-typed behaviors (Fausto-Sterling et al., 2012a) is more appropriate for

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addressing questions about the proximate and ultimate causes of sex-typed behavior. But because most research, thus far, has attempted to identify proximate causes of sex-typed behavior that are *either* somatic *or* social, my review of the literature will be divided thusly.

Research focused on identifying evolved human sex-typed behaviors in humans has generally sought to identify those that are likely to have somatic causation or to discover the somatic mechanisms that cause them. Here, I review the four major approaches researchers have taken to doing so. First, researchers document sex-typed behaviors that are not actively socialized in the populations that exhibit them. Most of this research focuses on identifying sex-typed visuospatial skills and attention (e.g., Ecuver-Dab and Robert, 2007). Once found, these sex-typed traits are presumed to result from sex differences in the visual processing system, which, in turn, are presumed to have been produced by selection pressures that favored different visual skills in males and females (e.g., Joseph, 2000). Currently, a major problem with this line of inquiry is its circularity, but this problem could be solved by clearly identifying the structural or physiological sex differences in the visual processing system that cause sex-typed visuospatial skills and attention (if they exist). Second, researchers have very recently begun attempting to identify sex-typed behaviors in individuals who have not yet experienced socialization (e.g., Connellan, 2000). Any such sex-typed behaviors are presumed to be somatically motivated because, by design, socialization is excluded as a cause. This is a promising avenue of research that has discovered tantalizing sex differences in individuals who have. However, as of yet, it is not clear that these early behavioral sex differences are exhibited consistently enough that they can be considered sex-typed behaviors, and the relevance of these early sex differences to the development of later sex-typed behavior has not yet been established. Third, researchers investigate the effects of hormonal variation on sex-typed behaviors in clinical populations with disorders that disrupt normative processes of somatic sex differentiation (e.g., Berenbaum and Hines, 1992). The biggest weakness of this approach is that it is unclear to what degree an understanding of developmental abnormalities is relevant to understanding normative development. And fourth, researchers identify correlations between hormonal variation and sex-typed behaviors in nonclinical populations comprising individuals who have apparently undergone normative somatic sex differentiation (e.g., Hines et al., 2002). A review of this work reveals good evidence that prenatal hormone exposure plays an important role in shaping later sex-typed behavior. But, despite a great deal of research, the details of that process remain surprisingly unclear.

Furthermore, a review of research on the social causes of human sex-typed behaviors shows that sex-typed socialization is probably equally important for their development. Overt socialization promoting the development of sex-typed behaviors starts early, is widespread, is persistent, occurs even when it is not deliberate (Sidorowicz and Lunney, 1980), and children adjust their behavior in response to it (Wilansky-Traynor and Lobel, 2008). Even nonovert socialization probably accentuates and helps to canalize sex-typed behaviors via a “separate-cultures” phenomenon that results when children voluntarily segregate and socialize primarily with members of their own sex (Maccoby, 2002). This body of evidence makes it all but impossible to exclude socializa-

tion as an alternative explanation for the development and expression of sex-typed behaviors in humans. As a result, despite the breadth and depth of research on both sides of the issue, interpretations of the data remain fiercely contested. Without consensus on the relative importance of somatic and social causes of sex-typed behavior, consensus on the evolutionary history of human sex-typed behaviors is out of reach.

In theory, data from nonhuman primates (hereafter, primates) has the potential to resolve questions of both proximate and ultimate causation of human sex-typed behavior. Primates have been good models for understanding the proximate causation of other important developmental phenomena in humans, making them promising candidates as models for understanding proximate causation of human sex-typed behaviors. For example, they have been important to understanding the workings of the infant attachment system (Harlow and Zimmerman, 1959; Bowlby, 1969; Ainsworth, 1979) and the hormonal and experiential determinants of parental behavior (Maestripieri, 1999, 2005a,b). If a particular mechanism drives the development of a particular sex-typed behavior in many primate lineages, that mechanism is likely to be driving the development of the same behavior in humans as well. While primates are less experimentally tractable than rodent model systems, primate models are more likely to yield insight into complex, human biobehavioral phenomena than rodents (Maestripieri, 1999, 2005a; Curry, 2001; Plant, 2001; Wallen, 2005).

Unlike human research, primate research has relied heavily on experimental manipulations of prenatal hormones and social experience to clearly establish their causal effects on the development of sex-typed behavior. As a result, drawing conclusions about causality from primate research is more straightforward than in work on humans. Even so, this review of research on both the somatic and social proximate causes of primate sex-typed development highlights the complexities of sex-typed developmental systems (the systems of interactive causal factors that produce sex-typed behaviors) and the major challenges that remain in this area of research.

A review of the somatic causes of primate sex-typed behavior reveals a number of complexities that are often underappreciated in human studies. Studies of navigational skills and the development of sex-typed prepubescent mounting behavior indicate that sex-typed behaviors are not apparently broadly conserved across mammals, and neither are their hormonal causes (Epple et al., 1990; Herman and Wallen, 2007). This calls for caution in using single primate or rodent models as direct analogs for humans. Studies of early sex differences in rhesus monkey visual skills suggest that sex differences in visual preferences or competence in human infants may be real (Hagger and Bachevalier, 1991), but highlight the fact that the relevance of very early visual sex differences to the development of later sex-typed behaviors is still unknown. Studies on the roles of prenatal hormones in driving the development of particular sex-typed behaviors reveal that the sex-typed developmental system is extremely complex—different sex-typed behaviors do not share the same hormonal causes, are not sensitive to hormonal input at the same times during development, and the same behavior may not share the same hormonal cause across the lifespan (Wallen, 2005). This highlights a great deal of causal complexity that cannot be captured by broad correlational studies. Similar to human research, primate research has had

the most success in determining the somatic causes of masculine behaviors in females exposed to abnormally high prenatal androgens, but much less success in determining the causes of masculine behaviors in normal males or the causes of feminine behaviors in females (Wallen, 2005). These results both call into question a linear model of sex differentiation and highlight substantial lacunae in our understanding of sex-typed development in both humans and primates that need to be resolved before we can claim full understanding of the somatic drivers of sex-typed behavior.

A review of the social causes of primate sex-typed behavior paradoxically reveals both the limitations of primate models for understanding proximate causation in human sex-typed development and their crucial role in better understanding it. While there is definitive evidence that some sex-typed behaviors in primates depend on social experience for their development (Harlow, 1965), the social mechanisms involved are much less clear for primates than for humans, and there are probably fundamental differences in social causation of sex-typed behavior between humans and primates. Most notably, the evidence for overt socialization of sex-typed behavior by adults in primates is weak. Social modeling and a “separate-cultures” phenomenon may be important causal factors in the development of sex-typed behavior, but clear evidence for them is scant. The lack of clarity about social causes of sex-typed behavior in primates is largely due to much less research attention having been paid to it in primates than in humans, leaving much room for future research to clarify these mechanisms. But the relative lack of overt socialization in primates compared with humans is probably real, indicating that overt gender socialization in humans is overlain atop a primitive system composed of simpler (but as of yet unclear) mechanisms of sex-typed socialization. Nevertheless, copious primate research confirms that sex-typed development occurs due to the interaction of the body with its environment. For example, even the most selectively critical behaviors of mating do not develop in some species without appropriate social experience (Fritz et al., 1992). This confirms that a dynamic systems perspective to research on the development of human and primate sex-typed behaviors is more appropriate than research that focuses on finding either somatic or social causes (Fausto-Sterling et al., 2012a). And even though primate models cannot be taken as stand-ins for humans, insofar as a dynamic systems approach is crucial to understanding these issues, primates remain important model systems for study, because research that simultaneously considers and quantifies somatic and social factors and their effects is more logistically feasible in primates than in humans. While no primate research on the causes of sex-typed behavior has used a dynamic systems approach thus far, some studies of the development of the neuroendocrine stress axis in primates (e.g., Suomi, 1997; Coplan et al., 2001) are excellent examples of how such research might proceed.

While the complexity and diversity of primate sex-typed development precludes uncritical extrapolation directly from primates to humans, this diversity is exciting from the perspective of understanding the *evolution* of human sex-typed behavior. Due to our close phylogenetic relationship and similar social complexity, primates are likely to share many homologous and analogous behavioral and psychological traits with humans (Maestripieri, 2005a). Comparative analysis can identify sex-

typed behaviors that are conserved across many lineages and are, therefore, likely to be adaptations maintained by stabilizing selection (Nunn, 2011). It can also identify repeated, independent origins of trait-function correlations and can identify the probability that they arose from a shared selective pressure (Nunn, 2011)—the homoplasy approach to identifying adaptation (Coddington, 1994). For example, Benenson et al. (2004, 2007) have proposed that infant sex differences in preference for particular types of visual stimuli are evolved human characteristics associated with adult human social structure. Nonhuman primates, with their tremendous diversity in adult social structure, make excellent comparative taxa with which to test this hypothesis and many others like it.

Adaptational hypotheses must link observed patterns of trait variation to observed patterns of variation in their hypothesized causes (Coddington, 1994). Specifically, trait originations must precede or temporally coincide with the origination of their hypothesized adaptive functions (Kay and Cartmill, 1977; Coddington, 1994). As such, knowledge of the historical origination or originations of a hypothesized adaptation and its proposed function are required to test adaptive hypotheses. When a trait has multiple historical originations, the homoplasy approach is the most efficient and reliable method available for testing adaptive hypotheses (Coddington, 1994), which requires knowledge of a trait and its proposed adaptive function in multiple species.

Adaptation can also be investigated using the homology approach, and this is the only approach available for testing hypotheses of adaptation for traits that are truly unique (Coddington, 1994). This approach requires careful testing and rejection of many competing hypotheses—all of which must be falsifiable, and of which adaptation is only one of many—before cautiously accepting a claim of adaptation, lest the adaptive hypothesis “persist by monopoly rather than competitive merit” (Coddington, 1994; p. 66). But even determining the uniqueness of a trait requires comparative knowledge of its absence in many other species.

Absent comparative knowledge of the proximate causes of sex-typed behaviors, I argue that we have slim chance of accurately identifying which human sex-typed behaviors are adaptive. First, comparative knowledge is crucial to determining whether a homoplasy or homology approach is most appropriate for elucidating the adaptive nature of a particular behavior. Second, even the homology approach (which can be used to study single instances of traits that are not unique) depends on knowledge of the historical origination of a particular sex-typed behavior before reasonable adaptive hypotheses can be proffered. For example, if a particular human sex-typed behavior originated at the divergence of the African and Asian apes, hypotheses about functions of that behavior that are unique to humans are unfounded. Third, the homology approach depends on the thoroughness of our imaginations in generating competing, falsifiable hypotheses to explain trait originations. But it is not uncommon for the diversity in the natural world to outpace our imagination of it. Comparative knowledge of the world’s diversity broadens our imaginations and should help us generate better alternative hypotheses, even if we are practically or theoretically confined to a homology approach to testing them. Unfortunately, relatively few comparative data are available for comparative study, but the diversity of causes of sex-typed

behavior already captured by study on just a few species illustrates the tremendous potential value of similar data from more species.

Several reviews of human sex-typed behavioral development are available from other theoretical and disciplinary perspectives and approaches (Collaer and Hines, 1995; Maccoby, 2000; Ruble et al., 2006; Alexander and Wilcox, 2012; Fausto-Sterling et al., 2012b). In this article, consideration of the human data will be limited to traits for which there are potential homologous or analogous traits in primates. Therefore, topics such as gender, sexual orientation, identity, identity construction, and the validity of a sex/gender dualism will not be addressed. I will refer to boys, girls, men, and women when discussing subadult and adult male and female humans, both because it is less cumbersome and to distinguish them from the primates. First, I will review work targeted at identifying somatic causes of human sex-typed behaviors, followed by a review of work targeted at identifying social causes of human sex-typed behaviors, highlighting the lack of consensus in this area throughout. Then, I will explore the conclusions that can be drawn from the available data on somatic and social causes of primate sex-typed behavior. Finally, I will highlight specific lines of primate research that illustrate the great potential of using a dynamic systems perspective to furthering our understanding of human sex-typed behavior. I conclude with an argument that more comparative primate data are needed to understand the evolution of human sex-typed behavior.

### SOMATIC CAUSES OF HUMAN SEX-TYPED BEHAVIOR

The most robust sex-typed behaviors exhibited by children are in toy choice, spontaneous aggression, rough and tumble play, sex-segregation during play, performance on mental rotation tasks (Ruble et al., 2006), and activity level (Eaton and Enns, 1986; Campbell and Eaton, 1999). Researchers aiming to identify the somatic underpinnings of human behavioral sex differences use several methods. They attempt to identify traits that are unlikely to be produced through socialization either because they are not traits that any culture is interested in shaping or because they occur in individuals so young that socialization has not yet had time to act. They also attempt to identify traits that covary with their hypothesized causes in clinical and nonclinical populations.

Historically, behavioral and cognitive differences between men and women that arise in the absence of deliberate socialization have been inferred to be innate characteristics of male and female bodies. The best documented sex differences of this type are in spatial and verbal skills and attention. Men typically outperform women in mental object rotation (Linn and Petersen, 1985) and tend to focus on the “geometrical positions of objects in space,” while women tend to concentrate on “the position of objects relative to one another” (Ecuyer-Dab and Robert, 2007). On the other hand, women demonstrate superior verbal and reading skills (Miller and Halpern, 2014) and outperform men in object and object location memory (Eals and Silverman, 1994; Duff and Hampson, 2001; Alexander and Hines, 2002). Sex differences in navigation and memory reflect differences in spontaneous attention rather than ability (Eals and Silverman, 1994), but they are reliably replicated across studies. Some authors conclude that because these sex

differences are spontaneous and are not socialized in any obvious way, they are likely to be innate differences that stem from sexually differentiated evolution of the neurocognitive visual processing system (Geary, 1995; Joseph, 2000; Duchaine et al., 2001).

However, an alternative explanation of enculturation is just as plausible. Most of these sex differences do not arise until after preschool (Linn and Petersen, 1985; Alexander and Wilcox, 2012), raising the possibility that they result from sex differences in experience with activities that demand different kinds of visual processing and attention (Bussey and Bandura, 1999; Berenbaum et al., 2012). Even basic visual competence depends on postnatal experience with the environment for its development in mammals (Blakemore, 1976), suggesting that whenever visual experience is sex-typed, visual development will be as well. Dramatic cross-cultural variation in the interpretation of identical visual stimuli (Henrich et al., 2010) indicates that human visual processing is strongly affected by cultural and/or environmental factors. Similarly dramatic cross-cultural variation in the magnitude of cognitive sex differences (Miller and Halpern, 2014) confirms the importance of cultural or environmental (i.e., experiential) variation in driving sexual differentiation in cognition.

Another way to pinpoint innate behavioral sex differences is to identify those that have not had time to be enculturated (Alexander and Wilcox, 2012). A number of behavioral sex differences have been reported for infants less than 1 year old, but most have not been replicated (reviewed in Alexander and Wilcox, 2012), making it unclear whether or not they represent sex-typed behaviors. However, consistent male advantage in mental rotation skills have been identified in children as young as 3 to 5 months (reviewed in Alexander and Wilcox, 2012). Sex-typed toy preferences are established as early as 3 to 8 months (Alexander et al., 2009b); sex-segregated play arises between 2 and 3 years (La Freniere et al., 1984); male-typed aggressive behavior arises between 3 and 5 years (Maccoby and Jacklin, 1980); and male-typed rough and tumble play develops by 4 years (DiPietro, 1981). But in postindustrial cultures, the physical environments of male and female infants tend to be sexually differentiated by the time they are 5 months of age (Pomerleau et al., 1990). Thus, researchers interested in identifying unenculturated sex differences have developed gaze-tracking methods in order to test for their presence in very young infants (Alexander et al., 2009b).

In the most ambitious attempt to exclude enculturation of which I am aware, Connellan et al. (2000) tested for sex differences in visual preference in 1-day-old infants. When presented with a picture of a human face and a mobile comprising jumbled fragments of a human face, more girls than boys looked preferentially at the face while more boys than girls looked preferentially at the mobile (Table 1) (Connellan, 2000). It is not clear from this experiment which elements of the objects appealed to infants in sex-differential ways, but one can imagine that this type of sex difference in visual preference could underlie the development of sex-typed toy preferences that arise by 3 to 8 months (Alexander et al., 2009b). Follow-up work has not yet identified the specific object characteristics that makes particular objects more attractive to individuals of one sex or the other, but has excluded sex-differential color preference in toddlers, in which both boys and girls prefer red to blue (Alexander et al., 2009a).

TABLE 1. Number and percent of subjects according to preference category

	Face	Mobile	None
Males ( <i>n</i> = 44)	11 (25.0%)	19 (43.2%)	14 (31.8%)
Females ( <i>n</i> = 58)	21 (36.2%)	10 (17.2%)	27 (46.6%)

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Critics point out that Connellan et al. (2000) did not control for infant handling during experimentation, and that, because adults treat infants differently by sex, even day-old infants may already have experienced sex differential treatment. Additionally, there is substantial overlap between the sexes (Table 1), meaning that some other mechanism must be involved in elaborating these preferences during infancy and childhood. Alexander (2003) posits that slight sex differences in visual preference would initiate a feedback loop between preference for and experience with sex-typed toys and activities that would promote sexually differentiated visual skill development over time. This idea may be supported by earlier findings that boys' visuospatial ability is positively correlated with the degree to which their activity preferences are sex stereotypical (Connor and Serbin, 1977). Studies of this type on newborn infants are logistically challenging, but have tremendous potential to clarify how sex-typed behaviors are initiated and to generate and test hypotheses about how they are perpetuated.

The most convincing evidence for somatic motivation of sex-typed human behavioral development comes from clinical studies of girls with congenital adrenal hyperplasia (CAH). CAH is usually caused by genetic mutations that produce defects in an enzyme needed for cortisol synthesis; the resultant cortisol deficiency elicits a compensatory response that ultimately results in fetal overproduction of adrenal androgens during gestation (Collaer and Hines, 1995; Minutolo et al., 2011). Compared with unaffected girls, girls with CAH have more interest in male-typical toys (Berenbaum and Hines, 1992; Pasterski et al., 2005), are more aggressive, are less interested in infants (reviewed in Collaer and Hines, 1995; Mathews et al., 2009), and perform better on mental rotation tasks (Berenbaum et al., 2012). Most girls with CAH are treated with cortisol starting at birth, which reduces postnatal androgen production to levels within the range of variation in unaffected girls (Ruble et al., 2006). Thus, the organizational effects of prenatal androgens are deemed responsible for the development of male-typical behaviors in girls with CAH and, by extension, girls and boys in general.

Studies of other clinical populations also suggest that postnatal sex-typed behavior is influenced by the prenatal hormone environment (reviewed in Berenbaum and Beltz, 2011), but results from these populations are less clear. For example, boys with CAH exhibit *less* than typical rough play (Hines and Kaufman, 1994) and poorer performance on mental rotation tasks than unaffected boys (Berenbaum et al., 2012), while their toy preferences and play partner preferences are unchanged (Hines and Kaufman, 1994). This has led researchers to infer that, in contrast to girls, boys with CAH are exposed to slightly *lower* than average levels of gestational androgens, perhaps because increased adrenal androgen production somehow "clamps" the production of gonadal

androgen in the fetus (Wallen, 2005). But this has not yet been demonstrated.

These interpretations of prenatal androgen effects on later sex-typed behavior have been questioned because only a few of the studies of CAH children's sex-typed behavior have used observational methods (Berenbaum and Hines, 1992; Hines and Kaufman, 1994; Pasterski et al., 2005). Most have used interviews and surveys (Table 2) (reviewed in Collaer and Hines, 1995; Jordan-Young, 2012). Unfortunately, self-reports do not always coincide with actual behavior (Bussey and Bandura, 1999). Additionally, with clinical populations, there are reasons to expect bias in interview and survey results. It is possible that caretakers perceive girls with CAH to be behaviorally masculinized based on their masculinized genitalia or because previous research on children's sex-typed behavior, visuospatial skills, and adolescent and adult sexuality suggests that they will be (reviewed in Collaer and Hines, 1995; Jordan-Young, 2012). Observational studies have confirmed the ubiquitously reported preference for male-typical toys in girls with CAH, (Berenbaum and Hines, 1992; Pasterski et al., 2005), but have found no evidence that girls with CAH engage in more rough and tumble play (Hines and Kaufman, 1994), indicating that observational studies are needed to assess real, replicable differences between children with CAH and nonclinical children.

Critics also caution that few of these studies have attempted to control for the possibility that behavioral tendencies of the subjects were produced through unconscious socialization by parents or others (Bleier, 1984; Resnick et al., 1986; Fausto-Sterling, 1992; Pasterski et al., 2005). They further point out that aspects of the CAH disease process and treatment may affect behavioral development (Fausto-Sterling, 1992; Jordan-Young, 2012). The most important criticism of this body of research is that making inferences about mechanisms of normative human sex-typed behavioral development based on results from atypical populations is suspect (Bussey and Bandura, 1999).

Another approach to identifying innate behavioral sex differences is to identify their somatic causation in non-clinical populations. Based on work in the aforementioned clinical populations as well as the classic model of mammalian sex-differentiation (Jost et al., 1970), prenatal androgen exposure is expected to be important in organizing male-typical behavior in nonclinical populations. Based on this expectation, researchers have attempted to identify correlations between prenatal androgen exposure and the development of later sex-typed behavior. An ambitious prospective study of nearly 14,000 pregnant British women tested for correlations between circulating maternal testosterone from 5 to 36 weeks of gestational age and their children's masculinity/femininity score on a 24-item psychometric survey at 3.5 years of age (the Pre-School Activities Inventory, or PSAI) (Hines et al., 2002). They found that girls of mothers with high levels of circulating gestational testosterone had more masculine scores, while girls of mothers with low levels of circulating gestational testosterone had more feminine scores (Hines et al., 2002).

Another study of 13-year-old twins (Cohen-Bendahan et al., 2005b) found that girls with twin brothers were more aggressive than girls with twin sisters. Because amniotic testosterone levels are significantly higher in male pregnancies than in female pregnancies (van de Beek et al., 2009), it is assumed that gestational

TABLE 2. Studies of children's gendered behavior comparing CAH children with unaffected children, partially reproduced and modified from Collaer and Hines (1995)

Study	Topic	Observational methods
Berenbaum and Hines, 1992	Play behavior and toy preference	Yes
Hines and Kaufman, 1994	Rough and tumble play, play partner preference	Yes
Pasterski et al., 2005	Toy preference	Yes
Dittmann et al., 1990	Play preference, hobbies, infant interest, assertiveness, dominance	No
Ehrhardt et al., 1968	Tomboyism	No
Money and Ehrhardt, 1972	Tomboyism	No
Money and Schwartz, 1976	Tomboyism	No
Ehrhardt and Baker, 1974	Tomboyism	No
Hurtig and Rosenthal, 1987	Sexuality, personality traits	No
Helleday et al., 1993	Personality traits	No
McGuire et al., 1975	Visuospatial ability, perceptual-motor speed, sexual identity, play preference, sex roles	No
Resnick, 1983	Personality traits, handedness	No
Slijper, 1984	Gendered behavior, sexuality, toy preferences, aggression, rough and tumble play	No
Slijper et al., 1992	Sexuality, hobbies, play, friend preference	No

androgens experienced by twin girls with brothers are higher than those experienced by twin girls with sisters. These results suggest that exposure to gestational testosterone exposure masculinizes behavioral tendencies in girls.

Results from studies that measure amniotic hormone levels directly, though, are mixed. Auyeung et al. (2009) found that amniotic testosterone concentration from 11 and 21 weeks gestational age explained 11% of variation in girls' PSAI scores at 6 to 10 years of age. But other studies of similar gestational ages found no relationship between amniotic testosterone and girls' reported sex-typed play behavior at 5 to 6 years of age (Knickmeyer et al., 2005) or between girls' observed toy preferences and amniotic testosterone, estradiol, or progesterone concentrations (van de Beek et al., 2009).

As with clinical studies of CAH, results from nonclinical studies on the role of prenatal hormones in determining later sex-typed behavior are less straightforward in boys than in girls. Hines et al. (2002) found no relationship between boys' reported play styles and maternal gestational testosterone, although this is probably to be expected. Amniotic testosterone levels are much higher in pregnancies of male fetuses than female fetuses, but maternal plasma testosterone levels do not differ significantly between the two (van de Beek et al., 2009). Thus, testosterone produced by male fetuses probably swamps any normal variation in maternal testosterone (Hines et al., 2002), rendering maternal testosterone variation that is titrated to the fetus effectively irrelevant to the testosterone exposure of males.

But amniotic testosterone also explained less of 6- to 10-year-old boys' masculinity on the PSAI than girls', at only 4% (Auyeung et al., 2009). And Knickmeyer et al. (2005) and van de Beek et al. (2009) found no relationship between amniotic testosterone and boys' reported play styles or observed toy preferences, respectively. Furthermore, van de Beek et al. (2009) found no relationship between amniotic estradiol concentrations and observed toy preferences in boys, but an unexpected positive relationship between amniotic progesterone concentrations and male-typical toy preferences. Again, this research indicates that variation in

prenatal testosterone exposure might encourage the development of male-typed behaviors in girls, but its role in determining variation in male-typed behaviors in boys is less clear.

Critics of this work point out that studies using maternal hormone measures cannot control for the possibility that mothers with higher circulating testosterone socialize their daughters in more masculine ways (Cohen-Bendahan et al., 2005a). Similarly, since having opposite-sex older siblings results in less sex-typed behavior in younger siblings (Rust et al., 2000), twin studies cannot rule out the possibility that increased aggressiveness in teenage girls with twin brothers results from a childhood of interacting with them. Among studies that quantify amniotic hormone levels, results have been mixed, and the only study that has found the expected relationship between masculinity and amniotic testosterone (Auyeung et al., 2009) used a survey that collapsed sex-typed toy preferences, activities, and personality characteristics into a single rating (Golombok and Rust, 1993). This particular rating conceives of masculinity and femininity as oppositional characteristics on a linear scale—as one becomes more feminine, he or she becomes less masculine by definition. Individuals who are feminine in some characteristics and masculine in others will be numerically rated as "neither." As such, it is unclear what behavioral characteristics, exactly, amniotic testosterone explained in this subject pool. Additionally, 89% of variation in masculinity/femininity in girls and 96% of variation in boys still requires explanation, apparently by other mechanisms. Finally, although there is no reason to expect bias in survey data as with the CAH survey data, only van de Beek et al. (2009) used actual observations of children's behavior.

### Summary

Most researchers, myself included, agree that elements of the prenatal environment are likely to shape postnatal sex-typed behaviors. But the details of that process remain murky. Results of studies from clinical populations are of questionable relevance to nonclinical ones (Bussey and Bandura, 1999), and results from

nonclinical populations are often mixed (Ruble et al., 2006). When positive results are found, effect sizes are often small (Connellan, 2000; Auyeung et al., 2009), leaving a large majority of behavioral sex differentiation needing explanation by other mechanisms. Studies of these issues are also plagued by logistical constraints. For example, it is unknown: if amniotic testosterone is a reliable proxy for gestational brain exposure to testosterone; if gestational age of 11 to 22 weeks is the sensitive period for the organization of sex-typed play behavior; or if commonly used survey data are reliable proxies of children's actual behavior (only a few have been validated) (Knickmeyer et al., 2005). In light of dramatic cross-cultural variation in sex-typed behavior (Whiting and Edwards, 1973), social constructionist-leaning researchers have little trouble downplaying the importance of somatic causes of sex-typed behavioral development and focusing on the importance of the social.

### SOCIAL CAUSES OF HUMAN SEX-TYPED BEHAVIOR

While the existence of sex-typed behaviors is ubiquitous across societies, their specific expressions are not (Whiting and Edwards, 1973). Furthermore, the expression of sex-typed behaviors can change rapidly within a culture through time (Tallichet and Willits, 1986). In such cases, socialization may be a more likely proximate cause of sex-typed behavior than evolution. Socialization can play a role in the development of sex-typed behaviors in several ways. In common parlance, gender socialization refers to children being treated differently by others according to their sex. This might cause children to internalize others' expectations of them or to simply adjust their behavior accordingly. More simply, individuals might model their behavior after same-sex role models of their own accord, seeking out sex-differential social experiences without being overtly encouraged to do so. In humans, all are evidenced to some degree.

#### Overt socialization

Observational studies of children in industrialized societies have found that both parents and nonparental adults treat children in sex-differential ways, even before the ages at which children exhibit obviously sex-typed behavior themselves. At later ages, when they begin acting in sex-typed ways, they are treated in sex-differential ways by their peers, a phenomenon that continues throughout development. For example, within 24 hours of birth, American parents have been found to describe their infants in sex-stereotyped ways (Rubin et al., 1974). Parents describe their newborn infant girls as softer, weaker, and more delicate and their newborn boys as firmer, stronger, and larger featured (Rubin et al., 1974). Even as gender equity has increased through time, and even though parents do not believe that neonates behave in sex-typed ways, this phenomenon has persisted (Karraker and Vogel, 1995). With respect to behavior directed toward infants, Greek mothers have been observed engaging in more strongly affective vocal expression when talking to their infant sons (Roe et al., 1985). American mothers have been observed to engage in more physical contact with infant sons (Moss, 1966), until they are 6 months old, after which time they engage in more physical contact with daughters (Lewis, 1972). By the time Canadian infants are 5 months old, their parents have created sex-typed physi-

cal environments for them in terms of clothing color, toy color, and toy type (Pomerleau et al., 1990). In interactions with their 1-year-old infants, American fathers have been observed to maintain closer contact and proximity to daughters and to offer more sex-typed toys to sons (Snow et al., 1983). American parents and teachers of 12- and 18-month-old children have been found to respond more positively to girls' attempts to communicate, to pay more attention to boys' negative/assertive behaviors (Fagot et al., 1985; Fagot and Hagan, 1991), and to respond more positively to children when they were engaged in sex-typed play behaviors and less positively to them when they were engaged in cross-sex play behaviors (Fagot and Hagan, 1991). American parents of 20- to 24-month-old children have been observed to respond more negatively to daughters' manipulations of objects and gross motor activities (e.g., running, jumping, etc.), more positively to daughters' solicitations for help, and more negatively to sons' solicitations for help (Fagot, 1978). American mothers have also been observed to look at and talk to infant daughters more than sons through the age of 2 (Lewis, 1972).

Sex-differential treatment of children by their peers arises at about the same time that children begin exhibiting sex-typed behavior of their own. At 2 years of age, girls respond more positively to other girls than to boys (Fagot et al., 1985). Boys also respond more positively to same-sex peers, but much more positively to boys engaged in male-typed behavior than to boys engaged in female-typed behavior (Fagot et al., 1985). From 3 to 5 years of age, Dutch and American parents, teachers, and peers reinforce sex-typed behavior by responding positively to it and by either ignoring or punishing cross-sex behavior (Fagot, 1977a,b). Boys tend to receive more punishment than girls. American boys receive criticism for cross-sex behavior from peers, teachers (Fagot, 1977a; Langlois and Downs, 1980), and fathers (Langlois and Downs, 1980), and peer punishment of cross-sex behavior continues throughout childhood (Ruble et al., 2006).

A major strength of this body of work is its observational nature—rather than asking people what they do, observers have documented what they do. That children are treated differently by others based on their sex is repeatedly evidenced. However, whether sex differential treatment by adults is what *causes* sex-typed behavior in children can still be questioned on two counts. First, instances of sex-typed socialization across these studies have been characterized by small effect sizes and large variances, such that particular types of socialization were not statistically significant across all samples (Table 3) (Fagot and Hagan, 1991). Second, it is possible that adults are simply responding to sex-differential behavior on the part of children. For example, perhaps parents are more punishing of sons because sons more often act in ways that deserve punishment. Spontaneous behavioral sex differences in very young children have been indeed been documented, even if they are subtle and have not been replicated. American girls have been found to vocalize more than boys at facial stimuli at 3, 6, 9, and 13 months (Lewis, 1969). At 3 months, Greek boys have been found to respond preferentially to their mothers' vocalizations compared with strangers' while girls showed no such preference (Roe et al., 1985). At 1 year, American boys have been shown to be more likely than girls to touch child-inappropriate objects in study settings (Snow et al., 1983). And in

TABLE 3. Proportion of parents' positive reactions to children's behaviors in two samples at three ages

	12 Months						18 Months						5 Years						
	Boy (n = 50)			Girl (n = 42)			Boy (n = 42)			Girl (n = 40)			Boy (n = 86)			Girl (n = 86)			
	Mom	Dad		Mom	Dad		Mom	Dad		Mom	Dad		Mom	Dad		Mom	Dad		
Large motor behavior																			
Sample 1	0.117 (0.05)	0.178 (0.151)	0.106 (0.083)	0.121 (0.091)	0.172 (0.122)	0.09 (0.08)	0.058 (0.043)	0.184 (0.294)	0.053 (0.058)	0.13 (0.152)	0.028 (0.036)	0.076 (0.08)							
Sample 2	0.089 (0.047)	0.15 (0.165)	0.079 (0.038)	0.108 (0.129)	0.145 (0.057)	0.074 (0.029)	0.077 (0.029)	0.094 (0.062)	0.02 (0.016)	0.117 (0.11)	0.012 (0.011)	0.074 (0.099)							
Male-typed toy use																			
Sample 1	0.073 (0.069)	0.147 (0.14)	0.061 (0.025)	0.014 (0.045)	0.095 (0.121)	0.099 (0.12)	0.103 (0.09)	0.001 (0.001)	0.056 (0.07)	0.063 (0.064)	0.021 (0.048)	0.018 (0.034)							
Sample 2	0.069 (0.112)	0.12 (0.115)	0.03 (0.035)	0.029 (0.052)	0.151 (0.118)	0.069 (0.114)	0.049 (0.043)	0.069 (0.163)	0.015 (0.01)	0.046 (0.045)	0.016 (0.036)	0.018 (0.05)							
Female-typed toy use																			
Sample 1	0.089 (0.114)	0.036 (0.061)	0.148 (0.217)	0.112 (0.137)	0.043 (0.062)	0.18 (0.117)	0.143 (0.117)	0.07 (0.071)	0.028 (0.052)	0.02 (0.032)	0.074 (0.098)	0.079 (0.127)							
Sample 2	0.093 (0.088)	0.028 (0.053)	0.164 (0.179)	0.113 (0.094)	0.014 (0.024)	0.085 (0.158)	0.103 (0.09)	0.123 (0.131)	0.013 (0.021)	0.03 (0.044)	0.123 (0.085)	0.077 (0.104)							
Communicative attempts																			
Sample 1	0.181 (0.094)	0.14 (0.109)	0.171 (0.105)	0.11 (0.064)	0.132 (0.05)	0.166 (0.06)	0.111 (0.05)	0.06 (0.025)	0.081 (0.077)	0.052 (0.036)	0.073 (0.037)	0.084 (0.036)							
Sample 2	0.119 (0.062)	0.096 (0.064)	0.127 (0.077)	0.115 (0.051)	0.137 (0.049)	0.143 (0.037)	0.105 (0.042)	0.116 (0.051)	0.056 (0.039)	0.067 (0.04)	0.058 (0.029)	0.081 (0.065)							

Standard deviations are in parentheses. Partially reproduced from Child Development, volume 62, Fagot and Hagan, Observations of parents reactions to sex-stereotyped behaviors: age and sex effects, page 625, copyright 1991, with permission from Wiley.



most of the studies of socialization detailed above, sex-typed behaviors were also documented in the children (Fagot, 1977a,b, 1978, 1985; Fagot et al., 1985). These results could indicate that sexually differentiated treatment of children by adults is in response to children's sex-typed behavior.

Proponents of the importance of socialization in generating sex-typed behavior in children respond to these criticisms by pointing out that even though effect sizes are small, the overt socialization of sex-typed toy play in children up to 4 years old is particularly robust across studies and through time (Fagot, 1977a; Fagot and Hagan, 1991), as is the general phenomenon of sex-typed interaction with adults. Additionally, two points suggest that sex-differential treatment of children by adults precedes and probably swamps the role of sex-typed behavior on the part of children. While the studies detailed above documented sex-typed behavior in children beginning at 2 years old, sex differential treatment of children was documented in the absence of sex-typed behavior in the youngest children in some studies (Fagot, 1985). Furthermore, these studies found more manifestations of sex-differential treatment by adults than sex-typed behaviors of children (Fagot, 1978). While I favor the interpretation that adult sex-differential treatment of children is spontaneous and does not depend heavily on children's behavior at young ages, this interpretation is not unimpeachable.

A series of experiments attempting to eliminate the confound of sex-typed behavior on the part of children in determining what drives adults' sexually differentiated treatment of them has shown that even adults' perceptions of children's sex influence the ways in which they interact with children (Seavey et al., 1975; Sidorowicz and Lunney, 1980).

The original "Baby X" experiment (Seavey et al., 1975) dressed a single 3-month-old girl in yellow and introduced her to American graduate students as a either a boy, a girl, or without sex identification, and observed which toys the graduate students used to play with her. If the baby was a perceived girl, both men and women chose a sex-typed toy for the infant. If the baby was a perceived boy, adults did not choose the sex-typed toy, but the authors posit that this was because the male-stereotypical toy they provided—a football—was not age appropriate (Seavey et al., 1975). In the sex unknown condition, the graduate students guessed the infant's sex and later justified their guesses by citing stereotypical behavioral and physical characteristics of the infant—i.e., softness for "girl" and strength for "boy" (Seavey et al., 1975). A repetition of this study on American undergraduates using infants of both sexes aged 3 to 11 months found a similar but stronger pattern of sex-typed toy offerings according to infants' perceived sex, even though the football was still used as sex-typed toy offering (Sidorowicz and Lunney, 1980). A third experiment on a group of American law students and their wives (most of whom were parents) used toddlers of both sexes aged 13 to 14 months and found that adults talked more and played with dolls and bottles more often when interacting with perceived girls, but chose a tricycle and ball more often when interacting with perceived boys (Frisch, 1977). A fourth experiment using a 6-month-old girl found that American parents of toddlers directed more verbal attention, more interaction without eye contact, and used more neutral facial expressions with a perceived girl, while they more often looked directly at a

perceived boy. This was despite the fact that most of the parents did not believe that children are sexually differentiated at 6 months, did not believe that it was important for them to be so, and reported that their own children's sex did not influence their parenting styles (Culp et al., 1983).

Taken together, this body of work suggests that sex dichotomous social signals are sent to children even when they are not intended (Fagot, 1978) and that these signals are not always responses to sex-typed behavior on the part of children. However, critics dismiss the small effect sizes in these studies as unimportant. They also point out because the adults in these studies did not know the children, they had nothing but stereotypes to rely on in structuring their interactions with the children and, therefore, may have gender-stereotyped more than usual (McIntyre and Edwards, 2009). I favor the interpretation that overt, sex-typed socialization is a real phenomenon that does not derive mostly from sex-typed behavior on the part of children. In other words, that sex-typed socialization communicates to children adults' expectations about them based on their sex. If that is the case, we might expect children to respond to their perceptions of others' expectations of them.

### Human gender performance

Prominent feminist theorists of the last century conceive of gender and gender roles as constructed through the act of repeated social performance that come to be believed by both the actors and the audience (Butler, 1988). The available evidence shows that sex-typed behaviors are probably not entirely socially constructed. But, given how early and often children receive cues from others about their own sex and the behaviors considered appropriate to it, children might adjust their behavior according to perceived sex-typed behavioral expectations. In doing so, they may internalize those expectations, or they may simply act them out without internalizing them.

A few studies show that sex-typed performances are indeed given to both adults and peers. Four- and 5-year-old American children who report a caretaker, sibling, or peer who thinks negatively of cross-sex play exhibit more sexually differentiated toy preferences than children who believe that their caretakers, siblings, and peers have a neutral position on cross-sex play (Raag, 1999), and this effect is stronger in boys. It is unclear whether these children internalized the expectations of their social partners or simply modified their behavior to satisfy them, but it suggests that children do at least modify their behavior according to the expectations of others. Two additional studies have borne this out more definitively. American 3- and 4-year-old children have been shown to make more strongly sex-stereotyped toy choices when peers are present than when they are alone, and again the effect is stronger in boys (Serbin et al., 1979). Similarly, less strongly sex-typed 5-year-old Israeli boys have been observed to choose more masculine toys in the presence of an adult observer than when playing alone. But the toy choices of stereotypically sex-typed children and less sex-typed girls were unaffected (Wilansky-Traynor and Lobel, 2008). These studies indicate that some children modulate their behavior when they have an audience, that the perceived expectations of the audience may influence that performance, and that this phenomenon is more pronounced in boys than

in girls (as expected, since boys are punished more or cross-sex behavior).

Another way in which social performance may be important in the creation of sex-typed behavior is through the repetition and canalization of sex-typed behavior. If boys and girls spend time in sex-segregated groups, sex-typed behaviors may arise through drift and conformity in those groups—the so-called "separate cultures" phenomenon (Maccoby, 1998). Several authors have suggested that sexually segregated social interactions might lead to behavioral sex differences that are perpetuated by within-group socialization (Maccoby, 1998; Bussey and Bandura, 1999). Indeed, children do prefer to interact with same-sex playmates at early ages (Jacklin and Maccoby, 1978), and when given the opportunity, they consistently self-segregate by sex during play by approximately 3 years of age (Maccoby, 1998; Ruble et al., 2006). But, is the acquisition of sex-typed behavior driven by exclusive interactions with same-sex partners or is segregation by sex an inevitable outcome of children already consistently exhibiting sex-typed behaviors (Ruble et al., 2006)? One longitudinal study of American children aiming to answer this question found that the degree of sex-segregation in children's play partners predicted the degree to which their play became sexually differentiated over time (Martin and Fabes, 2001). This supports the idea that behavioral sex differentiation is partly driven by the process of repeated performance of sex-typed behavior with same-sex others during childhood (Maccoby, 2002), but more testing of this idea is needed.

### Human social modeling

Because children are active agents of their own gender construction (McIntyre and Edwards, 2009), children may be likely to imitate or emulate same-sex behavioral models in order to acquire their sex-typed behavior (Perry and Bussey, 1979; Bussey and Bandura, 1984). Studies that aim to test the importance of modeling in behavioral development usually use an experimental setup that allows a child to observe one or more demonstrators modeling a particular behavior or behaviors that are assumed to be non-sex-typed before experimentation. Then, the child is observed to see whether or not he or she chooses to adopt a modeled behavior based on sex of the demonstrator. Human children have repeatedly been shown to engage in high-fidelity imitation of adult models (Whiten et al., 2009; Nielsen and Tomaselli, 2010; Over and Carpenter, 2012). But, they have also been shown to choose carefully which demonstrators and behaviors they imitate based on their own social goals and/or social pressures (Over and Carpenter, 2012). For example, even before they have a clear understanding of sex constancy, American children imitate the behavior of same-sex demonstrators over that of opposite-sex ones (Bussey and Bandura, 1984). This preference for imitating same-sex models has been found for boys as early as 6 to 9 months old (Benenson et al., 2011). Additionally, Australian third and fourth graders adopt the sex-typed object preferences demonstrated by older children and adults (Perry and Bussey, 1979; Bussey and Perry, 1982), but only if the demonstrators were previously shown to be acting in sex-typical ways (Perry and Bussey, 1979). Children did not imitate sex-atypical demonstrators.

Skeptics of this mechanism of gender acquisition point out that a number of studies have found no effect of

demonstrator sex on the adoption of behavior by children (Maccoby and Jacklin, 1974; Barkley et al., 1977). They suggest that experiments with positive results may have inadvertently assigned behaviors to demonstrators that children already considered to be sex-typed (Barkley et al., 1977). But proponents insist that experiments showing negative results have used an experimental procedure that does not appropriately test the question, as they provided children with only a single demonstrator, rather than with a mixed-sex group of demonstrators who enacted sexually differentiated behaviors (Perry and Bussey, 1979). The most rigorous experiments on sex-typed modeling (Perry and Bussey, 1979; Bussey and Perry, 1982; Bussey and Bandura, 1984) presented subjects with sexually differentiated behaviors to choose from and controlled for the possibility that the modeled behaviors adopted by their subjects were already sex-typed in children who were not tested for modeling. All these studies found positive effects of model sex on children's sex-typed choices, and Perry and Bussey (1979) further demonstrated that the degree to which preferences exhibited by groups of models were sex-typed determined the degree to which children adopted those preferences in sex-typed ways. Modeling, paired with self-selected sex segregation has strong potential to canalize sex differences in behavior into sex-typed behaviors.

### CONCLUSIONS FROM HUMAN RESEARCH

Overt gender socialization, gender performance, and same-sex modeling all occur in humans and, as such, are potentially important for the development of sex-typed behavior. But the importance of each compared with the others is unknown. Furthermore, the importance of any of them compared with somatic mechanisms of sex-typed development is unknown. One problem with all of these studies is that they focus on either somatic or social causes of behavioral sex differentiation even though, for decades, researchers have emphasized that human development is situated in a complex, reciprocal, biocultural, psychosocial system in which each causal factor acts in interaction with all others (Lewis and Weinraub, 1979; Collaer and Hines, 1995; Maccoby, 2000; Ruble et al., 2006; McCarthy and Arnold, 2011; Fausto-Sterling et al., 2012a). For example, overt socialization shapes modeling, as demonstrated by the famous Bobo doll experiments, in which American children 3.5 to 6 years old were less likely to imitate a demonstrator's aggressive behavior if he or she was seen to be punished for it (Bandura, 1965). Studies that investigate sex-typed development from a dynamic systems perspective are currently lacking and sorely needed (Fausto-Sterling et al., 2012a,b). Still, the tendency to dichotomize and oppose social and biological causes of sex-typed behavioral development persists. Even when we acknowledge that one does not occur without the other, discerning the relative importance of each is always open to interpretation, and those interpretations are often contested. Researchers with social constructionist leanings highlight the ubiquity of adult sex-differential treatment of infants, downplay the behavioral sex differences of infants, and point out that small differences in treatment by adults are potentially more important than is belied by their initial size due to the ways in which they can be elaborated through cumulative experience and response by children (Sidorowicz and Lunney, 1980).

Researchers with biologically mechanistic leanings highlight the small effect sizes of adult treatment of infants and emphasize the potential importance of early behavioral sex differences in structuring interactions with others and the environment (McIntyre and Edwards, 2009).

Sorting out how much of human sex-typed behavior derives from innate motivations, how much is experientially motivated or constrained, and how much interaction there is between the two is a formidable challenge. The methodological constraints of research on humans are greater than for any other species. Some tools that could solve the conundrum, such as experimental manipulation of prenatal hormone concentrations, are ethically prohibited (McIntyre and Edwards, 2009). Others, such as observing all of a subject's social interactions throughout development, are logistically infeasible. Yet, a comprehensive understanding of sex-typed development is required to make inferences about the evolution of human sex-typed behavior. If the human data are not yet up to that task, perhaps the primates can help.

### POTENTIAL CONTRIBUTIONS OF THE COMPARATIVE APPROACH

Behavioral sex differentiation in primates bears a number of similarities to that in humans. Primate infants are not strongly sexually differentiated in their behavior at birth, but develop many behavioral sex differences well before puberty (reviewed in Meredith, 2013). Additionally, many primate behavioral sex differences during development are similar to those in humans. For example, young males generally play longer, more frequently, and more vigorously than females (Owens, 1975; Altmann and Pereira, 1985; Brown and Dixon, 2000; Maestripieri and Ross, 2004; Förster and Cords, 2005). Preferential association with same-sex individuals is common, especially during play (reviewed in Meredith, 2013). Young females are more interested in infants than young males are (Chamove et al., 1967; Cheney, 1978; Crockett and Pope, 1993; Wallen et al., 1995; Clarke et al., 1998; Förster and Cords, 2005; Cords et al., 2010), and they engage in more infant handling (Maestripieri and Ross, 2004). Two species have even demonstrated human-like sex differences in human toy preference (Alexander and Hines, 2002; Hassett et al., 2008) and another in object preference (Kahlenberg and Wrangham, 2010). A great deal of experimental work has shown that both somatic and social factors are important in normative sex-typed development. Social influences on the normal development of sex-typed behaviors have not been the subject of nearly as much investigation as in humans, but somatic influences on sex-typed behavioral development have been and continue to be much more thoroughly investigated than is possible in humans. The ability to experimentally manipulate somatic and social causes of primate behavioral sex differentiation is one of the greatest strengths of primate research on this topic.

### SOMATIC CAUSES OF PRIMATE SEX-TYPED BEHAVIOR

While research on somatic causes of human behavioral sex differences must rely largely on correlative studies, research in primates is able to experimentally manipulate hypothesized causal factors. The most common experimental subjects in investigations of primate

behavioral sex differentiation are the macaques. In macaques, in addition to the sex differences common to most primates, juvenile sex differences in vocalizations (Tomaszycki et al., 2001, 2005), visual cognition (Herman and Wallen, 2007), and social interactions with mothers (Wallen et al., 1995) have also been reported. Experimental protocols used to investigate the somatic causation of sex-typed behaviors in macaques involve pharmacological androgen supplementation or suppression during gestation and the neonatal period (reviewed in Wallen, 2005). High gestational androgen dosage has achieved maternal levels of circulating testosterone in the range of 54 to 75 ng/ml (and possibly much higher in some studies) (Goy et al., 1988; Eaton et al., 1990; Wallen, 2005), which results in amniotic levels within the normal range for male fetuses, but approximately 10 to 20 times the normal range for female fetuses (Wallen, 2005). Low gestational doses have achieved maternal levels of circulating testosterone in the range of 2.4 to 42 ng/ml, and methods of gestational androgen suppression have achieved maternal levels of testosterone near zero (Wallen, 2005). Neonatal androgen manipulations have either eliminated, mimicked, or enhanced the normal infant male testosterone surge (Wallen et al., 1995; Nevison et al., 1997; Brown and Dixon, 1999). Macaque gestation is approximately 170 days long (Tomaszycki et al., 2001). Early gestational manipulations have generally targeted gestational days 40 through 70; late gestational manipulations have targeted gestational days 115 through 140 (Wallen, 2005). Some of the specific behaviors supposed to be somatically driven in humans have been experimentally investigated in primates. In addition, many lessons can be gleaned from primate research that does not directly replicate human research. This section will begin with direct comparisons with human sex-typed behaviors, followed by what can be learned from the primate literature, more broadly.

Similarities between human and rodent sex-typed spatial skills (Williams et al., 1990; Galea and Kimura, 1993; Galea et al., 1994) have led some authors to infer that sex differences in spatial abilities are broadly conserved across mammals, but the available primate data do not support this view. In rhesus macaques, global and landmark navigational performance does not distinguish the sexes in ways similar to rats and humans, as females outperform males in both global and landmark navigation (Herman and Wallen, 2007). Unlike in rats, adult female rhesus monkey global and landmark navigational skills are resistant to androgen supplementation and androgen blocking both early and late in gestation (Table 4). Also unlike in rats, adult male rhesus monkey global navigational skills are resistant to androgen administration and androgen blocking early and late in gestation. Only adult males' landmark navigational skills are responsive to prenatal hormone manipulation. Adult male landmark navigational skills improve with prenatal androgen blocking, but only if the androgen blocking occurs early in gestation (Table 5) (Herman and Wallen, 2007). In sum, prenatal hormone manipulation in rhesus monkeys appears to have minimal effects on their later navigational skills, and the pattern of sex differences found in rhesus monkeys and the hormone effects on those sex differences are both inconsistent with broad conservation of sex differences in navigational skills across mammals.

Similar to humans, small sex differences in visual discrimination are found in infancy in rhesus macaques.

TABLE 4. Behavioral outcomes of androgen supplementation and suppression in female Japanese and rhesus macaques according to level and timing of dosage

	Japanese		Rhesus								
	Early gestation		Early gestation			Late gestation			Neonatal		
	T +		T +			T +			T +		
	Low	High	Low	High	T -	Low	High	T -	Neonatal ♂ levels		
Global navigation	.	.	0	.	0	0	.	0	.	.	.
Landmark navigation	.	.	0	.	0	0	.	0	.	.	.
Visual discrimination	.	.	.	.	.	.	.	.	0	♂	.
Visual discrimination reversal	.	.	.	♂	.	.	.	.	♂	0	.
Vocalizations	.	.	♂	.	~♂	~♂	.	~♂	.	.	.
Maternal mounting	0	~♂	0	♂	0	0	0	0	.	.	0
Peer mounting	0	~♂	0	♂	0	0	♂	0	.	.	0
Maternal grooming	0	0	.	♂	.	.	0	.	.	.	0
Maternal proximity	0	0	.	.	.	.	.	.	.	.	0
Rough and tumble play	0	0	0	0	~♂	~♂	♂	~♂	.	.	0
Interest in infants	.	.	0	.	0	0	.	~♂	.	.	.
Play partner preference	.	.	0	0	.	0	0	.	.	.	0

Compilation of results from (Goy, 1970; Goy et al., 1988; Clark and Goldman-Rakic, 1989; Eaton et al., 1990; Hagger and Bachevalier, 1991; Wallen et al., 1995; Nevison et al., 1997; Brown and Dixson, 1999; Tomaszycy et al., 2001; Herman et al., 2003; Wallen, 2005; Herman and Wallen, 2007).

T + = androgen supplementation; T - = androgen suppression; . = not tested; 0 = no effect; ♂ = complete masculinization; ~♂ = partial masculinization.

Female rhesus monkey infants learn to distinguish between rewarded and unrewarded pairs of visual stimuli faster than males (Hagger and Bachevalier, 1991), but males learn the reversal of the reward pattern faster than females (Goldman et al., 1974). Males' slowness at learning the visual discrimination task is positively correlated with their circulating testosterone (Bachevalier et al., 1989), suggesting that androgens might inhibit performance on this task, which experimental manipulations have confirmed. Ovariectomized infant females dosed neonatally with dihydrotestosterone (DHT) lost their performance edge on the visual discrimination task during infancy (Table 4), while elimination of the neona-

tal testosterone surge by castration improved infant male performance (Table 5) (Hagger and Bachevalier, 1991). Additionally, females dosed neonatally with testosterone propionate (TP) performed as well as males on the reversal task (Clark and Goldman-Rakic, 1989), indicating that the sex differences in developmental curves in both of these skills are androgen dependent. However, these doses of prenatal TP failed to masculinize female performance on the visual discrimination task, even though they masculinized female genitalia more than DHT administration did (Hagger and Bachevalier, 1991). The authors suggest that the different effects of the two androgens are probably due to differences in their

TABLE 5. Behavioral outcomes of androgen supplementation and suppression in male Japanese and rhesus macaques according to level and timing of dosage

	Japanese		Rhesus					
	Early gestation		Early gestation		Late gestation		Neonatal	
	T +		T +	T -	T +	T -	T +	T -
	Low	High	Low	Zero	Low	Zero	Supra	Zero
Global navigation	.	.	.	0	.	.	.	.
Landmark navigation	.	.	.	♀	.	.	.	.
Visual discrimination	.	.	.	.	.	.	.	♀
Visual discrimination reversal	.	.	.	.	.	.	.	0
Separation-rejection vocalizations	.	.	0	~♀	0	0	.	.
Mounting	0	0	0	~♀	+♂	+♂	0	0
Maternal grooming	0	0	.	.	.	.	.	0
Maternal proximity	0	0	.	.	.	.	+♂	~♀**
Rough and tumble play	0	0	+♂	~♀	+♂	0	0	0
Interest in infants	.	.	0	0	0	0	0	0

Compilation of results from (Goy, 1970; Goy et al., 1988; Clark and Goldman-Rakic, 1989; Eaton et al., 1990; Hagger and Bachevalier, 1991; Wallen et al., 1995; Nevison et al., 1997; Brown and Dixson, 1999; Tomaszycy et al., 2001; Herman et al., 2003; Wallen, 2005; Herman and Wallen, 2007).

T + = androgen supplementation; T - = androgen suppression; . = not tested; 0 = no effect; ♀ = complete feminization; ~♀ = partial feminization; +♂ = hypermasculinization; \*\* = two other studies found no effect.

receptor-binding affinities in the brain—DHT binds preferentially with androgen receptors and TP is aromatized into estrogens and binds preferentially to estrogen receptors (Hagger and Bachevalier, 1991). This example highlights some of the complexities of hormonal causation of behavioral sex differentiation that are rarely appreciated by correlational studies. It also demonstrates that a precise understanding of the somatic mechanisms of sex differentiation of even the best-studied behaviors has not yet been achieved. Importantly, these sex differences disappeared at later ages (Goldman et al., 1974; Bachevalier et al., 1989), much like the visual skill differences that have been reported for infant boys and girls (Alexander and Wilcox, 2012). This calls into question the relevance of very early sex differences to understanding those that develop later and are more persistent. While it stands to reason that identifying very early sex differences will be crucially important to understanding behavioral sex differentiation in later object (toy) and activity preferences, care must be taken to establish their relevance via longitudinal study.

Experimental manipulations of female monkeys indicate that several other sex-typed behaviors are also androgen dependent in primates, but that individual sex-typed behaviors have different sensitivities to both levels and timing of early androgen exposure. For example, low doses of gestational testosterone given early in gestation masculinize females' separation-rejection vocalizations, but low doses given late in gestation only partially masculinize them (Table 4) (Tomaszycki et al., 2001). Doses of testosterone sufficient to masculinize vocalizations are insufficient to masculinize females' mounting, rough and tumble play, interest in infants, or preference for female play partners (Table 4) (Wallen, 2005). Higher doses of prenatal testosterone masculinize several more behaviors, but with time-sensitive effects. Maternal mounting and grooming are only masculinized by high doses of maternal testosterone early in gestation, while rough and tumble play is only masculinized by high doses of maternal testosterone late in gestation (Table 4) (Goy et al., 1988). Peer mounting does not appear to be time-sensitive to androgen exposure, being masculinized by high maternal testosterone dosage at any time during gestation. But female-typical preference for female play partners is strongly resistant to androgen administration, not being masculinized by these testosterone dosages at all (Table 4) (Goy et al., 1988; Herman et al., 2003).

Neonatal hormones, on the other hand, appear to have little effect on infant or juvenile sex-typed behavior (Table 4). In contrast to prenatal testosterone treatments, neonatal testosterone administration does not masculinize play or mounting behavior in females (Nevison et al., 1997; Brown and Dixson, 1999). In males, neither pharmaceutical suppression nor amplification of neonatal testosterone affects play or mounting behavior (Wallen et al., 1995; Nevison et al., 1997; Brown and Dixson, 1999). And gonadectomy at birth does not alter the play behavior of infants or juveniles of either sex (Goy, 1970).

In direct comparisons with humans, this research lends support to some commonly accepted ideas about human behavioral sex differentiation and calls others into question. The differences between rhesus macaques and humans/rodents in sex-typed visuospatial skills and the dissimilarity of macaques and rodents in the hormonal causes of those sex differences calls into question inferences of trait homology in humans and rodents. If

the trait similarity between rodents and humans is analogous, then their proximate causes may differ in each taxon. As such, rigorous research in this area should consider and test alternative hypotheses of proximate causation not limited to those derived from rodent models. Sex differences in the visual discrimination skills of infant rhesus macaques lend credence to the interpretation that small sex differences in visual attention in human neonates are real and potentially important in sex-typed development. The disappearance of these early sex differences in rhesus macaques reminds us that the importance of very early behavioral sex differences to the development of later sex-typed behavior must be tested rather than assumed. The successful induction of male-typical rough and tumble play in juvenile female rhesus macaques by administration of prenatal testosterone suggests that masculine play behaviors in girls with CAH do, in fact, result from abnormally high prenatal testosterone exposure. However, the finding that low dosages of exogenous gestational testosterone sufficient to masculinize female macaque fetus's later vocalizations are insufficient to masculinize their play behavior calls into question the idea that variation in prenatal androgen exposure within the range of variation in nonclinical populations determines girls' variation in feminine/masculine presentation during childhood. Lastly, a major conclusion to be drawn from the primate data overall is that any hypothesis about prenatal androgen exposure during gestation, *sensu lato*, causing a person to become more masculine, *sensu lato*, is inappropriately simplistic.

Another important finding of the primate research is that some individual sex-typed behaviors have different somatic drivers in juvenility and adulthood. Prenatal hormone exposure contributes to the organization of sex-typical adult macaque sexual and infant-directed behavior (Pomerantz et al., 1986; Thornton and Goy, 1986; Maestripieri and Zehr, 1998; Thornton et al., 2009). Neonatal hormones also contribute to the organization of adult male sexual behavior, because suppression of neonatal testosterone damps sexual behavior in adult males, causing them to masturbate and copulate less with receptive females than controls (Eisler et al., 1993). However, in adulthood, sexual and infant-directed behavior become strongly under the control of gonadal hormones. In adult rhesus macaques, pharmaceutical testosterone suppression extinguishes male mounting behavior (Wallen et al., 1991), and castration during adulthood causes a decline in rates of intromission and ejaculation that are completely restored by administration of exogenous androgen (Phoenix, 1974). Similarly, adult ovariectomy decreases female receptive and proceptive behavior, but normal rates are restored by treatment with estradiol (Thornton and Goy, 1986). The effects of gonadal hormones on infant interest in adults has not been reported for rhesus macaques, but in pig-tail macaques, administration of estradiol to ovariectomized females increases their rates of infant handling (Maestripieri and Zehr, 1998). This is in stark contrast to mounting and infant-directed behavior in juveniles, which develops normally in the absence of any postnatal gonadal hormone activation (Wallen, 2005). This work illustrates that the same behavior in childhood and adulthood may have different proximate and ultimate causes that should not be assumed to be the same.

Importantly, primate research has also shown that some sex-typed behaviors have different somatic causes

in different species. In Japanese macaques, high doses of prenatal testosterone masculinize rates of juvenile female mounting behavior but not rates of playing, displaying, or grooming (Table 4) (Eaton et al., 1990). This particular combination of effects has not been seen in rhesus macaques (Table 4). Eaton et al. (1990) used maternal testosterone implants calibrated to achieve the same maternal circulating testosterone levels as research that used high doses of testosterone appropriate injections in rhesus macaques (Goy et al., 1988; Eaton et al., 1990). However, they actually achieved maternal levels slightly lower than target levels (Eaton et al., 1990). It is possible, therefore, that slightly lower levels of maternal circulating testosterone were sufficient to masculinize mounting but not the other behaviors tested. If so, this might mean that male-typed mounting behavior has a lower critical testosterone threshold than male-typed play, display, and grooming that has simply not yet been captured in work on rhesus. It is also possible that these behaviors have different critical period and/or dosage thresholds in Japanese macaques compared with rhesus macaques (Table 4). Data from prenatal manipulations of males support the latter interpretation. Low androgen doses administered during gestational days 40 through 70 hypermasculinized male rhesus macaque play behavior (Wallen, 2005), but neither low nor high doses administered during gestational days 40 through 100 affected male play in Japanese macaques (Table 5) (Eaton et al., 1990). At the very least, sex-typed play behavior in males responds differently to hormone manipulations in Japanese and rhesus macaques.

More distantly related primates have markedly different relationships between sex-typed behaviors and hormones. In marmosets and tamarins, prepubertal castration does not affect the development of normal adult male mounting behavior (Epple et al., 1990; Dixon, 1993a), and in marmosets, even castration during adulthood does not suppress it (but this has not been tested in tamarins) (Dixon, 1993a). In contrast, neonatal castration completely feminizes adult male sexual behavior, eliminating mounting of receptive females altogether (Epple et al., 1990; Dixon, 1993a). Thus, in marmosets and tamarins, the neonatal testosterone surge seems paramount in the development of normal adult sexual behavior and the role of adult gonadal hormones in activating it seems absent (Epple et al., 1990; Dixon, 1993a). This is opposite to rhesus macaques, in which neonatal testosterone plays a small to moderate role in the development of adult male mounting (Eisler et al., 1993) and adult gonadal testosterone is paramount (Phoenix, 1974; Wallen et al., 1991). But hormonal control of mating behavior is not identical even in the closely related, socially similar marmosets and tamarins. Administration of testosterone normalizes the adult male mating behavior of neonatal castrates in marmosets (Dixon, 1993b), but has no ameliorative effect on neonatal tamarin castrates (Epple et al., 1990). The relationship between prenatal testosterone exposure and rough and tumble play also seems to be different in marmosets than it is in macaques and humans. In marmosets, levels of circulating maternal testosterone have been found to be negatively correlated with juvenile levels of rough and tumble play, especially in juvenile males (Birnie et al., 2012).

Altogether, this work suggests that individual behaviors may have proximate causes that vary widely across species. Studies of primate developmental endocrinology

to date have largely been limited to rhesus macaques (Thornton et al., 2009). Little is known about the normative developmental endocrinology of other primate taxa, but what is known demonstrates that assumptions about the somatic causation of a behavior in one species based on its proximate causes in another species are unfounded.

Lastly, this body of work suggests that a linear model of femininity and masculinity is inappropriate (Fitch and Denenberg, 1998; Fausto-Sterling, 2000; McCarthy and Arnold, 2011). Somatic causation of sex-typed behaviors in rhesus macaques is well studied and convincing (Wallen, 2005; Thornton et al., 2009), but even in this best-studied model system, questions about physiological causation remain. The role that supranormal levels of androgens play in inducing male-typed behavior in females is well established, but establishing the role of normal levels of androgens in causing male-typed behavioral development in *males* has proved challenging. Attempts to demasculinize males by prenatal androgen suppression have produced unexpected results. Daily maternal dosage with an androgen receptor blocker (flutamide) in early gestation partially feminized infant male vocalizations (Tomaszycki et al., 2001), rough play, and mounting at various times during development (Table 5) (Wallen, 2005). This is as expected because masculinization of these behaviors depends on prenatal androgen exposure. But, when administered in late gestation, flutamide treatment *hypermasculinized* juvenile male rates of juvenile mounting and did not affect rough play or (Wallen, 2005) separation-rejection vocalizations (Table 5) (Tomaszycki et al., 2001).

Androgen blocking has also produced unexpected patterns of masculinization in females. Juvenile female rough play was partially masculinized by flutamide when given at any time in gestation (Wallen, 2005), and late gestational flutamide treatment also partially masculinized infant female maternal separation vocalizations and interest in infants (Tomaszycki et al., 2001), but rates of mounting were unaffected (Table 4) (Wallen, 2005). These results have been interpreted by the authors as resulting from increased production of maternal androgen as a result of flutamide blocking negative feedback (Wallen, 2005), but this has not yet been demonstrated and the effects remain unexplained.

The failure, thus far, to demasculinize male-typical behaviors in males may seem trivial in light of the ability to induce them in females. But inferring that prenatal androgen exposure is the cause of male-typed behaviors in males because it is the cause of male-typed behaviors in experimentally manipulated females assumes that sex-typed development is nothing more than the imposition of male-typed characteristics on "an essentially female anlagen" (Wallen, 2005; p. 12). This linear model of sex differentiation (Jost et al., 1970) has been criticized as an oversimplification (Collaer and Hines, 1995; Fitch and Denenberg, 1998; Fausto-Sterling, 2000; McCarthy and Arnold, 2011). First, there may be causes of naturally occurring masculine behavior in males that are different from or additional to those that induce masculine behavior in females. Second, processes of feminization also need explanation. In rhesus macaques, juvenile female play partner preference (Goy et al., 1988), rates of play initiation (Goy, 1981), and infant interest were all resistant to defeminization by prenatal androgen exposure (Goy et al., 1988; Herman et al., 2003). What explains the persistence of these

primate-wide female-typed behaviors in females treated with androgens, and what explains their differences from males? The "essential female Anlagen" perspective falls short.

Experimental primate research has made great strides in identifying the somatic causes of sex-typed behavior and has also illustrated its complexity. There is substantial variation in the manifestation of behavioral sex differences across taxa. When sex-typed behaviors are common across taxa, there is substantial variation in their somatic causes. Within a taxon, specific behaviors have specific critical periods during which they are sensitive to specific androgens. The primate research impeaches the conception of masculinity as a suite of traits that shares a single cause and illustrates the inadequacy of a linear model of masculinity/femininity. It also highlights the need for more research into the causes of female-typical behavior, as, despite such thorough work on the behavioral effects of androgens, estrogenic effects on juvenile behavioral development are unknown (Wallen, 2005).

Research on prenatal hormone influences on sex-typed behavior has also demonstrated the importance of the social environment in linking somatic behavioral organization to realized behavioral outcomes. Early experiments that attempted to test the behavioral effects of prenatally androgenizing females did not induce masculinized behavior because these experiments reared animals in restricted social environments that eliminated competent social behavior entirely. The organizational effects of prenatal androgen exposure were only translated into sex-typed behavior when subjects were reared in socially complex groups of mothers and infants (Thornton et al., 2009), indicating that the social environment is just as important to sex-typed development as the soma. The degree to which captive experimental primate research has been able to investigate the role of social experience in determining behavioral outcomes is another major strength of primate research.

### **SOCIAL CAUSES OF PRIMATE SEX-TYPED BEHAVIOR**

Most of the evidence for social causation of primate sex-typed behavioral development comes from studies that constrain social interaction by removing entire classes of individuals from monkeys' rearing environments. Most of these studies have focused heavily on mating behavior in particular, but their results are still relevant to the question of social influence on the development of other kinds of sex-typed behavior. Of all sex-typed behaviors, we might expect mating behavior to be the most evolutionarily conserved, the most strongly driven by somatic factors, and the least dependent on socialization for its development. Thus, insofar as mating behavior depends on social interaction for its development, other kinds of sex-typed behavior probably do, too.

Male primates seem to require social experience in order to learn the kinematics of mating. Rhesus macaque males that are reared mostly alone, with only limited access to peers, fail to develop sex-typical juvenile mounting behavior at all (Harlow, 1965). And although juvenile mounting behavior is not reproductive in nature, it is apparently critical to the development of adult mating behavior. The rates of foot-clasp mounting exhibited by juvenile males from different social environ-

ments predicts their adult male reproductive competence (Goy and Wallen, 1979). Rearing without access to conspecifics has also been shown to impede the development of normal adult mating behavior in chimpanzees and aye-ayes. Human-reared males of both species exhibited sexual interest in receptive females as adults, but required training to successfully master the mechanics of mating (Dean Gibson, personal communication; Fritz et al., 1992). The specific elements of the social environment that are important for the development of normal male mating behavior are unknown, as are the learning mechanisms involved. However, these data indicate that social interactions with conspecifics at early ages are important to the development of sex- and species-typical primate behavior. Notably, this includes even a solitary foraging strepsirrhine (Nash, 1993, 2004), indicating the viability of heretofore untapped taxonomic avenues for future research on social determinants of behavioral development.

Research on rhesus macaques reveals several important points about the development of nonmating sex-typed behaviors as well. First, the manifestation of some sex-typed behaviors depends on the particular constellation of social partners experienced during rearing. For example, the development of sex-typical rates of foot-clasp mounting depends on social interaction with a full complement of peers. When reared in groups with their mothers and only same-sex peers, females developed higher rates and males developed lower rates of foot-clasp mounting than those reared with mothers and mixed-sex peers (Goldfoot et al., 1984). Second, rearing experience can also induce the development of sex differences that do not occur in all rearing environments. For example, when reared in groups with mothers and peers, juveniles rarely withdrew from peers and demonstrated no sex difference in withdrawal rates. But when reared without substantial access to peers during the first year of life, withdrawal from peers increased, and juvenile females withdrew from peers much more often than males did (Wallen et al., 1981). Similarly, when reared in peer groups without mothers, males threatened peers more often than females, but when reared with mothers, rates of threatening peers were low and not sexually differentiated, regardless of how often juveniles had access to peers (Wallen, 1996). This illustrates the point that not all behavioral sex differences are sex-typed behaviors. Finally, some behaviors are more strongly shaped by social interactions than others, and some behaviors are more strongly shaped by social interactions in one sex or the other. Male rates of rough and tumble play outpace female rates in all environments, but female rates of rough and tumble play do not change across rearing environments while male rates are highest when peer-reared, intermediate when reared with the mother and other mother-infant pairs, and lowest when reared with only male peers (Wallen, 1996). In this case, the sex difference is invariant and is probably somatically programmed, but its magnitude is modulated socially.

The relevance of much of this work for understanding normative developmental processes is open to criticism on the basis that most of the experimental manipulations used are well outside the range of variation that infants and juveniles would survive in natural settings (Schino et al., 2001). The effects of normal variation in social interactions on sex-typed behavior, specifically, have not been tested, but one set of studies has at least shown that differences in social experience well within

the range of variation expected in the wild can affect developmental outcomes in important ways.

An ingenious experimental manipulation that replicated real-world variation in foraging demand while controlling for variation in caloric intake found that foraging demand affects the social milieu, which, in turn, affects primate behavioral development. Groups of bonnet macaque mothers with infants ranging from 1 to 4 months of age were subjected to either low foraging demand, high foraging demand, or unpredictable foraging demand for a period of 3 months (Rosenblum and Paully, 1984; Andrews and Rosenblum, 1991). The total amount of food available was identical across foraging demand regimes; the only difference was in how hard mothers had to work to find their food. In the short term, these foraging demand regimes affected both female-female relationships and mother-infant relationships. Females subjected to low foraging demand (LFD) were the least aggressive and most affiliative; variable foraging demand (VFD) females were the most aggressive; and high foraging demand (HFD) females were intermediate (Rosenblum and Paully, 1984). Mother-infant dyads that experienced VFD were more often in contact, spent less time out of visual contact, and made and broke contact more often than dyads in the other groups. Infants reared in the VFD environment exhibited less social behavior, less object exploration, less play, and eventually showed signs of depression—long bouts of sitting hunched over with closed eyes, often self-clinging (Rosenblum and Paully, 1984). These early differences in social experience had important long-term effects. As adolescents, VFD-reared individuals were more avoidant of others, threatened others less, were less affiliative toward others than LFD-reared individuals, and were subordinate to LFD-reared individuals (Andrews and Rosenblum, 1994). This study illustrates that differences in social experiences during development that are well within the range of variation expected in natural populations can have important long-term effects on behavioral outcomes, even when those differences are short-lived. There is currently no experimental evidence to show that normal variation in early social experience is important in determining the development of primate sex-typed behaviors, but these results demonstrate its potential and probability.

### Overt socialization in primates

While the importance of socialization for primate behavioral development is clear, the specific mechanisms by which it occurs are less so. Due to the prevalence of overt socialization of sex-typed behavior in humans, it is a plausible hypothetical cause of behavioral sex differentiation in primates as well, but evidence for it is weak. Overall, sex-differential treatment of infants and juveniles by adults is much less pronounced in primates than in humans. In some species, sex differences in the treatment of offspring by mothers and others have been documented, but in other species, none has been found. And even when sex-differential treatment of infants and juveniles is documented, it is usually much subtler than in humans.

For example, studies of rhesus macaques have found that mothers inspect the genitals of sons more than the genitals of daughters (Goy et al., 1988) and that they are more responsive to distress calls of sons (Tomaszycki et al., 2001). They also produce more energy dense milk

for sons, but less milk volume, such that they spend more time nursing daughters (Hinde, 2009). In Japanese macaques, mothers are reported to break contact with and retrieve infant sons more often than infant daughters (Eaton et al., 1985). And blue monkey mothers groom sons more than daughters after the age of 6 months (Förster and Cords, 2005). One study of olive baboon development found no sex differences in maternal treatment of infants (Nash, 1978), but another with larger sample sizes found that mothers maintained contact more reliably with daughters than with sons throughout the first 2 weeks of their infants' lives (Bentley-Condit, 2003). Barbary macaque mothers of daughters limit their own social interactions to females within their matriline, while mothers of sons preferentially interact with females outside their matriline (Timme, 1995). While this is not a sex difference in how mothers treat their infants directly, maternal choice of social partners directly affects infant social opportunities and could be a way in which mothers influence their offsprings' social interactions in sex-differential ways. In yellow baboons, infant sex interacts with maternal characteristics to determine some aspects of the mother-infant relationship. Mothers do not maintain contact with or proximity to one sex of infant more than the other, nor does their maternal style differ according to infant sex (Altmann, 1980). But mothers of high maternal rank nurse and carry their infant daughters (but not sons) less than low ranking mothers (Nguyen et al., 2008; Samuels and Altmann, 2011), and experienced mothers (but not inexperienced ones) initiate contact more with sons than with daughters (Nguyen et al., 2012).

The ways in which mothers treat infants differently based on their sex are relatively few, some only characterize mothers of particular types, and they are not consistent across taxa. Whether nonmothers treat infants differently by sex has rarely been investigated. Japanese macaque nonmaternal group members punished infant females more than infant males (Eaton et al., 1985). But no sex differences have been found in treatment of infants by others in red-fronted brown lemurs (Barthold et al., 2009), or southern lesser galagos (Nash, 2003). One study of infant ring-tailed lemur development found no sex differences in infant treatment by others (Gould, 1990), but another found that infant males were approached more often by adult males than infant females were (Meredith, unpublished data).

Some researchers suggest that, despite their subtlety, adult behavioral sex differentiation might be rooted in these very early sex differences in social interactions (Nguyen et al., 2012). However, these sex-differential interactions might be initiated by infants rather than by mothers, as a number of infant behavioral sex differences have also been documented at these ages. Both rhesus (Tomaszycki et al., 2001) and pigtail macaque infants (Gouzoules and Gouzoules, 1989) exhibit sex differences in vocal fluency and expression. Perhaps the reason that rhesus macaque mothers are more responsive to infant male distress calls is because infant males tend to scream more when separated from their mothers than infant females do (Tomaszycki et al., 2001). Infant male Japanese macaques spend more time playing with and mounting nonmaternal group members and less time in proximity to other group members than female infants (Eaton et al., 1985). Perhaps mothers retrieve male infants more often because they more often need



retrieving. The age at which blue monkey mothers shift their grooming toward their female infants corresponds with the age at which male infants dramatically increase their rates of approaching and leaving their mothers (Förster and Cords, 2002). Perhaps mothers groom daughters more than sons because they are more often available for grooming. In the study that found sex differences in treatment of ring-tailed lemur infants by adults, infant males also approached and spent time near adult males more than infant females did (Meredith, unpublished data). Perhaps adult male attraction to infant males was a response to infant male attraction to them.

Certainly, when adults do not treat infants or juveniles differently by sex, overt socialization cannot be responsible for behavioral sex differentiation. Primate adults of some species do treat infants and juveniles differently by sex in some aspects of social interaction. But when this pattern is found, there seem to be complementary sex differences in the behavior of infants and juveniles, making it difficult to divine who is responsible for sex differences in adults' interactions with infants. Rather than being foisted on infants by adults, the process of sexual differentiation in social interactions seems to be largely reciprocal (Eaton et al., 1985). Some researchers (Nguyen et al., 2012) have even suggested that male and female fetuses may be responsible for initiating sexually differentiated mother-infant interactions in utero based on their differential effects on maternal gestational physiology. In any case, the evidence for overt socialization of sex-typed behavior is far weaker for primates than it is for humans.

### Sex-typed performance in primates

If overt sex-typed socialization is not a major driver of sex-typed behavioral development in primates, it is difficult to imagine a scenario in which primates would perform sex-typed behavior according to the perceived or imagined expectations of others. In order for this to occur, individuals would need both the ability to adjust their behavior according to an audience and to know that others expected particular behaviors of them. Many primate taxa have demonstrated the cognitive capacity to adjust their behavior based on the presence of a particular audience ("audience effects" *sensu lato* Zuberbühler, 2008). For example, when chimpanzees are attacked, they scream louder in the presence of individuals who outrank their attackers than when no superiors of their attackers are present (Slocombe and Zuberbühler, 2007). Chimpanzees also demonstrate audience effects in several other situations (Brosnan and Waal, 2003; Schel et al., 2013), as do bonobos (Krunkelsven et al., 1996), tufted capuchins (Di Bitetti, 2005), and vervet monkeys (Cheney and Seyfarth, 1985). However, only chimpanzees have demonstrated the ability to understand what other individuals know (Cheney and Seyfarth, 1990; Hare et al., 2001; Call and Tomasello, 2008), and no primate has yet demonstrated an ability to understand what others believe (Drea and Weil, 2008; Kaminski et al., 2008). Therefore, there is no evidence that primates are able to adjust their behavior to others' expectations of them (in sex-typed ways or otherwise).

On the other hand, the proposed "separate cultures" mechanism of human gender role creation has the potential to occur in many primates. As in humans, immature individuals of many primate species self-segregate by

sex. Juvenile wedge-capped capuchins (Robinson, 1981) and long-tailed macaques (van Noordwijk, 1993) associate preferentially with same-sexed individuals over opposite-sexed individuals. Juvenile blue monkeys (Cords et al., 2010), southern lesser galagos (Nash, 2003), rhesus macaques (Harlow, 1962), and Japanese macaques (Nakamichi, 1989) prefer same-sex play partners. Juvenile female talapoin monkeys prefer affiliative interaction with other females over males (Wolfheim, 1977). Juvenile male chacma baboons prefer male play partners (Cheney, 1978). And juvenile female Hanuman langurs prefer age-matched females as social partners (Nikolei and Borries, 1997). A common sex-differential pattern of infant and juvenile social interactions among female-philopatric species seems to be that developing females focus their social attention more on their matrilineal kin while developing males focus more of theirs outside it (Eaton et al., 1985; Goy et al., 1988; Pereira, 1988; Timme, 1995; Förster and Cords, 2002). For example, by 5 months of age, female barbary macaques are found in close proximity to their mothers more often than males (Timme, 1995), and female juvenile Japanese macaques show a pattern of increasing frequency of interactions with their mothers through time compared with males (Eaton et al., 1986). This tendency will inevitably create sexually differentiated social experiences for infants and juveniles. No evidence yet exists for a "separate cultures" mechanism of sex-typed behavioral development in primates. But whether social sex-segregation is associated with the degree of sex differentiation in other behaviors (e.g., aggression or rough and tumble play) has not been investigated in primates as it has been in humans. This is a plausible social mechanism by which sex-typed behavior might develop, and an area wide open for future investigation.

### Social modeling in primates

As with humans, primate infants and juveniles are expected to be active agents of their own social development (Pereira, 1988; Cords et al., 2010). One way that primates might acquire sex-typed behaviors is through patterning their behavior after same-sex role models. Most research testing for social modeling has focused on foraging behavior, but the results illustrate that juvenile primates do use modeling to acquire at least some sex-typed behaviors.

In a study of the development of sex-typed foraging behavior in tufted capuchins, Agostini and Visalberghi (2005) found that juvenile males but not females used same-sex adult models to acquire some of their sex-typed foraging behavior. Juvenile males preferentially associated with and directed their food interest toward adult males during foraging, and the amount of time juvenile males spent in association with adult males was positively correlated with their rates of targeting of animal prey (a male-typed foraging behavior). In contrast, juvenile females did not preferentially associate with or direct attention toward adult females during feeding. The authors suggest that some of the especially complex male-typical foraging behaviors may depend on social modeling for their development, while simpler foraging behaviors are learned independently.

This phenomenon also occurs in the acquisition of termite fishing behavior in chimpanzees. Termite-fishing is a complex, multistep foraging behavior that takes years to perfect, and adult females spend more time engaged

in and are more proficient at it than adult males (Lonsdorf, 2005). Adult females also exhibit consistent inter-individual preferences in termite-fishing tool length. Juvenile female chimpanzees pay more attention to their mothers' termite-fishing than juvenile males do, and juvenile females eventually adopt their mothers' tool-length preferences, whereas juvenile males do not (Lonsdorf, 2004, 2005). Instead, juvenile males eventually converge on the least efficient termite-fishing style (Lonsdorf, 2005). In this case, juvenile females learn termite-fishing through careful imitation of their mothers, while juvenile males learn it only through goal emulation (Lonsdorf, 2005; Whiten et al., 2009) and independently invent their own tool styles.

These are the only two studies yet to document the use of same-sex adult models by juveniles in acquiring their sex-typed behaviors. But some other juvenile primates do preferentially interact and associate with same sex adults, which is a necessary precursor to developing sex-typed behavior through modeling. Juvenile yellow baboons approach same-sex adults more often than opposite-sex adults (Pereira, 1988). Juvenile male chimpanzees associate preferentially with adult males as they age (Pusey, 1983, 1990; Lonsdorf et al., 2014), as do juvenile male black-handed spider monkeys (Milton, 1993), ring-tailed lemurs (Meredith, unpublished data), and mantled howling monkeys (Clarke et al., 2007). Infant male rhesus macaques target yearling males as play partners (Berman, 1982), and juvenile male rhesus macaques prefer to play with subadult and adult males (Wallen et al., 1995). While the data for the importance of modeling of sex-typed behavior in primates is currently limited, investigations of it have also been limited. Studies that experimentally demonstrate high fidelity imitation of novel foraging techniques in chimpanzees (Whiten et al., 2007) combined with observational studies in the wild that show correlational evidence of sex-typed modeling of foraging behaviors (Agostini and Visalberghi, 2005; Lonsdorf, 2005) illustrate that modeling of sex-typed behaviors is at least a possibility. Study of species in which immature individuals preferentially target same-sex adults (or same-sex older individuals) for social interaction and proximity may provide further comparative evidence of the phenomenon.

### SOCIAL-SOMATIC FEEDBACK IN PRIMATES

Just as in humans, there are currently no studies in primates that illustrate how the body and social experience interact to produce sexually differentiated behavior. But primate research has made substantial contributions to disentangling the effects of rearing experience on the body and later behavior via its effects on neuroendocrine stress axis development (reviewed in Kinnally, 2013). This work illustrates the potential for future research focused on elucidating how social environments interact with male and female bodies to produce sex-typed behavior.

Upon presentation with a stressor, the brain controls the secretion of corticotropin-releasing factor (CRF) from the hypothalamus, which stimulates secretion of adrenocorticotropin (ACTH) by the anterior pituitary gland, stimulating secretion of cortisol by the adrenal cortex, which feeds back negatively in the brain to shut down further cortisol production (reviewed in Kinnally, 2013). Studies using a peer-rearing versus mother-rearing experimental paradigm have shown that early social

environments can have important impacts on the development of the hypothalamic-pituitary-adrenal (HPA) axis in rhesus macaques (reviewed in Sánchez, 2006). They have also shown that genetic makeup affects HPA axis reactivity and interacts with early experience and sex to shape eventual HPA axis reactivity profiles.

The neurotransmitter serotonin is involved in the development of the central nervous systems as well as in the activation and control of the HPA axis (Barr et al., 2004b). In macaques, a polymorphism in a promoter region of the serotonin transporter gene influences serotonin uptake. The shorter of two alleles results in decreased serotonin uptake by reducing the transcriptional efficiency of the serotonin transporter gene (Lesch et al., 1996), and is associated with higher anxiety and behavioral reactivity in rhesus macaques (Champoux et al., 2002). But, genotype at serotonin transporter gene locus interacts with sex and rearing experience to shape HPA axis development. In 3- to 5-month-old macaques, males with a short allele (*l/s*) had higher ACTH responses to a short-term stressor than males who were homozygous for the long allele (*l/l*) regardless of rearing, indicating higher reactivity for male heterozygotes (Barr et al., 2004a). But heterozygous peer-reared females had the highest ACTH responses of all, and also had the lowest levels of cortisol (Barr et al., 2004a). In other words, the reactivity effects of the *s* allele were exacerbated by peer-rearing in females but not males. At 6 months, peer-reared animals had lower baseline levels of ACTH and cortisol than mother-reared animals, but peer-reared *l/s* individuals had the lowest cortisol levels of all (Barr et al., 2004b). Here, the suppressive effects of peer-rearing on baseline ACTH and cortisol were exacerbated by the short serotonin transporter allele. During a 30-min stressor, peer-reared *l/s* individuals had dramatically elevated ACTH levels compared with the other rearing-genotype groups (Barr et al., 2004b), indicating hyperreactivity of the HPA axis brought about by peer-rearing, but only for individuals with a short serotonin transporter allele. Considering only one genetic polymorphism is clearly an oversimplification of the process that generates complex behavioral responses to social experiences—countless other genes and their interactions with each other and the environment will also be important (reviewed in Kinnally, 2013). But these data illustrate the potential for study of the ways in which the soma and the environment interact to produce sex-typed behavioral outcomes.

Social deprivation is extreme and unlikely to be survived by animals in natural settings, so its relevance normative developmental processes may be questionable, but nonlethal maternal abuse in the first months of life has similar long-term physiological effects. Rhesus macaques living in mother-infant groups who experienced maternal abuse during their first months of life showed normal levels of baseline cortisol and ACTH throughout their first 3 years (Sánchez et al., 2010), but exhibited persistent, accentuated cortisol responses in response to administration of CRF compared with nonabused individuals. This suggests that early stressors led to greater adrenocortical responsiveness later in life (Sánchez et al., 2010). Serotonin transporter regulatory genotype also shaped HPA axis reactivity in these individuals. During the first 6 months of life, *l/l* infants showed no cortisol or ACTH elevations in response to a short-term stressor if their mothers were present, but *l/s* infants did, and the increase was most pronounced for *l/s*

infants who were abused (McCormack et al., 2009). The mechanism by which serotonin transporter regulatory genotype affected HPA axis reactivity in these experiments is not clear, because there were no significant differences in cerebrospinal fluid (CSF) serotonin metabolite levels between *l/l* and *l/s* genotypes during the first 3 years of life (Maestripieri et al., 2006). And unlike in the more severe rearing disturbances in the peer versus mother-rearing paradigm, no sex differences or interactions between sex and abuse or genotype were found in the abused and nonabused animals (Sánchez et al., 2010). But this work still illustrates that early experience and genotype interact to shape individual physiology, which has the potential to produce interindividual behavioral differences.

Variation in early experience within the range of variation that might be encountered by wild-living populations also seems to have long-term effects on neuroendocrine stress axis development. At 4 years of age and as adults, individuals who were reared in variable foraging demand environments had higher levels of baseline CRF and lower levels of baseline cortisol in their CSF compared with individuals reared in low foraging demand environments (Coplan et al., 1996, 2001). They were also hyper-responsive to a noradrenergic probe and hyporeponsive to a serotonergic probe (Roseblum et al., 1994), indicating that the functioning of their HPA axis differed from low foraging demand individuals.

The long-term effects of early stress on the responsiveness of the HPA axis are not yet completely clear (Sánchez, 2006), but regardless of how little we currently understand about these interactive systems, social effects on the soma are likely to be selectively important. For example, immunosuppression after maternal separation in bonnet macaques can be prevented if the infants are allowed access to a juvenile with whom the infant had an established friendship (Boccia et al., 1997)—having a good friend buffers infants from the negative somatic impacts of maternal loss. And functioning of the HPA axis has potentially selectively important outcomes because it determines how individuals respond physiologically and behaviorally to every day challenges in ways that are fairly consistent throughout the lifespan (reviewed in Kinnally, 2013).

Somatic effects on the social can also be selectively important. Macaques with a highly reactive phenotype—who exhibit above-average behavioral arousal and HPA axis activation in response to mild stressors, greater immunosuppression, shyness with peers, etc. (reviewed in Suomi, 1997)—typically fare less well than their less reactive counterparts. Reactive males immigrate later than their peers and reactive females have a higher risk of poor mothering with their first infants. But, highly reactive infants do very well if they are reared by the “right” kind of mother. In one of the few studies to examine the effects of especially positive early life experiences, highly reactive and normally reactive infant rhesus macaques were cross-fostered with either normal or especially nurturant mothers (reviewed in Suomi, 1997). Extra nurturing did not affect normal monkeys, but was dramatically ameliorative for highly reactive monkeys. Instead of suffering the behavioral deficits typical of their phenotype, highly reactive monkeys reared by especially nurturant mothers became behaviorally precocious. Later in life, they became adept at recruiting and maintaining allies in response to agonistic encounters,

rose to high rank, and stayed there. Furthermore, when these females had their own offspring, they exhibited the highly nurturant maternal style of their foster mothers, not the inadequate care typical of their biological mothers (Suomi, 1997).

This work does not explain the social-somatic interactions that govern the development of behavioral sex differences. But it clearly identifies some mechanisms by which the soma can affect behavior and experience and how those behaviors and experiences can be reincorporated into one's own and others' somas. Given that males and females differ in some aspects of their genetics, physiology, and anatomy, these differences may prime the sexes to have different outcomes from their interactions with the same environmental stimuli. Sex-differential somatic responses to similar social stimuli could serve as one mechanism by which social environment could drive sexual differentiation in behavior, and research on primates is much more feasible than research on humans in this area.

## SUMMARY AND CONCLUSIONS

There is good correlational evidence that somatic factors contribute to some human behavioral sex differences, and good experimental evidence that confirms their importance in determining similar sex differences in primates. Prenatal androgen exposure is well-accepted as a cause of male-typed rough play patterns (Smith et al., 2013), and the consistency of the evidence thus far from primates supports extrapolation of this causal mechanism of sex-typed play behavior to nonclinical human populations. The somatic causes of same-sex social partner preferences and female infant interest in infants are less clear in both humans and primates. The primate data do not currently support inferences that prenatal androgen exposure extinguishes female infant interest in humans. But, the persistence of these behaviors across a wide range of somatic and social manipulations suggests that they are somatically tied to sex, even if the proximate mechanism is not yet understood. On the other hand, somatic explanations for visual cognitive sex differences in humans and primates are dissimilar. The primate data do not confirm that navigational styles in humans are testosterone-mediated, because rhesus macaques' sex-typed navigational styles are different from humans'. The primate data highlight an important gap in research on the somatic causes of human female-typical behavior. Processes of feminization have thus far proved somewhat impenetrable in the primate research laboratory, but they have received almost no attention at all in human research. This deserves redress.

Primate research makes clear that even though some sex-typed behaviors are influenced by prenatal hormones, “more masculine” behavior does not follow simply from “more testosterone” exposure. Particular behaviors are affected by particular exposures of particular androgens at particular times during a lengthy gestation. Additionally, sex-typed behaviors do not always share the same somatic causes in adulthood and subadulthood. The complexity of somatic causation of sex-typed behavior in primates warrants a cautious eye toward the explanatory mechanisms implied by correlational studies between sex-typed adult behaviors such as proficiency in football (Manning and Taylor, 2001), financial trading (Coates et al., 2009), or object attention (Alexander, 2006) and proxies of prenatal androgen exposure such as

digit ratios. First of all, digit ratios were originally, themselves, correlationally derived proxies of prenatal androgen exposure. Second, recently available evidence shows that they are actually an indicator of androgen/estrogen ratios during a very narrow gestational window rather than a measure of absolute prenatal androgen exposure in general (Lutchmaya et al., 2004; Zheng and Cohn, 2011). Third, regardless of the validity of any particular proxy for gestational hormone exposure, the primate data have shown that for any link between prenatal hormone exposure and behavioral outcomes, there are surely at least one or two other causal factors involved.

There is strong evidence that the social environment is a critical driver of postnatal behavioral development in humans, and the same is true for primates. However, we still have relatively little understanding of the social factors that drive the development of sex-typed behavior in primates. Overt socialization of sex-typed behavior is nearly absent in primates. In contrast to humans, when sex differences in treatment of infants and juveniles by others are found, these usually co-occur with identifiable behavioral sex differences in infants and juveniles, suggesting that the social processes by which sex differential behavior is canalized are not due to unidirectional socialization by adults. Overt socialization and the sex-typed performance it elicits appear to be uniquely human inventions overlain on a primitive system of subadult-motivated sex differentiation that may include social modeling and a separate cultures phenomenon in addition to somatic causes. Social modeling of same-sex behaviors has been documented in the domain of foraging in primates, but not in any other. However, minimal research has been done in this area, and the potential of social modeling in facilitating sex-typed behavioral development deserves increased attention. The separate cultures phenomenon of sex-typed socialization has not been documented in primates, but no research has been done on this question, and the spatial and social sex-segregation necessary for this process to occur is common across taxa. This is another potential process of sex-typed socialization that merits attention in primate research, especially as it has the potential to work synergistically with sex-typed social modeling to produce sex-typed behavior.

Overall, the human research has more rigorously investigated social causes of behavioral sex differentiation and the primate research has more rigorously investigated somatic ones. While not much can be done about constraints on somatic research in humans, there is still a great deal of work to be done on social mechanisms of behavioral development in primates. Relatively little of the human and primate research has taken a dynamic systems approach to investigate how the two interact to generate sex-typed behaviors. However, primate research on early adversity and the development of neuroendocrine stress reactivity provides a good model for such investigations.

Often implicit (and sometimes explicit) in discussions of the primate data on sex differences is the assumption that elements of human sex-typed behavior that are shared with nonhuman animals must be somatically instead of socially mediated (Joseph, 2000; Lonsdorf et al., 2014). The data presented here directly contradict this. Individual phenotypes in both humans and primates result from complex interactions between individuals' somatic characteristics and their experiences with the

social and physical environment (Lewis and Weinraub, 1979; Capitano, 1984, 1985; Geary, 1995; Pereira, 1995; Deputte and Quris, 1996; Wallen, 1996; Kelly et al., 1999; Wallen and Zehr, 2004; Pasterski et al., 2005; Fausto-Sterling et al., 2012a). These interactions begin before birth. The fetus interacts with its mother throughout gestation, as she shapes and is shaped by her own environment. Thus, "we should not be tempted to think that even the bodies of infants are, so to speak, all biology and no culture" (McIntyre and Edwards, 2009; p. 90). There is no social organism on whom socialization has not yet had time to act. Therefore, research on behavioral sex differentiation should adopt a dynamic systems perspective over traditional approaches (Alexander and Wilcox, 2012; Fausto-Sterling et al., 2012a). In many ways, primate research is better positioned to simultaneously investigate multiple causal factors on sex-typed development than is human research. Primates have faster generation times; it is possible to observe all of their social interactions with all others during most or all of their waking hours; there is less environmental variation across different populations of primates than in humans; and invasive measures of somatic characteristics are more often possible to acquire. As such, in addition to the insights it has already produced, primate research on sex-typed development retains tremendous potential to clarify the evolved workings of human sex-typed behavioral developmental system.

Paradoxically, while primate models are indispensable for elucidating questions of proximate causation in human sex-typed development, the data already warn of their potential limitations in that regard. Careful experimental work has shown that androgenic influences on sex-typed behavioral development do not proceed identically in all primates. The same is likely to be true for social influences on behavioral development. Model systems are only models, and cannot be taken as stand-ins for humans. Hypotheses about the function of human developmental systems derived from the demonstrated function of primate models should still be tested in humans whenever possible. When testing in humans is beyond logistical or ethical limitations, primate data should be relied upon with due caution.

Despite a few limitations on their utility as models for understanding the proximate causes of human sex-typed behavior, the primates are crucial to understanding its evolution. The interspecific variation in sex-typed behaviors and their proximate causes in the few primate species studied so far indicate that similar data on other species will be useful in reconstructing the evolutionary histories of human sex-typed traits, in reconstructing the evolutionary histories of their causal mechanisms, and in testing adaptive hypotheses about them. Hypotheses of behavioral adaptation are challenging to test, but are best explored using the comparative method (Harvey and Pagel, 1991; Nunn, 2011). The comparative method can reveal elements of adult sex-typed behavior that vary little across many species and that may have experienced stabilizing selection, and it can test for evolutionary covariation between sex-typed behaviors and other, potentially selectively important factors, such as resource distribution, social system, or specific patterns of social interaction. Comparative study of sex-typed behavior and development across the primate order offers the

clearest way to gain insight into questions regarding the evolution of, and adaptation in, human sex-typed behavior. There are other methods available to study the evolution of traits that are unique to humans, but for traits that are shared with other taxa, the comparative method is both the most appropriate and the most incisive (Coddington, 1994). Thus, insofar as we are interested in understanding the evolution of human sex-typed behavior, the value of future comparative data on sex-typed behavior and its causes in primates cannot be overstated.

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