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REVIEWS

Opinion
Sex-Linked Behavior: Evolution, Stability, and Variability

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Common understanding of human sex-linked behaviors is that proximal mechanisms of genetic and hormonal sex, ultimately shaped by the differential reproductive challenges of ancestral males and females, act on the brain to transfer sex-linked predispositions across generations. Here, we extend the debate on the role of nature and nurture in the development of traits in the lifetime of an individual, to their role in the cross-generation transfer of traits. Advances in evolutionary theory that posit the environment as a source of trans-generational stability, and new understanding of sex effects on the brain, suggest that the cross-generation stability of sex-linked patterns of behavior are sometimes better explained in terms of inherited socioenvironmental conditions, with biological sex fostering intrageneration variability.

Sex, Brains, and Evolution

To many, including many scientists, to say that a **sex/gender** (see Glossary) difference in human brain and behavior reflects an evolved adaptation is to set limits on plausible future male/female patterns of behavior. Indeed, it is a tenet of the best-known evolutionary psychology research approach that the dispositions to behavior presumed to have been differentially adaptive for women versus men in our ancestral past should persist in contemporary, modern humans (for an overview of numerous evolutionary approaches, see [1]), with environmental and social factors only modifying their manifestation in behavior. For instance, it is often claimed that certain sex/gender differences, such as interest in casual sex, preferred partner characteristics, and willingness to compete for status and resources, reflect **sex-linked** adaptations for reproductive success that will always be observed to some degree at the population level, regardless of social and cultural context (e.g., [2–5]). This assumption is also common in public debates, evident in arguments that equality-promoting initiatives, such as gender-neutral toy marketing, are unlikely to be effective since the different preferences of girls and boys are due to sex-linked adaptive predispositions (reviewed in [6]).

Many criticisms have been leveled at such accounts (for major critiques, see [7,8]), such as the overlooked importance of competition for female reproductive success [9]; overstatement of both the benefits and prevalence of male promiscuity (e.g., [10,11]); shifting conceptualizations of 'male' and 'female' sexuality [12]; and the methodological and empirical weaknesses and inconsistencies in purported evidence for prenatal hormonal influences on sex-linked predispositions [12–14].

Another major theme has been the role of nature and nurture in the development of sex-linked behavioral traits (see [15]). Although the longstanding nature–nurture debate typically concerns the role of genes and environment in the development of behavioral traits in the lifetime of an

Trends

Recent advances in evolutionary theory point to the environment as a source of trans-generational stability for adaptive behavioral traits. Stability of environmental factors over generations can guarantee the reliable reproduction of a trait across generations, and also can remove any selective pressure for the development of parallel stabilizing genetic factors.

Recent models of sexual differentiation of the brain posit genetic and hormonal sex as a source of variability between individuals.

Together, these advances point to the possibility that sex-linked patterns of behavior are sometimes best explained in terms of inherited socioenvironmental conditions that provide cross-generation stability, while biological sex as well as other socioenvironmental factors foster intrageneration and interindividual variability.

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individual (i.e., ontogeny), our focus here is a discussion of the relative contributions of genes and the environment to the development and transfer of traits across generations (i.e., phylogeny). Specifically, we focus on a common assumption not always made explicit: that sex-linked adaptive traits persist across time and culture because they are passed on via inherited **biological sex**. That is, proximal mechanisms of genetic and hormonal sex, ultimately shaped by the differential reproductive challenges of ancestral males and females, affect brain and behavior in ways that predispose even contemporary Western women and men, living in very different conditions from their ancestors, to the same sex-linked behaviors and roles. In other words, it is assumed implicitly or otherwise that the cross-generational transmission of traits is largely mediated by genetics, with the environment being a source of variability in the development, or ontogeny, of the behavioral phenotype in each individual, and a source of selective pressure on genes. Given sufficient time, this selective pressure can drive changes in sex-linked traits, but since stabilized evolutionary change is thought to require the fixation of changes to the genome, only very long periods of consistent environmental influence can achieve genuine evolutionary change. The different timescales of changes to the environment and to the genome imply that the genome is largely responsible for the stable and the evolved influences on ontogeny, while the effects of the environment give rise to opportunistic and transitory influences [16].

Drawing on a much-expanded view of inheritance in recent evolutionary biology, and on contemporary understanding of sexual differentiation of brain and behavior, we question this division of labor between nature (genes) and nurture (environment) in the phylogeny of sex-linked behaviors. Specifically, we argue the need to consider the possibility that, for some sex-linked behavioral traits, socioenvironmental conditions provide the cross-generational inherited element while biological sex fosters interindividual variability.

The Role of the Environment in the Evolution of Behavioral Traits
According to the evolutionary perspective, the development and inheritance of adaptive behavioral traits depends on processes that allow both the creation of variation on which natural selection can act and the stable cross-generation transfer of these traits. There has been growing recognition in recent years that genetic inheritance is not the only such process, and that **epigenetic**, behavioral, and **symbolic systems** can create phenotypic variation, and provide the means of reliable transfer of these traits [17].

In parallel, there has been increasing criticism of mainstream evolutionary theory, the so-called 'Modern Synthesis', for overlooking the importance of development, and for assuming, implicitly or explicitly, that developmental outcomes are predetermined by genes. The disregard of the exact processes by which developmental outcomes are achieved has been criticized from various directions, especially from **evolutionary developmental biology** [18,19], **ecological evolutionary developmental biology** [20], and **developmental systems theory** [21,22]. The latter two perspectives, in particular, point to an important, yet often neglected, factor in ensuring accurate transfer of traits across generations: the environmental aspects of the developmental system. Every organism inherits a rich, dynamic developmental system comprising both genetic and extra-genetic resources that contribute to developmental processes from conception to death. Environmental aspects of the developmental system include, for example, local ecology, other individuals, and social and cultural constructions (from bee hives and beaver dams, to schools, the law, and literature).

Consider, for example, the apparently 'instinctual' preference of mallard ducks on hatching for vocalizations of their own species. Remarkably, this adaptive behavioral trait depends on auditory stimulation in the egg: mallard ducklings whose own prehatching vocalizations were muted, and that were put in auditory isolation, did not show the usual robust preference for the

Glossary

Biological sex: the genetic and hormonal components of sex that bring about sexual differentiation of the reproductive system.

Developmental systems theory: a theoretical lens on development, heredity, and evolution based on several themes that try to transcend oppositional conceptualizations in biological thinking, including the importance of 'extended inheritance' beyond the genetic, and an emphasis on traits as constructed through development.

Ecological evolutionary developmental biology: this research program additionally incorporates consideration of environmental factors in the creation of genetic and phenotypic variability and evolutionary processes.

Epigenetic/epigenetic modification: potentially heritable changes in **gene expression** and activity that do not involve changes to the DNA sequence itself.

Evolutionary developmental biology: traditionally, evolutionary biologists have been concerned with explaining why (ultimate cause) a particular trait exists, while developmental biologists explain the how (proximate causes). Evolutionary developmental research is located at the intersection of the two questions, exploring, for instance, the evolution of developmental processes and the role of developmental processes in evolutionary ones.

Gene expression: the process by which a section of genomic DNA sequence is transcribed into an RNA molecule. The RNA molecule may then undergo further processing and guide the synthesis of all or part of a protein. Many RNA transcripts are not translated into proteins and may have other functions, although the proportion that do remains controversial. Not all genes are expressed in all cells or at all times.

Sex/gender: an alternative term for either 'sex' or 'gender' intended to emphasize that comparisons of males and females capture contributions of both biological sex, social gender constructions, and their interaction (e.g., [57]). Note that, also captured in such comparisons and interactions are the effects of variables that correlate with sex, such as size or muscle mass.

maternal mallard call over the call of a chicken [23]. Likewise, the 'typical' adaptive behavioral responses of moose to the sounds and smells of their predators (vigilance, aggressive responses, and departure from a feeding site) are greatly reduced in populations in which those predators have recently disappeared, and appear to be rapidly acquired by mothers whose calves have been killed by a predator [24].

These examples (for fuller descriptions of these and numerous others, see [25]) illustrate the important point that genetic material is not the only stable inherited resource for development: a mallard duck reliably inherits a prehatching environment that includes the vocalizations of itself, mother, and siblings; a moose reliably inherits an ecology replete with stimuli correlated with predators, as well as a mother that has learned to respond in particular ways to those cues.

Thus, despite the widely assumed conceptual link between 'inherited' and 'genetic', the reliable development of adaptive behaviors can be contingent on specific environmental resources. Where the necessary environmental factors are stably reproduced, generation after generation, so too will be the (re-)production of the adaptive trait in each generation. The more nearly the environmental factors are sufficient for the development of a trait, the more the ability to quickly acquire or learn adaptive behaviors will be genetically selected for and inherited, rather than the behaviors themselves [17].

Another example of this principle is the reflex of the rat to right itself when dropped on its back into water. It turns out that the development of this reflex is facilitated by experience in gravity. Thus, 1-day-old rats that spent most of their gestation in space and were then brought down to Earth were half as likely to attempt to right themselves when placed in a water bath compared with control rats, although they quickly learnt to do so [26].

This last example nicely illustrates Griffiths' point that: 'Selection cannot favor a trait that compensates for the loss of a developmental input that is, as a matter of fact, reliably available. Evolution does not anticipate future contingencies.' ([27] pp. 74–75.) As a result, stability of environmental factors over generations not only guarantees the reliable reproduction of a trait across generations, but also removes any selective pressure for the development of parallel stabilizing genetic factors. Only regular space travel would provide any selective pressure for rats to evolve genetic determination of the water reflex. Genetically determined traits may also be lost when some reliable feature of the environment makes them unnecessary. One such example, provided in [27], is the loss of the ability to synthesize vitamin C in primates, because this vitamin is readily available in their fruit-based diet.

Whereas in some of the examples provided above, the stable environmental factor was a fixed aspect of the environment (e.g., gravity), in other examples the stable environmental factor comprised aspects of the environment that were heavily dependent on the behavior of organisms (e.g., the vocalizations of mallard ducks; the behavior of the mother moose and its predators). In the latter case, the fact that the environment is (ontogenetically) crucial in the development of behavior and that relevant aspects of the environment can be reliably generated by the behavior of organisms points to a phylogenetic pathway that is distinct from the familiar genetic one. Thus, as others have argued, we suggest that the currently dominant view, which focuses on genes as a source of cross-generation stability, should be extended to the view that many behavioral traits are stabilized by the interplay between intrinsic (e.g., genetic or epigenetic) and extrinsic environmental factors [17]. For some traits, this balance leans more toward the genetic side, whereas, for others, it leans more toward the environment side. Note that, also in the latter case, genetic inheritance is assumed to furnish critical neural capacity for acquisition of the trait [17]. The important aspect of our argument is that, to the extent that the 'content' of the trait is provided by stabilizing environmental factors, there will not be parallel

Sex-linked: referring to traits for which average differences are observed between the sexes. Given the overlap between the sexes in behavior, this is a more accurate term than 'sex-specific' or 'sexually dimorphic', which imply distinct categories.

Symbolic system: referring to information sent or received that derives its meaning from socially shared conventions or understandings. The word 'evolution', the symbol '=', and pink packaging on a toy are all examples of symbolic information.

stabilizing genetic factors. With this, we add to previous models, such as the biosocial construction model [51], the possibility that evolved environments do not necessarily augment genetic inheritance, but can sometimes obviate the necessity for the development of parallel genetic mechanisms.

What About Sex-Linked Adaptive Behaviors?

Until recently, models of mammalian sexual differentiation of brain and behavior focused on direct effects of the genetic and hormonal components of sex on the brain and behavior in explaining the stability of neural and behavioral endpoints. In this traditional 'organizational–activational' account (reviewed in [28]), the chromosome composition (XX or XY in most mammals) determines the form of the gonads (ovaries or testes, respectively), and the hormones secreted by the gonads permanently 'organize' distinct neural circuits relating to reproductive behavior in the brains of males and females. At sexual maturity (or in the breeding season), these sexually differentiated neural circuits are 'activated' by elevated levels of sex hormones (and, in females, also hormones triggered by pregnancy, birth, and lactation), facilitating sex-role behavior. In this traditional account, a genetic binary (XX versus XY), acting via gene-directed sex hormones, is a primary and stable source of sexually differentiated brain circuits that underlie sex-linked adaptive behavior. Although the traditional 'organizational–activational' theory has been widely criticized on different grounds (e.g., [12,28–30]), evidence from both *in vitro* and *in vivo* studies clearly demonstrates that the genetic and hormonal components of sex can affect the structure and function of brain cells *in utero* and throughout life (reviewed in [31]).

It has always been acknowledged, of course, that the biological components of sex interact with environmental factors. However, we think it reasonable to suggest that these sex × environment interactions have implicitly or explicitly been understood to be either conservative or additive in nature. In conservative interactions [32], internal (biological sex) and external (environmental) causes interact, but in such a way that the internal causes tend to keep the phenotype to a 'preferred' state, with strong external changes required to modify this (for an example of an expression of this view with regards to sex differences in brain and behavior, see [33]). Thus, in conservative interactions, biological sex is assumed to stabilize a particular sex-linked phenotype across a wide range of environmental conditions. In additive interactions, a particular environmental factor will have a similar effect on both sexual geno-types. For example, an environmental factor (such as a predator attack or food shortage) would influence brain and behavior in both females and males to the same degree (e.g., reduce neuronal density in a specific nucleus), meaning that a similar relative sex difference (e.g., male > female) will be observed across the entire range of stressful environments. In contrast to conservative interactions, additive interactions may result in overlap of phenotypes between females and males at the population level. This is because the phenotypes of some males under some environmental conditions may be similar to the phenotypes of some females under other environmental conditions (e.g., if the neuronal density in a specific nucleus is higher in males than in females, and is reduced by stress in both females and males, then neuronal density in stressed males may be similar to that found in nonstressed females).

However, it is now apparent that some of the interactions between sex and the environment are what Barker describes as 'radical' [32]; that is, the effects of an environmental condition on the brain may be different and even opposite in females and males. As a result, what is typical of females under some environmental conditions may be typical of males under other environmental conditions (reviewed in [34]). Moreover, these complex interactions between sex and the environment are region specific [28] thus giving rise to brains comprising unique 'mosaics' of features, some in a form that, at the population level, is more common in males than in females (i.e., 'masculine' form) and some in a form that, at the population level, is more common

in females than in males (i.e., 'feminine' form) [28,34]. Such mosaicism was recently demonstrated in human brains: analysis of structural characteristics in over 1400 brains from four data sets revealed that mosaic brains were much more common than brains with only 'feminine' or only 'masculine' features [35]. Similarly, although at the population level there are differences between women and men in a variety of behavioral and psychological characteristics, most humans have a mosaic of both feminine and masculine characteristics, rather than segregating into two categories, or aligning on a masculinity–femininity continuum [35].

Conservative sex × environment interactions would be consistent with the implicitly assumed role for biological sex as a source of stability in brain structure and function. By contrast, the existence of radical interactions and of mosaic brains suggests biological sex as a source of interindividual variability in brain structure and function. This may be seen as an extension of the hypothesized role of sexual reproduction in increasing interindividual genetic variation [36] to the level of brain and behavior.

That biological sex is a potential source of variability for at least some sex-linked neural and behavioral endpoints gives us even greater reason to consider the possibility that environmental factors are sometimes a source of stability for sex-linked behavioral traits, so long as the necessary resources are reliably reproduced and inherited by each generation [37]. Therefore, differentiation of behavior by sex, whether complete or partial, would require either a sex-differentiated predisposition to acquire or learn an adaptive trait and/or a reliably sex-differentiated environment. Evidence for a mechanism of the former kind may be provided by the recent finding that girls exposed to high levels of androgens *in utero* showed a reduced tendency to mimic the behavior of older girls compared with girls exposed to typical levels of androgens [38].

With regards to the second potential mechanism, one set of reliably inherited factors that can lead to stable and reproducible sex-differentiated environments are phenotypic markers of biological sex, such as appearance, size, strength, and smell. These are reliably inherited in ways that are largely, though by no means wholly, insensitive to environmental variables. These phenotypic markers can influence both the individual's behavior and others' responses to them, and these effects can in turn affect the development of brain and behavior. Consider, for example, evidence that mother rats are attracted to the higher level of testosterone in the urine of their male, compared with female, rat pups. This stimulates higher intensity anogenital licking, which, in turn, contributes to sexual differentiation of specific brain regions and of sexual behavior [39,40]. Recognition of such indirect effects of sex on development, via sex-differentiated experiences, is now growing [41,42].

Recognition of the role of stable experiential factors in the inheritance of adaptive behavioral traits helps to explain examples in which sex-linked traits fail to develop when environmental conditions change. Take, for instance, the finding that cross-species-fostered sheep and goat newborn males develop robust and persistent sexual preferences for mates of the cross-fostered species [43]. Likewise, contrary to the notion of a 'maternal instinct', adequate care of a firstborn by female Rhesus monkeys depends on early social experience [44]; or consider a study that found that, when put in close contact with pups, male Charles River strain rats showed 'maternal' behavior within 1 week [45].

As these examples illustrate, the typical sex-linked outcome for individuals at a particular stage in the lifecycle depends in part on deceptively unexceptional aspects of the environmental developmental system, such as early social experience. Moreover, the different examples demonstrate Griffiths' point above that, when the environmental conditions are reliably reproduced generation after generation, we should not assume that there must be additional endogenous (e.g., genetic) factors that support the stability of the neural or behavioral endpoint

[46], beyond those necessary for learning or acquiring the traits. As a consequence, 'sexual nature' can be eliminated or even reversed, when relevant features of the external developmental context change [47,48].

We of course make no claim that the examples we cite generalize across species or behavioral traits: this is a matter for empirical investigation (see Outstanding Questions). Nonetheless, these examples add, to the conventional understanding of sex, the realization that the genetic and hormonal components of sex sometimes act, along with some socioenvironmental factors, to increase interindividual and intrageneration variability of neural and behavioral endpoints, while other socioenvironmental factors can provide cross-generation stability.

Concluding Remarks

As we have seen above, stable environmental conditions can have a crucial role in the ontogenetic development and phylogenetic inheritance of adaptive behavioral traits. In addition, in the interplay between internal and external factors that stabilize selectively advantageous behavioral traits, in some cases what is genetically selected for and inherited is the ability to quickly acquire or learn adaptive behaviors, whereas the actual content of the behavior thus acquired may depend on sex-differentiated environmental processes.

What does all this mean for the claims that, in humans, adaptive sex-linked predispositions are directly and stably mediated by biological sex, and, therefore, will manifest at the population level over a wide range of socioenvironmental conditions? Several important features of humans deserve consideration in light of the insights presented above.

The inheritance of a rich, cumulative culture and an unprecedented capacity for social learning have been taken to explain how human populations have been able to successfully thrive and reproduce in such a wide range of vastly different environments [49]. We expand on this to note that humans reliably inherit physical markers of their biological sex and, notably, some socialization practices that are related to marking and emphasizing sex categories with gender labels, such as clothing, hair style, pronouns, and name (gender presentation). From an early age, these gender categories affect children's social learning, for example, in the form of preferences for novel items modeled by children of the same gender [38,50]. Our offspring also undergo the most extensive and elaborate period of childhood socialization of any species. This takes place in the context of a cultural inheritance that reliably includes gender constructions: stereotypes, norms, expectations, values, laws, customs, rituals, role models, and practices relating to maleness and femaleness (an elaborated documentation of the many sociocultural processes involved is provided in the biosocial construction model [51]). These multiple sources of gender socialization create stability through redundancy.

Together, all these sociocultural factors result in both short- and long-term effects of sex categorization on the development of skills, attitudes, experiences, and, of course, the brain, mediated by gender socialization, including self-socialization [51,52]. Notably, some of these sociocultural factors affect components of biological sex, which may, in turn, affect the development of behavioral and neural endpoints [41,51,53]. Recent research in social endocrinology, for instance, demonstrates the effects of gendered experiences and roles on testosterone level ([54–56]; and see Outstanding Questions).

In short, human developmental systems thus provide extensive cultural, behavioral, and environmental mechanisms for the transmission of sex-linked adaptive traits and to a much higher degree than any other species. This transmission, in turn, (re)produces to a more or less faithful degree the cultural conditions to enable transfer to the next generation. Thus, this view

Outstanding Questions

For any particular sex-linked behavioral trait in a given species, what are the causally relevant nongenetic features of the developmental system that influence its development, form, and expression? To study this, one needs to study the trait under different genetic (e.g., in different strains), developmental, and environmental conditions.

How are such causally relevant nongenetic features transmitted across generations and between members of the same generation?

Do other species, particularly other primates, display sex-linked imitation and social learning?

How does sex-linked morphology influence the behavior of individuals and their conspecifics?

How do causally relevant nongenetic features of the developmental system interact with genetic and hormonal mechanisms, including sex-linked mechanisms?

can account for both the considerable interindividual variability in sex-linked behaviors and the remarkable stability of gender as a social system. The wealth of environmental mechanisms should challenge a priori assumptions that, for any particular trait, it is biological sex, via direct effects on the brain, that does the heavy lifting when it comes to cross-generation transfer. Moreover, the extensive nature of the environmental factors involved in the development of sex-linked patterns of behavior means that many relevant aspects of the environment have to change for these patterns to significantly shift at the population level. However, a final important point of difference between ourselves and other species is our capacity to transform our material and cultural developmental systems. As history has shown, sufficient cultural change can produce remarkable changes in sex-linked patterns.

References

1. Laland, K. and Brown, G. (2011) *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour.* (2nd edn), Oxford University Press
2. Buss, D.M. and Schmitt, D.P. (1993) Sexual strategies theory: an evolutionary perspective on human mating. *Psychol. Rev.* 100, 204–232
3. Geary, D. (2010) *Male, Female: The Evolution of Human Sex Differences,* American Psychological Association
4. Kennair, L.E.O. *et al.* (2016) Sexual regret: tests of competing explanations of sex differences. *Evol. Psychol.* Published online December 26, 2016. http://dx.doi.org/10.1177/1474704916682903
5. Herbert, J. (2015) *Testosterone: Sex, Power, and the Will to Win,* Oxford University Press
6. Fine, C. and Rush, E. (2016) "Why does all the girls have to buy pink stuff?" The ethics and science of the gendered toy marketing debate. *J. Bus. Ethics* Published online February 24, 2016. http://dx.doi.org/10.1007/s10551-016-3080-3
7. Dupré, J. (2001) *Human Nature and the Limits of Science,* Clarendon Press
8. Fausto-Sterling, A. (1992) *Myths of Gender: Biological Theories about Women and Men.* (2nd edn), Basic Books
9. Hrdy, S.B. (1986) Empathy, polyandry, and the myth of the coy female. In *Feminist Approaches to Science* (Bleier, R., ed.), pp. 131–159, Pergamon Press
10. Pedersen, W.C. *et al.* (2002) Evolved sex differences in the number of partners desired? The long and the short of it. *Psychol. Sci.* 13, 157–161
11. Einon, D. (1998) How many children can one man have? *Evol. Hum. Behav.* 19, 413–426
12. Jordan-Young, R. (2010) *Brain Storm: The Flaws in the Science of Sex Differences,* Harvard University Press
13. Fine, C. (2010) *Delusions of Gender: How Our Minds, Society, and Neurosexism Create Difference,* Norton
14. Grossi, G. and Fine, C. (2012) The role of fetal testosterone in the development of "the essential difference" between the sexes: some essential issues. In *Neurofeminism: Issues at the Intersection of Feminist Theory and Cognitive Science* (Bluhm, R. *et al.*, eds), pp. 73–104, Palgrave Macmillan
15. Eagly, A. and Wood, W. (2013) The nature-nurture debates: 25 years of challenges in understanding the psychology of gender. *Perspect. Psychol. Sci* 8, 340–357
16. Dupré, J. (2008) Against maladaptationism: or what's wrong with evolutionary psychology? In *Knowledge as Social Order: Rethinking the Sociology of Barry Barnes* (Mazzotti, M., ed.), pp. 165–180, Ashgate

17. Jablonka, E. and Lamb, M.J. (2014) *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life.* (2nd edn), MIT Press
18. Carroll, S. (2008) Evo-devo and an expanding evolutionary synthesis: a genetic theory of morphological evolution. *Cell* 134, 25–36
19. Müller, G. (2007) Evo-devo: extending the evolutionary synthesis. *Nat. Rev. Genet.* 8, 943–949
20. Gilbert, S. and Epel, D. (2015) *Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution,* Sinauer Associates Inc.
21. Oyama, S. (2000) *The Ontogeny of Information: Developmental Systems and Evolution,* Duke University Press
22. Oyama, S. *et al.* (2001) *Cycles of Contingency: Developmental Systems and Evolution,* MIT Press
23. Gottlieb, G. (1997) *Synthesizing Nature and Nurture: The Prenatal Roots of Experience,* Erlbaum
24. Berger, J. *et al.* (2001) Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291, 1036–1039
25. Blumberg, M. (2005) *Basic Instinct: The Genesis of Behavior,* Thunder's Mouth Press
26. Ronca, A. and Alberts, J. (2000) Effects of prenatal spaceflight on vestibular responses in neonatal rats. *J. Appl. Physiol.* 89, 2318–2324
27. Griffiths, P.E. (2002) What is innateness? *Monist* 85, 70–85
28. McCarthy, M.M. and Arnold, A.P. (2011) Reframing sexual differentiation of the brain. *Nat. Neurosci.* 14, 677–683
29. de Vries, G. and Södersten, P. (2009) Sex differences in the brain: the relation between structure and function. *Horm. Behav.* 55, 589–596
30. McCarthy, M. *et al.* (2009) New tricks by an old dogma: mechanisms of the Organizational/Activational Hypothesis of steroid-mediated sexual differentiation of brain and behavior. *Horm. Behav.* 55, 655–665
31. Arnold, A.P. and Chen, X. (2009) What does the "four core genotypes" mouse model tell us about sex differences in the brain and other tissues? *Front. Neuroendocrinol.* 30, 1–9
32. Barker, G. (2015) *Beyond Biofatalism: Human Nature for an Evolving World,* Columbia University Press
33. Cahill, L. (2014) Equal ≠ the same: sex differences in the human brain. *Cerebrum* 2014, 5
34. Joel, D. (2011) Male or female? Brains are intersex. *Front. Integr. Neurosci.* 5, 57
35. Joel, D. *et al.* (2015) Sex beyond the genitalia: the human brain mosaic. *Proc. Natl. Acad. Sci. U. S. A.* 112, 15468–15473

36. Maynard Smith, J. (1978) *The Evolution of Sex,* Cambridge University Press

37. Dupré, J. (2014) The role of behaviour in the recurrence of biological processes. *Biol. J. Linn. Soc. Lond.* 112, 306–314

38. Hines, M. *et al.* (2016) Prenatal androgen exposure alters girls' responses to information indicating gender-appropriate behaviour. *Philos. Trans R. Soc. Lond. B Biol. Sci.* 371, 20150125

39. Moore, C.L. (1984) Maternal contributions to the development of masculine sexual behavior in laboratory rats. *Dev. Psychobiol.* 17, 347–356

40. Moore, C.L. *et al.* (1992) Maternal stimulation affects the number of motor neurons in a sexually dimorphic nucleus of the lumbar spinal cord. *Brain Res.* 572, 52–56

41. Joel, D. and McCarthy, M.M. (2016) Incorporating sex as a biological variable in neuropsychiatric research: Where are we now and where should we be? *Neuropsychopharmacology* 42, 379–385

42. de Vries, G. and Forger, N. (2015) Sex differences in the brain: a whole body perspective. *Biol. Sex Differ.* 6, 15

43. Kendrick, K.M. *et al.* (1998) Mothers determine sexual preferences. *Nature* 395, 229–230

44. Seay, B. *et al.* (1964) Maternal behavior of socially deprived rhesus monkeys. *J. Abnorm. Soc. Psychol.* 69, 345–354

45. Rosenblatt, J.S. (1967) Nonhormonal basis of maternal behavior in the rat. *Science* 156, 1512–1513

46. Gray, R. (1997) "In the belly of the monster": feminism, developmental systems, and evolutionary explanations. In *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers* (Gowaty, P.A., ed.), pp. 385–413, Springer

47. Fine, C. (2017) *Testosterone Rex: Myths of Sex, Science, and Society,* Norton

48. Dupré, J. (2016) Postgenomic perspectives on sex and gender. In *How Biology Shapes Philosophy: New Foundations for Naturalism* (Smith, D., ed.), pp. 227–246, Cambridge University Press

49. Henrich, J. and McElreath, R. (2003) The evolution of cultural evolution. *Evol. Anthropol.* 12, 123–135

50. Shutts, K. *et al.* (2010) Social categories guide young children's preferences for novel objects. *Dev. Sci.* 13, 599–610

51. Wood, W. and Eagly, A.H. (2012) Biosocial construction of sex differences and similarities in behavior. *Adv. Exp. Soc. Psychol.* 46, 55–123

52. Fausto-Sterling, A. (2012) *Sex/gender: Biology in a Social World,* Routledge

53. van Anders, S. (2014) Comment: the social neuroendocrinology example: Incorporating culture resolves biobehavioral evolutionary paradoxes. *Emot. Rev.* 6, 256–257

54. van Anders, S.M. *et al.* (2015) Effects of gendered behavior on testosterone in women and men. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13805–13810

55. Gettler, L.T. *et al.* (2011) Longitudinal evidence that fatherhood decreases testosterone in human males. *Proc. Natl. Acad. Sci. U. S. A.* 108, 16194–16199

56. Muller, M.N. *et al.* (2009) Testosterone and paternal care in East African foragers and pastoralists. *Proc. R. Soc. Lond. B: Biol. Sci.* 276, 347–354

57. Kaiser, A. (2015) Re-conceptualizing "sex" and "gender" in the human brain. *Z. Psychol.* 220, 130–136