

1 **Sex-Linked Behavior: Evolution, Stability, and Variability**

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15 **KEYWORDS:** sex; gender; variability; evolution; adaptive traits; sex roles

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17 **ABSTRACT:**

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

1 **SEX, BRAINS, AND EVOLUTION**

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

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

22 Another major theme has been the role of nature and nurture in the development of sex-
23 linked behavioral traits (see [15]). Although the long-standing nature-nurture debate typically
24 concerns the role of genes and environment in the development of behavioral traits in the
25 lifetime of an individual (i.e., ontogeny), our focus here, however, is a discussion of the
26 relative contributions of genes and environment to the development and transfer of traits
27 across generations (i.e., phylogeny). Specifically, we focus on a common assumption not
28 always made explicit: that sex-linked adaptive traits persist across time and culture because
29 they are passed on via inherited **biological sex**. That is, proximal mechanisms of genetic and
30 hormonal sex, ultimately shaped by the differential reproductive challenges of ancestral
31 males and females, affect brain and behavior in ways that predispose even contemporary
32 Western women and men – in very different conditions from their ancestors – to the same

1 sex-linked behaviors and roles. In other words, it is assumed implicitly or otherwise that the
2 cross-generational transmission of traits is largely mediated by genetics, with the
3 environment being a source of variability in the development – or ontogeny – of the
4 behavioral phenotype in each individual, and a source of selective pressure on genes. Given
5 sufficient time, this selective pressure can drive changes in sex-linked traits, but since
6 stabilized evolutionary change is thought to require the fixation of changes to the genome,
7 only very long periods of consistent environmental influence can achieve genuine
8 evolutionary change. The different time scales of changes to the environment and to the
9 genome imply that the genome is largely responsible for the stable and the evolved, while the
10 effects of the environment give rise to opportunistic and transitory influences on ontogeny
11 [16].

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

18

19 **THE ROLE OF THE ENVIRONMENT IN THE EVOLUTION OF BEHAVIORAL** 20 **TRAITS**

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

27 In parallel, there has been increasing criticism of mainstream evolutionary theory, the so-
28 called *Modern Synthesis*, for overlooking the importance of development, and for assuming,
29 implicitly or explicitly, that developmental outcomes are predetermined by genes. The
30 disregard of the exact processes by which developmental outcomes are achieved has been
31 criticized from various directions, especially from **evolutionary developmental biology** [18,
32 19], **ecological evolutionary developmental biology** [20], and **developmental systems**

1 **theory** [21, 22]. The latter two perspectives, in particular, point to an important, yet often
2 neglected, factor in ensuring accurate transfer of traits across generations: the environmental
3 aspects of the developmental system. Every organism inherits a rich, dynamic developmental
4 system comprising both genetic and extra-genetic resources that contribute to developmental
5 processes from conception to death. Environmental aspects of the developmental system
6 include, for example, local ecology, other individuals, and social and cultural constructions
7 (from bee hives and beaver dams, to schools, the law, and literature).

8 Consider, for example, mallard ducks' apparently 'instinctual' preference on hatching for
9 vocalizations of their own species. Remarkably, this adaptive behavioral trait depends on
10 auditory stimulation in the egg: mallard ducklings whose own pre-hatching vocalizations are
11 muted, and are put in auditory isolation, do not show the usual robust preference for the
12 maternal mallard call over the call of a chicken [23]. Likewise, the 'typical' adaptive
13 behavioral responses of moose to the sounds and smells of their predators – vigilance,
14 aggressive responses, and departure from a feeding site – are greatly reduced in populations
15 in which those predators have recently disappeared, and appear to be rapidly acquired by
16 mothers whose calves have been killed by a predator [24].

17 These examples (for fuller descriptions of these and numerous others, see [25]) illustrate the
18 important point that genetic material isn't the only stable inherited resource for development:
19 a mallard duck reliably inherits a pre-hatching environment that includes the vocalizations of
20 itself, mother, and siblings; a moose reliably inherits an ecology replete with stimuli
21 correlated with predators, as well as a mother who has learned to respond in particular ways
22 to those cues.

23 Thus, despite the widely assumed conceptual link between 'inherited' and 'genetic', the
24 reliable development of adaptive behaviors can be contingent on specific environmental
25 resources. Where the necessary environmental factors are stably reproduced, generation
26 after generation, so too will be the (re-)production of the adaptive trait in
27 each generation. The more nearly the environmental factors are sufficient for the
28 development of a trait, the more what will be genetically selected for and inherited is the
29 ability to quickly acquire or learn adaptive behaviors rather than the behaviors themselves
30 [17].

31 Another example of this principle is the rat reflex to right itself when dropped on its back into
32 water. The development of this reflex, it turns out, is facilitated by experience in gravity. So,

1 one day old rats mostly gestated in space then brought down to Earth are half as likely to
2 attempt to right themselves when placed in a water bath, although they do quickly learn to do
3 so [26].

4 This last example nicely illustrates Griffiths' [27] point that (pp. 74-5): "Selection cannot
5 favour a trait that compensates for the loss of a developmental input that is, as a matter of
6 fact, reliably available. Evolution does not anticipate future contingencies." As a result,
7 stability of environmental factors over generations not only guarantees the reliable
8 reproduction of a trait across generations, but also removes any selective pressure for the
9 development of parallel stabilizing genetic factors. Only regular space travel would provide
10 any selective pressure for rats to evolve genetic determination of the water reflex.
11 Genetically determined traits may also be lost when some reliable feature of the environment
12 makes them unnecessary. One such example, provided in [27], is the loss of the ability to
13 synthesize vitamin C in primates, as this vitamin is readily available in their fruit-based diet.

14 Whereas in some of the examples provided above, the stable environmental factor was a
15 fixed aspect of the environment (e.g., gravity), in other examples the stable environmental
16 factor consisted of aspects of the environment that are heavily dependent on the behavior of
17 organisms (e.g., the vocalizations of mallard ducks; the behavior of the mother moose and its
18 predators). In the latter case, the fact that the environment is (ontogenetically) crucial in the
19 development of behavior and that relevant aspects of the environment can be reliably
20 generated by the behavior of organisms, points to a phylogenetic pathway that is quite
21 distinct from the familiar genetic one. Thus, as others have argued, we suggest that the
22 currently dominant view, which focuses on genes as a source of cross-generation stability,
23 should be extended to the view that many behavioral traits are stabilized by the interplay
24 between intrinsic (e.g., genetic, epigenetic) and extrinsic environmental factors [17]. For
25 some traits this balance leans more toward the genetic side, whereas for others it leans more
26 toward the environment side. Note that also in the latter case, genetic inheritance is assumed
27 to furnish critical neural capacity for acquisition of the trait [17]. The important aspect of our
28 argument is that, to the extent that the "content" of the trait is provided by stabilizing
29 environmental factors, there will not be parallel stabilizing genetic factors. In this we add to
30 previous models, such as the biosocial construction model , the possibility that evolved
31 environments do not necessarily augment genetic inheritance, but can sometimes obviate the
32 necessity for the development of parallel genetic mechanisms.

1

2

3 **WHAT ABOUT SEX-LINKED ADAPTIVE BEHAVIORS?**

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

20 It has always been acknowledged, of course, that the biological components of sex interact
21 with environmental factors. However, we think it reasonable to suggest that these sex-by-
22 environment interactions have implicitly or explicitly been understood to be either
23 *conservative* or *additive* in nature. In conservative interaction [32], internal (biological sex)
24 and external (environmental) causes interact, but in such a way that the internal causes tend to
25 keep the phenotype to a “preferred” state, with strong external changes required to modify
26 this (for an example of an expression of this view with regards to sex differences in brain and
27 behavior, see [33]). Thus, in conservative interaction, biological sex is assumed to stabilize a
28 particular sex-linked phenotype across a wide range of environmental conditions. In additive
29 interaction, a particular environmental factor will have a similar effect on both sexual
30 genotypes. For example, an environmental factor (like a predator attack or food shortage)
31 would influence brain and behavior in both females and males to the same degree (e.g.,
32 reduce neuronal density), meaning that a similar relative sex difference (e.g., male > female)

1 will be observed across the entire range of stressful environments. In contrast to conservative
2 interaction, additive interactions may result in overlap of phenotypes between females and
3 males at the population level. This is because the phenotypes of some males under some
4 environmental conditions may be similar to the phenotypes of some females under other
5 environmental conditions (e.g., if the neuronal density in a specific nucleus is higher in males
6 than in females, and is reduced by stress in both females and males, then neuronal density in
7 stressed males may be similar to that found in non-stressed females).

8 However, it is now apparent that some of the interactions between sex and the environment
9 are what Barker describes as *radical* [32], that is, the effects of an environmental condition
10 on the brain may be different and even opposite in females and males. As a result, what is
11 typical of females under some environmental conditions may be typical of males under other
12 environmental conditions (reviewed in [34]). Moreover, these complex interactions between
13 sex and the environment are region-specific [35] thus giving rise to brains comprised of
14 unique ‘mosaics’ of features, some in a form that, at the population level, is more common in
15 males than in females (i.e., ‘masculine’ form) and some in a form that, at the population
16 level, is more common in females than in males (i.e., ‘feminine’ form) [34, 35]. Such
17 mosaicism was recently demonstrated in human brains: analysis of structural characteristics
18 in over 1400 brains from four datasets revealed that mosaic brains were much more common
19 than brains with only ‘feminine’ or only ‘masculine’ features [36]. Similarly, although at the
20 population level there are differences between women and men in a variety of behavioral and
21 psychological characteristics, most humans possess a mosaic of both feminine and masculine
22 characteristics, rather than segregating into two categories, or aligning on a masculinity-
23 femininity continuum [36].

24 Conservative sex-by-environment interactions would be consistent with the implicitly
25 assumed role for biological sex as a source of stability in brain structure and function. By
26 contrast, the existence of radical interactions and of mosaic brains suggests biological sex as
27 a source of inter-individual variability in brain structure and function. This may be seen as an
28 extension of the hypothesized role of sexual reproduction in increasing inter-individual
29 genetic variation ([37]) to the level of brain and behavior.

30 That biological sex is a potential source of variability for at least some sex-linked neural and
31 behavioral endpoints gives us even greater reason to consider the possibility that
32 environmental factors are sometimes a source of stability for sex-linked behavioral traits, so

1 long as the necessary resources are reliably reproduced and inherited by each generation [38].
2 Differentiation of behavior by sex, whether complete or partial, would therefore require either
3 a sex-differentiated predisposition to acquire or learn an adaptive trait, and/or a reliably sex-
4 differentiated environment. Evidence for a mechanism of the former kind may be provided by
5 the recent finding that girls exposed to high levels of androgens in utero showed a lower
6 tendency to mimic the behavior of older girls, compared with girls exposed to typical levels
7 of androgens [39].

8 With regards to the second potential mechanism, one set of reliably inherited factors that can
9 lead to stable and reproducible sex-differentiated environments are phenotypic markers of
10 biological sex, such as appearance, size, strength and smell. These are reliably inherited in
11 ways that are largely, though by no means wholly, insensitive to environmental variables.
12 These phenotypic markers can influence both the individual's behavior and others' responses
13 to them, and these effects can in turn affect the development of brain and behavior. Consider,
14 for example, evidence that mother rats are attracted to the higher level of testosterone in the
15 urine of their male, compared with female, rat pups. This stimulates higher intensity
16 anogenital licking, which, in turn, contributes to sexual differentiation of specific brain
17 regions and of sexual behavior [40, 41]. Recognition of such indirect effects of sex on
18 development, via sex-differentiated experiences, is now growing [42, 43].

19 Recognition of the role of stable experiential factors in the inheritance of adaptive behavioral
20 traits helps to explain examples in which sex-linked traits fail to develop when environmental
21 conditions change. Take, for instance, the finding that cross-species-fostered sheep and goat
22 newborn males develop robust and persistent sexual preferences for mates of the cross-
23 fostered species [44]. Likewise, contrary to the notion of a 'maternal instinct', adequate care
24 of a firstborn by female Rhesus monkeys depends on early social experience [45]. Or
25 consider a study that found that, when put in close contact with pups, male Charles River
26 strain rats showed 'maternal' behavior within a week [46].

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

1 neural or behavioral endpoint [47], beyond those necessary for learning or acquiring the
2 traits. As a consequence, ‘sexual nature’ can be eliminated or even reversed, when relevant
3 features of the external developmental context change [48, 49].

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

11

12 **CONCLUDING REMARKS**

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

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

23 The inheritance of a rich, cumulative culture and an unprecedented capacity for social
24 learning, has been taken to explain how human populations have been able to successfully
25 thrive and reproduce in such a wide range of vastly different environments [50]. We expand
26 on this to note that humans reliably inherit physical markers of their biological sex and,
27 notably, some socialization practices which are related to marking and emphasizing sex
28 categories with gender labels, such as clothing, hair-style, pronouns, and name (gender
29 presentation). From an early age these gender categories affect children’s social learning, for
30 example, in the form of preferences for novel items modeled by children of the same gender
31 [39, 51]. Our offspring also undergo the most extensive and elaborate period of childhood

1 socialization of any species. This takes place in the context of a cultural inheritance that
2 reliably includes gender constructions: stereotypes, norms, expectations, values, laws,
3 customs, rituals, role models, and practices relating to maleness and femaleness (an
4 elaborated documentation of the many socio-cultural processes involved is provided in the
5 biosocial construction model [52]). These multiple sources of gender socialization create
6 stability through redundancy.

7 Together, all these sociocultural factors result in both short- and long-term effects of sex
8 categorization on the development of skills, attitudes, experiences, and, of course, the brain,
9 mediated by gender socialization, including self-socialization [52, 53]. Notably, some of
10 these sociocultural factors affect components of biological sex, which may, in turn, affect the
11 development of behavioral and neural endpoints [42, 52, 54]. Recent research in social
12 endocrinology, for instance, demonstrates the effects of gendered experiences and roles on
13 testosterone level ([55-57]; and see Outstanding Questions).

14 In short, human developmental systems thus provide extensive cultural, behavioral, and
15 environmental mechanisms for the transmission of sex-linked adaptive traits, and to a much
16 higher degree than any other species. This transmission, in turn, (re-)produces to a more or
17 less faithful degree the cultural conditions to enable transfer to the next generation. This view
18 can thus account for both the considerable inter-individual variability in sex-linked behaviors
19 and the remarkable stability of gender as a social system. The wealth of environmental
20 mechanisms should challenge a priori assumptions that, for any particular trait, it is biological
21 sex, via direct effects on the brain, that does the heavy lifting when it comes to cross-
22 generation transfer. Moreover, the extensive nature of the environmental factors involved in
23 the development of sex-linked patterns of behavior means that many relevant aspects of the
24 environment have to change in order for these patterns to significantly shift at the population
25 level. However, a final important point of difference between ourselves and other species is
26 our capacity to transform our material and cultural developmental systems. And as history
27 has shown, sufficient cultural change can produce remarkable changes in sex-linked patterns.

28

29

GLOSSARY

Androgen receptors: These are present in many body tissues, including the brain. Androgens (a class of steroid hormones that includes testosterone) can bind to a receptor, enabling the regulation of androgen-responsive genes.

Autosomes: Referring to chromosomes other than the X and Y chromosomes.

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

Developmental systems theory (DST): A theoretical lens on development, heredity, and evolution based on a number of 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 (eco-evo-devo): 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 don’t involve changes to the DNA sequence itself.

Evolutionary developmental biology (evo-devo): Traditionally, evolutionary biologists have been concerned with explaining *why* (ultimate cause) a particular trait exists, while developmental biologists explain the *how* (proximate causes). Evo-devo 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

1 are not translated into proteins and may have other functions, though the proportion
2 that do remains controversial. Not all genes are expressed in all cells or at all times.

3
4 **Sex/gender:** An alternative term for either “sex” or “gender” intended to emphasize
5 that comparisons of males and females capture contributions of both **biological sex**,
6 social gender constructions, and their interaction (e.g., [58]). Note that, also captured
7 in such comparisons and interactions, are the effects of variables that correlate with
8 sex, such as size or muscle mass.

9
10 **Sex-linked:** Referring to traits for which average differences are observed between
11 the sexes. Given the overlap between the sexes in behavior, this is a more accurate
12 term than “sex-specific” or “sexually dimorphic”, which imply distinct categories.

13
14 **Symbolic system:** Referring to information sent or received that derives its meaning
15 from socially shared conventions or understandings. The word ‘evolution’, the symbol
16 “=”, and pink packaging on a toy are all examples of symbolic information.

1 **REFERENCES:**

- 2 1. Laland, K. and Brown, G. (2011) *Sense and nonsense: Evolutionary perspectives on*
3 *human behaviour*, 2nd edn., Oxford University Press.
- 4 2. Buss, D.M. and Schmitt, D.P. (1993) *Sexual strategies theory: an evolutionary perspective*
5 *on human mating*. *Psychol Rev* 100 (2), 204-232.
- 6 3. Geary, D. (2010) *Male, female: The evolution of human sex differences*, American
7 *Psychological Association*.
- 8 4. Kennair, L.E.O. et al. (2016) *Sexual regret: Tests of competing explanations of sex*
9 *differences*. *Evol Psychol*, DOI: 10.1177/1474704916682903.
- 10 5. Herbert, J. (2015) *Testosterone: Sex, power, and the will to win*, Oxford University Press.
- 11 6. Fine, C. and Rush, E. (2016) “Why Does all the Girls have to Buy Pink Stuff?” *The Ethics*
12 *and Science of the Gendered Toy Marketing Debate*. *J Bus Ethics*, DOI: 10.1007/s10551-
13 016-3080-3.
- 14 7. Dupré, J. (2001) *Human nature and the limits of science*, Clarendon Press.
- 15 8. Fausto-Sterling, A. (1992) *Myths of gender: Biological theories about women and men*,
16 *Second edn.*, Basic Books.
- 17 9. Hrdy, S.B. (1986) *Empathy, polyandry, and the myth of the coy female*. In *Feminist*
18 *approaches to science* (Bleier, R. ed), Pergamon Press.
- 19 10. Pedersen, W.C. et al. (2002) *Evolved sex differences in the number of partners desired?*
20 *The long and the short of it*. *Psychol Sci* 13 (2), 157-161.
- 21 11. Einon, D. (1998) *How many children can one man have?* *Evol Hum Behav* 19 (6), 413-
22 426.
- 23 12. Jordan-Young, R. (2010) *Brain storm: The flaws in the science of sex differences*,
24 *Harvard University Press*.
- 25 13. Fine, C. (2010) *Delusions of gender: How our minds, society, and neurosexism create*
26 *difference*, Norton.
- 27 14. Grossi, G. and Fine, C. (2012) *The role of fetal testosterone in the development of “the*
28 *essential difference” between the sexes: Some essential issues*. In *Neurofeminism: Issues at*
29 *the intersection of feminist theory and cognitive science* (Bluhm, R. et al. eds), pp. 73-104,
30 *Palgrave Macmillan*.
- 31 15. Eagly, A. and Wood, W. (2013) *The nature-nurture debates: 25 years of challenges in*
32 *understanding the psychology of gender*. *Perspect Psychol Sci* 8 (3), 340-357.

- 1 16. Dupré, J. (2008) Against maladaptationism: or What's wrong with Evolutionary
2 Psychology? In Knowledge as social order: Rethinking the sociology of Barry Barnes
3 (Mazzotti, M. ed), pp. 165-180, Ashgate.
- 4 17. Jablonka, E. and Lamb, M.J. (2014) Evolution in four dimensions: Genetic, epigenetic,
5 behavioral, and symbolic variation in the history of life, Revised edition edn., MIT Press.
- 6 18. Carroll, S. (2008) Evo-devo and an expanding evolutionary synthesis: A genetic theory of
7 morphological evolution. *Cell* 134 (1), 25-36.
- 8 19. Müller, G. (2007) Evo-devo: Extending the evolutionary synthesis. *Nat Rev Genet* 8 (12),
9 943-949.
- 10 20. Gilbert, S. and D, E. (2015) Ecological developmental biology: The environmental
11 regulation of development, health, and evolution, Sinauer Associates, Inc.
- 12 21. Oyama, S. (2000) The ontogeny of information: Developmental systems and evolution,
13 Duke University Press.
- 14 22. Oyama, S. et al. (2001) Cycles of contingency: Developmental systems and evolution,
15 MIT Press.
- 16 23. Gottlieb, G., Synthesizing nature and nurture: The prenatal roots of experience, Erlbaum,
17 Hillsdale, NJ, 1997.
- 18 24. Berger, J. et al. (2001) Recolonizing carnivores and naïve prey: Conservation lessons
19 from Pleistocene extinctions. *Science* 291 (5506), 1036-1039.
- 20 25. Blumberg, M. (2005) Basic instinct: The genesis of behavior, Thunder's Mouth Press.
- 21 26. Ronca, A. and Alberts, J. (2000) Effects of prenatal spaceflight on vestibular responses in
22 neonatal rats. *J Appl Physiol* 89, 2318-2324.
- 23 27. Griffiths, P.E. (2002) What is innateness? *Monist* 85 (1), 70-85.
- 24 28. McCarthy, M.M. and Arnold, A.P. (2011) Reframing sexual differentiation of the brain.
25 *Nat Neurosci* 14 (6), 677-683.
- 26 29. de Vries, G. and Södersten, P. (2009) Sex differences in the brain: The relation between
27 structure and function. *Horm Behav* 55 (5), 589-596.
- 28 30. McCarthy, M. et al. (2009) New tricks by an old dogma: Mechanisms of the
29 Organizational/Activational Hypothesis of steroid-mediated sexual differentiation of brain
30 and behavior. *Horm Behav* 55, 655-665.
- 31 31. Arnold, A.P. and Chen, X. (2009) What does the “four core genotypes” mouse model tell
32 us about sex differences in the brain and other tissues? *Front Neuroendocrin* 30 (1), 1-9.
- 33 32. Barker, G. (2015) Beyond biofatalism: Human nature for an evolving world, Columbia
34 University Press.

- 1 33. Cahill, L., *Equal ≠ the same: Sex differences in the human brain*, Cerebrum, The Dana
2 Foundation, 2014.
- 3 34. Joel, D. (2011) Male or female? Brains are intersex. *Front Integr Neurosci* 5:57.
- 4 35. McCarthy, M.M. and Arnold, A.P. (2011) Reframing sexual differentiation of the brain.
5 *Nat Neurosci* 14 (6), 677-683.
- 6 36. Joel, D. et al. (2015) Sex beyond the genitalia: The human brain mosaic. *Proc Natl Acad*
7 *Sci USA* 112 (50), 15468-15473.
- 8 37. Maynard Smith, J. (1978) *The evolution of sex*, Cambridge University Press.
- 9 38. Dupré, J. (2014) The role of behaviour in the recurrence of biological processes. *Biol J*
10 *Linn Soc Lond* 112, 306-314.
- 11 39. Hines, M. et al. (2016) Prenatal androgen exposure alters girls' responses to information
12 indicating gender-appropriate behaviour. *Philos T Roy Soc B*, 371 (1688).
- 13 40. Moore, C.L. (1984) Maternal contributions to the development of masculine sexual
14 behavior in laboratory rats. *Dev Psychobiol* 17 (4), 347-356.
- 15 41. Moore, C.L. et al. (1992) Maternal stimulation affects the number of motor neurons in a
16 sexually dimorphic nucleus of the lumbar spinal cord. *Brain Res* 572 (1), 52-56.
- 17 42. Joel, D. and McCarthy, M.M. (2016) Incorporating sex as a biological variable in
18 neuropsychiatric research: Where are we now and where should we be?
19 *Neuropsychopharmacol*, DOI: 10.1038/npp.2016.79
- 20 43. de Vries, G. and Forger, N. (2015) Sex differences in the brain: A whole body
21 perspective. *Biol Sex Differ* 6 (1), 15.
- 22 44. Kendrick, K.M. et al. (1998) Mothers determine sexual preferences. *Nature* 395 (6699),
23 229-230.
- 24 45. Seay, B. et al. (1964) Maternal behavior of socially deprived rhesus monkeys. *J Abnorm*
25 *Soc Psychol* 69 (4), 345-354.
- 26 46. Rosenblatt, J.S. (1967) Nonhormonal basis of maternal behavior in the rat. *Science* 156
27 (3781), 1512-1513.
- 28 47. Gray, R. (1997) "In the belly of the monster": Feminism, developmental systems, and
29 evolutionary explanations. In *Feminism and evolutionary biology: Boundaries, intersections*
30 *and frontiers* (Gowaty, P.A. ed), pp. 385-413, Springer.
- 31 48. Fine, C. (2017) *Testosterone Rex: Myths of sex, science, and society*, Norton.
- 32 49. Dupré, J. (2016) Postgenomic perspectives on sex and gender. In *How biology shapes*
33 *philosophy: New foundations for naturalism* (Smith, D. ed), Cambridge University Press.

- 1 50. Henrich, J. and McElreath, R. (2003) The evolution of cultural evolution. *Evol Anthropol*
2 12 (3), 123-135.
- 3 51. Shutts, K. et al. (2010) Social categories guide young children's preferences for novel
4 objects. *Developmental Sci* 13 (4), 599-610.
- 5 52. Wood, W. and Eagly, A.H. (2012) Biosocial construction of sex differences and
6 similarities in behavior. *Adv Exp Soc Psychol* 46 (1), 55-123.
- 7 53. Fausto-Sterling, A. (2012) *Sex/gender: Biology in a social world*, Routledge.
- 8 54. van Anders, S. (2014) Comment: The social neuroendocrinology example: Incorporating
9 culture resolves biobehavioral evolutionary paradoxes. *Emot Rev* 6 (3), 256-257.
- 10 55. van Anders, S.M. et al. (2015) Effects of gendered behavior on testosterone in women
11 and men. *Proc Natl Acad Sci USA* 112 (45), 13805-13810.
- 12 56. Gettler, L.T. et al. (2011) Longitudinal evidence that fatherhood decreases testosterone in
13 human males. *Proc Natl Acad Sci USA* 108 (39), 16194-16199.
- 14 57. Muller, M.N. et al. (2009) Testosterone and paternal care in East African foragers and
15 pastoralists. *Proc R Soc Lond B: Biol Sci* 276 (1655), 347-354.
- 16 58. Kaiser, A. (2015) Re-conceptualizing "sex" and "gender" in the human brain. *Zeitschrift*
17 *für Psychologie* 220 (2), 130-136.
- 18