Sex-Linked Behavior: Evolution, Stability, and Variability

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ABSTRACT:

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 socio-environmental conditions, with biological sex fostering intra-generation 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 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 overview, 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 girls' and boys' different preferences are due to sex-linked adaptive predispositions (for review, see [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 long-standing nature-nurture debate typically concerns the role of genes and environment in the development of behavioral traits in the lifetime of an individual (i.e., ontogeny), our focus here, however, is a discussion of the relative contributions of genes and 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 – 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 time scales of changes to the environment and to the genome imply that the genome is largely responsible for the stable and the evolved, while the effects of the environment give rise to opportunistic and transitory influences on ontogeny [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, socio-environmental conditions provide the cross-generational inherited element while biological sex fosters inter-individual 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, mallard ducks' apparently 'instinctual' preference on hatching for vocalizations of their own species. Remarkably, this adaptive behavioral trait depends on auditory stimulation in the egg: mallard ducklings whose own pre-hatching vocalizations are muted, and are put in auditory isolation, do not show the usual robust preference for the 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 isn't the only stable inherited resource for development: a mallard duck reliably inherits a pre-hatching 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 who 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 what will be genetically selected for and inherited is the ability to quickly acquire or learn adaptive behaviors rather than the behaviors themselves [17].

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

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

This last example nicely illustrates Griffiths' [27] point that (pp. 74-5): "Selection cannot favour 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." 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, as 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 consisted of aspects of the environment that are 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 quite 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, 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 stabilizing genetic factors. In this we add to previous models, such as the biosocial construction model , 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 have focused on direct effects of the genetic and hormonal components of sex on brain and behavior in explaining the stability of neural and behavioral endpoints. In this traditional 'organizational-activational' account (for review, see [28]), the chromosome composition (XX or XY) 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 (for review, see [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-by-environment interactions have implicitly or explicitly been understood to be either *conservative* or *additive* in nature. In conservative interaction [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 interaction, biological sex is assumed to stabilize a particular sex-linked phenotype across a wide range of environmental conditions. In additive interaction, a particular environmental factor will have a similar effect on both sexual genotypes. For example, an environmental factor (like 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), 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 interaction, 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 non-stressed 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 [35] thus giving rise to brains comprised of 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) [34, 35]. Such mosaicism was recently demonstrated in human brains: analysis of structural characteristics in over 1400 brains from four datasets revealed that mosaic brains were much more common than brains with only 'feminine' or only 'masculine' features [36]. Similarly, although at the population level there are differences between women and men in a variety of behavioral and psychological characteristics, most humans possess a mosaic of both feminine and masculine characteristics, rather than segregating into two categories, or aligning on a masculinity-femininity continuum [36].

Conservative sex-by-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 inter-individual variability in brain structure and function. This may be seen as an extension of the hypothesized role of sexual reproduction in increasing inter-individual genetic variation ([37]) 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 [38]. Differentiation of behavior by sex, whether complete or partial, would therefore 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 lower tendency to mimic the behavior of older girls, compared with girls exposed to typical levels of androgens [39].

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 [40, 41]. Recognition of such indirect effects of sex on development, via sex-differentiated experiences, is now growing [42, 43].

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 [44]. Likewise, contrary to the notion of a 'maternal instinct', adequate care of a firstborn by female Rhesus monkeys depends on early social experience [45]. Or consider a study that found that, when put in close contact with pups, male Charles River strain rats showed 'maternal' behavior within a week [46].

As these examples illustrate, the typical sex-linked outcome for individuals at a particular stage in the life-cycle 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 [47], 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 [48, 49].

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 socio-environmental factors, to increase inter-individual and intra-generation variability of neural and behavioral endpoints, while other socio-environmental factors can provide cross-generation stability.

CONCLUDING REMARKS

As we've seen in the foregoing, stable environmental conditions can play 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 will therefore manifest at the population level over a wide-range of socio-environmental conditions? Several important features of humans deserve consideration in light of these insights.

The inheritance of a rich, cumulative culture and an unprecedented capacity for social learning, has been taken to explain how human populations have been able to successfully thrive and reproduce in such a wide range of vastly different environments [50]. We expand on this to note that humans reliably inherit physical markers of their biological sex and, notably, some socialization practices which 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 [39, 51]. 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 socio-cultural processes involved is provided in the biosocial construction model [52]). 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 [52, 53]. Notably, some of these sociocultural factors affect components of biological sex, which may, in turn, affect the development of behavioral and neural endpoints [42, 52, 54]. Recent research in social endocrinology, for instance, demonstrates the effects of gendered experiences and roles on testosterone level ([55-57]; 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. This view can thus account for both the considerable inter-individual 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 in order 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. And as history has shown, sufficient cultural change can produce remarkable changes in sex-linked patterns.

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

are not translated into proteins and may have other functions, though 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., [58]). Note that, also captured in such comparisons and interactions, are the effects of variables that correlate with sex, such as size or muscle mass.

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.

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