Neuroscience and Biobehavioral Reviews 125 (2021) 26–32

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

Now you see them, and now you don't: An evolutionarily informed model of environmental influences on human sex differences

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ARTICLE INFO

Keywords:
Sex differences
Sexual selection
Cognition
Condition-dependent
Stressor

ABSTRACT

The contributions of evolutionary processes to human sex differences are vigorously debated. One counterargument is that the magnitude of many sex differences fluctuates from one context to the next, implying an environment origin. Sexual selection provides a framework for integrating evolutionary processes and environmental influences on the origin and magnitude of sex differences. The dynamics of sexual selection involve competition for mates and discriminative mate choices. The associated traits are typically exaggerated and condition-dependent, that is, their development and expression are very sensitive to social and ecological conditions. The magnitude of sex differences in sexually selected traits should then be largest under optimal social and ecological conditions and shrink as conditions deteriorate. The basics of this framework are described, and its utility is illustrated with discussion of fluctuations in the magnitude of human physical, behavioral, and cognitive sex differences.

1. Introduction

The existence of human sex differences is no longer debated, at least for some traits, but their origin, magnitude, and practical significance remain areas of contention (Archer, 2019; Hyde, 2005). The variable expression of sex differences across contexts adds to the contention and is often interpreted as evidence for the cultural origin of these differences (Wood and Eagly, 2002). I outline here how an evolutionary perspective helps us to understand these contextual effects and at the same time places the study of human sex differences within the same unifying framework used to study them in nonhuman species, that is, Darwin's (1871) sexual selection (for review see Andersson, 1994). In the following, I provide a brief introduction to sexual selection and condition-dependent traits in nonhuman species and then illustrate how these principles can be used to understand fluctuations in the magnitude of sex differences in human traits.

1.1. Sexual selection

Darwin's (1871) sexual selection provides the evolutionary framework for the study of sex differences and includes competition with members of the same sex over mates (intrasexual competition) and discriminative choice of mating partners (intersexual choice). These dynamics have traditionally focused on male-male competition and female choice but in recent decades it has become clear that female-female competition over access to mates or access to other resources (e.g., high-quality food) is common (Stockley and Bro-Jørgensen, 2011; West-Eberhard, 1983), albeit typically not as intense (e.g., resulting in serious injury) as that found among males of the same species. As with females, males often show discriminative mate choices, especially when they provide some level of investment in offspring (Berglund and Rosenqvist, 2001; Reynolds and Székely, 1997).

The result of competition and mate choices is the elaboration of the traits that contribute to them. One result, as shown in the top set of distributions in Fig. 1, is that sexually selected traits are typically larger or more elaborated (e.g., plumage color) in the sex that is subjected to more intense competition or more exacting mate choices (Janicke et al., 2016). These traits are often physical, such as the mandibles of the male and female beetles (*Chalcosoma atlas*) shown in Fig. 2 but can also include behavioral or cognitive traits. Behavioral traits range from courtship displays to the building of the elaborate wooden structures that male bowerbirds use to attract potential mates (e.g., Borgia, 1985). Birdsong is among the better studied brain and cognitive traits associated with female choice (Ball and Hulse, 1998), as is spatial ability associated with male-male scramble competition (Gaulin, 1992; Jašarević et al., 2012). For the latter, males expand their home range during the breeding season and search for prospective mates that are dispersed throughout the ecology. Males with better navigational

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https://doi.org/10.1016/j.neubiorev.2021.02.020
Received 1 October 2019; Received in revised form 5 August 2020; Accepted 10 February 2021
Available online 17 February 2021
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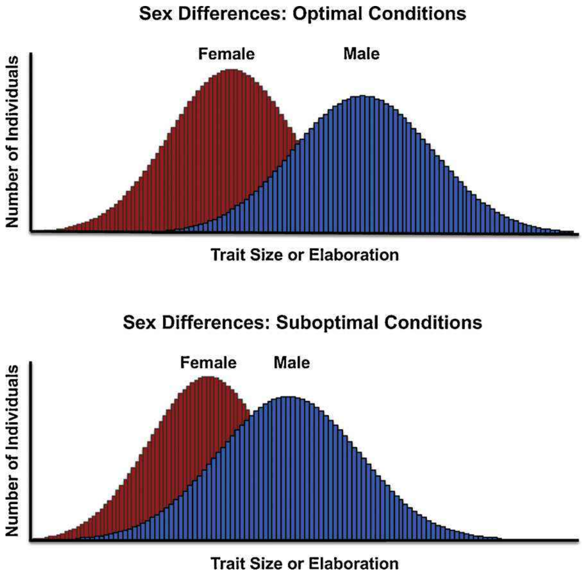

Fig. 1. Sexual selection will result in the evolution of elaborated traits that signal competitive abilities or influence mate choices. The development, maintenance, and expression of these traits are highly sensitive to stressors and thus reveal the individuals' exposure and resilience to them. The top distributions show larger sexually selected traits (blue) in one sex versus the other; or larger sexually selected than naturally selected traits in the same individual. Exposure to stressors has stronger effects on the elaborated trait than the contrast trait, such as the same trait in the other sex (red). Note that it is not well represented in the Figure, but the population variability in the trait of interest will increase under stressful conditions, with some individuals greatly affected and others only mildly affected by stressor exposure.

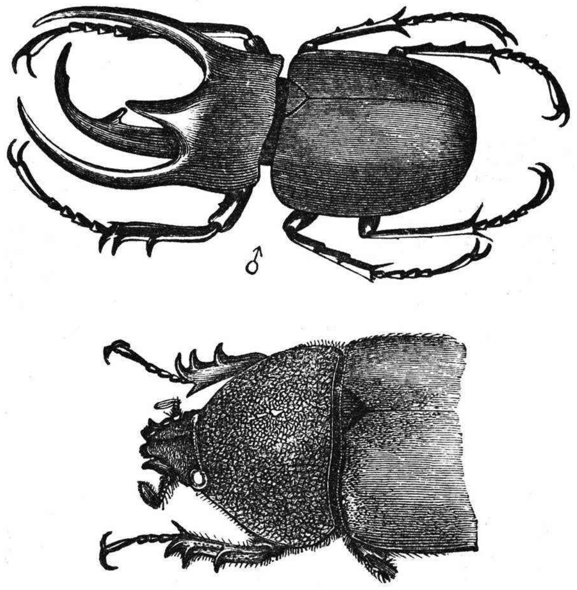

Fig. 2. Male and female beetles (*Chalcosoma atlas*) from *The descent of man, and selection in relation to sex* Vol. I, by C. Darwin (1871), London, John Murray, p. 368. Males compete by searching for mates in trees and hook their mandibles under the wings of competitors and attempt to throw them from the tree.

abilities find more mates and generally have higher reproductive success than their less adventurous peers (Spritzer et al., 2005).

1.2. Condition-dependent traits

The dynamics of competition and choice not only lead to the evolution of sex differences in trait size or degree of elaboration (e.g., plumage color), they also result in a heightened sensitivity of these traits to social and ecological stressors. The basic idea is shown in the bottom set of distributions in Fig. 1, whereby current or developmental exposure to stressors will compromise the development and expression of sexually selected traits more severely than other traits. The result is that sex differences become smaller and more variable than they would be under better conditions. The heightened sensitivity of these traits makes their expression dependent on the condition (e.g., physical health) of the individual and reduces the ability of unfit individuals to bluff in the context of intrasexual competition or cheat in the context of mate choices (Zahavi, 1975). Across species, the most common stressors that compromise these traits are nutritional deficits, parasitic diseases, and chronic social stress (Geary, 2015). Many man-made toxins have similar effects, that is, they compromise sexually selected traits more severely than other traits (e.g., Bortolotti et al., 2003; Jašarević et al., 2011).

The mechanisms underlying the heightened vulnerability of these traits are not yet fully understood but might include the efficiency of mitochondrial functioning (Hill, 2014). Mitochondria are the primary source of cellular energy and thus the common currency for the development and functioning of all biological traits. They are also the source of cell-damaging oxidative stress, and contribute to hormone synthesis, immune functioning and other basic cellular processes (von Schantz et al., 1999; Weinberg et al., 2015). The stressors that typically compromise condition-dependent traits can directly or indirectly compromise one or several aspects of mitochondrial functioning and result in a reduction in cellular energy production (Koch et al., 2017; Picard et al., 2016). On this view, the vulnerability of condition-dependent traits follows directly from their exaggerated size or other elaborations because these require more cellular energy to build, develop, and maintain than do other traits. By analogy, consider that it takes more energy to heat a 300-square-meter house than a 100-square-meter house. A drop in available energy will be noticed first in the larger house and result in a more rapid drop in ambient temperature relative to the smaller one. In fact, if available energy is sufficient for the latter, then a change in energy availability will go unnoticed.

The main point is that any advantages in trait size or elaboration enjoyed by one sex necessarily come with the attendant costs of building, maintaining, and expressing these traits. On the basis of this proposal, conditions with abundant nutritional resources, low disease risk, and muted social competition will result in near maximal trait expression, within any genetic constraints, and large sex differences for sexually selected traits. As these conditions deteriorate, many members of the advantaged sex can no longer build and maintain exaggerated traits and thus the magnitude of any sex difference for these traits will become smaller and the variation among members of the advantaged sex will become larger.

1.3. Human sexual selection

Sex differences in physical size and strength are consistent indicators of male-male competition and a polygynous mating system in mammals (Andersson, 1994). Males of these species also grow more slowly than females, mature at a later age, and have a shorter lifespan (Clutton-Brock and Isvaran, 2007; Leigh, 1995). Human physical and developmental sex differences fit this general pattern (Tanner, 1990), in keeping with an evolutionary history of physical male-male competition. Examination of the likely size differences between our male and female ancestors suggests that intense reproductive competition among males stretches back at least four million years (Leakey et al., 1998). In traditional contexts, male-male competition includes fights for dominance within the ingroup and smaller- to larger-scale raids of competing groups, with 20 % or more of men dying as a result of such conflicts (e.g., Walker and Bailey, 2013). The historical record and population genetic studies indicate the intensity of conflict and the attendant variation in men's reproductive success intensified with the emergence of agriculture and early empires (Betzig, 2012; Zeng et al., 2018). The exercise of dominance-related physical male-male competition was slowly suppressed in modern nations over the past few centuries (Pinker, 2011), and partially replaced by knowledge- and skills-based competition (Geary, 2021); also known as prestige-based competition (Henrich and Gil-White, 2001).

Female-female competition is common in mammals and especially among primates but does not reach the same intensity as that found in same-species males (Smuts, 1987). Competition is typically over access to high-quality foods rather than mates, and females or female kin-groups that achieve access to these resources have a higher reproductive success than their less competitive peers (Silk, 1993). Competition among women for social influence and access to resources–often competition among cowives in polygynous marriages–is well documented in the cross-cultural record (Stockley and Campbell, 2013). Rather than being physical, the competition typically involves relational aggression that includes attempts to sully the reputation and undermine the social-support network of competitors. Although it is not as well documented as for men, in many contexts socially dominant women often have healthier and more surviving children than do submissive ones (Jankowiak et al., 2005; Ji et al., 2013). Female and male choice are also evident in humans but beyond the scope of this article (see Geary, 2021).

The point is there is ample evidence that at least some currently observed sex differences are the result of sexual selection during human evolution. The goal here is to illustrate that an understanding of sexually selected traits as condition-dependent has the potential to expand our understanding of human sex differences, especially in terms of social and ecological factors that can influence the magnitude of these differences. An important prediction is that the magnitude of human sex differences, as in other species, will be largest for populations living in favorable conditions and smaller for populations living in more stressful conditions. This is not, however, a blanket statement about all sex differences, but rather those that have a clear evolutionary history related to competition for mates and other resources and related to mate choices. I provided *a priori* predictions regarding which traits will be most vulnerable to stressors in an earlier book (Geary, 2015, see Table 5.1, pp. 156–159) and more precisely define stressors elsewhere (Geary, 2017, 2019). The goal here is to illustrate the potential utility of this approach for understanding human sex differences and fluctuations in the magnitude of these differences, but before providing these illustrations I discussion some limitations to the approach.

1.3.1. *Limits to and nuance in the proposed model*

As noted, the use of condition-dependent trait expression as a principled means to understand fluctuations in the magnitude of human sex differences does not directly apply to all of these differences. One important class of exceptions are evolutionarily novel academic abilities, such as reading, writing, and mathematics, that only emerge with the massive cultural intervention of formal schooling (Geary, 1995, 2007). Although there may be indirect relations between sex differences in sexually selected traits and academic abilities (e.g., language as related to reading acquisition), sex differences for the latter are not expected to be as strongly influenced by stressor exposure as sexually selected traits. This is because the development of academic abilities is heavily dependent on exposure in school, instructional approaches, and other experiences that will more strongly influence the development of these abilities, and any sex differences in them, than will any indirect influence of evolved abilities. Thus, the pattern of larger sex differences under favorable conditions might not manifest in these domains (e.g., Guiso et al., 2008).

There are in addition social dynamics and constraints that can influence the magnitude of some behavioral and psychological sex differences that are independent of or interact with condition-dependent trait expression (Kaiser, 2019; Salk et al., 2017; Schmitt, 2005, 2015). As an example, religious prohibitions and proscriptions are associated with increases in social cooperation and decreases in self-serving behaviors that in turn decrease the magnitude of the sex differences in the personality trait of agreeableness (favoring women) and in use of Machiavellian social strategies (favoring men). This is because these prohibitions and proscriptions influence men's behaviors more strongly than those of women (Schmitt, 2015). These types of changes are sometimes correlated with changes in ecological conditions that could influence the expression of condition-dependent traits in ways similar to that found in other species (Kaiser, 2019), but this need not be the case.

The next section describes how improvements in living conditions resulted in an increase in many physical sex differences that can be linked to an evolutionary history of male-male competition and thus in line with condition-dependent trait expression in other species. These same changes are also associated with some evidence for a widening of the sex differences (favoring women) in anxiety and perhaps depression (Högberg et al., 2020; Salk et al., 2017; Schmitt, 2015; Thorisdottir et al., 2017). Women's anxiety and depression are not condition-dependent traits in the same way as men's physical competencies, although they may be condition-dependent social signals associated with men's resilience in the face of physical male-male competition (see Geary, 2015, pp. 224–226). In other words, men have a bias to suppress behavioral indicators of anxiety and depression, because these will undermine their status in male dominance hierarchies; there are also hormonal mechanisms that reduce men's reactivity to threat in competitive contexts (Stanton et al., 2009).

This perspective, however, is not a satisfactory explanation of why women's rates of anxiety and depression remain elevated in the modern, low-risk world or, more critically, why they may have increased over the past several generations (e.g., Högberg et al., 2020; Thorisdottir et al., 2017), despite reductions in risk (e.g., crime) and improvements in overall living conditions (Pinker, 2011). Del Giudice (2018) proposed that anxiety and depression are evolved psychological defense mechanisms that reduce engagement in risky behaviors and withdrawal from risky social dynamics and are more easily triggered in women than in men. The benefits include reduced injury and death due to accidents and homicides at the extreme end, and lower social risks overall (Wilson and Daly, 1985). Sex differences would be expected to remain in low-risk contexts, but this leaves unanswered the recent secular increase in the magnitude of these differences. One possibility is concept creep, whereby reductions in serious threats (e.g., physical assault) are associated with increased sensitivity to what were once considered minor threats (e.g., unpleasant verbal statements; Levari et al., 2018). The latter are more common in the context of normal social dynamics and thus increased sensitivity to them could result in an increased triggering of the psychological defense mechanisms of anxiety and depression. The triggering would occur more often in women than in men and result in a corresponding increase in the sex differences in these areas.

Whatever is contributing to the sex differences in anxiety and depression, it is clear that the magnitude of many such differences can vary across contexts and time (for addition examples, Geary, 2021). It is also clear that such fluctuations are not necessarily evidence against sex differences in evolved biases, as is often assumed (e.g., Costa et al., 2001; Wood and Eagly, 2002), but rather reflect context-dependent plasticity in their expression (Geary, 2015; Kaiser, 2019; Schmitt, 2015). Much remains to be learned about contextual influences on the expression of evolved biases and any associated sex differences. The study of these interactions in the context of what is known about condition-dependent traits in nonhuman species provides a principled means to study some of these interactions, as illustrated in the following sections, but will not be sufficient to explain all of them.

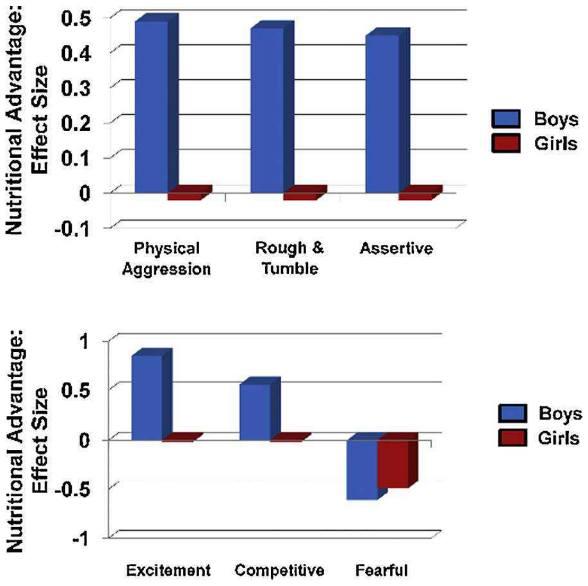

Fig. 3. Chronic poor nutrition during early childhood compromises the social-competitive play of boys more than that of girls. The *x*-axis shows the strength of the relation (*d*) between variation in nutritional supplementation and later social behavior. The top graphic shows engagement in social behaviors across 5 h of observations, and the bottom one engagement in a competitive game. Except for fearfulness, the effects for girls were small and not significant. Based on data reported in Barrett et al. (1982) and Barrett and Radke-Yarrow (1985).

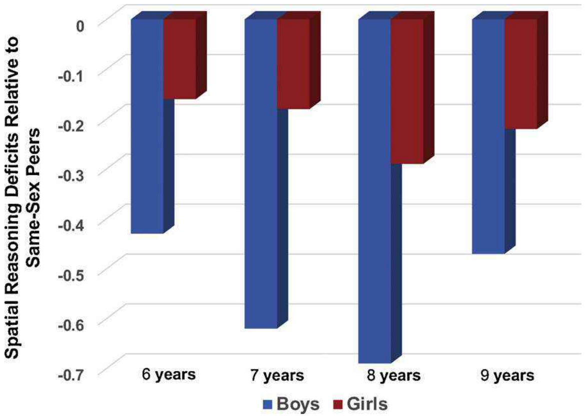

Fig. 4. Boys who were prenatally exposed to polychlorinated biphenyls (PCBs) showed more substantive deficits (*d*) in spatial reasoning than did girls exposed to PCBs. Deficits are in standard deviation units (*d*) and in comparison to unexposed and demographically matched same-sex peers. Based on data reported in Guo et al. (1995).

1.3.2. Human sex differences during physical and behavioral development

The evolutionary echo of male-male competition includes sex differences in height, skeletal structure of the upper body, lean muscle mass, and cardiovascular fitness, among other traits (Tanner, 1990). Most of these differences are small to moderate during childhood and become quite large during pubertal development. If these traits follow the pattern illustrated in Fig. 1, then exposure to stressors and especially during puberty should more severely compromise them in boys than in girls. In other words, the magnitude of the male advantage in these areas should be largest in well-nourished populations with access to modern health care and sheltered from intense (i.e., life threatening) social competition and smallest in stressed populations, and this in fact the case.

As one example, men's relative advantage in height is universal but the magnitude of this sex difference varies across populations and generations within populations, with the largest differences in the healthiest nations (Perkins et al., 2016). For the latter, adult stature is highly heritable but chronic poor nutrition and disease are important environmental contributors to adult height in suboptimal conditions and more so for men than women (Perkins et al., 2016; Zemel et al., 2007). Secular increases in height during the 20th century, a period of marked by substantive gains in overall health, illustrate the point (e.g., Kuh et al., 1991; Papadimitriou et al., 2002). From 1900–1958 in Great Britain, Kuh et al. found a 1.09 cm/decade increase in men's height as compared to a 0.36 cm/decade increase for women. In 1900, the average British man was 11 cm taller than the average woman ($d = 1.4$), but this increased to 15 cm ($d = 2.2$) by 1958, a 36 % increase in less than three generations. The same pattern of a fluctuating sex difference is found in developing nations today. For young adults in nutritionally stressed regions of Nigeria, for instance, men are 7.5 cm shorter than their better-nourished peers, whereas women are 3.2 cm shorter (Omigbodun et al., 2010). The result is a sex difference in height that is 38 % smaller than it would be if these adults had received better nutritional and medical care during childhood and adolescence.

In a review of the social play of mammals, Power (2000) found that young males of polygynous species with intense physical male-male competition nearly always engaged in more play fighting than females. This form of play likely results in improved social competencies and later social-competitive advantage (Graham and Burghardt, 2010), as well as establishing dominance relationships before play merges into potentially harmful fighting (Pellis and Pellis, 2007). The same is true with children. Boys engage in various forms of rough-and-tumble and competitive group play at least three times more frequently than girls (DiPietro, 1981; Lever, 1978), and by adolescence this form of play merges into physical intimidation and aggression and influences status among their peers (Pellegrini and Bartini, 2001). Boys who do not engage in these forms of play are often bullied and at risk for anxiety and depression (Fagot, 1977).

As with height, stressor exposure more strongly disrupts boys' sex-typical play and these aspects of social behavior than that of girls. These stressors include prenatal exposure to man-made toxins (Swan et al., 2010), as well as chronic malnutrition during childhood (Barrett et al., 1982). Barrett and colleagues provided a unique and semi-natural assessment of the social play of 6- to 8-year-old Guatemalan children. These were children from a larger study of the benefits of prenatal and early postnatal (up to four years of age) nutritional supplements on physical growth and cognitive development. Girls and boys with higher levels of nutritional supplements were more active and socially engaged than their poorly-nourished peers. As shown in Fig. 3, five hours of observation of natural behavior revealed that the better-nourished boys' social potency and thus dominance was consistently higher than that of poorly nourished boys, but there were few differences in the social potency of better- and poorly-nourished girls. During participation in a competitive game, poorly-nourished boys were the least engaged and well-nourished boys were the most engaged and competitive (Barrett and Radke-Yarrow, 1985). The engagement and competitiveness of the poorly- and better-nourished girls was in-between that of the two boys' groups. In other words, the most active and socially potent children were well-nourished boys and the least potent were malnourished boys, with girls somewhere in between the boys' groups independent of their nutritional status.

1.3.3. Human sex differences in cognition

Male-male competition in traditional contexts often involves long-distance travel to raid competing groups or to hunt, as well as the use of projectile weapons (MacDonald and Hewlett, 1999). These activities are associated with male advantages in various areas of visuospatial cognition, including more accurate navigation, an enhanced ability to identify targets in large-scale 3-dimentional space, and more accurate tracking of the movement of objects as they travel through space. The

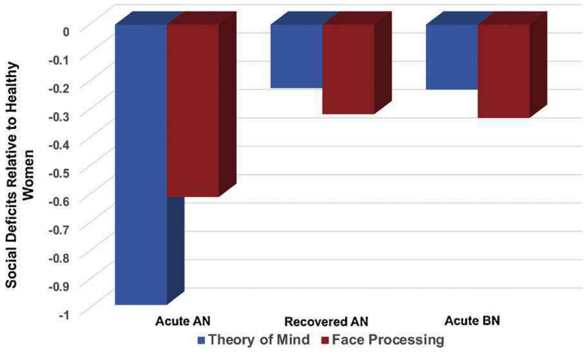

Fig. 5. Women with acute anorexia nervosa (AN) have deficits in theory of mind and face processing relative to healthy women. The deficits of women who have recovered from AN or with bulimia nervosa (BN) are more modest. Deficits are in standard deviation units (d). Data are based on Bora and Köse's (2016) meta-analysis.

sex differences in these areas are well documented and range from small ($d = 0.2$) to large ($ds > 0.7$; Peters, 1997; Peters et al., 1995; Voyer et al., 1995).

An example of a male-specific vulnerability in this area is provided by the accidental exposure of thousands of people in Taiwan to PCB-contaminated cooking oil, including 74 women who were pregnant at the time or became pregnant soon thereafter. A longitudinal assessment of these children from 6- to 9-years of age, inclusive, and relative to a group of demographically matched peers revealed that exposed boys' but not girls' spatial reasoning abilities were compromised (Guo et al., 1995), as shown in Fig. 4. One result was that healthy boys' among the youngest group had a small spatial reasoning advantage over healthy girls ($d = .09$), but girls had an advantage among the exposed children ($d = -.19$). Among the oldest group, healthy boys had a moderate advantage over healthy girls ($d = .57$), but boys' advantage was 70 % smaller among the exposed children ($d = .17$).

There are also indications that exposure to one or more toxins can compromise men's visuospatial memory and performance on more complex spatial cognition tests (Farahat et al., 2003; Schwartz et al., 2000). Akila et al. (1999) assessed Finnish factory workers' level of aluminum exposure (through welding) and performance on a variety of cognitive measures. With control of demographic and other factors, the primary deficits associated with men's exposure were "in tasks requiring working memory, particularly that relating to processing of visuospatial information" (Akila et al., 1999, p. 632). The magnitude of the sex differences in spatial abilities also varies across nations (Lippa et al., 2010). As overall health improves, men's advantages in visuospatial abilities increase modestly ($r = .33$) to substantially ($r = .68$), depending on the type of spatial competence assessed.

Female-female relational aggression may have contributed to girls' and women's advantages in interpreting nonverbal communication cues and facial expressions, and for theory of mind, that is the ability to infer the thoughts and feelings of others. The sex differences in these areas range from modest ($ds = 0.2$) to substantial ($ds > 1.0$; e.g., Hall, 1984; Thompson and Voyer, 2014). Girls and women also have small to moderate ($d = 0.1$ to 0.4) advantages in many basic aspects of language (Leaper and Smith, 2004; Majeres, 2007). The subtlety of women's relational aggression may be one reason they rehash social episodes with a best friend (Rose et al., 2014); to evaluate and decipher ambiguous messages. Rehashing in turn is dependent on a strong episodic memory (i.e., memory for personal experiences) and a strong verbatim recall of what was said (memory for language) and how it was said (e.g., memory for faces). Girls and women do indeed have advantages ($d = 0.2$ to 0.3) over boys and men in the later recall of social information (Herlitz et al., 1997; Pauls et al., 2013).

Stressor exposure can reduce or eliminate girls' and women's advantages for these cognitive traits in the same way that stressors reduce boys' and men's advantages for other traits. An example is provided by the social-cognitive deficits that are associated with the acute of phase of anorexia nervosa (AN), which involves severe calorie and nutrient restriction. Women who eventually develop AN tend to have social-cognitive deficits independent of weight loss and thus contrasts of women in acute and recovered stages of AN are important (Zucker et al., 2007). Women with bulimia nervosa (BN) have similar psychological issues but do not have the severe weight loss that is associated with AN and thus provide a useful contrast group. As shown in Fig. 5, acute AN is associated with substantial deficits in women's ability to make inferences about the thoughts of other people (theory of mind) and their ability to infer others' emotions using facial cues (Bora and Köse, 2016). Deficits in making inferences about the emotions of others conveyed through voice and body posture are also common in AN (Oldershaw et al., 2010).

As with men's spatial ability, the magnitude of women's advantage in verbal episodic memory increases with improvements in the social and economic conditions of the population, as shown in Fig. 6. Asperholm et al.'s (2019) meta-analysis indicted that women have the largest advantage in verbal memory in countries with higher levels of gender equality, better educational and employment opportunities and higher income, with this advantage disappearing or reversing in more stressful

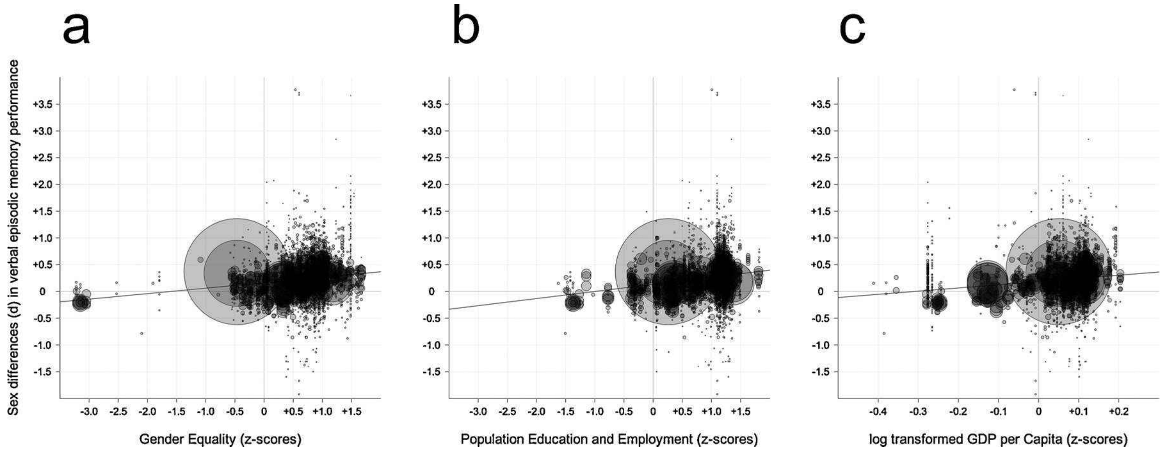

Fig. 6. Indicator of (a) Gender equality, (b) Population Education and Employment, (c) Gross Domestic Product (GDP) per Capita (*x*-axis) plotted against sex differences in Verbal episodic memory performance (*y*-axis). The diameter of each data point is equal to the inverse of its squared variance. The lines indicate the best-fitting regressions. From The magnitude of sex differences in verbal episodic memory increases with social progress: Data from 54 countries across 40 years by Asperholm et al. (2019). Creative comments license. https://journals.plos.org/plosone/article/figure?id=10.1371/journal.pone.0217033.g002.

contexts.

2. Conclusions

Sexual selection provides a powerful, theory-driven approach for the study of sex differences across all sexually reproducing species (Andersson, 1994; Darwin, 1871), including our own (Geary, 2021). Competition for mates and discriminative mate choices provide the mechanisms that drive the evolution of the associated traits and their condition-dependent expression provides social signals regarding the individuals' exposure to and resilience against social and ecological stressors (Zahavi, 1975). Sexual selection and the condition-dependent expression of the associated traits provides a unique perspective on the study of human sex differences and a principled approach for the identification and prediction of sex-specific vulnerabilities associated with chronic malnutrition, disease, social stressors, and man-made toxins (Geary, 2018, 2019). The critical point here is that exposure to these stressors reduces the magnitude of any sex differences and thus might provide an evolutionarily informed framework for the study of environmental influences on the magnitude of human sex differences. At the same time and as described earlier, condition-dependent trait expression does not explain fluctuations in all human sex differences, but it does provide a means to identify traits for which sex differences are expected and are sensitive to social and ecological conditions (Geary, 2015).

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