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The reality and evolutionary significance of human psychological sex differences

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ABSTRACT

The aims of this article are: (1) to provide a quantitative overview of sex differences in human psychological attributes, and (2) to consider evidence for their possible evolutionary origins. Sex differences were identified from a systematic literature search of meta-analyses and large-sample studies. These were organized in terms of evolutionary significance as follows: (1) characteristics arising from inter-male competition (within-sex aggression; impulsiveness and sensation-seeking; fearfulness; visuospatial and object-location memory; object-centred orientations); (2) those concerning social relations that are likely to have arisen from women's adaptations for small-group interactions and men's for larger co-operative groups (person-centred orientation and social skills; language; depression and anxiety); (3) those arising from female choice (sexuality; mate choice; sexual conflict). There were sex differences in all categories, whose magnitudes ranged from (1)

small (object location memory; negative emotions), to (2) medium (mental rotation; anxiety disorders; impulsivity; sex drive; interest in casual sex), to (3) large (social interests and abilities; sociosexuality), and (4) very large (escalated aggression; systemizing; sexual violence).

Evolutionary explanations were evaluated according to whether: (1) similar differences occur in other mammals; (2) there is cross-cultural consistency; (3) the origin was early in life or at puberty; (4) there was evidence for hormonal influences; and (5), where possible, whether there was evidence for evolutionarily derived design features. The evidence was positive for most features in most categories, suggesting evolutionary origins for a broad range of sex differences. Attributes for which there was no sex difference are also noted. Within-sex variations are discussed as limitations to the emphasis on sex differences.

Key words: aggression, emotions, empathizing, evolution, gender similarities hypothesis, meta-analyses, sex differences, sexuality, social relations, systemizing.

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I. INTRODUCTION

Two major issues have recurred in analyses of psychological sex differences: whether these are minimal, or whether they are large and widespread, and if so, what is their theoretical significance? Explanations of sex differences began with the theory of sexual selection (Darwin, 1871/1901), which covered both physical and behavioural differences in animals, including humans. The alternative social role explanation can be traced to Woolley (1910), who concluded that sex differences in mental processes are likely to be “of sociological rather than of biological origin” (p. 342). In the 1970s, the debate was rekindled by Maccoby & Jacklin’s (1974) comprehensive synthesis of research, in which they concluded that there were few well-established differences. This was disputed on the grounds that their evidence base was incomplete, and that the tabulated results showed further differences (Block, 1976). Maccoby & Jacklin (1974) had drawn their conclusions from the proportion of studies that found statistically significant sex differences, although they also specified the magnitude of effects (pp. 351–352), in terms of units of standard deviation, thus heralding the next major innovation in summarizing sex differences, which was meta-analysis. This method places findings on the firmer basis of effect-size measures.

The first meta-analysis of sex differences was on decoding non-verbal cues (Hall, 1978). Further meta-analyses of sex differences followed in the 1980s (15 in all), and the debate about whether they were few or many continued (e.g. Baumeister, 1988; Eagly, 1987, 1990; McHugh, Koeske & Frieze, 1986). There were more meta-analyses through the 1990s and beyond. Hyde (2005) summarized those available at the time, concluding that sex differences were minimal, a position she termed the Gender Similarities Hypothesis (GSH). Hyde’s method of counting the proportion of effect sizes showing no or minimal differences overlooks the significance of specific

sex differences for theoretical explanations, in particular those derived from evolutionary principles (Archer, 2006c). Using the same method for physical features would likewise lead to the conclusion that men's and women's bodies are essentially similar, but would have missed the substantial differences in their primary and secondary sexual characteristics. It would also have directed attention away from the evolutionary questions these differences raise. From an evolutionary viewpoint, it is unsurprising that men and women show minimal, if any, differences in a range of psychological attributes. Both sexes have been subject to the same selective forces that comprise natural selection. By contrast, we would expect substantial differences in those characteristics that have been subject to different selection in males and females, as a direct or indirect consequence of the parts the sexes play in reproduction.

II. AIMS AND SCOPE

The aims of this article are: (1) to extend previous overviews of the quantitative evidence for sex differences (Hyde, 2005, 2014; Zell, Krizan & Teeter, 2015); and (2) to evaluate the extent to which the evidence is consistent with evolutionary explanations. With regard to the first aim, I show that there is a considerable number of substantial sex differences, particularly in attributes that can be linked to sexual selection. The most obvious and largest of these differences lie in three domains: (1) same-sex aggression; (2) sexuality and mate choice; and (3) sexual conflict.

Evolutionary analyses also point to sex differences in other psychological domains, notably impulsiveness, fearfulness, and visuospatial skills, and in social attributes and interests.

Reviews that use meta-analytic summaries (Hyde, 2005; Zell *et al.*, 2015) have the crucial advantage over narrative reviews in that they use the same metric (Cohen's *d*) for a wide range of different attributes. This is particularly suitable for comparing men and women. Like Zell *et al.* (2015), I carried out a systematic literature search, so as to lessen the possibility of biased selection. I supplemented this with additional sources not considered previously: (1) cross-national surveys of

personality traits, social attributes, mate choice and sexuality; (2) large-sample ($N > 1000$) online studies; (3) social surveys on attributes related to health and crime; and (4) crime statistics. These often involve more participants than meta-analyses do (Hedges & Nowell, 1995; Lippa, 2006b).

Hyde (2005) used the classification of effect sizes based on Cohen's (1988) criteria, which pre-dated meta-analysis and were intended for power analyses. The criteria were intended to apply generally to the social sciences, and ranged from close to zero ($d = 0-0.10$) to large ($d = 0.66-1.0$). Since some of the effect sizes considered here are greater than 1.0, Cohen's scheme has been extended to encompass larger values, as shown in Table 1. An intuitive way of understanding these effect sizes is the probability that a randomly selected person of one sex will be higher or lower on the particular measure than a randomly selected person of the other sex (Grissom, 1994). This is 50% (chance level) when the effect size is zero, and it increases to 100% as the effect size approaches a non-overlapping distribution. From the values for the mid-points of each category (Table 1), it is apparent that the term 'sex difference' covers a wide range, from nearly overlapping to practically no overlap.

Hyde's (2005) review was criticized from a methodological perspective (del Giudice, Booth & Irwing, 2012), on the grounds that using bivariate effect sizes (Cohen's d), and averaging these, minimizes the extent of the sex differences in coherent sets of related attributes, such as personality measures: they suggested that an alternative multi-variable effect-size measure, Mahalanobis Distance (D), be used to summarize related sex differences. If this is computed, for example for global personality, the sex differences are much larger than for individual traits or facets. Hyde (2012) noted that such aggregation would not be meaningful if it were at too high a level, and further criticized this approach (Hyde, 2014) on the grounds that D artificially inflates differences, and that it is not readily interpretable. Lippa (2012) commented that D may be a useful statistic for a coherent set of interrelated characteristics, for example personality (del Giudice, 2009; del Giudice *et al.*, 2012), facial features (del Giudice, 2013), and mate-choice preferences (Conroy-

Beam *et al.*, 2015): the issue is what is meaningfully related. In most cases covered in this review there are not such coherent sets of characteristics, but where there are, this is noted.

A further methodological point (del Giudice *et al.*, 2012; Schmidt, 2010) is that bivariate effect sizes for self-reports are typically underestimates compared with estimates for the same traits as latent values. Such corrections are not typically made in the meta-analyses considered here, so that my inferences about sex differences stand or fall on the basis of uncorrected bivariate effect sizes. They may well be underestimates, but to avoid methodological criticisms on this point I have adopted a conservative approach.

Darwin (1871/1901) proposed that human psychological sex differences could be explained in terms of sexual selection, mainly inter-male competition, and to a lesser extent female choice. Inter-male competition is still the primary evolutionary explanation of human sex differences (Archer, 2009a; Buss, 1995; Daly & Wilson, 1988; Puts, 2010). It has been used to explain sex differences in aggression, impulsiveness, fearfulness, visuospatial skills, and understanding physical systems. The last of these was attributed to selection pressures (arising from inter-male competition) enacted in the changing environments of hominin evolution, such as tool-use, hunting, tracking, trading, and achieving status (Baron-Cohen, 2003). In animals, particularly in mammals, inter-male competition has been explained in terms of females generally being a limiting resource for males (Clutton-Brock & Vincent, 1991; Trivers, 1972).

Sex differences in social attributes have been linked to women's need to attend more closely to social signals, and to form fewer, closer, relationships than men do: again, these selection pressures have been viewed as a direct result of greater female than male parental investment (Campbell, 1999) and in terms of the need to form bonds with other women (Baron-Cohen, 2003, pp. 126–130; Geary *et al.*, 2003; Hrdy, 2009). An alternative is that women's social skills may have evolved to facilitate attachments to male providers (R.F. Baumeister, personal communication).

The second aspect of Darwin's theory of sexual selection is female choice. It can be traced to females' greater parental investment (Trivers, 1972), and female choice has been used to explain sex differences in sexuality, mate-choice attributes, and in both physical and sexual aggression to members of the opposite sex.

The ordering of the topics covered here follows these evolutionary principles. In Section V, I cover sex differences that have been explained primarily in terms of inter-male competition: these are: (1) aggression and related attributes; (2) risk-taking, impulsiveness and sensation-seeking; (3) fearfulness; (4) visuospatial skills; and (5) understanding physical systems. I then cover sex differences in aspects of social relations that have been variously attributed to the greater need for women to bond with infants, with other women, or with men (Section VI). In Section VII, I cover sex differences that are viewed as being the consequence of female choice, notably those in sexuality, mate-choice criteria, and in aggression between the sexes.

A second aim of this article is to explore evidence for an evolutionary background in each case. Table 2 summarizes the specific questions that are asked. Answers to these, when taken together, can be viewed as 'tell-tale signs' of the imprint of evolutionary processes. This does not mean that such sex differences are not subject to variability arising from individual differences or from social processes. These have been addressed extensively in terms of gender roles (e.g. Eagly, 1987; Wood & Eagly, 2012), and it is beyond the scope of this review to consider how these sources of variability have interacted with evolutionarily based sex differences over the course of human history and prehistory. Since evolutionary processes pre-date the societal influences conceptualized as gender roles, a full explanation would have to recognize evolutionary processes as precursors of social roles. It is therefore necessary to clarify these evolutionary processes before social roles can be fully understood.

The first question posed in Table 2 is whether there is a plausible adaptive explanation, i.e. whether it is likely that the attribute contributed differentially to the reproductive success of men

and women at some stage in the evolutionary past. Ideally, such an explanation should be testable, although tests of adaptive significance are limited to whether the character is likely to be adaptive under current conditions. The second question is whether there are similar differences in other mammals, and particularly in humans' nearest relatives. The third question is whether the sex difference is found in humans living under different cultures and conditions, particularly in surviving hunter-gatherers. These three questions address the plausibility of an evolved origin for the sex difference. The fourth question concerns the developmental trajectory: if a sex difference has an adaptive origin, it is likely to be present either early in infancy, or to be first found at puberty, or in young adulthood to coincide with reproductive competition. We should note that lack of early sex differences does not provide evidence against an evolutionary origin, and that sex differences found in childhood may be precursors of adult adaptations. The fifth question is whether the sex difference is associated with neonatal or pubertal reproductive hormones.

A sixth question is whether evolutionarily derived design features are apparent in the mechanisms underlying the sex difference. It has long been argued in evolutionary psychology that features that have evolved to solve adaptive problems should reflect this in their mechanisms (Tooby & Cosmides, 1992). Although this may be too simple as a comprehensive explanation, since mechanisms can reflect function in diverse ways (see Archer, 1988, 2009*b*), there will be many instances where there is sensitivity to specific adaptive cues in the environment. For example, if the primary function of male competition is related to obtaining mates, it should be accentuated when potential mates are present. I have cited such studies where they are available.

III. SELECTION OF EVIDENCE

A systematic literature search was used to provide a comprehensive overview of previous meta-analyses. The search involved *PsycINFO*, *ERIC*, *Medline*, and *Web of Science*, from 1970 to December 2016, using the key words “(sex or gender) differences” and “meta analy*”: this

produced 178 sources. I also searched the reference sections of key publications (e.g. Hyde, 2005, 2014; Geary, 2010; Zell *et al.*, 2015); and I searched the following journals from 1970 onwards: *Aggressive Behavior*, *Aggression and Violent Behavior*, *Archives of Sexual Behavior*, *Child Development*, *Developmental Psychology*, *Journal of Interpersonal Violence*, *Journal of Personality and Social Psychology*, *Personality and Individual Differences*, *Psychological Bulletin*, *Review of General Psychology*, *Sex Roles*, and *Violence and Victims*. The meta-analytic evidence was supplemented by large-scale surveys (here defined as 1000 or more participants). Many large-sample cross-national studies and national surveys relevant to sex differences were found during the searches for meta-analyses; others were obtained by searching for government reports, and from previous publications (e.g. Archer, 2004, 2009a; Archer & Lloyd, 2002). Using “sex or gender differences” and “survey” in the databases used for the meta-analyses produced few relevant sources. Thus, while the evidence base is likely to be near to 100% for meta-analyses, the coverage of other sources is likely to be less exhaustive.

Excluded from consideration were the following: (1) studies involving specialist populations, such as gifted youth or medical patients, since prior selection would have distorted any sex differences; (2) studies on attributions or attitudes, except where these relate to core topics, such as sexuality and interests; (3) medical conditions or psychopathology, again except when these are related to psychological attributes, such as rates of depressive disorder; (4) studies where the two sexes were evaluated by others on an attribute, such as leadership or personality (i.e. measures of gender stereotypes); (5) neuroimaging studies; and (6) physical differences associated with men’s greater muscularity, such as strength, muscle size, and throwing ability: some of these were included in Hyde (2005) under the heading “motor activities”.

These searches yielded 216 relevant sources (127 describing meta-analyses; 85 describing surveys; and four describing both), all of which are listed as supporting online information (Tables S1–S13). In these tables, values from selected studies are highlighted for inclusion in a summary

table (Table 3) using asterisks (145 studies: 106 meta-analyses and 39 surveys). I chose which studies to highlight based on the following criteria: (1) the most recent large-scale meta-analysis or survey that used adult samples; (2) when there were overall and specific subsets of data, the overall value was selected unless specified otherwise; (3) where frequency and intensity values were available, I chose frequency; (4) where lifetime and the last 12 months were provided, I chose data for the last 12 months; (5) where there was a choice between a western or North American sample and a cross-national sample, the cross-national one was chosen. Where there was more than one study fitting these criteria, a mean value was calculated. This selective procedure was used rather than performing a meta-analysis of the different sources shown in Tables S1–S13, since these sources typically used at least some of the same studies, i.e. they were not independent. In the case of large-scale surveys, these often used different methods and samples and for this reason could not be aggregated in a meta-analysis. The metrics in Tables S1–S13 were checked from the original sources.

To provide an indication of the coverage of this review compared to previous sources, 38 of the 45 studies listed by Hyde (2005) are included. There are a further 88 sources reporting meta-analyses, including 10 cited in Hyde's (2014) update. Of the 127 meta-analytic sources used in the present article, 20 were cited in Geary's (2010) book considering human sex differences in an evolutionary context. 75 of the meta-analyses shown in Tables S1–S13 were in the supplementary material of Zell *et al.* (2015) [they did not include some of the older meta-analyses included here, they omitted some relevant studies, and some additional studies have been published since their paper]. In addition, Tables S1–S13 include 85 sources reporting large-sample surveys, 11 of which were cited by Geary (2010).

In the following discussions, I mainly use effect sizes. Where these were not shown in the source, I converted metrics (mainly means and standard deviations, and *t*-values) to Cohen's *d*, using Comprehensive Meta-Analysis (CMA) (Borenstein *et al.*, 2009).

IV. EVOLUTIONARY THEORIES OF PSYCHOLOGICAL SEX DIFFERENCES

Inter-male competition has been the prevailing evolutionary explanation for physical and psychological sex differences since Darwin (1871/1901): human males show a range of features indicating an adaptive complex shaped by inter-male competition. These features include: greater male size and strength; facial and vocal features associated with aggressive displays; inter-male violence (particularly among young males); shorter average male than female life span, associated with a male-biased sex ratio at conception; and slower male maturation. All these are characteristic of sexually selected species (Andersson, 1994), and are associated with greater male than female variation in reproductive success, which is apparent in humans (Archer, 2009a; Betzig, 2012; Brown, Laland & Borgerhoff Mulder, 2009). It is clear that sex differences in features such as aggression, risk-taking, and fear fit this pattern. Other sex differences whose origin may be a consequence of inter-male competition include: (1) better performance by males than females on tests of visuospatial ability, which may result from selection for larger ranges among males; (2) better performance by males than females in understanding physical systems, which as indicated in Section V.5, may result from selection in hominin evolution for achieving status through more efficient understanding of the physical world.

The focus on inter-male competition has detracted from consideration of a parallel set of selection pressures arising from the part played by female mammals in reproduction. Campbell (1999) argued that greater female avoidance of escalated aggression, risk aversion, and fear evolved as a direct consequence of the importance of mothers not risking their lives, and thus those of their offspring.

Owing to viviparity and lactation, parental investment is necessarily female-biased during the early years of offspring life in mammals. At some stage in human evolution, the context of parental care became widened to include paternal care associated with pair-bonding (Geary, 2000),

and shared or alloparenting with other women (Hrdy, 2009). It is within this context of the generally greater (and initially obligatory) parental investment by females that sex differences in a range of features associated with the social life of women have been considered (e.g. Baron-Cohen, 2003, pp. 126–130; Hrdy, 2009). These include sensitivity to social signals, the nature of friendship groups, and empathy. Alternative explanations involve adaptations for bonding with other women or with men.

Darwin (1871/1901, p. 847) identified female choice as an important part of sexual selection: as a consequence of the typically greater female than male parental investment (Trivers, 1972), females are usually the more discriminating sex when choosing a mate. This has been applied to human sexuality, to explain the greater male than female preference for casual sex and for short-term relationships (Buss & Schmitt, 1993). Other predictions about criteria underlying mate choice arise from specifically human characteristics, such as the menopause and pair-bonding (Buss, 2012, pp. 103–162). When female choice is combined with greater male coercive power, it can lead to sexual coercion, and physical violence to female partners. Clutton-Brock & Parker (1995) considered this theoretically in animals, and their analysis forms the basis of the present consideration of human sex differences associated with sexual conflict. Thus conflict between the sexes in humans can be viewed as being derived from the diverging fitness interests of men and women, arising from their different roles in the reproductive process.

Although I have identified different evolutionary principles, in practice they are likely to operate together. Thus while men have evolved characteristics for inter-male competition leading to sex differences in escalated aggression, selection pressures on women may have led to sexual selection in the same direction: as Darwin (1871/1901) noted, features such as strength and muscularity in men, which aid direct physical aggression, are also those chosen by women (Frederick, & Haselton, 2007; Sell, Lukazsweski & Townsley, 2017). Similarly, antler size in male red deer is attractive to female deer (Morina *et al.*, 2018).

In the following sections, I consider behavioural and psychological attributes in relation to evidence for sex differences and their magnitude, and I evaluate the evidence for an evolutionary origin in each case, based on the criteria in Table 2. These attributes are considered in three broad sections, according to the main evolutionary explanations outlined above: first the consequences of inter-male competition; second, social relations; and third, the consequences of female choice.

V. INTER-MALE COMPETITION AND PARENTAL INVESTMENT

(1) Within-sex aggression, violence and dominance

(a) Evolutionary rationale

Following Darwin (1871/1901), the main evolutionary explanation for greater male than female physical aggression to same-sex others is inter-male competition (Archer, 2004, 2009a; Daly & Wilson, 1988, 1990). This links sex differences in aggression to those in size and strength (Archer, 2009a; see also Durkee, Goetz & Lukaszewski, 2018; Sell, Cosmides & Tooby, 2014; Sell *et al.*, 2009). The avoidance of escalated physical aggression by females (Campbell, 1999), as a consequence of the greater importance of mothers in rearing their offspring, is likely to have co-evolved with inter-male competition. Inter-male competition is also likely to have produced secondary differences, for example the cognitive elaboration of violent fantasies, as assessed by measures of revenge (McCullough, Kurzban & Tabak, 2013), and a belief in hierarchical social systems (Pratto *et al.*, 1994).

(b) Sex differences

Most studies involving general measures of direct aggression, where the target is unspecified, show sex differences in aggression in the male direction that are identical to those when the target is specified as someone of the same sex (Archer, 2004, 2009a). Table S1 presents findings for

measures of aggression and for fights, weapon-carrying, violent crime, and homicide. Summarizing this evidence (see Table 3), there are: (1) no sex differences in anger (most $d < 0.10$; see Table 1); (2) no differences for forms that do not involve face-to-face confrontation (indirect or relational aggression: Archer & Coyne, 2005), although there is evidence for greater female involvement during adolescence (Archer, 2010); (3) small differences in the male direction for direct verbal aggression; (4) medium differences in the male direction for inclusive measures of physical aggression; (5) large or very large differences in the male direction for weapon-carrying and use, and violent crime; (6) very large differences for homicides involving adults of the same sex. From this sequence of increasing effect sizes, it can be inferred that there is a difference in the degree to which men and women escalate aggressive exchanges to dangerous levels. Consistent with this, Campbell & Muncer (2009) found that sex differences in verbal and physical aggression were mediated by risky impulsivity or the tendency to act without deliberation in situations that are likely to have dangerous consequences.

Table S1 also shows attributes related to aggression. There is a very large difference in the male direction for violent computer-game use, and a large difference for revenge, which may be associated with masculine values such as honour and reputation (Archer, 1994); there was a small difference in the female direction for forgiveness. Men also showed higher values for ‘social dominance orientation’, indicating their greater approval of social hierarchies (a medium-sized difference). This measure mostly involves approval of dominance over other groups (rather than hierarchies within groups). Finally there were no differences for a measure of competitiveness: however, this meta-analysis was restricted to laboratory measures of dyadic interactions between North American students, involving negotiation and bargaining. This is very different from the concept of competition in an evolutionary sense, and from real-life competitiveness for status and for attracting a sexual partner: there are no meta-analyses or large surveys on such measures. However, there is evidence from an observational study of real-life dyadic conversations in a

British city centre. Those between two males involved much more competitive communication, both verbal and non-verbal, than those between two females (Granger & Dunbar, 2009).

(c) Evidence for evolutionary origins

The highest levels of escalated physical contests take place among young males at the peak of their reproductive activity, i.e. during late-teenage and young adult years, conforming to predictions if male aggression evolved in response to inter-male competition. Men's fighting ability is linked with physical sexually dimorphic features, such as upper body strength (see Section V.1a), and (even in a modern western sample) this is related to mating success to a greater extent than is physical attractiveness (Kordsmeyer *et al.*, 2018).

Comparable sex differences in same-sex aggression are found in many other mammals, notably those with polygynous mating systems (Archer, 1988). Studies of primate aggression indicate that males typically show more ritualized threats than do females, and that the risk of injury is considerably higher in male than in female fights (Smuts, 1987). The effect size for the sex difference in the rates of aggression in a small sample of free-living chimpanzees was $d = 1.02$ (from Fig. 9 in Zinner & Wheeler, 2013; data from Müller, 2002). Inter-male aggression is typically more intense and more prolonged than that between females. In humans, higher male physical aggression is found across several nations (Archer, 2004). A large sex difference ($d = 0.86$) was found for physical aggression in an observational study of hunter-gatherer children aged 4 to 5 years (Blurton-Jones & Konner, 1973),

The sex difference in physical aggression occurs from early in life (Archer & Côté, 2005; Baillargeon *et al.*, 2007). The role of hormones in this is not straightforward in that there is no evidence for a direct effect of either prenatal or pubertal hormones on aggressive behaviour (Archer, 2006b). However, a longitudinal study covering ages 6 to 22 years (Nguyen *et al.*, 2016) found that testosterone modulates the covariance between the amygdala (a limbic structure

associated with aggression) and the prefrontal cortex (associated with self-control). This covariance was associated with levels of aggression, and also modulated the relationship between testosterone and aggression. These findings suggest that testosterone is associated with the regulation of brain areas associated with aggression from childhood to young adulthood.

Testosterone administered at high doses to young women promotes more engagement with angry faces, i.e. those associated with social threat. Thus, testosterone considerably increased the cardiac defence reflex to subliminally presented angry faces (van Honk *et al.*, 2001); led to longer maintenance of eye contact with angry faces (Terburg, Aarts & van Honk, 2012); and lessened avoidance of an angry face in approach–avoidance tests (Enter, Spinhoven & Roelofs, 2014). There was more prolonged activation of brain regions associated with aggression, such as the amygdala and hypothalamus, in response to these angry faces (Hermans, Ramsay & van Honk, 2008). Men’s testosterone levels were highly correlated with amygdala and ventromedial prefrontal cortex responses to angry faces (Stanton *et al.*, 2009). Administering testosterone to young men decreased their approach distance to an angry person in a computerized task (Wagels *et al.*, 2017).

There is also evidence of a link between testosterone and measures of dominance. A meta-analysis of several correlational studies showed an overall medium-sized association between the two measures when outliers were removed (Archer, 2006b, pp. 332–333). Another study showed that testosterone administered to men increased their perceptions of their dominance, assessed by asking them to pick which face corresponded to their own from an array differing in facial masculinity (Welling *et al.*, 2016). A five-week longitudinal study of young women found an association between the level of competitiveness with other women and their testosterone levels (Hahn *et al.*, 2016).

The levels of aggression in both sexes vary in response to evolutionarily relevant cues. One such cue is the operational sex ratio (OSR) (Emlen & Oring, 1977): the ratio of males to females available for mating in the population. In non-humans, inter-male competition is accentuated when

the OSR is male-biased. In humans, historical analyses show more individual and collective violence when there was a surplus of young men, i.e. the OSR was high (Hudson & den Boer, 2004). If the OSR is female-biased, female competition is accentuated. This occurs when young men have been removed from the local population, through mortality, imprisonment or migration (Campbell, 2013), and it results in more overt physical aggression between young women (Campbell, 1995).

Maternal aggression is a neglected form of aggression that has been found in a range of mammals and birds, and has been studied experimentally in rodents (Archer, 1988, pp. 69–104). Hahn-Holbrook *et al.* (2011) found that mothers who were breastfeeding had considerably higher levels of aggression than either formula-feeding mothers or nulliparous women, indicating that it is lactation rather than motherhood that is associated with greater aggression at this time. It is also likely that both sexes show additional protective adaptations to being a parent. For example, parents perceived a potential opponent to be more physically formidable than did non-parents (Fessler *et al.* 2014). It is likely that such evaluations will make men less likely to engage in or escalate an aggressive encounter with such an opponent, and hence would tend to decrease the sex difference in escalated aggression.

(2) Impulsiveness and sensation-seeking

(a) Evolutionary rationale

Sex differences in impulsiveness and sensation-seeking have – like those in same-sex aggression – been attributed both to inter-male competition (Daly & Wilson, 1988, 2001), and to the importance of females for offspring survival (Campbell, 1999). Thus the higher levels of male reproductive competition lead to selection for higher male risk-taking, and the greater importance of females for parental care produces selection for lower female risk-taking. This is likely to be reflected in measures of impulsiveness and sensation-seeking.

(b) Sex differences

The broadly defined construct of impulsiveness can be divided into four categories (Cross, Copping & Campbell, 2011): (1) reward sensitivity, a tendency for rewards to have a strong attraction; (2) punishment sensitivity, the tendency for punishment to have a strong effect; (3) sensation-seeking and risk-taking; and (4) poor effortful control, a weakness of the higher-order control of impulses, often referred to as impulsivity or (lack of) self-control.

Table S2 summarizes the major findings regarding these four components and related attributes. There is no overall sex difference in reward sensitivity, although women show higher scores indicating a medium effect on a personality measure involving sociability (Miettunen *et al.*, 2007), on which women typically score more highly than men (Section VI), whereas men show higher scores on questionnaires containing items associated with ambition and success (Cross *et al.*, 2011). Thus sex differences in reward dependency reflect whether the domain is interpersonal or competitive.

Women score higher than men (to a small extent) on the second component, punishment sensitivity, which is represented as “harm avoidance” in a measure of temperament (Table S2). Thus, women experience more negative feelings in response to punishment, or its anticipation. These are strongest for measures of the Behavioural Inhibition System (BIS), one of the three components of Gray’s (1970, 1982) reinforcement-sensitivity theory of personality, related to anxiety-proneness (Table S2).

The third component is sensation-seeking and risk-taking. Men show moderately higher values than women on a variety of measures of sensation-seeking, and the related personality measure, excitement-seeking, which shows a small difference in the male direction (Table S2). Men are also higher on risk-taking, assessed by the Eysenck Venturesome Scale (EVS: Eysenck *et al.*, 1985) (Table S2). An earlier meta-analysis (Byrnes, Miller & Schafer, 1999) found small sex

differences (in the male direction) for specific measures of risk-taking, such as driving and gambling, and medium ones for physical risk-taking. Combining two studies of real-life risk-taking by pedestrians and cyclists (Cobey *et al.*, 2013; Pawlowski, Atwal & Dunbar, 2008) produces a small overall difference in the male direction ($d = 0.34$; $N = 1715$).

The fourth component is often assessed by a variety of measures labelled as impulsivity. Meta-analyses of general measures find no sex difference (Table S2), as is the case for delay of gratification and resistance to temptation. Sex differences in behavioural measures of impulsivity occur in both directions, depending on the task. There is a very large difference in the female direction for a cognitive measure related to impulsivity, effortful control, from ages 3 months to 13 years, based on six studies; inhibitory control shows a similar, but smaller, difference at the same ages. An online sample found a small sex difference for risky impulsivity in the male direction (Cross, 2010).

(c) Evidence for evolutionary origins

A large-sample study from 53 countries found consistent and large sex differences indicating that men are more likely to take risks for potential gain than are women (Rieger, Wang & Hens, 2014). A further study showed sex differences in the male direction for risk preferences in two gambling contexts among Hadza hunter-gatherers, with small to medium effects (Apicella, Crittenden & Tobolsky, 2017).

There is evidence for a sex difference in the female direction for inhibitory and effortful control early in life (Table S2). Correlational and experimental evidence shows a link between testosterone and risk-taking. Testosterone levels were associated with risk-taking in 14 year olds (Vermeersch *et al.*, 2008) and in 18 to 24 year olds (Dariotis, Schen & Granger, 2016). Testosterone levels were correlated with a laboratory measure of impulsivity in samples of young women (Bjork *et al.*, 2001) and of both sexes (Dariotis *et al.*, 2016; Stanton, Lienen & Schultheiss,

2011). Cerebrospinal fluid levels of testosterone were positively correlated with EVS rating in a sample of personality-disordered men (Coccaro *et al.*, 2007). Testosterone administered to young men increased their impulsivity (Goudriaan *et al.*, 2010), as assessed by the Balloon Analogue Risk Test (BART). Testosterone administered to young women lessened their sensitivity to punishment (van Honk *et al.*, 2004). Cortisol levels were found to modulate the association between testosterone and risk-taking, so that risk-taking was more prominent in individuals with low rather than high cortisol levels (Mehta *et al.*, 2015).

If higher male risk-taking and impulsivity are a result of inter-male competition, we would expect them to be most pronounced in young adulthood. An analysis of mortality rates in US statistics for 2000, at five-year intervals throughout the lifespan, found that the peak male-to-female mortality ratio (M:F MR) from external causes was 4.03 and occurred in young adulthood (20–24 years), and that the ratio declined thereafter (Kruger & Nesse, 2006). Such deaths largely reflect the greater male than female engagement in risky activities at these ages (Kruger & Nesse, 2006). There is also experimental evidence that young men engaged in substantially higher risk-taking when they were paired with a young man than when alone ($d = 0.87$; Fischer & Hills, 2012); women showed substantially lower risk-taking when paired with an infant ($d = 0.71$) than when alone. Another study found that the presence of an attractive woman increased risk-taking by young male skateboarders, resulting in them having both more successes and more crash landings (Ronay & von Heppel, 2010). As has been noted previously (Section V.1*b*), the characteristic of ‘risky impulsivity’ (Campbell & Muncer, 2009) mediates the sex difference in physical and direct verbal aggression.

(3) Fearfulness

(a) Evolutionary rationale

Courage – absence of fear – is an important component of successful inter-male competition and of willingness to pursue dangerous activities. There will therefore have been stronger selection for overcoming fear reactions in men than women, in particular in resisting fear of physical danger. The same selection pressures could have operated to raise the pain threshold in men and lower it in women, since pain has evolved to signal physical danger. Sex differences in fear have also been attributed to stronger selection on female than male mammals to avoid danger, given their greater role in parental care (Campbell, 1999, 2009; Cross & Campbell, 2011). Thus, women’s greater fear reactions have been attributed to selection for harm avoidance.

(b) Sex differences

The results in Table S3 show small to medium differences in the female direction for general measures of fear. The scales used in these studies over-represent phobic items, and conflate fear with anxiety: therefore Campbell *et al.* (2016) devised a scale avoiding these and other confounds, so that fear was assessed as “a situated and short-lived emotional response to risky or potentially dangerous situations that might be encountered in the real world” (p. 212). This measure, the Situated Fear Questionnaire (Campbell *et al.*, 2016), showed very large sex differences in three samples from the UK and Romania (overall $d = -1.16$; $N = 869$). Men also show a moderately higher pain threshold and substantially greater pain tolerance than women (Table S3).

(c) Evidence for evolutionary origins

The finding that there are large sex differences in measures of real-life fear suggests that the evolutionary explanations outlined above are plausible. In the nearest extant relative of humans, the chimpanzee, large sex differences were found in the female direction for ratings of timidity in a small-sample field study (Buirski, Plutchik, & Kellerman, 1978). Sex differences in fear show cross-national consistency (Brebner, 2003) and are found during childhood (Else-Quest *et al.*,

2006). Jacklin, Maccoby & Doering (1983) found that, in boys, an absence of timidity at 6, 9, 12 and 18 months was correlated with higher levels of testosterone in umbilical cord blood.

Testosterone has a fear-reducing effect in other mammals (Aikey *et al.*, 2002; Boissy & Bouissou, 1994; Bouissou & Vandenheede, 1996; Vandenheede & Bouissou, 1993). When administered to young women, it significantly reduced unconscious fear in response to an emotional face (van Honk, Peper & Schutter, 2005), and fear-induced startle (Hermans *et al.*, 2006a). Testosterone also lessened gaze avoidance in women who showed social anxiety (Enter *et al.*, 2016; Terburg *et al.*, 2016).

(4) Visuospatial ability and object-location memory

(a) Evolutionary rationale

This section concerns differences in spatial abilities. The first is visuospatial ability, in particular mental rotation of spatial images, where men perform better than women. The second is object-location memory, remembering the spatial location of objects in an array, where women outperform men. The first has been attributed to inter-male competition and the second to selection for a low-risk female reproductive strategy [Ecuyer-Dab & Robert (2004a) following Campbell (1999)], involving a small home range and restricting attention to nearby spatial cues. Thus, the same underlying explanations apply as those offered for aggression, impulsivity and fear.

An alternative explanation for male visuospatial ability involves an advantage when ranging over larger and potentially unknown territories for hunting (Kolakowski & Malina, 1974; Wynn, Tierson & Palmer, 1996). Although this may have been a selection pressure later in human evolution, a link between male polygynous mating, larger home ranges, and greater spatial skills has been found widely in mammals (Gaulin & Fitzgerald, 1986, 1989; Gaulin & Hoffman, 1988; Geary, 1995; Perdue *et al.*, 2011) suggesting that this sex difference is likely to be of earlier origin than hunter–gatherer specialization, i.e. that greater visuospatial ability arose from an advantage

provided by larger ranges in inter-male competition. An explanation for the advantage to females of an enhanced object-location memory is that it is an adaptation for gathering plant food (Silverman & Eals, 1992); another possibility (Geary, 2010, p. 399) is that it is related to women having a better memory for personal experiences ('episodic memory'; Herlitz & Rehnman, 2008), which may be a consequence of their greater social skills (Herlitz, Nilsson & Bäckman, 1997; Section VI).

Sex differences in some mathematical abilities have been linked to visuospatial abilities, particularly mathematical problems that require such abilities, where there is a significant sex difference (Halpern *et al.*, 2007). Geary (1996) proposed an interactive model whereby sex differences in some mathematical abilities have arisen from sexually selected tasks being co-opted for new tasks in novel environments, such as the teaching of mathematics. On this view, certain latent abilities, originally adaptive in the context of spatial skills for route-finding, manifest themselves as mathematical skills. Another important part of Geary's (1996) model is the impact of sex differences in person-centred and object-centred orientations (see Sections V.5 and VI), which could bias males towards mechanical and abstract interests, and females towards social ones.

(b) Sex differences

Table S4 shows sex differences in tests involving the mental rotations of visual patterns, where d values are medium to large in the male direction. Mental rotation involves keeping a three-dimensional image in the working memory while making mental transformations (Halpern *et al.*, 2007), and is linked with navigation, route-finding, and performance in computerized labyrinth tests (Geary, 1996; Kimura, 2002; Silverman *et al.*, 2000). Table S4 also shows differences in visuospatial perception and line angle judgment, which are medium in size, and in spatial visualization, which is small in size. Again, these are in the male direction.

Tests of memory for objects involve showing drawings of an array of objects to participants, asking them first to remember the objects when further ones are added ('object identity

memory task'), and second to identify which objects had been moved when shown an array of the same objects in different places ('object location memory task'). The first series of studies (Eals & Silverman, 1994; Silverman & Eals, 1992) reported a large female superiority in object-location memory in five adult samples (mean weighted $d = -0.71$), with more varied findings in object-identity memory. However, a meta-analysis of these and other studies (Voyer *et al.*, 2007), and a 40-nation survey (Silverman, Choi & Peters, 2007) both found only small overall differences in the female direction for object-location memory (Table S4).

Table S4 also shows findings for mathematical abilities, which are variable but mostly show a small difference in the male direction if a difference is present. Concentrating on mean differences is likely to underestimate any more substantial differences at the ends of the distribution, since there is a wider variation in this ability among males than females (e.g. Feingold, 1992*b*; Hedges & Nowell, 1995). Studies of mathematically precocious pre-schoolers, and mathematical high-achievers find that males substantially outnumber females. Thus there is clear male superiority on more difficult mathematical problems (Geary, 1996; Halpern *et al.*, 2007; Kimura, 2002; Stoet & Geary, 2013). The issues surrounding sex differences in the distribution of mathematical abilities are beyond the scope of this review and readers are referred elsewhere (Geary, 1996; Stoet & Geary, 2012).

(c) Evidence for evolutionary origins

In non-human mammals there is a link between male polygynous mating, larger home ranges, and greater spatial skills. Applying this to humans, it is predicted that men will have larger home ranges than women and that their range size will be linked to their spatial ability. Both predictions were supported in a modern western sample (Ecuyer-Dab & Robert, 2004*b*), and in two samples of traditional cultures in Namibia (Vashro & Cashdan, 2015). Larger male than female ranges have also been found for extant hunter-gatherers (Ecuyer-Dab & Robert, 2004*b*, p. 235). From several

hunter–gatherer data sets, it was concluded that “for all societies with appropriate data, males, on average, travel considerably farther than females in a lifetime but especially in young adulthood, when competition for mates is greatest” (MacDonald & Hewlett, 1999, p. 513).

If object-location memory is an adaptation for gathering plant food, we would expect it to co-vary with plant-gathering ability and thus predict a female-biased sex difference. For object-location memory, there were sex differences in the female direction in a study of 40 nations (Silverman *et al.*, 2007), and in 35 cases the difference was statistically significant. Evidence from other western samples is conflicting (Neave *et al.*, 2005; Stoet, 2011). A study of Hadza hunter–gatherers (Cashdan *et al.*, 2012), and one of two other traditional African cultures (Vashro & Cashdan, 2015) found that men were better at object-location memory than women. Cashdan *et al.* (2012) found plant-gathering ability and object-location memory to be unrelated in women. Consistent with this, Stoet (2011) argued that it is unnecessary for women to have specific adaptations for gathering, or for them to be more efficient than men at such tasks: their role in gathering plant food in many societies may simply result from adaptations to child care and their lesser size and strength that would make gathering convenient for women, rather than something for which they possess specific skills [see also Wood & Eagly (2002, 2012) for a similar view of behavioural sex differences in general].

A male-biased sex difference in visuospatial ability has been found in a range of nations and cultures, including Australia, India, Indonesia, Japan, Norway, Sierra Leone, South Africa, Sweden and the UK (e.g. Berry, 1966, Lynn, 1994; Silverman & Phillips, 1998). Berry (1966) found no sex difference among the Inuit of Baffin Island, and subsequently among several other subsistence-level people (Berry, 1971). However, there was a medium-sized difference in the male direction for visuospatial ability ($d = 0.50$) in the Hadza hunter–gatherers studied by Cashdan *et al.* (2012), and in a subsequent study (Vashro & Cashdan, 2015) of traditional people in Namibia ($d = 0.44$). Two

cross-national studies, of 53 (Lippa, Collaer & Peters, 2010) and 40 nations (Silverman *et al.*, 2007), both found a consistent sex difference in mental rotation.

Sex differences in spatial abilities such as mental rotation are found early in life. Two studies found substantial sex differences for two types of mental rotation task, at 3 to 4 months (Quinn & Liben, 2008; $d = 1.33$, calculated from their t values using CMA) and at 5 months (Moore & Johnson, 2008; $d = 0.66$). Very large sex differences were found in spatially related play in 7 year olds (Grimshaw, Sitarenios & Finegan, 1995; $d = 1.31$, calculated from their one-way F values using DSTAT: Johnson, 1989), and in two types of spatial tasks at 7 to 10 years of age (Auyeung *et al.*, 2012; $d = 0.60$ and 1.15). However, small differences were found from 4 to 7 years of age in another study ($d = 0.25$; Levine *et al.*, 1999), and a meta-analysis (Voyer *et al.*, 2007) found no significant sex differences before puberty.

There is mixed evidence for an influence of prenatal androgens on visuospatial ability, (Kimura, 1996). Girls who had experienced high androgen levels prenatally (from congenital adrenal hyperplasia) showed better visuospatial performance than their unaffected siblings ($d = 0.80$ – 0.94 , calculated from means and standard deviations in the source, using CMA), when measured between 13 and 23 years of age (Resnick *et al.*, 1986). A study involving girls subject to excess androgens *via* exposure to diethylstilbestrol found no influence on spatial performance (Hines & Sandberg, 1996). Both studies involved small samples, and involved assessment at one time point only. Two longitudinal studies (Auyeung *et al.*, 2012; Grimshaw *et al.*, 1995) measured foetal testosterone levels in non-clinical samples. The first found a positive association for one spatial task (the Embedded Figures Test), but not another (mental rotation); the second found a positive association among girls for mental rotation. There is therefore mixed evidence for an organizational effect of androgens on visuospatial ability.

Evidence for the effects of activational hormones – both testosterone and oestrogen – comes from clinical and non-clinical samples. A substantial increase in visuospatial performance occurred

among female-to-male transsexuals treated with androgens for 3 months (van Goozen *et al.*, 1994, 1995) and for longer periods (Slabbekoorn *et al.*, 1999). A summary of 13 correlational studies in non-clinical populations up to the mid-2000s indicated mixed results (see Table 1 in Thilers, MacDonald & Herlitz, 2006), although three of five male samples that exceeded 100 participants showed a positive association between testosterone and spatial performance. In their empirical study, Thilers *et al.* (2006) found a positive association between visuospatial ability and testosterone that became larger with age in a Swedish sample of men ($N = 1107$) aged 35 to 90 years. Dettenborn *et al.* (2013) also found a positive association in a small sample of middle-aged men. Overall, there is reasonable evidence for a positive association between testosterone and visuospatial performance in men.

Consistent with these findings, a double-blind placebo-controlled cross-over study found that women's spatial performance improved following testosterone administration (Aleman *et al.*, 2004). By contrast, visuospatial performance decreased following high doses of testosterone (O'Connor *et al.*, 2001) in a community sample of men. These and other conflicting findings could be reconciled if there is a curvilinear relationship between testosterone levels and spatial ability across the whole range for both sexes (Moffat & Hampson, 1996; Shute *et al.*, 1983): thus in women and older men, higher testosterone levels will be associated with better spatial performance, whereas among younger men, where circulating levels are higher, higher testosterone levels will be associated with lower performance. However, this hypothesis is contradicted by findings of a positive association among younger men (e.g. Christiansen & Knussmann, 1987; Hooven *et al.*, 2004; Silverman *et al.*, 1999) and a lack of association between testosterone and visuospatial performance in several studies [those tabulated by Thilers *et al.* (2006)].

Two studies have reported a negative association between spatial performance and oestrogen levels (Hampson, Levy-Cooperman & Korman, 2014; Hausmann *et al.*, 2000), with

performance better during menses than during the mid-luteal phase when oestrogen levels are higher (e.g. Kimura, 1996; Phillips & Silverman, 1997).

(5) Object-centred orientation

(a) Evolutionary rationale

An interest in objects or things, and how physical systems work, which underlies an interest in science and technology is more pronounced in males than in females (McGuinness & Pribram, 1979; Su, Rounds & Armstrong, 2009). Baron-Cohen (2003, 2011) characterized the essential psychological sex difference as ‘systemizing’, contrasting it with the ability to empathize (see Section VI). Systemizing is defined as the ability to see patterns in systems and to understand how they work, and Baron-Cohen argues that this has formed a key aspect of the human ability to modify the natural world in an adaptive manner. There are several ways in which systemizing could have conferred a selective advantage to males during hominin evolution (Baron-Cohen, 2003, pp. 118–126): (1) making and using tools; (2) hunting and tracking; (3) trading; and (4) achieving and maintaining power or status. These attributes would all affect reproductive success, and therefore would have been additional traits on which inter-male competition could act.

(b) Sex differences

All four variables assessing object-centred orientation show very large differences in the male direction (Table S5). The measures are: (1) systemizing, measured by the Systemizing Quotient Questionnaire (Baron-Cohen *et al.*, 2003), which is strongly related to an interest in technology and science (Nettle, 2007); (2) occupational interests (from a list that were mostly object or person-centred; Lippa, 2010); (3) engineering interests; and (4) ‘Thing Orientation’ (from the people–things scale: Su *et al.*, 2009).

(c) Evidence for evolutionary origins

In a study of 53 nations, men consistently scored much higher than women on systemizing (Manning *et al.*, 2010). There is also evidence for early sex differences in attributes associated with object-centred orientation, when this is contrasted with person-centred orientation (Section VI). Twelve-month-old infant boys showed a greater relative preference than infant girls for a car than for a moving face ($d = 0.64$: Lutchmaya & Baron-Cohen, 2002). At 4 years of age, boys scored higher than girls ($d = 0.64$) on restricted interests, an attribute related to systemizing (Knickmeyer *et al.*, 2005). When these children were 6 to 9 years of age, boys also scored higher than girls ($d = 0.69$) on a measure of systemizing designed for children (Auyeung *et al.*, 2006). In the same longitudinal study, foetal testosterone level was a strong predictor of restricted interests at 4 years of age, and of systemizing at 6 to 9 years, independent of other variables, including the child's sex (Chapman *et al.*, 2006). A further study (Belz, Swanson & Berenbaum, 2011) found that androgenized girls showed more interest in things ($d = 0.75$), systemizing ($d = 0.64$) and scientific occupations ($d = 0.56$) than their unaffected siblings.

VI. SOCIAL RELATIONS AND RELATED ATTRIBUTES

(1) Characteristics directly associated with social relations

(a) Evolutionary rationale

Women are viewed as being more interested in, and having better skills for, social relations. There are three main ways of characterizing these differences, and their evolutionary origins. One is that women tend to show interdependence in their construals of social relations, whereas men tend to show independence in their self-construals (Cross & Madson, 1997). This follows earlier characterization of women and men as being 'communal' and 'agentic', respectively, in their behaviour (e.g. Eagly, 1987). An alternative view is that the characteristic of 'empathy' is central to sex differences in personal relations (Baron-Cohen, 2003, 2011), and that it contrasts with the male

characteristic of ‘systemizing’ (see Section V.5): Baron-Cohen (2003) regarded this as the “essential difference” between the brains of women and men.

A radically different view (Baumeister & Sommer, 1997) is that men and women are equally social, but in different ways: women have a small number of close relationships whereas men relate to other men in larger groups. Women’s social relations involve skills such as empathy and decoding non-verbal signals, whereas men’s social relations involve skills for negotiating status and power relations. This characterization follows earlier accounts of boys’ and girls’ social relations (Archer, 1992), and more recent findings supporting the view that the sex difference lies in social styles rather than in greater or lesser degrees of engagement in social relations (Benenson, 2009; Benenson *et al.*, 2009; Benenson, Morganstein & Roy, 1998).

This section investigates how women are adapted for different types of social relations relative to those of men. A range of relevant attributes (social skills and interests, empathy, helping behaviour, and aspects of morality) are thus all likely to be more characteristic of females. Aspects of leadership style, such as task-oriented leadership, can be viewed in relation to male–male coalitional competition.

A general difference in the degree of sociability may reflect greater female than male parental investment (a general mammalian feature), whereas the detailed differences could have originated during hominin evolution when men became specialized for operating in larger groups and women for fewer closer relationships. One suggestion is that women’s adaptations to form close relationships arose as an adaptation for relating to other women (Baron-Cohen, 2003, pp. 126–130; Hrdy, 2009). This has been attributed to patrilocal dispersal in humans, which would have led to women having to negotiate social relations with unrelated individuals (e.g. Geary *et al.*, 2003; Smuts, 1995). Others have doubted this origin, citing evidence for a mixed and flexible pattern of dispersal among modern hunter–gatherers (Alvarez, 2004; Hrdy, 2009, pp. 239–250; Marlowe,

2004). However, genetic analyses do suggest patrilocal dispersal in modern hunter–gatherers (Destro-Bisol *et al.*, 2004), and in Neanderthals (Lalueza-Fox *et al.*, 2011).

An emphasis on bonding with other women can be questioned on the grounds that a meta-analysis of cooperation (Balliet *et al.*, 2011) found that women cooperate well in mixed-sex settings but show very low levels of cooperation with other women. Thus, men cooperate with both sexes, whereas women cooperate with men, but not well with other women. One evolutionary scenario that can be derived from such findings (R.F. Baumeister, personal communication) is that following the evolution of pair-bonding and paternal care in the hominin line, initially in the form of defence and carrying (Gettler, 2010), women developed interpersonal skills so as to be able to relate to, and bond with, male providers of paternal care and of resources. Men, on the other hand, obtained their resources partly from group hunting, and they had to defend their resources in group fighting: thus, male sociality is more oriented towards large groups. In this scenario, female social skills are derived from the need to form an attachment to a male provider rather than from adaptations for bonding with other women.

Baron-Cohen (2003) also argued that men’s comparative lack of empathy would be advantageous in the violent power struggles that have been common throughout human history (Betzig, 1986, 1992; Pinker, 2011), and that possibly have their origins in pre-human evolution in the light of violent inter-group attacks by chimpanzee males (Wrangham, 1999; see also Geary, 1996, p. 235). Such conflict would have arisen due to the involvement of men in larger social groups involving hierarchies, and in the hostile interactions between such groups.

(b) Sex differences

The first section of Table S6 shows sex differences in social interests and social skills. Women show higher values than men for all of these measures. Those for the people-things dimension and social interests are in the large range, and those for skills (i.e. face recognition, emotional

intelligence, and decoding non-verbal cues) are mostly in the medium range. The measures in the second section of Table S6 concern social interactions in dyads or small groups: there are higher female scores, in the medium range, for the following: (1) degree of peer attachment; (2) affiliation motivation; (3) smiling; (4) seeking emotional support; and (5) disclosure to same-sex others. Differences for agreeableness, friendship expectations, and intimacy in relationships are in the small range, again higher in women. Measures of touch initiation, personal space and adult attachment style showed no differences.

The third section of Table S6 includes a measure of empathizing, the Empathizing Quotient (EQ) (Baron-Cohen *et al.*, 2003), for which a cross-national survey showed a large female advantage. An ability measure of empathizing provided by the ‘Reading the Mind in the Eyes’ test (Baron-Cohen *et al.*, 2001), involving inferring emotional states from depictions of a person’s eyes, showed only a small difference in the female direction.

From Table S6, women show more helping behaviour, to a small degree. There is practically no difference in cooperation, as measured in social dilemma tests. As posited in Section VI.1a, men are likely to cooperate in same-sex interactions whereas women are more cooperative in mixed-sex interactions: the entries in Table S6 support this, although both differences are small in magnitude. Table S6 also shows differences in measures related to morality. There were medium differences in the female direction for basing moral judgments on norms rather than consequences, and for moral self-esteem; men had more positive attitudes to cheating (a small effect). There were small differences for moral orientation (women showing more care-orientation), and for moral sensitivity, and justice-based moral reasoning, again in the female direction.

Measures of emergence of leaders in a group mostly show small differences: when there is a specific task, men lead to a greater extent than women (to a medium extent), whereas when groups have no structured task, women tend to become leaders (to a small extent). Differences in measures of leadership effectiveness depend on who is rating the effectiveness. Women tend to adopt more

democratic leadership styles than men. Finer-grained distinctions in leadership style yield differences in both directions (Table S6). Negotiation outcome yields conflicting findings for sex differences (Table S6). Men influence others more than women do, to a small extent (Table S6).

(c) Evidence for evolutionary origins

Two large-scale studies of captive chimpanzees (King, Weiss & Sisco, 2008; Lutzman *et al.*, 2015) found medium-sized differences for agreeableness, both in the female direction. The smaller human sex difference in agreeableness (women scoring higher than men) is consistent across nations (Costa & McCrae, 1992; Lippa, 2008; Schmitt *et al.*, 2008). In a study of 53 nations, women consistently scored much higher than men on empathizing (Manning *et al.*, 2010).

There are early sex differences in attributes associated with a person-centred orientation, when this is contrasted with an object-centred measure. Thus, 12-month-old infants showed a substantial sex difference ($d = -0.64$) in their relative preference for a moving face over a moving car (Lutchmaya & Baron-Cohen, 2002). At the same age, there was a sex difference in the female direction ($d = -0.53$) for eye contact with parents (Lutchmaya, Baron-Cohen & Raggatt, 2002). In the same sample, at 4 years of age, early signs of understanding others' mental processes were assessed by asking the children to describe cartoon depictions of moving triangles which interacted in a way that suggested psychological motives and emotions (Knickmeyer *et al.*, 2006). Girls used more mental ($d = -0.50$) and affective ($d = -0.82$) terms to describe the cartoons, and more intentional propositions ($d = -0.62$), whereas boys used more neutral terms ($d = 0.63$). When the children were 6 to 9 years of age, there was a large sex difference ($d = -0.76$) in a child's version of the EQ, and a smaller one ($d = -0.31$) in the Reading the Mind in the Eyes test (Chapman *et al.*, 2006).

These comparisons involving children should have the caveat that girls grow up faster than boys, a characteristic of sexual selection (Andersson, 1994), so that in theory any female

advantages may not reflect real sex differences. However, in these studies, boys showed advantages in other domains (reflecting their orientation to objects), and there is evidence that the measures used are related to testosterone levels. For example, in the same longitudinal study, there was an association between eye contact and foetal testosterone levels at 12 months of age (Lutchmaya *et al.*, 2002), which was negative in the lower testosterone range and positive in the higher range. In the cartoon-description study (Knickmeyer *et al.*, 2006), foetal testosterone level was negatively correlated with the use of intentional propositions, and positively with the use of neutral propositions, at 4 years of age. At 6 to 9 years, both the EQ and the reading-the-eyes tests showed a negative association with foetal testosterone levels (Chapman *et al.*, 2006), although for the EQ this was restricted to boys.

It has long been known that male primates show a surge in testosterone during the first few months of postnatal life, after which there is a return to low levels until puberty (Forest *et al.*, 1974; Winter *et al.*, 1976), and that this applies to humans (Dixson, Brown & Nevison, 1998). Urinary testosterone levels, measured during the first 6 months of postnatal life in boys, were positively correlated ($\rho = 0.54$) with a measure of gender-typed activities at 14 months (Lamminmäki *et al.*, 2012). Playing with a doll or a train showed the expected sex differences; playing with the doll was negatively correlated with testosterone levels ($\rho = -0.48$) in boys, and playing with the train was positively correlated with testosterone levels ($\rho = 0.43$) in girls, whose levels are much lower than those of boys during the early postnatal months.

There is both correlational and experimental evidence for a link between testosterone and measures of empathy later than this early postnatal stage. Nine-year-old girls showed a negative correlation between circulating testosterone levels and cognitive empathy (Pascual-Sagastizabal *et al.*, 2013). In a laboratory task designed to foster self-disclosure, lower basal testosterone and decreases in testosterone levels during the task were both associated with greater perceived closeness (Ketay, Welker & Slatcher, 2017). In an experimental study, young women administered

with testosterone showed less unconscious facial mimicry in a masked Stroop test than did controls, a finding attributed to lowered empathy (Hermans, Putman & van Honk, 2006b).

(2) Language and related attributes

(a) Evolutionary rationale

Language skills presumably evolved much later than non-verbal skills: sex differences have been attributed to the central importance of language for female social relations (Geary, 2010, pp. 362–264), although we should add the caveat that this is for small-group or dyadic relations. Widespread reading and writing obviously arose in recent historical times. Here too there are sex differences in the female direction and they are likely to be linked with differences in language ability, which in turn arose from social skills. It is useful to distinguish in an evolutionary context between the primary results of selection, such as sex differences in size and fighting ability, and secondary effects, such as mathematical ability, and skills in reading or writing (Geary, 1996), which are presumably expressions of primary effects visible in modern environments such as schools.

(b) Sex differences

Table S7 shows evidence for sex differences in overall verbal abilities, and for language ability, speech, vocabulary, verbal reasoning, reading, writing, and spelling. There are variable findings for overall verbal abilities, a medium difference in the female direction for language ability, and a small one for speech production, or the ability to put thoughts into words. There are variable differences in aspects of conversation. Women show more affiliative and tentative speech, whereas men are more talkative and interrupt more, although all these differences are small. There is little sign that either sex is more talkative than the other. Medium-sized differences in the female direction are found for reading, writing, and spelling. Reading showed a medium difference in a large-scale study of 15-year-olds from 75 nations (Table S7), and a small difference in

representative US samples of 17-year-olds (Table S7). Two large international surveys found that the sex difference in reading occurs from around 8 years (Halpern *et al.*, 2007), and that there are more girls at the higher end of the distribution (Halpern *et al.*, 2007; Stoet & Geary, 2013).

(c) Evidence for evolutionary origins

Kung *et al.* (2016) found that salivary testosterone levels measured at 1 to 3 months of age were negatively correlated with expressive vocabulary at 16 to 30 months, and that they mediated the higher values in girls than in boys at this age, suggesting that any differences cannot be attributed to the slower development of boys than girls. There is some evidence from adults that verbal fluency is lower when circulating testosterone levels are higher: for example, a negative correlation in a large sample ($N = 1276$) of women aged 35 to 90 years (Table 1 in Thilers *et al.*, 2006); a decline following 3-months of testosterone administration in female-to-male transsexuals (van Goozen *et al.*, 1994, 1995); and an improvement when women's testosterone levels were reduced in a small clinical sample (Schattmann & Sherwin, 2007). In apparent contrast, another study found greater verbal fluency following injections of supra-physiological levels of testosterone in a non-clinical sample of men (O'Connor *et al.*, 2001). As in the case of visuospatial ability (Section V.4), it is possible that circulating testosterone has a curvilinear effect, so that there would be lower verbal fluency at both low and high hormone levels. At present this is highly speculative, particularly in view of evidence against such a pattern for visuospatial performance. Studies involving female hormones have produced mixed results for verbal fluency (Geary, 2010, p. 367).

(3) Depression and anxiety

(a) Evolutionary rationale

Women's higher rates of depression and anxiety, in both sub-clinical and clinical ranges, have been attributed to their different approach to personal relationships, in this case their greater sensitivity in

such relationships (Geary, 2010, p. 416). Increased depression in teenage girls has also been linked to indirect aggression, which is pronounced in groups of girls of this age (Geary, 2010, p. 416), operates in the context of their social groups, and may be linked to avoidance of escalated aggression (see Section V.1). It is likely that both selection pressures are in operation.

(b) Sex differences

Women show more depression, anxiety, and related attributes, than do men, to a small to medium extent (Table S8). Earlier narrative reviews (Nolen-Hoeksema, 1987; Weissman & Klerman, 1977), covering studies from the US and other geographical regions, found a mean ratio of two women to every one man for depressive disorders, suggesting a larger difference than for depressive symptoms, or alternatively a larger difference in the tails of the distribution despite a more modest mean difference. The most recent meta-analysis of representative samples from 90 nations (Salk, Hyde & Abramson, 2017) confirms these earlier findings, with an overall effect size in the small range. There are also small or medium-sized differences in the female direction for sadness, and for rumination, the coping style associated with depression (Table S8). Anxiety and social anxiety show medium-sized differences in the female direction. There is a small difference in neuroticism, one of the ‘Big Five’ personality measures related to anxiety and depression [e.g. the Revised NEO Personality Inventory (NEO-PI-R); Costa & McCrae, 1992]: the value shown in Table S8 is the weighted mean from a combination of one meta-analysis and nine large-scale surveys including two of over 50 nations. Details of these studies, together with the other four personality measures are provided in Table S13). There are small differences in the female direction for shame and guilt.

(c) Evidence for evolutionary origins

Two large-scale studies of captive chimpanzees (King *et al.*, 2008; Latzman *et al.*, 2015) found small differences in the female direction for neuroticism, corresponding with the small differences

reported for humans. There is cross-national consistency in the sex differences for depressive symptoms (Gater *et al.*, 1998; Salk *et al.*, 2017), anxiety (Abdel-Khalek & Alansari, 2004), social anxiety (Caballo *et al.*, 2014), anxiety disorders (Lindal & Stefánsson, 1993), and neuroticism and its facets anxiety and depression (Costa & McCrae, 1992; Lippa, 2008; Schmitt *et al.*, 2008). A large-sample multi-nation meta-analysis of depressive symptoms (Salk *et al.*, 2017) showed a peak at age 16 ($d = -0.47$), followed by a small decline and then stability in adulthood, confirming a pattern found in other studies (Twenge & Nolen-Hoeksema, 2002; Patten *et al.*, 2016). Sex differences in anxiety disorders are also found during childhood (Lewinsohn *et al.*, 1998; McLean & Anderson, 2009; Salk *et al.*, 2017). Testosterone administration was found to increase functional connectivity in cortical regions of the brain where low connectivity has been found in depressed patients (Schutter *et al.*, 2005).

VII. THE CONSEQUENCES OF FEMALE CHOICE

(1) Sexuality

(a) Evolutionary rationale

One consequence of unequal parental investment (Trivers, 1972) is greater discrimination by females when choosing a mate, and a male preference for more sexual partners. Although this has been to some extent mitigated in humans by the evolution of male parental care (Geary, 2000), males of many monogamous species retain traits associated with polygynous mating (Andersson, 1994, pp. 157–158; Trivers, 1972). This is possibly reflected in human males by a greater liking for impersonal sex, and its substitutes, such as pornography use and masturbation.

(b) Sex differences

In the pre-AIDS homosexual communities of the US, gay men had far more sexual partners than heterosexual men, whereas lesbians had a similar number to women in heterosexual

relationships, leading Symons (1979) to conclude that a male preference for a greater variety of sexual partners is constrained by a female preference for exclusive longer-term relationships. Subsequently, an individual-difference measure of the degree to which people are willing to engage in uncommitted sex was designed (the sociosexuality index, SOI; Simpson & Gangestad, 1991). The SOI shows wide individual variation in both sexes, but overall men show higher scores on this measure, with medium or large effect sizes (Table S9). In a revised version of the SOI (Penke & Asendorpf, 2008), there are three components: behaviour, attitude and desire. Consistent with Symons' (1979) argument, the sex difference in the male direction was large for desire but close to zero for behaviour (for details, see footnote d in Table S9).

The following sex differences were identified in a systematic review of whether men have a stronger sex drive than women (Baumeister, Catanese & Vohs, 2001): (1) men masturbate more than women; (2) they have more permissive sexual attitudes; (3) they think and fantasize more about sex than women do; (4) they use pornography more; (5) they desire sex more frequently; (6) they want sex earlier in a relationship; (7) they want and report having more partners; (8) they prefer more varied sexual activities; (9) they are more likely than their heterosexual partners to want more sex; and (10) they adapt less readily to periods of abstinence.

Many of these differences are reflected in the measures of sexuality found in meta-analyses and surveys (Table S9). Men showed more frequent pornography use, greater sex drive, and masturbation, typically to a medium or large extent. Men report a greater interest in casual sex, and desiring more partners over specific time periods, effects typically medium or large, with some studies showing smaller values (Table S9). Men also perceive young women to be more seductive, promiscuous and flirtatious, than women do (to a small or medium degree), indicating that men tend to view young women in a sexualized way. Men also show more mate poaching, again to a medium extent, and this is consistent with their greater interest in sexual variety (Table S9).

(c) Evidence for evolutionary origins

Men's greater preference for casual relationships is found across more than 50 different nations (Schmitt & ISDP, 2003; Lippa, 2009). Since sexuality is characteristic of adults, the criterion of early appearance in development does not apply. Sexuality develops at puberty in both sexes, following rises in gonadal hormones (Tanner, 1989). Testosterone facilitates sexual behaviour in boys (Halpern, Udry & Suchindran, 1998). Androgens administered to surgically menopausal women increase the intensity of their desire and arousal, and the number of sexual fantasies they experience (Sherwin, Gelfand & Brender, 1985). In men, higher testosterone levels are associated with lower marital satisfaction (Julian & McHenry, 1989), lower investment in spouses (Gray *et al.*, 2002), more partners (van Anders, Hamilton & Watson, 2007), and a greater interest in erotic stimuli (Daitzman & Zuckerman, 1980).

Baumeister & Twenge (2002) reviewed evidence to show that where there is an unequal OSR (see Section V.1c), the majority sex modifies their behaviour in the direction of the minority's preferences: thus, when there are fewer men, women's mate choices become less discerning and more short term; when there are fewer women, men's mate choices becomes more restrained and long term. Both situations lead to a reduction in sex differences in sexual behaviour for these measures. Thomas & Stewart-Williams (2017) investigated the possibility of changes in preferences for short- and long-term mates in an experimental study. When a prime for parental care was present, in the form of a video of men and women caring for infants, preference for a long-term relationship was enhanced in women. When a prime for wealth was used, both sexes showed an enhanced preference for short-term mates. Using a prime for danger increased both long-term mating interest (as predicted) but also short-term mating interest.

(2) Mate-choice criteria

(a) Evolutionary rationale

Men and women differ in their reproductive capacity throughout life: men's ability to fertilize women shows only a gradual decline with age whereas women's ability to bear children ceases at the menopause. In addition, a mother's youth and health are more important than a father's for the developing offspring. These considerations, and the importance for offspring survival of having a father who can provide for and protect the family, have led to predictions about sex differences in preferred mate-choice attributes (Buss, 1987, 1989, 2012, pp. 105–173): thus, when choosing a long-term mate, men should regard youth and good looks as important and women should regard financial prospects, industriousness and social status as important. These predictions are specific to humans as they are based on the presence of the menopause and on the need for long-term relationships, both of which are absent in humans' nearest primate relatives.

(b) Sex differences

Table S10 shows sex differences in mate-choice preferences. These range from small to very large for most of the attributes studied. Women show a much greater preference for an age difference than men do, a medium or high preference for good financial prospects, ambition/industriousness, and a small preference for dominance/social status. Men show a medium preference for looks and cook–housekeeper skills, and a small preference for chastity. These preferences were present in a 37-cultures study (Buss, 1989), but more restricted samples often show smaller differences for some characteristics, such as 'cook–housekeeper', but not for others, such as age difference (Table S10). A re-analysis of the 37-cultures data showed that when viewed as a coherent set of related attributes (see Section II), the resulting sex difference is in the very large range (Conroy-Beam *et al.*, 2015).

(c) Evidence for evolutionary origins

The sex differences in preferred mate-choice characteristics are found cross-nationally: Buss's (1989) study involved 37 nations, and the subsequent BBC internet study 53 nations (Lippa, 2007, 2008, 2009). Although sex differences in mate-choice criteria occur consistently across nations, their magnitude varies considerably, and is related to a national measure of women's societal power [Eagly & Wood (1999); see Zentner & Mitura (2012) and Schmitt (2012) for qualifications]. Mate choice is characteristic of adults, so presumably develops after puberty, although there are no studies of possible hormonal influences.

(3) Sexual conflict

(a) Evolutionary rationale

Greater female discrimination in choosing mates leads to a conflict between the sexes' fitness interests. This, together with greater male size and strength, has led to male sexual coercion being widespread in mammals. Coercion can occur at all stages of the reproductive cycle, from copulation through to relations between parents in bi-parental species. Clutton-Brock & Parker (1995) described three forms of sexual coercion in animals: (1) forced copulation; (2) harassment: repeated attempts to copulate with an unreceptive female; and (3) physical intimidation and punishment. The equivalents of these in humans are: (1) rape and sexual aggression; (2) sexual harassment (persistent unwanted sexual advances); and (3) male violence to partners.

Sexual coercion is not an area where there has been much interest in measuring sex differences since it is assumed (consistent with the evolutionary analyses) that male victimization is generally negligible. Evolutionary accounts of rape and sexual coercion have concentrated on the adaptive significance and motivational basis of coercive sex by males to females (Malamuth, 1996; Malamuth *et al.*, 1995; Thornhill & Thornhill, 1992). These accounts have identified individuals prone to sexual coercion as possessing two characteristics more common among men than women: an interest in impersonal sex and a willingness to use force to obtain what they want (Malamuth,

1996; Wilson & Daly, 1992b). Another male-typical characteristic, lack of empathy (Baron-Cohen, 2011), is also likely to be involved.

Physical aggression to partners has been viewed as equivalent to male mate-guarding in non-human animals (Wilson & Daly, 1992a); sexual jealousy has been viewed similarly to mate-guarding, i.e. the emotional consequence of paternity uncertainty (Wilson & Daly, 1992a, 1998) and thus as a male characteristic. An alternative view (Buss *et al.*, 1992) involves the different circumstances evoking sexual jealousy in the two sexes: whereas men (as a result of paternity uncertainty) show more jealousy when their partners are sexually unfaithful, women show more when their partners are emotionally unfaithful (and hence likely to divert time and resources to another woman).

(b) Sex differences

Evolutionary theory and common sense indicate that male victimization from sexual coercion is likely to be minimal. Consistent with this, women form the majority of victims of rape and other forms of sexual coercion (Table S11), producing very large effect sizes for sex differences. Nevertheless, several large-scale surveys indicate that men form a sizeable minority of victims of sexual aggression, including rape (Table S11), leading to a reduction in the effect size for sexual victimization. However, most incidences of sexual coercion, including rape, involve male perpetrators whether the victim is male or female (Basile *et al.*, 2007; Black *et al.*, 2011; Tjaden & Thoennes, 1998). A study of German students (Krahé & Berger, 2013) reporting their experiences since they were 14 years old found only a medium-sized sex difference in sexual coercion for heterosexual sexual encounters ($OR = 0.41$; $d = -0.49$) when these were distinguished from homosexual encounters. In the case of heterosexual partners, the recipients of male sexual victimization will of course be female, and here sex differences are large or very large (Table S11). Consistent with women's greater likelihood of victimization, women also perceive a wider range of

sexual behaviour as more harassing than do men, and they are more likely than men to opt for conviction in simulated sex-abuse cases (Table S11): these are both small differences.

Table S11 also shows effect sizes for verbal and physical aggression to partners, from meta-analyses and homicide data. A large number of studies in western settings find either no sex difference, or a small one in the female direction, for inclusive measures of physical aggression (Archer, 2000). A cross-cultural analysis (Archer, 2006a) found a high correlation between the sex difference in partner violence and a national-level measure of women's relative societal power, such that sex differences were in the male direction in nations with lower gender empowerment (e.g. Papua New Guinea: $d = 0.53$), and slightly in the female direction in nations with higher empowerment (e.g. Finland: $d = -0.06$). The greater size and strength of men means that even where women have more societal power, they are still subject to more severe injuries in response to male aggression than *vice versa*; consistent with this is the increasing effect size with escalating forms of physical aggression to a partner (Table S11), albeit smaller than expected from size and strength differences (Archer, 2013, 2018).

A meta-analysis of sex differences in sexual jealousy found a small overall difference in the female direction (Table S11), which is inconsistent with predictions from the paternity uncertainty theory (Archer, 2013). There is better support for the hypothesis that men are more upset by physical infidelity and women by emotional infidelity. An earlier meta-analysis (Harris, 2003) found the sex difference (a medium effect in the male direction) to be restricted to studies using forced choices rather than continuous measures of the degree of upset to each possible scenario. Subsequent meta-analyses (Table S11) found a large difference for forced-choice measures. In one (Carpenter, 2012), it was concluded that the evolutionary prediction was unsupported, because both sexes were more upset by emotional than sexual infidelity. However, Table 2 of that study shows medium to very large differences [effect sizes ranged from $d = 0.36$ to 1.29 depending on the comparison in the scenario (calculated from the author's r values using

formula 2.21 in Rosenthal, 1984)] in the degree to which men show relatively greater upset to sexual stimuli than women do to emotional stimuli: the large effect size in the male direction shown in Table S11 is the value for the overall sample of 54 studies involving forced-choice measures of upset to sexual *versus* emotional stimuli (the value in the first line of Table 2 from the source).

In the only meta-analysis of studies using continuous measures (Sagarin *et al.*, 2012), the single effect-size metric, taken from an interaction term, indicated the difference between (1) the degree to which men showed greater upset when confronted by sexual than emotional infidelity, and (2) the degree to which women showed the reverse. The difference was small but reliable. In a recent empirical study (Bendixen, Kennair & Buss, 2015), sex differences in the large range were found across four samples of Norwegian students, for both forced choice and continuous measures (Table S11). The interpretation of such findings continues to be controversial (Carpenter, 2012; Sagarin *et al.*, 2012), although a recent careful analysis of the evidence over 25 years concluded that the meta-analyses do support the predicted sex difference both in hypothetical and in real-life situations (Edlund & Sagarin, 2017).

(c) Evidence for evolutionary origins

In many nations, and throughout history, there are circumstances in which rape was perpetrated by a wide range of the male population; in situations involving dehumanizing members of an out-group, peer-pressure, and with no prospect of retribution. This has been documented in the contexts of warfare and conquest from ancient times to the present day (e.g. Beevor, 2002; Brownmiller, 1975). Sanday's (1981) cross-cultural analysis concluded that rape is not universal. However, it is clear that rape did occur in many of the 47% of societies she identified as "rape-free": in one, men were fined for rape; in another, rape was viewed as a sin; and in a third, men stated that "our women never resist". More realistically, Brown (1991) included rape as a human universal.

From an evolutionary view, why surveys in western nations show evidence of sexual assaults in which males are the victims is puzzling. However, the majority of these record male-to-male sexual assault, particularly for rape, where in one survey only 7% of male victims reported a female perpetrator (Black *et al.*, 2011). Some of these surveys included a substantial number of cases where the rape occurred while the respondents were children. Such indiscriminate targets suggest that the male liking for impersonal sex goes beyond the evolutionarily appropriate target of male sexual desire, i.e. young women. Nevertheless, the preference of most rapists does reflect the reproductive potential of the victim, the peak age being older teenagers (Felson & Cundiff, 2012, 2014).

Physical coercion of females by males is well known in other animals, including many primates (e.g. Clutton-Brock & Parker, 1995; Smuts, 1992, 1995). Likewise, it is known from historical accounts and cross-national studies (Archer, 2006a) that physical aggression between spouses is widespread, and that in traditional societies, wife-beating is far more common than husband-beating (Levinson, 1989). It appears that it is only in modern technologically advanced nations that women show a comparable level of physical aggression to men, and even here men commit the more damaging acts. The pattern of differences across cultures today may be attributable to marked differences in societal roles and attitudes among nations (Archer, 2006a).

In one meta-analysis (Archer, 2013), sex differences in sexual jealousy did not fit predictions from paternity uncertainty theory of a large sex difference in the male direction. Nevertheless, it is clear that despotic rulers throughout history showed pronounced mate-guarding, often going to great lengths to avoid the possibility of paternity uncertainty (Betzig, 1986). Studies concerning the hypothesis that men are more upset by sexual infidelity and women by emotional infidelity have generally supported this prediction (Table S11)

VIII. OTHER ATTRIBUTES

(1) Sex differences

The present review involved all sex differences for which there are meta-analyses or large-sample studies, and thus includes a number of measures that do not fit easily within an evolutionarily driven classification. Table S12 shows these attributes: there are no large differences, 10 (13.5%) in the medium range, and the remainder showing small or no differences. The largest difference is for two components of schizotypy (proneness to schizophrenia-like symptoms): men showed physical and social anhedonia (the inability to feel pleasure in positive activities) to a greater extent than women, with medium-sized effects. There were no differences in two other aspects of schizotypy, magical ideation and perceptual aberration. Body image showed a medium-sized difference in the male direction, whereas physical attractiveness showed a small difference in the female direction.

There was likewise a small difference for simple reaction-time tasks, men being faster, and studies of positive emotions identifying a small difference in the female direction or no effect. Women reported more dream recall (a small effect) from adolescence to old age, and female adolescents and young adults reported more nightmares than their male counterparts (again a small effect). These differences are hard to explain from any theoretical viewpoint. There was a small difference in the male direction for narcissism. The coping styles of rumination (Table S8) and seeking social support (Table S6) were considered previously (they showed a small and medium difference, respectively, in the female direction). Three other coping styles are listed in Table S12, two of which (wishful thinking and active problem-focussed coping) showed small differences in the female direction. Men reported slightly higher self-esteem than women (Table S12), although this declined with age, and varied across ethnic groups (Zuckerman, Li & Hall, 2016). Men showed higher physical self-esteem and body self-image (Table S12).

There were small sex differences in the female direction in episodic memory. Differences in working memory were related to the material involved (Table S12) in that there was a small effect

in the male direction for a spatial task. Word recall also showed a small difference in the female direction. Men were slightly more achievement-oriented in their learning style, and women showed slightly more vivid mental imagery than men.

A large-sample meta-analysis of scholastic achievement showed a small difference in the female direction (Table S12), although there were indications of higher male scores in more difficult tests. Early intelligence tests were constructed so as to balance items favouring men with those favouring women: by definition, there should be no sex difference in such tests. From the 1930s onwards, Raven's Progressive Matrices (Raven, 1939) were regarded as the best test of abstract, non-verbal reasoning, which corresponds to Spearman's *g*, the general factor underlying all cognitive abilities. Two meta-analyses of general-population (Lynn & Irwing, 2004) and student (Irwing & Lynn, 2005) samples found a small overall male advantage on the advanced version of this test. Tests of general knowledge show no differences, as do time judgement, reaction to occupational stress, and the extent to which people feel more effective in the morning or evening.

(2) Measures for which there are limited data

The present review covers sex differences for which there are meta-analyses and large-sample surveys. There are other attributes that are relevant to an evolutionary analysis, for which these sorts of studies are unavailable. They are mentioned here briefly for future reference. One is rough-and-tumble play, an energetic form of play with bodily contact, which mimics fighting, but in a playful context. It is more common among boys than girls, a sex difference found in children from non-western (including hunter-gatherer) samples (e.g. Blurton-Jones & Konner, 1973; DiPietro, 1981; Peterson & Flanders, 2005; Whiting & Whiting, 1975). The sex difference is maintained into young adulthood (Gergen, 1990). Comparable differences are found in other mammals, especially those with high levels of inter-male competition (Pellis, Pellis & Foroud, 2005; Smith, 1982). There is evidence for the involvement of prenatal androgens in facilitating rough-and-tumble play in non-

human mammals (e.g. Olioff & Stewart, 1978; Wallen, 1996), and possibly in humans, although this is based on clinical evidence that is open to other interpretations (Hines & Kaufmann, 1994).

Interest in infants tends not to be covered in summaries of psychological sex differences, but it is clearly of evolutionary relevance in light of the greater female investment in the reproductive process and women typically having a major role in child care. Women show greater interest than men in stimuli associated with infants (Berman, 1980; Charles, Alexander & Saenz, 2013; Maestriperi & Spelka, 2002). Sex differences for self-reports of interest in infants are medium to very large in the female direction (Cárdenas, Harris & Becker, 2013; Charles *et al.*, 2013; Maestriperi & Spelka, 2002). There is some evidence that this difference develops at puberty and that it is influenced by female gonadal hormones, although female socialization clearly plays an important part as well. Further evidence for a hormonal involvement comes from studies measuring ratings of the cuteness of baby faces (Sprenelmeyer *et al.*, 2009), on which there is also a sex difference (Archer & Monton, 2011).

Several studies have found that women are more distracted than men by task-irrelevant information (Bayliss, di Pellegrino & Tipper, 2005; Judge & Taylor, 2012; Merritt *et al.*, 2007; Stoet, 2010). Testosterone decreases distractibility by task-irrelevant stimuli in birds (Andrew & Rogers, 1972; Archer, 1974; Klein & Andrew, 1986) and rodents (Archer, 1977; Thompson & Wright, 1979). Evolutionary explanations for this effect involve the greater need for males to avoid distraction when engaged in aggressive (Andrew & Rogers, 1972; Archer, 1976, p. 267) or sexual (Andrew, 1978) encounters. Whether the human sex difference is testosterone dependent awaits future study.

Both sexes underestimate the time of arrival of a rapidly approaching stimulus, whether it is visual or auditory. Two articles describe five experiments where sex differences were measured under different conditions (Schiff & Oldak, 1990; Neuhoff, Planisek & Seifritz, 2009). The overall effect size is in the large range ($d = -0.68$, $N = 320$; calculated from t and F values and then

aggregated, using CMA), indicating that women allow more margin of safety. Neuhoff (2001) suggested that underestimating the time of arrival of a rapidly approaching object evolved in both sexes to maximize safety, since the cost of making a false negative is greater than that for making a false positive response. There are two possible reasons why this occurs to a greater extent in women than men: the first is their lesser size and strength, and hence greater vulnerability to predation or assault (Neuhoff *et al.*, 2009); the second is their greater aversion to physical danger, a consequence of the mammalian maternal role (Campbell, 1999).

IX. GENERAL CONCLUSIONS

(1) The extent of psychological sex differences

The present review extends considerably the database for psychological sex differences used in previous accounts (Geary, 2010; Hyde, 2005, 2014; Zell *et al.*, 2015), and organizes it within an evolutionary framework. This should direct researchers towards areas where differences are more likely to be found. Theory and comparisons with other mammals suggest that: (1) differences that can be attributed directly to inter-male competition are escalated aggression, impulsiveness and risk-taking, fearfulness, spatial abilities, and object-centred orientation; (2) differences that arose from selection for fewer closer social relationships in women and more extensive but less-close relationships in men include a variety of social abilities such as greater decoding of non-verbal cues, empathy, language abilities, and depression and anxiety, and (3) differences that arose from female choice are more restricted female sexuality, different mate-choice criteria, sexual aggression, partner violence, and sexual jealousy.

Summarizing the evidence collated here (Table 3), there are no overall differences in anger and indirect aggression, a small difference in the male direction for verbal aggression, a medium difference for general physical aggression, and larger differences for measures involving use of weapons and violent crime, culminating in very large differences in homicides. All these measures

concern conflicts between adults of the same sex. Clearly, the sex difference in aggression does not arise from men having more angry episodes than women, or scoring higher on all forms of aggression. Rather, the sex difference increases as the physical risk of the aggressive encounter increases. Males also show more violent computer game use (a very large difference), more revenge feelings (a large difference), and greater approval of social hierarchies (a medium difference).

Sex differences in impulsiveness were considered in terms of four categories (Cross *et al.*, 2011). The first of these, reward sensitivity, showed no difference for a composite measure, although women scored higher on a personality measure that reflected social contexts. Women scored higher for harm avoidance, a measure of punishment sensitivity, to a small extent. Although there was no difference on a composite measure of impulsivity, men did show more sensation-seeking and risk-taking (medium effects) and risky impulsivity (a small effect) than women. Measures associated with self-control showed a small difference in the female direction (delayed gratification), or no difference (resisting temptation). It appears that sex differences are most pronounced for sensation-seeking, risk-taking and a personality measure of reward sensitivity.

Sex differences were found in the female direction for fearfulness. When confounds were removed to produce a purer measure of fear reactions to dangerous real-world situations, a very large sex difference was found in the female direction. This supports the view that it is fear of physical danger, rather than fear in general or specific phobias or anxiety, that differs between the sexes. There were also differences in pain threshold (medium effect) and pain tolerance (very large effect), with men showing higher thresholds and greater tolerance.

Men scored higher than women on visuospatial tests involving the mental rotation of objects (a large difference), and women performed better than men (to a small extent) on tests of object-location memory. There was a large or very large difference in the male direction in the ability to understand how systems work (systemizing), interest in engineering and interest in things.

Women showed higher scores on measures related to social skills. Social interests in general showed a large difference in the female direction. Emotional intelligence and face recognition showed medium-sized differences, and there was a small difference for decoding non-verbal cues. Women showed stronger peer attachment, affiliation motivation, and more smiling and disclosure to the same sex, all medium-sized effects. Small differences were found for agreeableness, and intimacy in relationships. There was a large difference in the ability to empathize with others, which is crucial for social relations in small groups. Women are also more inclined to help others, and showed medium to small differences in measures of moral reasoning. Men emerged as leaders more frequently than women when there was a specific task, whereas women were more likely to be influenced than men were, to a small extent.

Women show better language ability than men (medium-sized effect), and greater speech production (small effect), the ability to put thoughts into words. These differences are consistent with women's greater social skills for close relationships. Women also showed better reading, writing and spelling than men (all medium in magnitude).

It has been suggested that women's higher rates of depression and anxiety are a negative aspect of their greater engagement in fewer closer relationships compared to men's engagement in larger groups. Consistent with this, there were small differences for depressive symptoms and depressive disorders, and also for rumination. Measures of anxiety showed medium differences. Neuroticism showed small differences in the female direction, as did guilt and shame.

Several aspects of sexuality show differences in the male direction: men show a greater willingness to engage in uncommitted sex than do women, to large extent. There were medium-sized differences for pornography use, sex drive, masturbation, interest in casual sex, and preference for a larger number of partners. Men also showed more mate poaching and perceptions of sexual interest. Features people seek out when choosing a mate also showed sex differences: these were very large (female preference for an older age), large (female preference for good

financial prospects), medium (male preference for good looks and cook–housekeeper skills; female preference for ambitiousness), and small (female preference for social status; male preference for chastity).

As expected there were large sex differences in the male direction for rape but only medium-sized differences for sexual aggression, based on victims' reports from large-scale surveys. The larger than expected number of male victims is to some extent the result of men targeting other men and boys as their victims, but also because men can be victims of women's sexual coercion, even the most serious forms, in heterosexual relationships, particularly in modern western societies. Physical aggression between partners from western nations showed little overall difference between the sexes, a likely consequence of strong negative attitudes in western societies regarding male aggression to their female partners, which override or replace beliefs associated with honour, and considerations of size and strength. Severe physically aggressive acts to a partner, however, are in the male direction, a likely reflection of male physical superiority, with a very large difference in the male direction for partner homicide. Sexual conflict also encompasses sexual jealousy, where women show more jealousy than men, to a small extent, again mainly from western samples. However, men show more sexual than emotional jealousy, and women the reverse, and this difference is large.

For attributes that were more difficult to explain in an evolutionary context, there were mainly small or no sex differences.

(2) Evolutionary origins of sex differences

The evolutionary principles underlying psychological sex differences are – like those for physical differences – to be found ultimately in the sexual method of reproduction and its manifestation in female mammals. Some differences can be traced to the impact of this on reproductive competition, principally inter-male aggression, risk-taking and impulsiveness, fearfulness and spatial abilities.

Others are likely to reflect its impact on the types of social relations shown by men and women: this includes adaptations specifically for a smaller number of close relationships, such as empathizing, but also women's greater language ability and higher rates of depression. Female choice is reflected directly in women's preference for more restricted sexuality, in men's greater interest in casual sex, and in the preferred mate-choice characteristics of both sexes. With the exception of adaptations for social relationships, few sex differences can be traced to the more recent human division of labour into hunters and gatherers, although there may have been enhanced selection on pre-existing male attributes, such as visuospatial ability, with the advent of hunting. For object-location memory, the evidence does not support the explanation that it evolved to enhance plant-gathering skills in women.

Table 4 summarizes the evolutionary explanations for the sex differences included in this review. Some sex differences, such as same-sex physical aggression, visuospatial ability, variables related to sexuality and sexual coercion, are comparable to sex differences observed in other mammals. Attributes such as language ability, systemizing, and empathizing, are only found in humans.

Large-scale multinational surveys indicated a degree of cross-national consistency for same-sex physical aggression, visuospatial ability, object location memory, systemizing, empathizing, sexuality, mate choice, sexual aggression, and (with some qualifications) partner violence. Most sex differences showed an origin early in life, or developed at puberty. There are direct links with neonatal gonadal hormones (principally testosterone) for fearfulness, empathizing and systemizing, although there are few longitudinal studies. There was more evidence for the involvement of gonadal hormones at and after puberty: testosterone is likely to be involved in risky impulsivity, (lack of) fear, empathizing, visuospatial skill, and uncommitted sex.

(3) Limitations: within-sex variations

The coverage of psychological attributes was based on available meta-analyses, supplemented by large-sample surveys. As noted in Section VIII.2, there are also attributes on which the sexes differ, and which have plausible evolutionary explanations, for which there are currently no meta-analytic summaries. There are also large differences in the interests and activities of the two sexes (e.g. Ellis, 2008; Carothers & Reis, 2013), many or most of which are related to the psychological differences considered here

As indicated above, men and women may not differ on all, or even the majority, of psychological and behavioural attributes. Both sexes have been subject to common selection pressures in terms of their ability to counteract diseases, find food and shelter, and avoid predators and other dangers. Selection pressures will only differ when the adaptive norm differs for men and women as a consequence of their different roles in the reproductive process. These features have been highlighted herein, as have been those measures on which there are no, or only minimal differences. For example, there is little or no difference for anger, or for indirect aggression during adulthood; these findings are consistent with a sex difference being located only in more risky forms of aggression. For fearfulness, the difference was only large for fears associated with physical danger. For verbal abilities, there was no overall difference in vocabulary, and only a small one for verbal reasoning. For mathematical abilities, differences were related to those associated with mechanical reasoning or found only at higher ability levels.

Concentrating on mean differences between the sexes can lead to neglect of their overlap. However, it is possible to use the common metric of effect size to acknowledge this degree of overlap, in terms of the extent to which the measure enables a person to be correctly classified as male or female. Thus, as shown in Table 1, a small difference means that 56% of people would be correctly classified – a relatively small increase from chance level; by contrast, a d value of 2.00 would enable 91% to be classified correctly.

Carothers & Reis (2013) distinguished between differences that are dimensional, in which men and women differ to a degree, and those that are categorical, i.e. can be used to classify men and women correctly in most cases. Primary sexual characteristics – the reproductive organs – and some secondary sexual characteristics – such as beards, or voice pitch – are of the latter sort. Most of the attributes covered herein show at least some overlap. Using several statistical methods to determine whether sex differences were categorical or dimensional, Carothers & Reis (2013) found a categorical grouping for a composite measure of sex-typed activities: these involved an interest in construction, pornography, boxing, talking on the phone, golf, taking a bath, and cosmetics. In these cases, the distribution of men and women formed two categories, so that it is possible to use the measure to classify most people correctly into male or female. Many other sex differences were found to be dimensional, i.e. continuously distributed, with the means for men and women positioned differently along the dimension. This applied to intimacy in relationships, empathy, interest in science, and sexual attitudes and behaviour, all covered herein. It should be noted, however, that according to the metric used most often in psychology, the effect size, there is no distinction between dimensional and categorical differences, since effect size is a continuous metric.

Nevertheless, the categorical–dimensional distinction does highlight the overlap between the sexes as well as their mean differences, the topic of interest here. It also draws attention to a number of other issues. These include the distribution of individual men and women at different points along the dimension, within-sex variability, and moderator variables that influence the magnitude of sex differences. Considering the first, we would expect – if there is a normal distribution – that both sexes would be well represented around the mean value for the whole sample. At the higher and lower tails of the distribution, there will be considerably more of one sex than the other. If the particular attribute is of practical importance, for example a cognitive ability, possessing a high score on this attribute will be valued if it underlies a specific skill. This applies

even when the effect size is relatively small (Feingold, 1995). In addition, if one sex has greater variability than the other, there will be even more of that sex at the tails of the distribution. In practice, it is usually males who show more variability (Feingold, 1992*b*), and if the male mean is higher than the female mean, males will be over-represented at the higher end, even if the mean effect size is small. This applies particularly to mathematical ability (Feingold, 1992*b*; Halpern *et al.*, 2007) but also to physical aggression, mate-choice criteria (Archer & Mehdikhani, 2003), and physical attributes (Lehr *et al.*, 2009).

Greater male than female variability, particularly in aggression and mate choice, has been linked to an aspect of sexual selection, alternative reproductive strategies, particularly among males (Archer & Mehdikhani, 2003). One such distinction is between mating and parental strategies: males may pursue an uncommitted sexual strategy or alternatively be more committed to a female and their offspring. In human males, such differences are associated with stable individual differences in testosterone levels (Archer, 2006*b*). The extent to which psychological sex differences found in a particular sample reflect such individual differences among males (and females) is an interesting question for future studies.

Sex differences may also be influenced by the same individuals showing variable characteristics under different circumstances. Daly & Wilson (2001) found lower levels of homicide in married men than in those who were divorced, single or widowed. Although this analysis was cross-sectional, Norwegian archival data (Skarôhamer & Lyngstad, 2009) showed that criminal offending declined when men married or cohabited, and when they became a father. There is also evidence from longitudinal studies that men's testosterone levels decline when they become fathers (e.g. Archer, 2006*b*; Gettler *et al.*, 2011).

Other analyses have conceptualized life-history strategies as adaptations found in both sexes for particular environments, especially those experienced early in life (e.g. Chisholm, 1996; Draper & Harpending, 1988; Geary, 2002). These life-history strategies may affect the two sexes

differently: for example a high-risk short-term strategy may be associated with escalated aggression in males, thus increasing the typical sex difference; in females, it may produce more interest in short-term mating, hence decreasing the typical sex difference. Thus, some forms of adaptive alternative reproductive strategies may apply to both sexes, but result in different sex differences.

The occurrence and magnitude of sex differences are likely to be influenced by other environmental circumstances. In animals, heightened inter-male competition, leading to polygynous mating, occurs when certain males obtain a higher proportion of the resources necessary for reproduction (Orians, 1969). Throughout human history, despotic rulers have been able to obtain a greater monopoly of material resources, including women, than is possible for non-humans (Betzig, 1986, 1992, 2012). A number of studies link rates of violent crime (which principally involves young males) with greater inequality, at a neighbourhood (Wilson & Daly, 1997), state, and national level (Wilkinson & Pickett, 2009). A study of homicide figures in post-World-War 2 Japan (Hiraiwa-Hasegawa, 2005) showed a decreased rate from 1960 to 1996, which was partly predicted by a measure of equality that increased during these years. The point about such analyses for escalated aggression is that since it is characteristic of conflicts between young males, we would expect larger sex differences among young adults in areas with greater resource inequality.

This is an illustrative rather than an exhaustive list of environmental influences that are likely to affect the magnitude of psychological sex differences, and it is intended to make the point that an evolutionary approach to psychological sex differences incorporates variability and flexibility. Indeed, it goes beyond this to enable variability and flexibility to be understood in terms of ecological variables. This perspective on within-sex variability indicates ways in which an evolutionary approach can explain such variability. Some critics of evolutionary analyses of sex differences do not appreciate this point, regarding evolutionary analyses as only being concerned with consistencies across cultures and contexts (e.g. Hyde, 2014).

X. CONCLUSIONS

(1) Although men and women share many psychological features, they also differ in important ways that can be understood in terms of evolutionary principles, primarily as a consequence of mammalian reproduction. The present article involved a systematic review of the evidence from meta-analyses and surveys of psychological sex differences, which are expressed in terms of Cohen's d , ranging from 0 (no difference) to over 1.0 (very large difference).

(2) Measures of intra-sex aggression showed an increase in effect size in the male direction with increasing physical risk of the aggressive encounter, so that measures of anger showed no difference, whereas those involving weapons and homicide showed large or very large differences.

(3) Components of risky impulsivity, risk-taking and sensation-seeking showed small or medium-sized effects in the male direction; there were medium differences in the female direction for fears in general, and very large differences in reactions to danger in real-world situations. There was a very large difference in the male direction for pain tolerance.

(4) Men scored higher (to a large extent) than women on visuospatial tests involving the mental rotation of objects, and women performed better (to a small extent) on tests of object-location memory.

(5) Men showed higher scores (to a very large extent) in the ability to understand how systems work (systemizing). There were comparable differences for interest in engineering and in things rather than people.

(6) Social interests in general showed a large difference in the female direction, as did the ability to empathize with others, which is crucial for small-group interactions. Women showed greater emotional intelligence and face recognition, and there was a smaller difference for decoding non-verbal cues. Women showed stronger peer attachment, affiliation motivation, and more smiling and disclosure to same-sex others. Smaller differences were found for agreeableness, and intimacy in

relationships. Women were more inclined to help others. Men emerged as leaders more frequently when there was a specific task, and men were more likely to influence others.

(7) Women showed better language ability than men, and greater speech production (the ability to put thoughts into words), differences that are consistent with their greater social skills.

(8) Men showed a greater interest than women in uncommitted sex, to a large extent. More specific measures, such as pornography use, sex drive, masturbation, preferred number of partners, and mate poaching, showed medium-sized differences in the male direction. Features people seek when choosing a mate also showed sex differences, ranging from small (female preference for social status) to very large (female preference for an age difference).

(9) Evolutionary analyses of sexual conflict in animals provided a framework for considering sexual aggression, physical aggression between partners, and sexual jealousy. As expected, there were very large differences in the male direction for rape, and for escalated forms of physical aggression to a partner. The current evidence indicates that men are more upset by sexual than emotional jealousy, and the reverse is the case for women.

(10) There were mostly small or no sex differences for attributes where no sex difference would be expected from evolutionary analyses.

(11) Sources of variation that produce degrees of overlap between the sexes were considered within an evolutionary framework, namely alternative reproductive strategies and flexible responses to environmental conditions.

(12) For each psychological attribute, the evidence for an evolutionary basis was considered in terms of the following criteria: (1) comparable sex differences in other mammals; (2) cross-cultural consistency; (3) whether the difference develops early in life or at puberty; (4) whether there is evidence for links with neonatal gonadal hormones (principally testosterone); (5) the involvement of gonadal hormones at and after puberty; (6) in some cases, whether evolutionarily derived design features were apparent. For each attribute considered, there was considerable evidence that the

range of psychological sex differences covered did show indications of an evolutionary background.

(13) The evidence reviewed here shows that although men and women share many psychological features, they also differ in important ways that can be understood in terms of evolutionary principles, primarily sexual selection and extensions of this. The present-day consequences of this evolutionary process are that men and women are, on average and to varying degrees, psychologically as well as physically different in aspects that are primarily or secondarily related to their role in the reproductive process.

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XIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Aggression, violence and dominance.

Table S2. Sensation-seeking, risk-taking, and impulsivity.

Table S3. Fearfulness.

Table S4. Visuospatial and mathematical abilities.

Table S5. Object-centred orientation.

Table S6. Characteristics directly associated with social relations.

Table S7. Language and related attributes.

Table S8. Depression and negative emotions.

Table S9. Sexuality.

Table S10. Mate choice criteria.

Table S11. Sexual conflict.

Table S12. Evidence for sex differences and similarities in other attributes.

Table S13. Personality factors: *d* values for sex differences in the ‘Big Five’ from meta-analysis and large samples.

Table 1. Classification of effect sizes (based on Cohen, 1988) and per cent of cases correctly classified.

| <i>d</i> values | Effect size magnitude | Description | Midpoint | % correctly classified ^a |
|-----------------|-----------------------|---------------|----------|-------------------------------------|
| 0–0.10 | 0 | close to zero | 0.05 | 51.4 |
| 0.11–0.35 | 1 | small | 0.23 | 56.5 |
| 0.36–0.65 | 2 | medium | 0.50 | 63.8 |
| 0.66–1.0 | 3 | large | 0.83 | 72.1 |
| > 1.01 | 4 | very large | 2.00 | 90.9 |

Note. For each category, the percentage correctly classified is for the mid-point in the range of *d* values (shown in the previous column). An arbitrary midpoint of 2.0 was used in the table for the mid-point in the ‘very large’ category.

^aThis refers to the probability that a randomly selected person of one sex will be higher (or lower) on a particular measure than a randomly selected person of the other sex (Grissom, 1994).

Table 2. Criteria used for assessing a possible evolutionary origin of sex differences.

1. Is there a plausible adaptive explanation? Is it testable?
 2. Is there a similar difference in other mammals, in particular the great apes?
 3. Is the difference found in different nations and cultures, and in particular in surviving hunter–gatherers?
 4. Does the difference occur early in life, or begin at puberty, and is it pronounced in young adulthood?
 5. Is the difference associated with neonatal or pubertal reproductive hormones?
 6. Are evolutionarily derived design features apparent in the mechanisms underlying the sex difference?
-

Table 3. Summary of effect sizes (*d*) for sex differences in different measures. Rating refers to size of effect (from 0 to 4), details of which are shown in Table 1 below.

| domain | measure | summary value | effect size magnitude (0–4) | <i>CI</i> |
|--|----------------------------------|---------------|-----------------------------|--------------|
| aggression, violence & dominance | anger (frequency) | −0.003 | 0 | −0.03, 0.02 |
| | indirect | −0.02 | 0 | −0.07, 0.02 |
| | verbal | 0.30 | 1 | 0.27, 0.33 |
| | physical | 0.59 | 2 | 0.56, 0.62 |
| | weapon use | 0.88 | 3 | 0.82, 0.95 |
| | violent crime | 1.11 | 4 | 1.10, 1.12 |
| | homicide ^a | 2.54 | 4 | NA |
| | violent computer-game use | 1.41 | 4 | 1.33, 1.49 |
| | forgiveness | −0.28 | 1 | −0.36, −0.21 |
| | revenge | 0.83 | 3 | 0.43, 1.24 |
| | social dominance orientation | 0.43 | 2 | 0.39, 0.47 |
| competitiveness | 0.07 | 0 | 0.02, 0.13 | |
| sensation-seeking, risk-taking and impulsivity | reward sensitivity (personality) | −0.63 | 2 | −0.78, −0.49 |
| | reward sensitivity (overall) | 0.01 | 0 | −0.17, 0.19 |
| | harm avoidance | −0.33 | 1 | −0.41, −0.24 |
| | sensation-seeking | 0.39 | 2 | 0.35, 0.43 |
| | excitement-seeking | 0.29 | 1 | 0.14, 0.44 |
| | risk-taking | 0.49 | 2 | 0.43, 0.56 |
| | impulsivity (overall) | 0.07 | 0 | 0.05, 0.10 |
| | delay of gratification | −0.12 | 1 | −0.27, 0.03 |
| | resistance to temptation | −0.06 | 0 | −0.10, −0.02 |
| | effortful control | −1.01 | 4 | −1.37, −0.64 |
| | inhibitory control | −0.41 | 2 | −0.61, −0.21 |
| | risky impulsivity | 0.34 | 1 | 0.28, 0.41 |
| fearfulness | fear questionnaires | −0.41 | 2 | −0.46, −0.36 |
| | fear in real-world situations | −1.16 | 4 | −1.32, −1.01 |
| | pain threshold | 0.51 | 2 | 0.46, 0.56 |
| | pain tolerance | 1.17 | 4 | 1.16, 1.18 |
| spatial abilities | mental rotation | 0.66 | 3 | 0.52, 0.80 |
| | visuospatial ability | 0.48 | 2 | 0.10, 0.86 |
| | spatial visualization | 0.23 | 1 | 0.01, 0.46 |
| | line angle judgment | 0.49 | 2 | 0.48, 0.50 |
| | object location memory | −0.31 | 1 | −0.32, −0.30 |
| mathematical ability and science | quantitative ability | 0.03 | 0 | 0.03, 0.04 |
| | mathematics | 0.09 | 0 | −0.02, 0.19 |
| | mechanical reasoning | 0.98 | 3 | 0.97, 0.98 |
| | science | 0.28 | 1 | 0.19, 0.37 |
| object-centred orientations | systemizing quotient scale | 1.21 | 4 | 1.20, 1.22 |
| | occupational interests | 1.39 | 4 | 1.38, 1.40 |
| | engineering interests | 1.11 | 4 | 1.01, 1.20 |
| | interest in things | 0.97 | 3 | 0.80, 1.15 |

Table 3 contd.

| domain | measure | summary value | effect size magnitude (0–4) | <i>CI</i> |
|---------------------------------|----------------------------------|---------------|--------------------------------|--------------|
| social relations | people-things dimension | –0.93 | 3 | –0.99, –0.87 |
| | social interests | –0.68 | 3 | –0.74, –0.62 |
| | emotional intelligence | –0.47 | 2 | –0.72, –0.24 |
| | face recognition | –0.36 | 2 | –0.44, –0.29 |
| | decoding non-verbal cues | –0.27 | 1 | –0.32, –0.23 |
| | peer attachment | –0.51 | 2 | –0.59, –0.42 |
| | implicit affiliation motivation | –0.45 | 2 | –0.53, –0.37 |
| | smiling | –0.41 | 2 | –0.42, –0.39 |
| | seek emotional social support | –0.41 | 2 | –0.49, –0.32 |
| | disclosure (to same sex) | –0.37 | 2 | –0.42, –0.32 |
| | agreeableness | –0.29 | 1 | –0.39, –0.19 |
| | friendship expectations | –0.17 | 1 | –0.22, –0.12 |
| | intimacy in relationships | –0.11 | 1 | –0.13, –0.09 |
| | touch initiation | –0.09 | 0 | NA |
| | personal space | 0.08 | 0 | 0.04, 0.11 |
| | adult attachment style: anxious | –0.04 | 0 | –0.07, –0.01 |
| | adult attachment style: avoidant | 0.02 | 0 | –0.01, 0.05 |
| | empathy | –0.91 | 3 | –0.97, –0.85 |
| | Empathy Quotient | –0.87 | 3 | –0.88, –0.86 |
| | reading the mind in the eyes | –0.18 | 1 | –0.24, –0.12 |
| | helping behaviour | –0.34 | 1 | –0.36, –0.32 |
| | cooperation (overall) | –0.05 | 0 | –0.11, 0.001 |
| | moral norms vs consequences | –0.57 | 2 | –0.62, –0.52 |
| | moral self-esteem | –0.38 | 2 | –0.48, –0.29 |
| | attitudes to cheating | 0.35 | 1 | 0.32, 0.37 |
| | moral orientation (care) | –0.28 | 1 | –0.32, –0.25 |
| | moral sensitivity | –0.24 | 1 | –0.34, –0.14 |
| | justice-based moral reasoning | –0.21 | 1 | –0.26, –0.16 |
| | leadership (task) | 0.41 | 2 | 0.34, 0.48 |
| | leadership (social) | –0.18 | 1 | –0.29, –0.06 |
| democratic leadership style | –0.22 | 1 | –0.29, –0.15 | |
| influencing others | 0.26 | 1 | 0.19, 0.33 | |
| language and related attributes | overall verbal abilities | –0.27 | 1 | NA |
| | language ability | –0.37 | 2 | –0.43, –0.32 |
| | speech production | –0.33 | 1 | –0.46, –0.20 |
| | talkativeness | 0.14 | 1 | 0.08, 0.19 |
| | affiliative speech | –0.12 | 1 | –0.18, –0.06 |
| | tentative speech | –0.23 | 1 | –0.32, –0.13 |
| | interrupting | 0.15 | 1 | 0.07, 0.23 |
| | vocabulary | –0.10 | 0 | –0.11, –0.09 |
| | verbal reasoning | –0.15 | 1 | –0.16, –0.14 |
| | reading | –0.36 | 2 | –0.48, –0.24 |
| | writing | –0.57 | 2 | –0.72, –0.42 |
| | spelling | –0.50 | 2 | –0.51, –0.49 |

Table 3 contd.

| domain | measure | summary value | effect size magnitude (0–4) | <i>CI</i> |
|--------------------------------|---------------------------------------|-------------------|-----------------------------|--------------|
| depression & negative emotions | depressive symptoms | –0.27 | 1 | –0.29, –0.26 |
| | Major Depression diagnosis | –0.34 | 1 | –0.35, –0.34 |
| | sadness | –0.23 | 1 | –0.28, –0.18 |
| | ruminatation | –0.24 | 1 | –0.27, –0.21 |
| | anxiety | –0.59 | 2 | –0.67, –0.51 |
| | social anxiety | –0.36 | 2 | –0.38, –0.33 |
| | neuroticism | –0.31 | 1 | –0.38, –0.24 |
| | negative emotions | 0.03 | 0 | –0.03, 0.08 |
| | shame | –0.29 | 1 | –0.34, –0.24 |
| | guilt | –0.27 | 1 | –0.32, –0.23 |
| sexuality | sociosexuality | 0.74 | 3 | 0.74, 0.75 |
| | pornography use | 0.63 | 2 | 0.39, 0.85 |
| | sex drive/arousal | 0.62 | 2 | 0.62, 0.63 |
| | masturbation | 0.53 | 2 | 0.51, 0.55 |
| | casual sex | 0.49 | 2 | 0.42, 0.56 |
| | preferred number of partners | 0.46 | 2 | 0.43, 0.49 |
| | perceptions of sexual interest | 0.30 ^b | 1 | 0.22, 0.38 |
| mate poaching | 0.41 ^c | 2 | 0.34, 0.48 | |
| mate choice preferences | age difference | –2.00 | 4 | –2.05, –1.95 |
| | financial prospects | –0.76 | 3 | –0.81, –0.72 |
| | good looks | 0.55 | 2 | 0.55, 0.56 |
| | ambition/industriousness | –0.50 | 2 | –0.54, –0.46 |
| | social status/dominance | –0.34 | 1 | –0.38, –0.30 |
| | cook–housekeeper | 0.56 | 2 | 0.52, 0.60 |
| | chastity | 0.30 | 1 | 0.25, 0.34 |
| sexual conflict | rape | 2.32 | 4 | 0.77, 3.86 |
| | sexual aggression | 0.62 | 2 | 0.56, 0.67 |
| | perceptions of sexual harassment | –0.30 | 1 | –0.30, –0.30 |
| | convictions in rape/child abuse cases | –0.32 | 1 | –0.36, –0.28 |
| | verbal partner aggression | –0.25 | 1 | NA |
| | physical partner aggression (any) | –0.02 | 0 | –0.03, –0.00 |
| | physical partner aggression (severe) | 0.42 ^d | 2 | 0.32, 0.52 |
| | partner homicide | 1.06 | 4 | NA |
| | sexual jealousy overall | –0.20 | 1 | –0.36, –0.04 |
| sexual vs emotional jealousy | 0.87 | 3 | 0.83, 0.91 | |
| other attributes | schizotypy: physical anhedonia | 0.59 | 2 | 0.52, 0.66 |
| | schizotypy: social anhedonia | 0.44 | 2 | 0.37, 0.50 |
| | schizotypy: magical ideation | –0.01 | 0 | –0.08, 0.06 |
| | schizotypy: perceptual aberration | –0.08 | 0 | –0.17, –0.00 |
| | body image | 0.52 | 2 | 0.51, 0.53 |
| | physical attractiveness | –0.26 | 1 | –0.28, –0.24 |
| | simple reaction time | 0.35 | 1 | 0.31, 0.38 |
| | positive emotions | –0.20 | 1 | –0.29, –0.11 |
| | dream recall | –0.24 | 1 | –0.29, –0.19 |

| | | | | |
|--|--|--|--|--|
| | | | | |
|--|--|--|--|--|

Table 3 contd.

| domain | measure | summary value | effect size magnitude (0–4) | CI |
|-------------------------|------------------------------------|--------------------|-----------------------------|--------------|
| other attributes contd. | nightmare frequency | –0.26 | 1 | –0.32, –0.21 |
| | narcissism | 0.26 | 1 | 0.23, 0.28 |
| | wishful-thinking coping | –0.26 | 1 | –0.42, –0.10 |
| | problem-focussed coping | –0.26 | 1 | –0.29, –0.23 |
| | self-esteem physical appearance | 0.41 | 2 | 0.38, 0.45 |
| | self-esteem | 0.18 ^e | 1 | 0.18, 0.19 |
| | episodic memory | –0.25 ^f | 1 | –0.48, –0.02 |
| | working memory (overall) | 0.09 | 0 | 0.04, 0.14 |
| | working memory (spatial) | 0.26 | 1 | 0.21, 0.31 |
| | learning orientation (achievement) | 0.19 | 1 | NA |
| | vividness of visual imagery | –0.16 | 1 | –0.31, –0.02 |
| | scholastic achievement | –0.25 | 1 | –0.28, –0.23 |
| | abstract reasoning | 0.15 | 1 | 0.12, 0.18 |
| | general knowledge | 0.04 | 0 | –0.12, 0.20 |
| | time judgment | –0.06 | 0 | –0.11, –0.01 |
| | occupational stress | –0.02 | 0 | –0.06, 0.02 |
| | morningness–eveningness | –0.08 | 0 | –0.14, –0.03 |

Note. Effect size (*d*) magnitudes are defined in Table 1. Effect sizes are taken from Tables S1–S12, as summary values. In selecting the summary value, I chose the most recent large-scale meta-analysis or survey that used adult samples (identified using asterisks in Tables S1–S12). Where there are overall and specific subsets, the overall value was selected unless otherwise stated. Where frequency and intensity values were used, I chose frequency; where lifetime and the last 12 months were provided, I included values for the last 12 months. Where there was a choice between largely western or North American samples and cross-national samples, the cross-national one was chosen. Where there was more than one value fitting these criteria, the mean or median is shown here, and stated in a footnote.

^a Killing an adult member of the same-sex.

^b Mean of three values for flirtatiousness, seductiveness and promiscuousness.

^c Mean of values for short- and long-term mate poaching.

^d Median of the three measures shown in Table S10. Note that these are different from the values in the source for reasons explained in footnotes ^f and ^g of Table S11.

^e Mean of two values shown with * in Table S12.

^f Mean of five values shown with * in Table S12.

Table 4. Summary of evolutionary explanations advanced for psychological sex differences and a summary of the evidence for features associated with an evolutionary origin.

| Attribute/measure | Adaptive explanation | Evidence | | | | |
|--|----------------------|---------------|----------------|----------------|----------|-----------|
| | | other mammals | cross-cultural | develop-origin | hormones | mechanism |
| escalated aggression to same sex | 1,2 | 1,2,3 | 1,3 | 1 | 2 | 1 |
| risky impulsivity, sensation-seeking & impulsivity | 1,2 | 0 | 1 | 1 | 2 | 1 |
| fearfulness | 1,2 | 3 | 2 | 1 | 1,2 | 0 |
| visuospatial ability | 1,2 (6) | 1 | 2,3 | 1 | 1M, 2 | 0 |
| object location memory | 2 (7) | 0 | 2,3C | 2 | 0 | 0 |
| object-centred orientation | 8 | 0 | 2 | 1 | 1 | 0 |
| social relations and related attributes | 3,7,8,2 | 3 | 2 | 1 | 1,2 | 0 |
| language | 3 | NA | 0 | 1 | 1,2 | 0 |
| depression & anxiety | 3 | 3 | 0 | 2 | 2 | 0 |
| uncommitted sex | 4 | 0 | 2 | 2 | 2 | 1 |
| mate-choice preferences | 9 | NA | 2 | 2 | 2 | 0 |
| rape & sexual aggression | 4,5 | 1,2,3 | 2 | 2 | 0 | 0 |
| partner violence | 5 | 1,2,3 | 2 | 2 | 0 | 0 |

Notes. Adaptive explanation. 1 = direct inter-male competition; 2 = greater parental investment of females; 3 = greater importance of social relations for women than men, probably as adaptations for small close-knit groups *versus* larger cooperative groups, respectively; 4 = female choice; 5 = sexual conflict; 6 = hunting by men; 7 = plant gathering by women; 8 = extensions of inter-male competition in specifically human environments (Baron-Cohen, 2003), such as tool-use, hunting and tracking, trading, and achieving status; 9 = menopause and prolonged parental care. Parentheses indicate that for reasons discussed in the text this explanation is regarded as unlikely.

Evidence: **other mammals** i.e. comparable sex difference in other mammals (1 = mammals; 2 = non-human primates; 3 = chimpanzees); **cross-cultural** i.e. cross-cultural consistency (1 = evidence from at least one non-western sample; 2 = evidence from over 30 diverse nations; 3 = evidence from surviving hunter-gatherers); **develop-origin** – evidence of an early (= 1) or pubertal (= 2) developmental origin; **hormones** – evidence for organizational (= 1) or activational hormonal effects (= 2); **mechanism** – evidence for adaptive flexibility in mechanism underlying one or more of these features (= 1 if present). O indicates no evidence on a specific topic; NA is not applicable, M indicates mixed evidence; C indicates contrary evidence.