Review

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The evolutionary psychology of women's aggression

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Evolutionary researchers have identified age, operational sex ratio and high variance in male resources as factors that intensify female competition. These are discussed in relation to escalated intrasexual competition for men and their resources between young women in deprived neighbourhoods. For these women, fighting is not seen as antithetical to cultural conceptions of femininity, and female weakness is disparaged. Nonetheless, even where competitive pressures are high, young women's aggression is less injurious and frequent than young men's. From an evolutionary perspective, I argue that the intensity of female aggression is constrained by the greater centrality of mothers, rather than fathers, to offspring survival. This selection pressure is realized psychologically through a lower threshold for fear among women. Neuropsychological evidence is not yet conclusive but suggests that women show heightened amygdala reactivity to threatening stimuli, may be better able to exert prefrontal cortical control over emotional behaviour and may consciously register fear more strongly via anterior cingulate activity. The impact of testosterone and oxytocin on the neural circuitry of emotion is also considered.

1. Introduction

Before scientists can begin to explain a phenomenon, they need to be able to describe it. In 1981, Sarah Hrdy pointed out that the 'competitive component in the nature of women remains anecdotal, intuitively sensed, but not confirmed by science' [1, p. 130]. Happily, since that time, quantitative analyses and qualitative descriptions of women's aggression have been published. I begin by outlining what these studies have told us, before considering an evolutionary-informed account of the psychological basis of sex (and individual) differences in aggression. Following this, I review whether such a proposal is supported by neuropsychological studies. This ambitious interdisciplinary trajectory takes us from sociology, through psychology, to neuropsychology and endocrinology.

2. The shape of young women's violence

In the United States, girls account for 33% of arrests for simple assault and 24% of aggravated assaults [2]. Despite a 24% increase in female arrests for simple assault between 1996 and 2005, victimization and self-report data indicate that this reflects changes in police practice rather than girls' behaviour. The male-to-female ratio for assault has remained remarkably stable over time. The gender gap is considerably greater for aggravated than simple assault, reflecting girls' less injurious behaviour and their lower likelihood of using weapons. Surveys indicate that in the previous year, 40.5% of boys and 25.1% of girls had been in a physical fight [3]. In the previous month, 60% of girls had called another girl names, 50% had sworn at them and 35% had pushed or shoved them [4]. Boys and girls predominantly engage in same-sex aggression, although girls are more likely than boys to target members of the opposite sex. Here, I will focus specifically on same-sex aggression by young women.

The media depiction of girls' aggression—as an anomalous violation of the feminine gender role—ignores the way that femininity is constructed differently in different cultural contexts. Female aggression is more prevalent in disorganized neighbourhoods with high levels of poverty and low social cohesion [5].

For families living in these neighbourhoods, the frequent absence of a consistent father figure means that mothers (and grandmothers) play a pivotal role. They are strong figures who must cope alone with daily stresses of subsistence living. Many mothers are themselves involved in fighting, especially in defence of their family's good name. Some become actively involved in their daughters' fights also and, in doing so, become role models and allies [6]. Even when they do not go this far, mothers' concern for their daughters' welfare translates into tolerance (and sometimes encouragement) of fighting. Most mothers acknowledge that a girl needs to be able to 'stand her ground' and 'hold her own'. The strength and resilience of women (both mothers and daughters) is not seen as incongruent with femininity: indeed passivity is viewed as a weakness rather than an asset. As Irwin & Adler [7, p. 319] noted, 'Given the emphasis on female strength, girls lost respect for and even targeted other girls who fell short in fulfilling idealized notions of feminine resilience circulating in the local communities'.

If weakness makes a girl a target, an important benefit of willingness to fight is the avoidance of victimization. Girls' reports of their fights present aggression as a form of self-defence by emphasizing that their opponents 'started it'. In some cases, 'starting it' refers to a physical assault but more often to verbal taunts to which physical aggression is seen as the appropriate response. The slippery divide between physical and verbal provocation is mirrored in the equally fuzzy distinction between self-defence and reputation enhancement. For many girls, success in a public fight achieves more than the immediate goal of causing an opponent to back off: it promotes a 'crazy' or 'mean' reputation that will deter others from future attacks [6,8–11]. Reputation enhancement involves a disproportionate response to any perceived act (or rumour) of 'disrespect' including staring, failing to move out of the way, behind-the-back gossip and an offensive demeanour that presumes social superiority (a girl who 'thinks she's all that'). Once established, reputations must be defended against others who are seeking to enhance their own. Girls who start fights are '. . . trying to make their name. They'll go fight somebody so somebody can be like 'so-and-so' fought her, just so their name will be known' [10, p. 53]. One response to such reputation-seeking challengers is for tough girls to get their retaliation in first. In this way, a self-reinforcing loop develops between self-defence, reputation enhancement, sensitivity to challenge and pre-emptive aggression. But these overarching principles of deterring disrespect and maintaining a reputation obscure the specific triggers that provoke fights. What accusations or provocations constitute acts of 'disrespect' worthy of a violent response?

Although girls will fight out of loyalty to family and friends, the ethnographic literature leaves little doubt as to the central role played by boys. Romantic rivalry is one cause. Girls understand their own value in terms of the quality of boys they can attract: 'Say one guy is good looking, we're all in a fight over who's getting who . . . If all the girls are fighting for this one really popular guy and one girl gets him, everyone will think she's more popular too' [12, p. 148]. Once a boyfriend is secured, the relationship must be protected from takeover by other girls: jealousy is another major cause of female fights. When a girl spends too much time with another girl's boyfriend, the anger is firmly targeted at the female interloper rather than at the male partner. This is all the more remarkable because many young men ('playas') enjoy trading off girls against one another: 'He was being with both of 'em at

the same time, and they ended up fighting over him or whatever. In the end, they found out that both of 'em was getting played by him' [10, p. 55]. Commentators have noted that jealousy-motivated fights may not be entirely about the boy but about the kudos that a relationship with a high-status boy can bring [12]. At other times, the dividing line between defending a relationship and maintaining a reputation becomes blurred: 'I don't care about the guy or anything but I'm gonna mess that girl up cause she deserves it. The bitch just be asking for it. The way I see it, I ain't fighting over the boy. I'm fighting the girl because she be acting in a way that says she thinks I'm a punk' [13, p. 84]. Jealousy can be even more extreme when financial incentives are added, such as when the wronged girl is the mother of her boyfriend's baby [13].

Attractive girls are both the strongest rivals for male attention and the greatest threats to an ongoing relationship. However, it is the combination of attractiveness together with a self-confident awareness of it that seems particularly provocative. Girls who advertise their attractiveness through dress, make-up or demeanour are often targeted [10]. These girls offend on two fronts: they attract more than their fair share of boys and they communicate their felt superiority over other girls. This becomes a form of 'disrespect' which adds to the rivalry. While disrespect is often synonymous with status challenge among young men, the same is not true for girls. Girls do not show the hierarchical structure typical of boys' groups [14]. Girls chiefly want to fit in rather than stand out and it is this which explains the paradoxical finding that girls who are nominated as 'popular' (visible, charismatic) are not well liked as friends [15]. Girls who communicate their attractiveness too confidently are targeted not just because they are conspicuous to boys but because they set themselves apart from other girls. This refusal to blend in means that those girls who disdain concern with their appearance or with securing a boyfriend can also be picked on: an inherent sense of superiority is read into their non-conformity [7,10].

Perhaps the strongest evidence that boys lie at the heart of female competition is the terms used to insult others. The same epithets appear frequently in accounts of girls' fights: 'slag', 'slut', 'whore (ho)' and 'tart' [7,10,12,13,16]. The second most common insults are about a girls' appearance ('ugly', 'fat'). Whether it is delivered directly to an opponent's face or reaches her via gossip and rumour, these terms are often the immediate trigger to physical confrontation.

Sociologists have interpreted the prominence that girls accord to their appearance, boyfriends and sexual reputation as reflecting male hegemony and girls' internalization of men's sexual objectification of women [12,17]. They argue that girls come to view themselves through the 'male gaze', evaluating their worth in terms of boys' approval and respect. But this obscures a more fundamental issue: why is male approval so important to teenage girls? Why are terms that impugn their sexual reputation so effective at triggering fights? An evolutionary approach goes beyond chastizing girls for their 'false consciousness'.

3. Moderators of young women's mate competition: an evolutionary perspective

Male aggression (and the paucity of female aggression) has been explained in terms of the greater male variance in reproductive success contingent on polygyny [18]. However,

recent developments in evolutionary biology have queried the simplicity of the traditional view of sexual selection which highlights intense male (but not female) competition for mates [19,20]. Rates of female competition are higher in species (like our own) with biparental care and diminished sexual dimorphism. Attempts to trace the evolution of biparental care have used estimates of increased infant cranial size (leading to earlier births, protracted offspring dependence and greater maternal need for assistance) and dated it to 1.5–2 Ma [21]. In terms of sexual dimorphism, archaeological evidence suggests that the relatively modest difference in skeletal size between men and women has remained stable over about 2 Myr and possibly longer [22]. The long history of human biparental care is mirrored in the fact that the vast majority of the world's population live monogamously, despite the large number of societies that permit polygyny. The consequences of monogamy for women have been under-appreciated. When a man commits himself to a single woman, his criteria for mate choice shift dramatically upwards [23]. Monogamy entails two-way sexual selection: women as well as men must compete to attain the best possible mates.

While men and women share a preference for mates who are intelligent and kind, there are some traits that assume a higher priority for one sex than the other [24,25]. Women value resources, ambition and generosity which reflect their need for material and emotional support in raising children. Men value youth, attractiveness and fidelity which reflect preference for high reproductive value and the avoidance of cuckoldry. When women compete for well-resourced men, their intersexual competition will entail advertising those qualities that men value and their intrasexual competition will entail discrediting such traits in their rivals. When viewed from this perspective, girls' preoccupation with enhancing their appearance and defending their sexual reputation becomes more comprehensible, as does the provocative power of accusations of sexual availability and ugliness.

But, as recent theorists have pointed out [26], the severity of mate competition in both sexes is dependent on a range of individual and ecological moderators. Factors such as adult sex ratio, sex-biased mortality, population density and variation in mate quality can impact strongly on the degree of intrasexual competition. Below, I consider how such factors can moderate the intensity of women's aggression.

It is no surprise that *age* is a strong predictor of female aggression. For both sexes, the teenage years signal entry into the mating arena and a concomitant increase in aggression that is visible in criminal statistics. In line with girls' earlier sexual maturity, their offending peak occurs 2 years earlier than boys [27]. Allied to this, early menarche is predictive of girls' aggression. Life-history theory forms the basis for expecting that age of menarche should be responsive to cues from the local environment that canalize development toward a 'fast' or 'slow' reproductive tempo. These cues have been variously identified as resource scarcity, high rates of early mortality, psychosocial stress, low-quality parental investment, father absence and stepfather presence [28]. By signalling environmental uncertainty and unpredictability, these variables are thought to accelerate pubertal timing and reproduction in an adaptive fashion. In deprived neighbourhoods, girls may experience many of these risk factors simultaneously. These girls begin their sexual careers earlier, putting them at a significant advantage over their peers. In addition, older girls are acutely sensitive to the entry of younger competitors into the mating arena and this may increase their likelihood of victimization and retaliation. Girls who reach menarche early are more likely to be involved in delinquent and aggressive behaviour, and this is especially true for maltreated girls [29] and those living in disadvantaged neighbourhoods [30,31].

The *sex ratio* in the local neighbourhood determines the intensity of mate competition that a girl faces and in a number of urban centres in the United States this can be markedly skewed. In 2000, the male–female ratio in New York was 90 : 100 and in Philadelphia, 86.8 : 100 [32]. The mortality rate among men is considerably higher than among women especially between the ages of 15 and 35 [33]. At the age of 25, men are three times more likely to die from all causes than women and this rises to a four times greater mortality rate for deaths from external causes. This effect is conditioned by social class and educational achievement so that in poverty-level neighbourhoods, the sex ratio imbalance is especially marked. In addition to mortality, imprisonment also removes a substantial portion of men from the mate pool.

In addition to a paucity of men, there is also considerable *variance in male resources*. Ambitious and able men leave the neighbourhood as they acquire education and professional employment. Of those that stay, some are destined to unemployment and reliance on welfare (their own or that of their 'baby mother'). Unable to effectively contribute to the household, such men congregate on stoops and street corners where alcohol and drug abuse is common. At the other end of the income spectrum are 'flossers': drug dealers and other members of the underworld economy who are conspicuous spenders and 'high rollers' [10]. Their earn-and-burn lifestyle may not be long lasting but their resources make them attractive to many women. 'Dope guys is straight if they think you ain't dissing them . . . I date whoever is treating your girl the right way. Me, if a guy got some paper well, it's okay with me. I like fellas that's rolling, least they making it' [34, p. 130]. The paucity of resource-rich alternatives means that these men are able to impose their preferred short-term mating strategy on local women. This may be far from ideal from young women's point of view but market forces mean that such men often get their way, with young women adapting their resource-extraction tactics accordingly. 'I tell her take all his paper, all of it, 'cause it's just a matter of time and he's gonna do some rotten dog shit on her . . . Got to get it when you can. You never know when it's gonna stop and you better get much as you can while you can . . . When fellas get tired of your pussy, it's good-bye girl, naw, it's get the fuck out of my life bitch! Next bitch!' [23, pp. 97, 131]. Young women in these neighbourhoods compete for access to men who can supply lavish (if short-lived) resources and whose consumer lifestyle contrasts markedly with the hand-to-mouth existence of the unemployed. Among middle-class women, male resource variance is much less extreme, parental support is available, and consequently the need to resort to physical aggression is less: female competition is generally restricted to intersexual rivalry for male attention.

In impoverished neighbourhoods, the willingness of some women to trade sex for resources makes verbal assaults on a woman's sexual reputation particularly apt and creates fear among others that they will tarred with the same brush. But everywhere (regardless of social class, race or ethnicity) accusations of promiscuity are powerful forms of verbal attack because they jeopardise a young woman's

chance of finding a reliable long-term mate. The sexual revolution has done little to diminish men's reluctance to marry 'easy' women. In addition to damaging a rival's reputation, women as a sex benefit by using verbal attacks to control other woman's sexuality [35]. Because sex is a resource that men want and women can supply, women gain by maintaining a high 'market price' for sex. By making sex contingent on commitment, women encourage men to pursue a more monogamous strategy. Women who dispense sex too cheaply reduce the bargaining power of other women. In underclass neighbourhoods, the intense competition and the paucity of men who are willing to commit increases the temptation to offer sex at a low level of male investment. The term 'whore' is used not only to tarnish a rival in men's eyes but also to mark her out as someone who has selfishly sold other women out.

4. Psychological mediators of sex differences in aggression

Close description of the ecological setting, culture and dynamics of young women's fighting is illuminating, but it should not distract us from the fact that, everywhere and at every historical period, physical aggression between women is less frequent and less severe than between young men. As the dangerousness of the aggressive act increases so does the magnitude of the sex difference. Just as the sex difference is greater for aggravated than simple assault, so same-sex homicides show the greatest imbalance with 97% committed by men around the world [36]. Meta-analysis of self-report studies find effect sizes of $d = 0.59$ for physical aggression, $d = 0.19$ for verbal aggression and $d = 0.05$ for indirect aggression [37]. In other primate species also, aggression between males is more injurious than between females [38].

This pattern of sex differences has been explained in terms of sexual selection [37]. Daly & Wilson [18] focused on the greater variance in male reproductive success which offers incentives for intrasexual aggression in the quest for dominance and resources. While not denying the existence of female aggression, they emphasized its relative paucity which they explained in terms of the absence of reproductive incentives: females in polygynous species do not need to compete for copulations. My approach [39,40] focuses on the greater costs attendant on females' aggression. It does not assume a polygynous mating system and recognizes that incentives other than copulation opportunities can support female aggression.

For both sexes, reproductive success is measured in the number of offspring who survive to adulthood and who themselves reproduce. Given that maternal investment exceeds paternal investment, this burden is disproportionately borne by females. Following gestation, mothers expend calories in lactation and in feeding young children who must also be monitored and defended from natural accidents and attack by conspecifics. The advantages that high rank could confer in accomplishing these tasks make it all the more surprising that females do not engage in dominance contests to the same extent as males. In many species, dominant females have priority of access to food, supplant others from feeding sites and are less subjected to predation. They can suppress reproduction in subordinates, have shorter interbirth intervals and produce more surviving offspring [41].

Among primates, dominance relations are most discernible in female-bonded species (where daughters remain in their natal group). Dominance in such groups is inherited through matrilines rather than achieved by aggression. Matrilines can be ranked with respect to one another with virtually no overlap. There are three rules that predict a female's rank [42]. First, daughters inherit their mother's rank on her death without requirement for direct combat. Second, mothers dominate daughters for life. Third, in adulthood, younger sisters dominate older sisters. This may be a maternal strategy to ensure that a younger daughter cannot improve her rank by forming a coalition with her sister [43]. Matrilineal inheritance creates a remarkably stable system. In baboons, a juvenile female's rank at birth correctly predicted her adult rank in 97% of cases [44]. In female gelada baboons, there was no alteration in rank position over a 4-year period despite the disruptive potential of births, deaths, fissions and male takeovers [45]. Among capuchins, the female hierarchy was stable over 22 years [46]. Studies which have experimentally manipulated female groupings demonstrate that challenge for dominance is rare and occurs only when the odds are strongly in favour of the challenger, referred to as a 'minimal risk' strategy [42]. By contrast, in non-female bonded primates, for instance chimpanzees (in which females transfer to a new group at adolescence), dominance relations are hard to detect and rarely involve outright aggressive confrontation [47]. In bonobos also, female relationships are egalitarian and aggression between females constituted only nine out of 325 aggressive episodes recorded [48].

The advantages of dominance combined with the reluctance of females to risk aggression in its pursuit suggest that there must be associated costs. Aggression involves the possibility of injury and death and their consequences on reproductive success are not equal for men and women. For women, with their limited variance in fecundity, child survival plays a critical role in their ultimate reproductive success. A review of 45 studies of natural fertility populations with limited access to medical care indicated that a mother's death has uniformly detrimental effects on her children's chances of survival [49]. The effect is strongest in the early years of a child's life. Pavard et al. [50] conducted a careful study of births in seventeenth- and eighteenth-century Quebec. They excluded cases in which the baby died immediately following birth (to exclude obstetric complications and cross-infection) and corrected for between-family heterogeneity (intrinsic family mortality levels). A mother's death during the neonatal period increased the odds of her child dying in the postnatal period (28–299 days) by 5.52. Although the effect was less extreme at later ages, the death of a mother in early childhood (3–5 years) increased the odds of her child dying in the same period by 2.48 and by 1.45 if her death occurred during late childhood (5–15 years).

A contrast with the effect of paternal death is instructive. In every study in which there was a direct comparison of the effect of maternal and paternal deaths, the loss of a father had substantially less impact [49]. Indeed in 15 out of 22 (68%) studies, the presence of a father had no impact at all on child survival. Although it is commonly assumed that fathers are important in provisioning, paternal death had no effect on child survival among the South American Hiwi who live in nuclear families in which fathers contribute meat and direct child care. (This is not to deny the contemporary evidence that fathers improve their children's educational and social

life chances [51]. My concern here is with the centrality of the mother during human evolution.) It appears that paternal care is facultative rather than obligatory in our species and that a father's death can be compensated for by help from grandmothers (especially maternal grandmothers) and older siblings.

Infancy and early childhood are vulnerable periods. Among the Ache of Paraguay, 13% of children die before the end of their first year and 27% before the age of five [52]. The mother is the infant's most important line of protection from starvation, attack and accidents. Given the short interbirth interval in our species, women would have been caring for a vulnerable infant and/or pregnant for a substantial proportion of their reproductive career [53]. A woman's reproductive success may have depended on the avoidance of risky behaviours, including aggression.

This raises the question of the psychological adaptation that mediates women's greater avoidance of risky confrontations. Aggression can be conceived of as a trade-off between anger (approach) and fear (avoidance) which suggests that alterations in the intensity of these fundamental affective responses may underlie willingness to aggress. The possibility that women's lower level of anger might explain their greater desistance is not supported by research. Meta-analyses indicate no sex difference in anger either in adults [37] or in children [54]. In addition, a raised threshold for anger might protect women from aggressive confrontations but not from other risky forms of behaviour. Yet, there is ample evidence that women are more risk averse than men [55].

By contrast, there is a considerable body of work suggesting that women are more fearful than men. This difference is visible in childhood [54] and international surveys have found significant sex differences in the reported intensity and duration of fear in adults [56]. Women and girls show more corrugator muscle and electrodermal activity than men when viewing negative images and a stronger startle response to a noise blast delivered during exposure to fear-inducing pictures [57]. Cross-culturally, women exceed men on trait neuroticism [58] and are more prone to phobic fears and anxiety [59]. Under conditions of threat, women judge the danger to be greater than men do [60]. Women orient away from (rather than toward) threat and with greater intensity then men do [61]. Following the tragedy of the World Trade Center, a nationally representative sample of Americans participated in a survey which included assessments of fear and anger [62]. Women reported significantly higher levels of fear and gave higher risk estimates than men did. Some research suggests that fear has stronger aggression–suppressing effects on women than men [63]. After being subjected to stressors which both sexes rated as inducing fear, women in the high-stressor condition subsequently gave lower intensity shocks while, among men, stressor intensity was not related to shock delivery. Two meta-analyses have concluded that the magnitude of sex differences found in laboratory studies of aggression is positively correlated with the sex difference in ratings of participants' personal danger [64,65].

This emphasis on fear as a key factor in explaining sex differences carries implications for individual differences among young women. In deprived and dangerous neighbourhoods, girls frequently note the need to suppress expression of fear in order to avoid victimization. This theme echoes through much of the qualitative work on female violence, from Philadelphia ('If I seem like I'm scared to fight, some girl is gonna think she can mess with me all the time' [6, p. 38]) to Glasgow (' . . . 'Cos if you show fear of somebody they're just gonna walk all over the top of you. If you show fear of them, they always come back tae you' [66, p. 130]). Among young people with high exposure to violence in their communities, reduced levels of fear (reflected in lower heart rate) are associated specifically with proactive (unprovoked) forms of aggression [67]. This mirrors the narratives of aggressive girls who describe the importance of fearlessness and the use of pre-emptive aggression in the development of a fierce reputation.

5. Neuropsychology of sex differences in emotion

We now turn to the question of whether we are yet able to identify neuropsychological, hormonal and physiological correlates of sex differences in aggression-related emotion. Before doing so, it is important to bear in mind the visual stimuli that are used to induce emotions in neuroimaging studies. Of special relevance to understanding sex differences in aggression are responses to 'threatening' stimuli. These are chiefly facial expressions of fear and/or anger and, less frequently, aggressive stimuli such as weapons.

(a) Amygdala

I have noted the considerable behavioural evidence that women are more fearful than men. Indeed the twofold greater prevalence of anxiety disorders among women has been the impetus to many imaging studies looking for neural correlates of this sex difference. The chief focus of such studies has been the amygdala. The amygdala is an almond-shaped subcortical structure (composed of more than 10 nuclei) in the temporal lobe. For many years, it was believed that the amygdala was uniquely associated with fear responses, although it is now thought to register other strong or salient stimuli. Afferent sensory inputs to the lateral nucleus of the amygdala are coordinated with efferent outputs from the central nucleus which control behavioural, autonomic and endocrine fear responses. We would expect to see a stronger amygdala response to threat in women reflecting their greater fearfulness.

Meta-analyses conclude that women do show greater activation to threat in the limbic system, especially the amygdala ([68,69], but see [70]). In one study, women showed a greater extent (rather than magnitude) of activation together with a more extended time course: during exposure to threatening stimuli, women exhibited sustained amygdala activation (and skin conductance), whereas men's response diminished more quickly [71]. This suggests that women may register external threat more strongly and more persistently than men. However, because the majority of neuroimaging studies use participants of only one sex, meta-analytic conclusions are based on comparisons of neural responses in men and women to different stimuli [68].

Although amygdala activation has been chiefly implicated in fear, it has also been linked to aggression. Despite experimental bracketing of fearful and angry faces as representing 'threat', there is evidence that perception of these two stimuli may activate different brain regions. While fearful faces reliably activate the amygdala associated with avoidance, angry faces preferentially (or additionally) activate oribitofrontal areas implicated in emotional control [72,73]. Studies that include men and women in the same study are

important in establishing whether there are sex differences in brain activation to identical 'threatening' stimuli. McClure *et al*. [74] compared men's and women's reactivity to angry and fearful faces. The relative engagement of the amygdala bilaterally to angry faces was greater in women suggesting that women react more fearfully than men to unambiguously threatening (angry) faces. Relative to baseline fixation, women showed significantly greater activation than men over the whole 'fear circuit' (amygdala, orbitofrontal and anterior cingulate cortex (ACC)) to angry but not fearful faces. By contrast, men showed a less specific pattern of increased orbitofrontal (but not amygdala) activation to both stimuli. Men's reactivity to angry faces varies as a function of trait anxiety and anger [75]. In men, but not women, heightened amygdala reactivity is associated with a combination of high anxiety and high reactive anger. There is then some support for the proposal that amygdala activation may be more closely associated with fearful responses to threat in women and (fear-related) reactive anger in men.

As with other regions that are sexually dimorphic in size, the amygdala contains a high concentration of sex hormone receptors. Because testosterone (T) has been linked to aggression, we might expect to see T-linked differences in neural response. Depending on whether amygdala activity is viewed as reflecting fear or anger, different predictions follow. From the fear viewpoint, T has anxiolytic effects suggesting that endogenous T levels should reduce amygdala reactivity to threat, as has been found in men but not in women [76]. The amygdala also controls automatic responses to threat: T administration to young women reduced attention to fearful faces [77], skin conductance during viewing of negative pictures [78] and the magnitude of fear-potentiated startle response [79]. On the other hand, some have assumed that amygdala activity reflects anger rather than fear [80]. If so, we would expect to see a positive association between T and amygdala activity in response specifically to angry faces (since fearful faces are less likely to elicit anger). Although in both sexes, higher levels of endogenous T are associated with a stronger amygdala response to 'threatening' stimuli [81], many studies do not analyse fear and anger stimuli separately [82,83]. In one study that did, young men's amygdala reactivity did not differ significantly to angry versus fearful faces and their endogenous T levels were equally correlated with their amygdala responses to both stimuli [84]. However, administration of T to young women increases amygdala reactivity to angry faces [85]. Despite these inconclusive results, many researchers interpret the pattern of data as indicating that T causes a shift toward a more 'male typical' response with enhanced amygdala activity (reflecting anger registration) combined with a reduction of fear both physiologically (skin conductance) and behaviourally (startle response).

The neuropeptide oxytocin (OT) is widely recognized for its anxiolytic properties associated with enhanced trust and cooperation [86]. While OT administration reduces amygdala reactivity to threat in men, it has the opposite effect in women [87,88]. The full implications of this finding have yet to be appreciated and underscore the importance of studying both sexes in relation to hormonal effects. Despite the disproportionate use of male participants in OT studies, OT is thought to be particularly relevant to women because oestrogen stimulates OT release, and promotes OT receptor gene expression and OT binding in the amygdala. Given women's stronger fear response to threat, exogenously administered

(and by implication endogenously synthesized) OT has been interpreted as enhancing the female fear response as an adaptation for maternal survival and infant protection [88]. The fact that OT enhances, rather than diminishes, attention to potential threat in the environment casts doubt on the popular 'tend-and-befriend' hypothesis which is based on the presumed anxiolytic effect of OT [89]. In contrast to men's fight-or-flight response to threat, this hypothesis proposed that OT-mediated stress reduction enabled women to remain calm, blend into the environment and bond with their infants and with other females.

Comparing T and OT studies, we see that the interpretation of results is often selective. Studies which administer OT interpret enhanced amygdala activity as reflecting fear and avoidance, whereas T administration studies interpret the same effect as enhanced anger and approach. With respect to both hormones, we should consider the possibility that the effects of exogenous hormones on male and female brains are likely to differ. Given the greater OT receptor density in the female brain, administration of OT may result in very high levels of uptake and dosage effects may be non-linear, as has been found with other hormones. It is possible that at least some part of T's neural effects occur via aromatization to oestradiol in presynaptic terminals which in women may enhance sex-typical fear in response to threat. T is likely to produce very different effects on the female brain which, unlike the male brain, has not been prenatally organized by T. Gene expression in the brain is sexually dimorphic and controlled by sex hormones: the same hormone can result in the expression of different genes in male and female brains [90,91].

(b) Amygdala – frontal connectivity

Lower-level affective tendencies to approach or avoid stimuli located in the limbic system are part of a 'reflexive' behavioural control system sculpted chiefly by evolutionary forces. In humans, these tendencies are subject to higher level 'reflective' control. Emotional intensity and behavioural response can be modulated by the prefrontal cortex, especially the orbitofrontal (OFC) region, which has direct connections to the amygdala. In neuroimaging studies, negative correlations are found between amygdala and OFC activity in impulsively aggressive individuals [92]. In studies in which participants are instructed to imagine aggressing against [93] or harming [94] another person, deactivation of the OFC has been found. Given the modulatory role of the prefrontal cortex (PFC), studies have looked for sex differences in these regions. Women have a larger ventromedial PFC and right lateral OFC [95,96]. A meta-analysis of 88 studies reported greater OFC activity in women to facial stimuli depicting negative emotion ([68], see also [69]). This suggests that women may be more efficient in spontaneously regulating emotional responses.

This is supported by studies of hormones and the neurotransmitter serotonin. While progesterone increases functional connectivity between the amygdala and PFC [97], T reduces it, while leaving connectivity to the brain stem unaffected [82,98]. OT, a neuropeptide upregulated by oestrogen, appears to have opposite effects to those of T. OT enhances amygdala–prefrontal connectivity [99] while reducing amygdala coupling with the brain stem [100].

Serotonin (5-HT) plays a key role in the functional connectivity between the PFC and the amygdala. There is a dense

concentration of 5-HT receptors in the limbic system (including the amygdala) with projections to the prefrontal cortex. Dietary tryptophan depletion (which reduces 5-HT levels) reduces connectivity in the prefrontal–amygdala circuitry specifically when viewing angry faces [101]. Women have higher 5-HT transporter availability and, because this regulates 5-HT neurotransmission, baseline serotonin may be higher in women than men. Studies have reported a higher density of $5-HT_{1A}$ receptors in women in areas including the amygdala and medial and orbital PFC [102]. Receptor density in these areas is significantly negatively correlated with lifetime aggression. In animal research, 5-HT receptor density is also negatively correlated with T. Although this has not been replicated with humans, men (but not women) with high levels of aggression are characterized by a combination of high T and low 5-HT [103]. Reduced serotonin availability or uptake, associated with high T, may explain men's diminished prefrontal control over emotion-driven behaviour.

(c) Amygdala – peripheral connections

The central amygdala projects downward to the hypothalamus and brain stem to initiate autonomic and hypothalamic–pituitary–adrenal (HPA) responses to threat. Sex differences in self-reported and behavioural measures of fear are not matched by differences in sympathetic nervous system reactivity. When fear is induced through incremental behavioural approach to spiders [104], inhalation of CO_2-enriched air [105], affective images [106], scary movie clips [107] or emotional imagery [108], sex differences in heart rate and blood pressure are not found. In the HPA system, evidence indicates somewhat higher salivary cortisol measures in men after experimental stress induction [109].

(d) Anterior cingulate and anterior insula cortices

It has been suggested that this anomaly—higher self-reported fear in women combined with an absence of sex differences in physiological reactivity—might be resolved by sex differences in the conscious experience of emotion. Two structures which are often jointly activated have been implicated: the anterior insula cortex (AIC) and the anterior cingulate cortex (ACC). These structures monitor bodily states (including thirst, touch and sexual arousal) and are also activated in response to a wide range of emotions, including fear and anger. Their co-activation makes it difficult to tease out their respective contributions to emotional states, but it has been proposed that the AIC monitors the internal neural and visceral state (interoception) and the ACC mediates the subjective experience of emotion [110,111].

Women have greater grey matter volume and higher resting-state blood flow to the ACC. They show stronger ACC (as well as amygdala) activity than men in an electric shock conditioning paradigm, despite no sex difference in autonomic system reactivity [112]. A meta-analysis of 65 studies examining sex differences in neural activation to emotional stimuli found that women showed greater density of activation in the ACC [68] and men in the AIC [113]. In response to specifically negative stimuli, women showed greater reactivity than men in the ACC suggesting that women process stimuli in terms of subjective emotional state. Women but not men when asked to imagine acts of aggression show enhanced ACC activity [114]. OT enhances activity in the ACC and increases its connectivity with the amygdala [115,116]. Men

respond to negative stimuli with greater activity in the AIC. It has been suggested that this may be because men process emotional information in terms of interoceptive states and implications for action. The possibility that women have a more intense subjective experience of emotion than men goes some way to explaining the paradoxical finding that women's self-reports of the intensity of many emotions is generally higher than men's despite few sex differences in autonomic indices. This is especially true of fear.

Some have suggested that the absence of sex differences in autonomic correlates of fear is explicable by men's reluctance to admit fear because of male gender role proscriptions on acknowledging vulnerable emotions. Although self-reports of fear and anxiety are correlated negatively with masculinity and positively with femininity [59], studies which control for gender role still find a significant effect of biological sex in self-reports [117]. In a behavioural task in which some participants were told that their self-report of fear was verifiable by heart rate monitors, the significant sex difference in fear ratings was unaffected [104]. While social and cultural expectations about gender are important, it appears that they cannot fully explain sex differences in self-reported emotional experience.

To summarize, the available data suggest that women register threat more strongly in the amygdala, although the sexes differ little in their autonomic and HPA responses. Women may have a stronger subjective awareness of fear associated with greater ACC activity. They show a stronger OFC reactivity to negative emotion, have a higher density of serotonin receptors and lower levels of T (which reduces connectivity between the OFC and amygdala) perhaps making them better able to exert control over the behavioural expression of emotion.

6. Conclusion

Like all living organisms, women compete. The real questions concern what they compete about and how lethal their competition is. Among young Western women living in deprived circumstances, aggression often revolves around competition to acquire and retain mates. The same finding has been reported in a cross-cultural survey of the Human Area Relations File [118], as well as data from Zambia [119] and Aboriginal women [120]. Among the Tsimane of Bolivia [121], conflict about men constituted 25% of women's arguments, compared to 28% about social relationships (e.g. defecting on a social exchange) and 19% about food sharing or theft. However, these percentages varied significantly by age. Under the age of 20, men were the leading cause of conflict (Tsimane girls marry much younger than in the West) although this was overtaken by quarrels over mutual social obligations between women in the 30–40 age range. However, as we have seen, physical forms of aggression are most common among younger women. Anthropological research alerts us to the importance of cultural factors in female aggression. Young women's behaviour is shaped by local understanding of the meaning of 'femininity' and expectations of appropriate response to challenge. These cultural values in turn are likely to be responsive to ecological factors including sex ratio, poverty and variance in male resources.

The critical role that mothers play in infant survival is now well documented and provides an evolutionary platform for expecting that, despite the benefits of achieving dominant status, there are associated costs. I have emphasized the need

to avoid escalated aggression if women are to ensure the survival of infants with their high replacement costs. Others have pointed out that biological 'masculinization' associated with intense competition may compromise female fertility and fecundity, limiting the evolution of extreme female aggressiveness [19,41]. In our own species, the psychological evidence points strongly toward greater fear (rather than lower anger) as the proximate mediator of women's less intense aggression. A sex difference in fear also explains women's lower involvement in a range of risky activities such as extreme sports, dangerous driving and criminal activities [55,122]. It converges with considerable evidence of women's greater punishment sensitivity and vulnerability to anxiety and depression [123].

Despite abundant self-report and behavioural evidence of sex differences in fear, neuropsychological research is still in its infancy. Understanding aggression (in both sexes) requires more reliable tools to distinguish between qualitatively different emotional and motivational responses to threat stimuli. A fearful face communicates the possibility of danger at an undetermined place in the environment and may evoke corresponding fear in the viewer. An angry face directed to the viewer more clearly indicates threat but this may evoke either fear or anger (or both). Because fear and anger are associated with amygdala reactivity, there is a tendency for researchers' interpretation of their results to be driven by their knowledge of sex differences. Hence, heightened amygdala activity is taken to indicate fear in women and anger in men. At present, evidence suggests that women show a stronger amygdala registration of threat, combined with a stronger subjective awareness of emotion and, perhaps, stronger inhibitory prefrontal control. Further studies are needed in which men and women experience the same stimuli and their neural responses are directly compared. Ultimately, these emotional responses must be linked to aggressive behaviour and this is challenging for neuropsychology because a scanner restricts natural movement. However, asking participants to vividly imagine aggression may be the way forward: a number of studies now confirm that neural responses elicited when participants imagine acts or feelings correspond to those seen during the authentic experience [124,125].

From an evolutionary viewpoint, variance between women in reproductive outcomes tells us that women are in competition. The extent to which that competition takes the form of aggressive confrontation varies as a function of ecological pressure. Ethnographic studies can provide important descriptions of the causes, context and culture of female fighting. The challenge for psychology is to identify the psychological and neural mechanisms that underpin its expression and form, and that restrict its severity relative to men's.

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