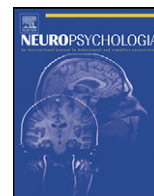




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Reviews and perspectives

Sex differences in processing emotional signals of others

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ABSTRACT

Interest in sex-related differences in psychological functioning has again come to the foreground with new findings about their possible functional basis in the brain. Sex differences may be one way that evolution has capitalized on the capacity of homologous brain regions to process social information between men and women differently. This paper focuses specifically on the effects of emotional valence, sex of the observed and sex of the observer on regional brain activations. We also discuss the effects of and interactions between environment, hormones, genes and structural differences of the brain in the context of differential brain activity patterns between men and women following exposure to seen expressions of emotion and in this context we outline a number of methodological considerations for future research. Importantly, results show that although women are better at recognizing emotions and express themselves more easily, men show greater responses to threatening cues (dominant, violent or aggressive) and this may reflect different behavioral response tendencies between men and women as well as evolutionary effects. We conclude that sex differences must not be ignored in affective research and more specifically in affective neuroscience.

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1. Introduction

The expression and interpretation of emotions play an important part in human interactions. Research indicates that men and women possess different skills related to the sending and receiving

of emotional messages. In general, women are more emotionally expressive, whereas men conceal or control their emotional displays (Buck, Miller, & Caul, 1974). In addition to their encoding ability, women tend to express emotion through facial expression and interpersonal communication, whereas men generally express emotion through actions such as engaging in aggressive behavior.

Sex differences in brain activation patterns associated with the processing of emotional expressions have been identified in numerous studies and described in many meta-analysis studies. However, from this gathered information, many questions are still left unanswered. Do women express their emotions and recognize others'

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emotions better or differently than men in all situations? If so, is this an inherent tendency or a product of socialization and cultural expectations? Do women feel more emotions than men and could this possibly be reflected in enhanced brain activity levels? These and other questions will be discussed in a very broad context, broader than most of the earlier review articles. Different factors that could possibly underlie sex differences in emotional processes—including chromosomal, hormonal, structural and functional differences on the brain level, as well as environmental (including cultural) factors and their interactions are discussed. Besides these factors that all affect the participant, we also discuss the effect of the sex of the stimulus.

In this review article we want to consider the evidence about the common view popular outside science that women are more emotional than men. The most problematic conflicting evidence with the stereotype is that men do not conceal their emotions or control their responses when it comes to aggression. The size of this bias toward hostility is closely related with testosterone levels and is reflected in increased brain activity levels as compared to females. In this review we pull apart emotional expressivity from emotional experience and show that whereas women may be more expressive than men and tend to recognize emotions better, this is highly dependent on the situation and type of emotion and does not reflect brain activity patterns.

2. Recognizing emotions

Men and women show differences in their ability to recognize facial expressions of emotion. Much of the evidence shows that women are better in identifying facial affect (Campbell et al., 2002; Collignon et al., 2011; Hall, 1978; Hampson, van Anders, & Mullin, 2006; Thayer & Johnsen, 2000). In a task which involved choosing a photograph that corresponded to a described emotion, 3.5-year-old girls were as accurate as 5-year-old boys (Boyatzis, Chazan, & Ting, 1993). However, boys and girls performed equally well on finding a line drawing of a target face among an array of eight distracter line drawing faces (LoBue, 2009). Nevertheless, a review article concluded that across development, a small yet reliable enhancement in performance on emotion tasks in females relative to males has been observed. This difference was largest in infancy and early childhood (McClure, 2000). Taken together with Hall's (1984) meta-analytic findings of a consistent female advantage for expression processing in adults, these findings suggest that sex differences wax and wane at different points in the lifespan, with a small tendency for females to perform better. Despite this evidence, there is controversy about the specificity and the size of the female advantage (Derntl et al., 2010; Grimshaw, Bulman-Fleming, & Ngo, 2004; Rahman, Wilson, & Abrahams, 2004).

One suggestion is that sex differences in the reaction to face stimuli may be greatest when the intensity of the emotions portrayed is maximal (Wild, Erb, & Bartels, 2001). Another study advocated that the differences might be explained by different looking patterns of male and female participants. In that study women were faster (not more accurate) in identifying happy facial expressions and males spent a significantly longer time viewing the nose and mouth (Vassallo, Cooper, & Douglas, 2009). However, we could not replicate these findings. In a group of 37 students, looking patterns of male and female participants on angry, fearful and happy facial expressions were similar. Even when including a high and low socially anxious group and increasing the sample to 79 individuals did not reveal any difference between the sexes (Kret, Roelofs, Stekelenburg, & De Gelder, in preparation) (see also Jansari, Rodway, & Goncalves, 2011). In another study showing the emotional expressions for a short duration – less than 200 ms – looking patterns were the same for both genders, yet women

showed higher accuracy rates than men (Hall & Matsumoto, 2004). Other studies suggest that these sex differences depend on the type of emotion. Women are said to be better in recognizing facial expressions of fear and sadness (Mandal & Palchoudhury, 1985; Nowicki & Hartigan, 1988), while men are superior at identifying anger (Mandal & Palchoudhury, 1985; Rotter & Rotter, 1988; Wagner, 1986).

All the above studies used photographs. In real life, emotional expressions are highly dynamic and researchers recently explored the influence of movement in emotional paradigms. Sex differences have not always been observed in the explicit recognition of dynamic expressions (Kret, Pichon, Grèzes, & De Gelder, 2011; Nelson & Russell, 2011a, 2011b; Rahko et al., 2010). However, in women, dynamic expressions have been associated with higher intensity ratings for anger and happiness whereas in men, dynamics' influence was limited to anger (Biele & Grabowska, 2006).

Common sense suggests that being confronted with a physically stronger man who expresses anger is a greater threat than being confronted with a woman who is less strong. For this and other reasons, some researchers looked at the effect of the sex of the stimulus and its interaction with the sex of the observer and some interesting observations resulted from that. As one would predict, evidence suggests that pictures of males versus females expressing anger are stronger cues. In an approach-avoidance-task, Seidel, Habel, Kirschner, Gur, and Derntl (2010) found significantly faster responses following male than female faces expressing disgust and anger. They also observed that female participants rated female faces more positively than male faces (Seidel et al., 2010). Anger posed by males was more accurately perceived than anger posed by females (Goos & Silverman, 2002). On the other hand, Marsh, Adams, and Kleck (2005) observed that their participants responded faster to female than to male faces and most quickly to women expressing fear. Armony and Sergerie (2007) observed that female participants better remembered fearful (but not neutral or happy) female versus male faces but it is unclear whether this difference was larger than in male participants. It has also been reported that female subjects better recognized females' than males' expressions whereas there was no difference for males (Wagner, 1986).

To conclude this section, there appears to be a female advantage when it comes to emotion recognition but due to conflicting results it is still not clear if this is true for all emotions in all situations and all expressers (McClure, 2000). More naturalistic stimuli and taking into account the sex of the actor, could provide further insight into the issues at stake. How these observations translate to differential brain activation patterns and how other factors such as chromosomal and hormonal differences can mediate these effects is discussed later on. But before we move to those issues, we will first clarify that differences in emotion recognition, expression or intensity ratings do not necessarily mean that the emotional experience between men and women differs. This issue will often come back in the remaining of this manuscript.

2.1. Are women more emotional than men?

Common sense views women as more emotional than men. Yet research suggests this presumed difference is based more on an expressive than on an experiential difference (Dimberg & Lundquist, 1990). Kring and Gordon (1998) assessed the expressive, experiential, and physiological emotional responses of men and women in two studies. In Study 1, participants viewed emotional films. Compared with men, women were more expressive, showed a different pattern of skin conductance responses but reported similar levels of experienced emotion. In Study 2, men and women completed self-report scales of expressivity, gender role characteristics, and family expressiveness after viewing the films. Results replicated

those from Study 1, and gender role characteristics and family expressiveness (as measured by rating the extent to which different expressive behaviors occurred in their families) modulated the relation between sex and expressivity. So, the higher gender role characteristics and family expressiveness, the higher expressiveness (Kring & Gordon, 1998). Wagner, MacDonald, and Manstead (1986) videotaped participants' facial expressions as they watched emotional slides. After each slide, participants named the emotion term that best described their affective reaction. Similar uses of emotion terms were later made by another group who watched the videotaped expressions. Females' neutral and surprised faces were more accurately recognized than those of males.

All this suggests that the stereotype of women "being" more emotional than men is probably derived from an expressive difference. It has been suggested that women might appear to be more emotional because they are more facile with emotion language (Fugate, Gouzoules, & Barrett, 2009) see also (Azim, Mobbs, Jo, Menon, & Reiss, 2005). Aside from this, across cultures, women show their tears five times more often than men (Walter, 2006). Women also tend to smile more, but results from a meta-analysis suggest that they do so especially in situations where they are expected to smile more (LaFrance, Hecht, & Paluck, 2003). In sharp contrast, men feel anger more frequently and tend to be more aggressive than women (Biaggio, 1980, 1989; Doyle & Biaggio, 1981). This provides evidence against the idea that women are generally more emotional than men and instead, it depends on the type of emotion and on the situation. Sex differences in crying, smiling and aggressive behavior therefore seem partly based on gender-specific display rules. Many sex differences are context-dependent, and socialized in accordance with display rules, prescriptive social norms that dictate how, when and where emotions can be expressed by males and females (Brody & Hall, 1993; Fischer, 1993; Fischer, Rodriguez Mosquera, van Vianen, & Manstead, 2004; Shields, 1987; Stoppard & Gruchy, 1993; Underwood, Coie, & Herbsman, 1992). We will elaborate on this issue in the next section.

2.2. Cultural prescriptions shaped by evolution

One of the many still unanswered questions regarding sex differences and their origin is whether they came into existence within a specific culture or whether they became evolutionary adaptive at some point and thereby modified culture. Either way, cultural influences probably socialize males and females to act in accordance with certain expectations. While socialization of aggressiveness might involve learning to control and inhibit angry behavior, pressures for this may be stronger on females than on males (Eron & Huesmann, 1984). Interestingly, women are more likely to use direct aggression in private, and are more likely to use indirect aggression in public (Chrisler & Donald, 2010). By age 4–5, girls tend to suppress the expression of anger consciously. By about 7–8 years of age, adult-like differences become more consistent, with boys expressing more anger (Potegal & Archer, 2004). But when it comes to positive emotions, women are not inhibited to express their feelings. Fischer and Dubbe (2003) showed that females' responses to advertisements that contain happiness or sentimentality were not influenced by social context effects. But the presence of another male in the viewing environment affected male responses when the emotional appeal was incongruent with stereotypes. Under private viewing conditions, male participants' self-reports were similar to that of females.

These cultural expectations also modify the meaning of emotional expressions as a function of the sex of the expresser. Men who display sadness, depression, fear, or dysphoric self-conscious emotions including shame and embarrassment are evaluated more negatively than females (Siegel & Alloy, 1990), and are less likely

to be comforted than women (Barbee, Cunningham, Winstead, & Derlega, 1993). On the opposite side, anger and aggression are seen as socially acceptable for men and aggressive boys have been found to be judged as more likable and socially competent than non-aggressive boys (Hart, DeWolf, & Burts, 1992; Serbin, Marchessault, McAffer, Peters, & Schwartzman, 1993), whereas this is not the case for girls (Crick, 1997). Men who expressed neutral and angry emotions were rated as higher in dominance when compared with men expressing sadness or shame (Hareli, Shomrat, & Hess, 2009). Female smiles are appealing to males, increasing physical attractiveness and enhancing sex appeal. However, a man's smile may not be most effective in attracting women, and facial expressions such as pride or even shame might be more effective (Tracy & Beall, 2011).

More evidence that the interaction between emotion and sex is highly socialized and changes the meaning or interpretation of emotional expressions comes from a study by Barrett and Bliss-Moreau (2009). When participants in an experiment looked at photos of women's and men's faces looking sad, afraid, angry, or disgusted, that are shown with a sentence beneath the image purporting to explain the emotion ("buried a family pet" for a sad face, for instance, and "was threatened by an attacker" for a fearful one), they offered starkly different explanations for the emotions. Women in the photos were said to feel sad, angry or afraid because they were "emotional", but the pictured men felt those emotions because they were "having a bad day"—even when the expressions and their explanations were identical (Barrett & Bliss-Moreau, 2009). The society we live in with its normative expectations has a massive impact on our gender identity. What is more, being forced to act in conflict with these scripts causes feelings of frustration. Bosson and Vandello (2011) observed that asking men to do jobs traditionally associated with women made them more aggressive when their masculinity was being threatened (Bosson & Vandello, 2011) see also (Bosson, Vandello, Burnaford, Weaver, & Arzu Wasti, 2009).

If these sex differences go a long way back in the course of evolution, they are probably best detectable via implicit paradigms and may also be apparent in young children. In an old binocular rivalry study, a relatively cultural bias-free technique, it has been found that males reported more violent scenes than females (Moore, 1966). As will be outlined in the next section, this enhanced sensitivity to threat in males, may be mediated by testosterone. Recent findings suggest that also ovarian hormones play an important role in emotional functions and may influence behavior directly or via brain plasticity and functionality (Derntl et al., 2008; Guapo et al., 2009; Hiroi & Neumaier, 2011; Zeidan et al., 2011).

2.3. Hormones and sex differences

Gonadal hormones, and testosterone in particular, are known to influence the regulation of emotional responses and affective states and may mediate some of the sex differences that are seen in emotional processes. Also, there is growing evidence that the neuropeptides oxytocin and vasopressin modulate complex social behavior and social cognition (Bos et al., in press) and oxytocin and vasopressin receptors are abundantly present in the hypothalamic nuclei and in limbic areas including the amygdala (Landgraf & Neumann, 2004).

Although normally released from the hypothalamus during the activation of the sympathetic autonomic nervous system, when administered exogenously, oxytocin produces opposite effects of the fight-or-flight response (Jezova, Skultetyova, Tokarev, Bakos, & Vigas, 1995). Oxytocin has caused relaxation and sedation as well as reduced fearfulness and reduced sensitivity to pain (Uvnas-Moberg & Petersson, 2005). Williams, Carter, and Lightman (1985) observed higher stress-induced increase in oxytocin levels in male rats of

which the testes had been surgically removed. This might suggest an inhibitory action of testosterone (Williams et al., 1985). In addition to the increased quantity of oxytocin released in females versus males, McCarthy (1995) found that estrogen enhances the effects of oxytocin. Thus, oxytocin may be vital in the reduction of the fight-or-flight response in females.

In males, the fight-or-flight response is characterized by the release of vasopressin. The effects of vasopressin are enhanced by and probably dependent on testosterone and influence the defense behavior of male animals (Taylor et al., 2000). Van Honk et al. (1999) showed positive relationships in both men and women between testosterone levels and vigilance to angry faces. Similarly, Wirth and Schultheiss (2007) observed that higher testosterone predicted better learning on sequences paired with sub-threshold (i.e., presented too fast for conscious awareness) angry faces. The authors suggest that testosterone may generally decrease aversion to threatening stimuli, and may facilitate approach toward signals of dominance. Testosterone level is also a good predictor of the presence of aggressive behavior and dominance (van Honk & Schutter, 2007).

At the level of brain responses, a recent review article (van Wingen, Ossewaarde, Backstrom, Hermans, & Fernandez, 2011) concludes that studies that have investigated women during different phases of the menstrual cycle (Derntl et al., 2008; Goldstein et al., 2005) suggest that progesterone and estradiol have opposing actions on the amygdala and prefrontal cortex. Endogenous testosterone concentrations are generally positively correlated to amygdala and OFC responses, and exogenous testosterone increases amygdala reactivity (van Wingen et al., 2011). Stanton et al. (2009) document associations between endogenous testosterone levels and BOLD responses to anger faces in the amygdala and vmPFC in men. The results further support the negative associations between amygdala and vmPFC activity. It has been suggested that this may contribute to sex differences in the vulnerability to psychiatric disorders (Kessler et al., 2005).

The above studies looked at hormonal effects in adulthood. But already very early in life androgens act to masculinize various human behaviors. There is evidence that the ratio of the length of the second digit divided by the length of the fourth digit (2D:4D) is affected by prenatal androgens. Many sexually differentiated behaviors have been correlated with digit ratios and replicated, including aggression (Benderlioglu & Nelson, 2004) and risk taking (Schwerdtfeger, Heims, & Heer, 2010) (for an overview, see Breedlove, 2010). It has been suggested that fetal testosterone comes into prominence when its priming is experimentally activated by testosterone administration in adulthood. A single administration of testosterone in female subjects leads to an impairment in the ability to infer emotions, intentions, and mental states of others. However, the 2D:4D ratio fetal testosterone marker predicted more than 50% of the variance in this effect, that is, effects of testosterone on cognitive empathy were only seen in subjects who were highly prenatally primed by testosterone (van Honk et al., 2011).

To conclude this section, there is a lot of discussion about the effects of circulating sex hormones and the prenatal organizing effects of sex hormones. But some differences between men and women cannot be not fully explained by gonadal hormones. Diversity in the genetic regulation of the receptors of neuropeptides (such as oxytocin and vasopressin) and perhaps also interactions between hormones levels and gene expression seem to underlie natural variation in social behavior.

2.4. Chromosomes and sex differences

As discussed in the former section, there is vast evidence for gonadal hormone control of sex differences (Morris, Jordan, &

Breedlove, 2004). But some neural and non-neural phenotypes have been found in which sex differences are not explained by the action of gonadal hormones (Arnold & Chen, 2009; Ngun, Ghahramani, Sanchez, Bocklandt, & Vilain, 2010; Sanchez & Vilain, 2010). In some cases, sex differences were found at developmentally earlier stages, before the onset of sex differences in levels of gonadal hormones.

Sex chromosomes are the only factors known to be represented differently in the male and female zygote. A strong test of the role of sex chromosome complement is the 'four core genotypes' (FCG) mouse model that produces XX and XY gonadal males, and XX and XY gonadal females (De Vries et al., 2002). Gatewood et al. (2006) used FCG mice in home cage intruder tests. Intruders were gonad-intact submissive males. The FCG mice were gonadectomized as adults, and testosterone was administered prior to the tests. XX-males, XY-males, and XY-females showed equal levels of aggression toward the intruder. XX-females showed less aggression. Thus, the effects of testicular secretions or an XY genome dominated. In another experiment, Barker, Torregrossa, Arnold, and Taylor (2010) used FCG mice and found that alcohol drinking was predicted by gonadal phenotype independent of sex chromosome complement. Various human sex chromosome disorders exist, which might be considered as a human model for sex chromosome effects similar to the four core genotypes. The most common variants in men involve additional X or Y chromosomes: Klinefelter Syndrome (47,XXY and 47,XYY). In women, the most common variants entail the addition or absence of X-chromosomes including 47,XXX; 48,XXXX; and Turner's Syndrome (TS) (45,X).

TS is a common chromosomal disorder in women, and provides a valuable paradigm to investigate genotypic contributions to social cognition. First of all, emotion recognition is impaired in women with TS (Lawrence, Kuntsi, Coleman, Campbell, & Skuse, 2003; Mazzola et al., 2006; Skuse, Morris, & Dolan, 2005). Skuse et al. (1997) observed differences in social skills between 45,Xp Turner-syndrome girls (in which the X was of paternal origin) and 45,Xm girls (in which the X was maternally derived). 45,Xp had superior social competence and better social skills than 45,Xm girls, suggesting that the genes in this locus are expressed only from the paternal X. A parallel may be drawn between the TS data and that of healthy men; both groups inherited the maternal X-chromosome and lack Xp-linked genes. Both demonstrate decrements in face and affect recognition (Skuse et al., 1997). The deficits in TS co-exist with neuro-anatomical abnormalities of the amygdala and other regions implicated in social processing (for a review, see Burnett, Reutens, & Wood, 2010).

2.5. Sex differences in brain structures

Sex differences in brain structure are well-documented, although not necessarily consistent. During critical periods of development in fetal and neonatal life, testicular secretions have permanent effects on the brain (Arnold & Gorski, 1984; Phoenix, Goy, Gerall, & Young, 1959). Exposure to androgens influences neuronal survival and connections (De Vries et al., 2002; Negri-Cesi, Colciago, Celotti, & Motta, 2004).

One robust finding is that the volume of the total brain is significantly larger in males than in females (Giedd et al., 1996), which is observed as early as infancy (Gilmore et al., 2007). When controlling for total volume, women have a higher percentage of grey matter and men a higher percentage of white matter (Gur et al., 1999; Luders, Steinmetz, & Jancke, 2002) for a review see (Cosgrove, Mazure, & Staley, 2007). Researchers have reported anatomical differences in limbic areas such as the amygdala and the caudate in male and female children (Durston et al., 2001) as well as in regions of the cingulate, hippocampus, parietal, and occipital regions in adults (Raz et al., 2004).

A negative correlation between the number of X-chromosomes and amygdalar volume has been observed in subjects with sex chromosome aneuploidies (Warwick et al., 1999). Women with TS have reduced volumes in structures connected with the amygdala, such as the right hippocampus, orbitofrontal cortex, and superior temporal sulcus (Kesler et al., 2004; Molko et al., 2004). But also sex hormones exert organizing effects on the brain and on regional grey matter in particular (Witte, Savli, Holik, Kasper, & Lanzenberger, 2010).

As mentioned previously, brain structure may also have consequences for function, and perhaps differently for men and women. For example, there are sex differences in locus coeruleus dendritic structure that allow for an increased receipt and processing of limbic information in females compared to males (Valentino, Reyes, Van Bockstaele, & Bangasser, 2011). Amygdala volume correlates positively with fearfulness in girls but not in boys (van der Plas, Boes, Wemmie, Tranel, & Nopoulos, 2010). Aggressive and defiant behavior is associated with decreased right anterior cingulate cortex (ACC) volume in boys (Boes, Tranel, Anderson, & Nopoulos, 2008). Not surprisingly, besides the structural differences between the male and female brain, a growing body of research demonstrates sex differences in the neural network involved in processing emotions (Lee, Liu, Chan, Fang, & Gao, 2005). Two observations are a stronger right hemispheric lateralization and also a higher activation level in males as compared to females.

2.6. Hemispheric lateralization in affective neuroscience

Some studies suggest that hemispheric cerebral activation differences in emotion processing are sex dependent (Hall & Matsumoto, 2004; Kesler-West et al., 2001; Killgore & Yurgelun-Todd, 2001; Williams et al., 2005). A meta-analysis of neuroimaging studies on valence, sex and lateralization in functional brain anatomy in emotion concluded that lateralization of emotional activity is complex and region-specific (Wager, Phan, Liberzon, & Taylor, 2003) (see also, Wager & Ochsner, 2005; Zald, 2003).

Many researchers focused the search for sex differences on the amygdala (Cahill, 2003; Cahill et al., 2001; Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004; Canli, Desmond, Zhao, & Gabrieli, 2002). Whereas these studies about memory for emotional stimuli show quite a consistent sex-related lateralization, studies that focus on just the processing of emotional stimuli do not find such steady patterns. A recent meta-analysis does not confirm a consistent pattern of sex differences in this area as a function of sex or valence (Fusar-Poli, Placentino, Carletti, Allen, et al., 2009; Sergerie, Chochol, & Armony, 2008; Wager et al., 2003). So, the debate about sex regarding general emotional processing is not over. Using a large sample of 235 male adolescents and 235 females matched for age and handedness, Schneider et al. (2011) recently investigated the sex-specific lateralization of amygdala activation during an emotional face perception task. Performing a sex by hemisphere analysis, they observed stronger right amygdala activation in males compared to females. Moreover, only male participants showed enhanced right (not left) amygdala activation following angry versus neutral dynamic faces.

To examine developmental sex differences in affective processing, Killgore et al. (2001) investigated children and adolescent hemodynamic response while viewing pictures of fearful faces. Males and females differed in their pattern of the amygdala versus prefrontal activation during adolescent maturation. Females showed a progressive increase in prefrontal relative to amygdala activation in the left hemisphere, whereas males failed to show a significant age related difference.

Hemispheric lateralization differences between men and women have also been observed in electrophysiological studies. In a task of judging facial expressions and pictures of infants, Proverbio,

Brignone, Matarazzo, Del Zotto, and Zani (2006) found an asymmetrical activation of the visual cortex (early face-sensitive P1 and N1 components) in men (with right-hemisphere predominance), and bilateral activity in women. Gasbarri et al. (2007) observed a sex-related hemispheric lateralization of electrical potentials evoked by arousing negative pictures. Negative pictures elicited more robust P300 effects in the left hemisphere in women and in the right hemisphere in men. This ERP finding was later replicated by using a different paradigm. A set of slides was accompanied by a simple narrative, either a neutral version or an arousing one. In addition to their previous ERP finding, they also found that men, not women, recalled the arousing story better than the neutral version (Arnone, Pompili, Tavares, & Gasbarri, 2011).

However, controversy around the lateralization hypothesis remains. In fact, it has recently been suggested that greater left than right frontal cortical activity is associated with *approach motivation*, which can be positive (enthusiasm) or negative in valence (anger) (Harmon-Jones, Gable, & Peterson, 2010). Thus, the lateralization differences between men and women that are sometimes observed may arise from differential approach motivation tendencies to emotional stimuli. Female and male behavioral tendencies on response to threat should be further investigated, for example in approach-avoidance paradigms (Seidel et al., 2010).

2.7. Activation patterns in males as compared to females

Wager et al. (2003) performed a quantitative meta-analysis on 65 neuroimaging studies of emotion. They found that females showed more brainstem activation in affective paradigms than males. A review article published one year later and which included 105 fMRI studies found that when processing human emotional faces, female participants showed greater activation than male participants in the right subcallosal gyrus. Male participants showed a greater neural response than female participants, in the right medial frontal gyrus, the left fusiform gyrus and in a cluster spanning the right parahippocampal gyrus and the amygdala (Fusar-Poli, Placentino, Carletti, Landi, et al., 2009). However, Sergerie et al. (2008) who in their review focused on the amygdala, could not find evidence for a difference in the proportion of amygdala activations between men and women.

Nevertheless, elevated activation of the amygdala in males compared to females following emotional stimuli has been observed regularly. While viewing pictures of attacks by humans or animals, men exhibited greater activation in the bilateral amygdala and the left fusiform gyrus than women (Schienle, Schafer, Stark, Walter, & Vaitl, 2005). Male subjects demonstrated right amygdala activation compared to baseline while observing sad faces, which was not present in females. Moreover, in male subjects, signal intensities in the right amygdala increased with intensified subjective experience of sadness. The same pattern was not confirmed for women and also not for the left amygdala (Schneider, Habel, Kessler, Salloum, & Posse, 2000). Men also showed more right amygdala activity following the passive observation of dynamic angry versus neutral faces which was not the case in women (Schneider et al., 2011).

Elevated activation in males versus females has also been observed in other brain areas than the amygdala. For example, Fine et al. (2009) showed greater male than female activation following photos and videos of positive and negative content in a range of frontal and temporal areas, and in the cingulate cortex. Remarkably, there was only one small area in the left middle temporal gyrus that showed more activation in females versus males. In another study by Rahko et al. (2010), during the observation of dynamic happy (but not fearful) faces, male adolescent subjects showed increased activity in the right frontal pole (MFG-paracingulate). Wrase et al. (2003) reported that men showed more activity than women in the

amygdala, inferior frontal gyrus, medial frontal gyrus and fusiform gyrus following exposure to emotional pictures. Again, there were no areas that responded stronger in female than male participants. Also Lee et al. (2005) observed enhanced activity in male participants during emotion recognition, in the right insula and left thalamus. Although women showed stronger neural responses than men to facial expressions of disgust, men displayed stronger brain activation than women to facial expressions of contempt (Aleman & Swart, 2008).

Derntl et al. (2009) observed that females and males showed equal bilateral amygdala activation following emotional faces but calculation of correlation coefficients for females and males separately revealed a significant association between recognition accuracy and amygdala activation to fearful faces only in the male group. Schneider et al. (2000) reported a correlation between mood parameters and amygdala activation during sad mood induction only in the male subjects. While viewing fearful versus neutral facial expressions, male but not female observers showed attenuation of tonic arousal all across early to late phases of the experiment. By contrast, when amygdala responses to fear perception were averaged for the whole experiment, females showed a relatively greater extent of amygdala activity than males, but there were no differences in the magnitude of the response (Williams et al., 2005). Han, Gao, Humphreys, and Ge (2008) examined if there exists a neural network supporting the processing of evolutionary unprepared threat cues that is independent of the fear or emotion-related system and whether this differed between male and female participants. As stimulus material they used a person with a neutral facial expression in either a safe situation (e.g., walking besides a stationary car) or a potentially dangerous situation (e.g., walking in front of a moving car). The results showed that the detection of threat cues was associated with stronger posterior parietal activation for males than females. This finding suggests that neural processing of evolutionary unprepared threat cues in social environments is influenced by evolutionary pressure on sex differences (Han et al., 2008).

In the preceding sections we discussed male-female differences in brain activity without taking situational factors into account. However, some male-female differences can only be observed when participants are brought into a stressful state. A recent study shows that acute stress affects face perception in opposite ways for men and women. Mather, Lighthall, Nga, and Gorlick (2010) did not find sex differences in overall amygdala or fusiform face area (FFA) activity. In their study, they observed that both in the stress and in the control conditions, women showed greater functional connectivity between the insula and the FFA and the amygdala when viewing angry faces than men did. FFA activity was greater under stress for women but diminished under stress for men, a relationship that was correlated with baseline testosterone but not estrogen levels (Mather et al., 2010). These findings are particularly interesting in the light of another recent study by Ino, Nakai, Azuma, Kimura, and Fukuyama (2010). They suggested that the reduced activation of women's brains during processing emotions suggest that the relevant neural systems are more efficiently recruited in women than in men.

Some EEG studies found enhanced activity in females versus males. Especially when looking at visual areas, women tend to have a larger beta response when observing facial expressions, yet this is independent of the type of emotion (O2, Guntekin & Basar, 2007; P300, Proverbio et al., 2006; but see Oliver-Rodriguez, Guan, & Johnston, 1999). Female participants seem to show significantly longer latency and higher amplitude P450 components than male subjects to both happy and sad faces (Orozco & Ehlers, 1998). Moreover, the N2b component, functionally considered as an attentional orienting mechanism, was delayed in men for happy stimuli as compared with fearful ones in a task in which they had to quickly

detect deviant happy or fearful faces among a train of neutral ones (Campanella et al., 2004).

We already briefly mentioned at the beginning that angry male cues may be more threatening than female ones, possibly even more so for men than for women and we return to that issue at the end of the next section. In the following part, we discuss how men and women differentially process emotional cues as a function of the sex of the actor.

2.8. Sex of the actor and sex of the observer

Expressions of anger should be more readily associated with aversive events than should expressions of happiness. Indeed, research has shown that electrodermal conditioning to pictures of faces, with electric shock as the unconditioned stimulus, worked best in the case of pictures of angry males, better than with happy pictures or pictures of angry females (Öhman & Dimberg, 1978). Moreover, in a fear-conditioning experiment, it has been observed that conditioned fear to the face of a male out-group target resists extinction, but conditioned fear toward the face of a female out-group target readily extinguished (Navarrete et al., 2009). Rotteveel and Phaf (2004) reported that their female sample reacted faster to male than to female faces, particularly to angry ones.

Research suggests that especially male participants respond to threatening male cues. Enhanced physiological arousal in men but not in women during exposure to angry male as opposed to female faces has been observed (Mazurski, Bond, Siddle, & Lovibond, 1996). Fischer et al. (2004) observed that exposure to angry male as opposed to angry female faces activated the visual cortex and the ACC more in men than in women. A similar sex-differential brain activation pattern was present during exposure to fearful but not neutral faces (Fischer et al., 2004). In line with these results, Aleman and Swart (2008) report stronger activation in the medial frontal gyrus, inferior frontal gyrus, and superior temporal gyrus in men than women in response to faces denoting interpersonal superiority. Kret et al. (2011) observed that men showed a higher blood de-oxy hemoglobin (BOLD) response following fearful and angry male bodily expressions in several regions of interest: extrastriate body area, fusiform gyrus, superior temporal sulcus and the premotor and supplementary motor area.

These studies suggest a defensive response in men during a confrontation with threatening males. Not surprisingly, aggression in men is often directed toward their own sex. In the evolutionary history, men were more often engaged in aggressive behavior, especially in situations connected with reproduction. Brutal rivalry between males is a part of human evolution and in most cultures men not only commit more violent offences but also more often the victims (Daly & Wilson, 1988). Therefore, it may be especially relevant for men to recognize anger in other men.

There is a large literature on the own race bias, the finding that people are better at recognizing faces of people from their own race but there may also be an own sex bias. For example, the left amygdala was more active for successfully remembered female fearful faces in women, whereas in men the right amygdala was more involved in memory for male fearful faces. At the behavioral level, female participants remembered better fearful (but not neutral or happy) female than male faces. Male participants remembered all face categories equally but the activation within the right amygdala was associated with stronger activity for successful memory for male, compared to female, fearful faces (Armony & Sergerie, 2007). Fischer et al. (2004) found that men and women rated male and female faces as being equally expressive. Although no differences between the participating men and women regarding the degree of expressiveness in the overall ratings were observed, an increased fMRI signal was found in the left amygdala and adjacent anterior temporal regions in men, but not in women, during exposure to

693 faces of the opposite versus the same sex (Fischer et al., 2004). In
694 an EEG study, Doi, Amamoto, Okishige, Kato, and Shinohara (2010)
695 observed a late positive component presumably reflecting the cog-
696 nitive evaluation stage of the stimuli that was larger to neutral but
697 not happy expressions of own-sex faces than to those of opposite-
698 sex faces. Furthermore, the late positive component amplitude to
699 male neutral expressions was larger in the male viewers than in the
700 female viewers (Doi et al., 2010). The P300 evoked in female par-
701 ticipants when observing neutral faces was larger to female than
702 to male faces (Oliver-Rodriguez et al., 1999).

703 3. Discussion

704 In the past decades we have witnessed something like a pendu-
705 lum swing with interest in sex differences going through alternative
706 phases of stressing and denying their existence. The reasons for
707 these differences between men and women are numerous. They
708 can be looked at from different perspectives, measured with dif-
709 ferent techniques and interpreted in multiple ways, which make it
710 hard to explain and completely understand them and which causes
711 some researchers to ignore them. However, they should be investi-
712 gated and researchers should take advantage of and combine new
713 research methods including brain imaging, the analysis of genetic
714 factors, and hormone manipulations. This way, we will get a closer
715 and closer view of the issues at stake.

716 Vigil (2008) suggests that sex differences in emotion are an
717 adaptation to a presumed social structure exhibited by early homi-
718 noids, in which males tended to stay in their natal groups and
719 females migrated from their natal group and later took care of
720 preverbal offspring. Over history, women have been mostly respon-
721 sible for childcare. Consistent with that, selection pressures for
722 responses to threat that benefit both self and offspring would
723 have been greater for females than for males. Research shows that
724 women are more likely to seek the company of others in times of
725 stress, compared to men (Taylor et al., 2000). Therefore, for women
726 it is of much importance to pick up emotional cues from others
727 and to facilitate communication and increase social bonding by also
728 being expressive themselves. For men, anger recognition, especially
729 the recognition of threatening cues from other men (competitors)
730 might have proven particularly adaptive over the course of evolu-
731 tion.

732 Although both men and women show the biological fight or
733 flight pattern of arousal (e.g., elevated heart rate and blood pres-
734 sure) sex differences exist in the consequent behavior. Men's
735 behavior under stress is typically characterized by fight (aggression)
736 and by flight (social withdrawal, substance abuse) (Geary &
737 Flinn, 2002). So, men and women may be biologically primed to
738 react to threat in a certain way, but the environment reinforces
739 these reaction patterns. For example, aggression is seen as socially
740 acceptable for men but not for women which positively reinforces
741 men and women to behave in a gender-stereotypical way (Hart
742 et al., 1992; Serbin et al., 1993). This can in some cases become
743 maladaptive in the long run, for example in the case of male vio-
744 lent offenders in which biological predispositions of aggressiveness
745 came too much to expression in the violent environment in which
746 they grew up (Lansford et al., 2007).

747 Paradoxically, while women might report finding emotional
748 stimuli more distressing, for men they may provide more behav-
749 iorally relevant cues, which elicit a more potent orienting response
750 and consequently different behavioral tendencies. This is in line
751 with an earlier suggestion made by Kesler-West et al. (2001) that
752 men may recruit more neurons when processing agonistic displays
753 than when processing affiliative emotions. In this context, a closer
754 examination of the effects of stimulus presentation duration is war-
755 ranted. It is possible that the activation patterns that are observed

517 in studies with long presentation times reflect different aspects of
518 emotion processing than those from short presentation times (ini-
519 tial stress response versus more elaborative cognitive processes
520 including reappraisal or emotion regulation). Systematic evalua-
521 tion of the role that stimulus duration plays inactivation during
522 emotion processing could facilitate reconciliation of different find-
523 ings across studies.

524 Sexual differentiation of the human brain is a multifactorial pro-
525 cess. The differences are not thought to be only consequence of
526 the influence of sex hormones on brain organization during devel-
527 opment but also of genetic factors (Cosgrove et al., 2007; Davies,
528 Isles, Burgoyne, & Wilkinson, 2006). Several studies have provided
529 evidence that some sex differences do occur very early during
530 development, before fetuses are exposed to endogenous sex steroid
531 hormones. The genetic makeup of individuals tends to dictate
532 physiological differences. So, male and female brain cells carry a
533 different complement of sex chromosome genes and are influenced
534 throughout life by a different mix of gonadal hormones. Testos-
535 terone exposure in males during both early brain formation and in
536 puberty is critical for the development of the sexually dimorphic
537 male brain (MacLusky & Naftolin, 1981). Throughout evolution, the
538 simple sexual-regulatory actions of oxytocin, vasopressin, testos-
539 terone and estradiol gradually extended to more complex social
540 behavior such as bonding between mothers and infants, partner
541 bonding, social recognition, aggression between conspecifics, and
542 ultimately the regulation of social cognition in primates. The broad
543 spectrum of social behavior can range from violent acts of aggres-
544 sion against a conspecific to apparent altruistic behavior. At both
545 ends of the spectrum, steroid and neuropeptide mechanisms are
546 involved and have a firm grip on human behavior (Bos et al., in
547 press).

548 In their view of sexual differentiation of the brain, McCarthy and
549 Arnold (2011) stress the importance of genetics and environment
550 being incorporated along with the effects of hormones to provide
551 a more nuanced portrayal of the types of variables that cause sex
552 differences. Included in this view are the principles that hormones,
553 sex chromosome genes and sex-specific environments (which used
554 to be discussed almost exclusively by social psychologists) have
555 independent parallel differentiating effects that can interact with
556 each other to cause sex differences in the brain.

557 While men have greater overall brain volume than women, rela-
558 tive to total volume, sex-specific regional differences exist. Men
559 have a larger amygdala and hypothalamus, while women have a
560 larger caudate and hippocampus. To what extent these structural
561 differences contribute to functional differences remains largely
562 unknown and this warrants further investigation. Research has
563 shown a marked dissociation between men and women in activa-
564 tion patterns following emotional stimuli. Males tend to show
565 greater responses in neural systems that encode aggression related
566 affective and perceptual features of stimuli, functions often asso-
567 ciated with the amygdala and temporal cortex but also motor
568 preparation areas. But it is necessary to make some critical remarks.

569 BOLD effects depend on multiple physiologic parameters and
570 it is impossible to extract a single physiologic parameter from
571 the observed signal changes. Some physiologic parameters differ
572 between men and women and some of the above-discussed results
573 can possibly be explained by those. Before moving to a more the-
574 oretical discussion about if we should, want to or even can control
575 for these possibly confounding or possibly interesting factors, we
576 first briefly discuss some parameters that could be confounding.
577 Notably, these are not specific for sex differences but are relevant
578 whenever groups are compared such as in clinical studies.

579 The amplitude and time course of the BOLD signal are dynamic.
580 Structural differences can be of influence, as well as cerebral
581 metabolic rate of oxygen, blood volume and rCBF (Cohen, Ugurbil,
582 & Kim, 2002; Kastrup, Li, Glover, Kruger, & Moseley, 1999; Kemna,
583

Posse, Tellmann, Schmitz, & Herzog, 2001). Also hematocrit, the concentration of red blood cells in blood, is of influence on the BOLD response and differs between men and women (45% in men, 40% in women) (Levin et al., 2001). Women have higher global and rCBF levels than do men which affects the BOLD response (Gur et al., 1982; Rodriguez, Warkentin, Risberg, & Rosadini, 1988).

Levin et al. (1998) applied gradient echo-echo planar imaging to measure BOLD signal response in the primary visual cortex in response to binocular photic stimulation. They found that the BOLD signal response was 38% lower in women than in men, and much of the difference was lateralized to the right hemisphere. They concluded that lower BOLD signal response in women may reflect a sex difference in the brain's response to a primary visual stimulation or in the physiology underlying BOLD fMRI signal changes (Levin et al., 1998), both interpretations are relevant for affective neuroscience in which for example emotional pictures are presented. There is also evidence to support an endocrine effect upon functional brain activity and brain perfusion. A review of the literature suggests that estrogen replacement may increase CBF, alter regional brain activation patterns during cognitive processing, and have effects on various neurotransmitter systems (Smith & Zubieta, 2001).

Of particular relevance here is the possibility that the interpretation of functional imaging findings may change once certain parameters (such as size differences of certain brain areas) are controlled for. For example, an activation decrement observed in one group might actually be explained by a corresponding reduction in cortex in that group. A reduction of grey matter might appear as a reduction in measured brain activity due to partial volume averaging effects (Drevets, 2000). But if a structural difference or some baseline blood flow difference is detected, how can we know whether these facts explain the BOLD signal differences? Moreover, if the size of the particular structure implicated is taken into account (Asllani et al., 2009), if different baseline levels that have been shown to affect the BOLD response are controlled for, if hormonal factors are balanced out, if contextual factors are manipulated, if . . . , if . . . then, can we still say we are measuring sex differences? Studies combining functional and structural information will give more insight in this potential confound. We presume that at least these questions should be discussed much more, especially between researchers from different fields of research. The different parameters should be investigated in detail in order to find out when and to what extent they might be of influence. Interesting in this context is a point made by De Vries (2004): neural sex differences could also prevent behavioral sex differences or differences in emotional processing instead of creating them. . .

Besides these theoretical considerations, we should think about the many conflicting results that have been reported and often not replicated. Because of the many different brain areas that have been found to be differentially involved in emotional processes in men and women, it may be better to conduct whole brain analyses and focus on patterns and connectivity between areas rather than focusing on specific ROIs. A lot of fMRI studies (most of them conducted before 2004) that are discussed in this article and in cited review articles and meta-analyses did not conduct a multiple comparison correction, leading to false positives. Small sample sizes may be another explanation for the diversity of findings, especially in fMRI research. But also in behavioral studies, many conflicting findings have been published. Not all studies replicated the female advantage for recognizing emotions: the specific task (verbal labelling versus emotion matching), the number of included emotions, the presentation duration of the stimuli (very often ceiling effects were not accounted for), the presence of another person such as a test leader or even the type of reward and many other factors may influence men and women differently. Moreover, research in this area may suffer from a publication bias, positive results are more easily published. Besides, it is likely that various studies that

report sex effects were not initially set up for this purpose which raises statistical questions.

Ironically, results are often written up in a stereotype-consistent way (that women are more emotional than men) and therefore it is sometimes hard, as a reader, to pick up "inconsistent" results that do diverge from the overall picture. For example, in Whittle, Yucel, Yap, and Allen (2011) one reads that a study by McClure et al. (2004), found increased female activation in response to angry face stimuli. However, it is not mentioned that this was only observed in the adult and not in the adolescent group. More importantly, in this study, enhanced female activation was only found when comparing the difference score between angry and neutral stimuli with male participants. But in fact, for men, angry, fearful and neutral faces all elicited more activation relative to fixation, which was not the case for women. Unfortunately, these differences with fixation were not compared between men and women but a completely different conclusion could have been drawn.

4. Conclusion

Taken together, there are strong indications that males and females differ in the recruitment of cerebral networks following female and male emotional expressions. This clearly suggests that in order to generalize findings about the neural correlates of processing emotions, we definitely should consider the sex of the subjects. To conclude, many studies observed strong effects of threatening stimuli, ranging from recognition performance effects to enhanced physiological arousal and brain activity in male observers, especially when observing a threatening or dominant male stimulus. Research has also shown that males use more physical aggression, especially toward other males. Future studies need to further investigate the interaction between sex of the observer and observed in various emotion paradigms.

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