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Review

Emotion recognition and regulation in males: role of sex and stress steroids

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Abstract

Understanding emotions in males is crucial given their higher susceptibility to substance use, interpersonal violence, and suicide compared to females. Steroid hormones are assumed to be critical biological factors that affect and modulate emotion-related behaviors, together with psychological and social factors. This review explores whether males' abilities to recognize emotions of others and regulate their own emotions are associated with testosterone, cortisol, and their interaction. Higher levels of testosterone were associated with improved recognition and heightened sensitivity to threatening faces. In contrast, higher cortisol levels positively impacted emotion regulation ability. Indirect evidence from neuroimaging research suggested a link between higher testosterone levels and difficulties in cognitive emotion regulation. However, this notion must be investigated in future studies using different emotion regulation strategies and considering social status. The present review contributes to the understanding of how testosterone and cortisol affect psychological well-being and emotional behavior in males.

Keywords

Males, testosterone, cortisol, dual-hormone hypothesis, emotion recognition, emotion regulation, sex hormones, emotions, cognitive reappraisal, approach-avoidance.

Contents

1. Introduction

"The only emotion regulation strategy that men consistently report doing more often than women is drinking to cope" (Nolen-Hoeksema, 2012).

Emotion recognition is defined as understanding the emotional state of another individual from an ensemble of sensory stimuli (Ferretti & Papaleo, 2019). In contrast, the ability to influence one's emotions is known as emotion regulation (McRae & Gross, 2020). Both these abilities are associated with sex or gender-related differences (Berke et al., 2018; Nolen-Hoeksema, 2012; Thompson & Voyer, 2014). Males tend to perform worse in emotion recognition tasks than females (Thompson & Voyer, 2014) and females report using more emotion regulation strategies than males (Nolen-Hoeksema, 2012). Impairments in emotion recognition and the use of maladaptive emotion regulation strategies are related to difficulties in social relationships, mood disorders, and the development of psychopathology (Baez et al., 2023; Krause et al., 2021; Marsh & Blair, 2008; McRae & Gross, 2020). Males are diagnosed with depression (3.6% vs. 5.1%) and anxiety disorders (2.6% vs. 4.6%) less often than females (World Health Organization, 2017). However, they are more prone to substance use, interpersonal violence, and suicidality compared to women (Fisher et al., 2021).

This discrepancy might be due to several reasons. For example, it has been suggested that both depression (Lenz et al., 2019) and anxiety disorders (Fisher et al., 2021) might be underreported in men because of inadequate diagnostic tools (Fisher et al., 2021). On the other hand, male emotional behavior might be influenced by social factors such as perceived masculinity (Berke et al., 2018; Fisher et al., 2021) or pressure from others to subscribe to various social roles (Mckenzie, 2016). Moreover, males exhibit higher levels of alexithymia (i.e., difficulty understanding and describing one's own emotions) than females (Levant et al., 2009). Alexithymia has been associated with both an unwillingness to communicate personally distressing information (O'Loughlin et al., 2018), and negative attitudes toward professional psychological help-seeking (Sullivan et al., 2015). Nevertheless, the impact of biological factors such as levels of stress and sex hormones on males' emotion processing, socioemotional behavior and mental health should not be excluded. Probably the most powerful sex steroid in males, testosterone, was suggested to affect the emotion regulation system (Rice & Sher, 2017). Testosterone has been shown to contribute towards higher rates of suicide in adolescent males (Rice & Sher, 2017; see also Ho et al., 2022). Moreover, both prenatal and adult levels of androgens have been shown to

increase the risk of suicide (for review: Lenz et al., 2019). In contrast, cortisol was suggested to positively affect emotion regulation (Putman & Roelofs, 2011).

By acting via both slow genomic and faster non-genomic pathways, sex and stress steroids affect many brain regions, including the prefrontal cortex, amygdala and hippocampus (Joëls et al., 2012; McEwen & Milner, 2017). The presence of androgen, estrogen, mineralocorticoid (MC), and glucocorticoid (GC) receptors in these regions has been reported in animals (Handa & Weiser, 2014) with overlapping findings in humans (e.g., Beyenburg et al., 2000, 2000; López et al., 1998, 1998; Perlman et al., 2004, 2007; Xing et al., 2004; for the putative distribution of estrogen and progesterone receptors in the human brain, see: Barth et al., 2015). These brain structures are also involved in emotion recognition (Adolphs, 2002) and regulation (Etkin et al., 2015), therefore, the effects of cortisol and sex hormones on these processes are plausible.

The release of both sex and stress hormones is coordinated by the hypothalamus, where the hypothalamic-pituitary-gonadal (HPG) and hypothalamic-pituitary-adrenal (HPA) axes start (Figure 1). In the HPG axis, gonadotropin releasing hormone (GnRH) is released from the preoptic area (POA) and carried to the anterior pituitary. Stimulation of gonadotroph cells by GnRH leads to the release of luteinizing hormone (LH) and follicle stimulating hormone (FSH). Then, LH stimulates the synthesis of testosterone by Leydig cells (Oyola & Handa, 2017). During stress, corticotropin-releasing hormone (CRH) and vasopressin (VP) are released by parvocellular neurons of the paraventricular nucleus (PVN). In turn, these hormones stimulate the secretion of adrenocorticotropic hormone (ACTH) from the anterior pituitary, which leads to the release of glucocorticoids by the adrenal cortex (Aguilera, 2011; Lightman et al., 2020). Accordingly, cortisol is essential for stress adaptation (Aguilera, 2011) and is routinely used as a marker of the response of the HPA axis to stress (Hellhammer et al., 2009). However, there is evidence that sex steroids impact the activity of the HPA axis (for review: Handa & Weiser, 2014). Furthermore, alterations of the HPA axis have been linked to alexithymia (for review: Goerlich & Votinov, 2023). It has also been shown that the HPA and HPG axes influence each other via multiple mechanisms (Burnstein et al., 1995; Chen et al., 1997; Oyola & Handa, 2017; Tilbrook et al., 2000; Viau, 2002) (Figure 1). Hence, it is important to consider interactions between the HPA and HPG axes while evaluating effects of sex and/or stress hormones on emotional behavior.

Reciprocal interactions between the HPG and HPA axes might be related to the inconsistent findings between cortisol and stress perception. A systematic review of studies considering links between HPA activity and feelings after acute stress, revealed significant associations between cortisol and subjective stress experience in only 8 out of 30 studies (27%). Sex was suggested to be one of multiple possible factors influencing this discrepancy (Campbell & Ehlert, 2012). Furthermore, a quadratic association between the cortisol response and subjective stress was found in females (Admon et al., 2017) but no significant relationship was found in males (Dalile et al., 2022). Moreover, although higher cortisol reactivity to acute psychological stress was shown in males than in females (Reschke-Hernández et al., 2017), controlling for testosterone, estradiol, and progesterone eliminated this difference (Juster et al., 2016) and diminished cortisol reactivity to the acute stress (Barel et al., 2018). Considering these findings, it is also important to evaluate the fluctuations of sex hormones. There are no well-organized monthly fluctuations or dramatic changes in the levels of sex hormones in males as there are in females. However, some changes exist, such as ultradian fluctuations with higher testosterone levels in the morning compared to the evening (Beaven et al., 2010), potential seasonal variations (Smith et al., 2013), a slow decrease in testosterone levels with age starting at approximately 30 years (Kanabar et al.,

2022), variations related to the use of exogenous androgens or decline due to the androgen suppression, which is routinely used to treat conditions such as prostate cancer (Buchan & Goldenberg, 2010). Hence, due to differences in the levels of sex hormones and cortisol reactivity and associations between the cortisol response and subjectively perceived stress in males and females, it is important to investigate hormonal effects on emotional behavior in both sexes separately.

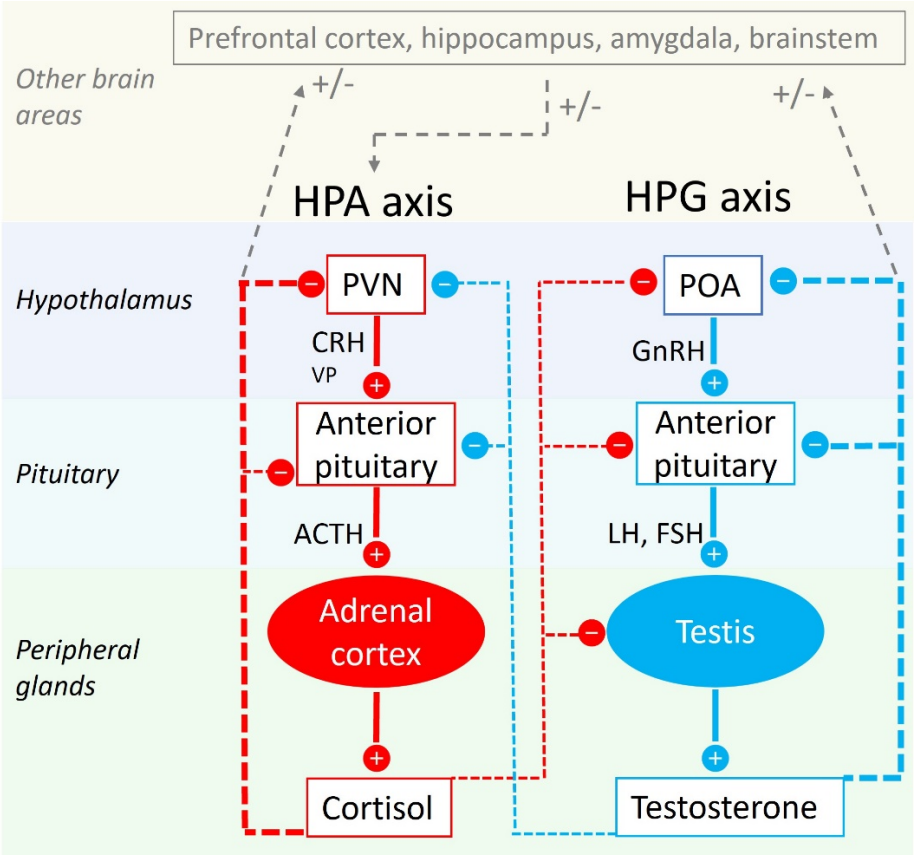

Figure 1. Schematic representation of the complex interaction between the hypothalamic-pituitary-adrenal (HPA) (red) and hypothalamic-pituitary-gonadal (HPG) (blue) axes. HPA: Parvocellular neurons of the paraventricular nucleus (PVN) release corticotropin-releasing hormone (CRH) and vasopressin (VP). In turn, these hormones stimulate the secretion of adrenocorticotropic hormone (ACTH) from the anterior pituitary, leading to the release of cortisol from the adrenal cortex. In the HPG axis, gonadotropin releasing hormone (GnRH) is released from the preoptic area (POA) and carried to the anterior pituitary. Here, gonadotroph cells are stimulated by GnRH, leading to the synthesis and release of luteinizing hormone (LH) and follicle stimulating hormone (FSH). Thereafter, LH stimulates the synthesis of testosterone by Leydig cells. Dashed red and blue lines represent multiple levels of how the HPA and HPG axes are inhibited by cortisol and testosterone, respectively. Thicker lines represent stronger (or main function-related) effects. Dashed gray arrows represent interactions of other brain areas with the HPA/HPG axes.

Due to the mutual inhibitory effects of the HPA and HPG axes, the dual-hormone hypothesis was proposed (Mehta & Josephs, 2010). The hypothesis states that testosterone's role in status-relevant behavior depends on the circulating cortisol level (for review and meta-analysis on the dual-hormone hypothesis, see Dekkers et al., 2019; Grebe et al., 2019; Knight et al., 2020; Mehta & Prasad, 2015). According to the dual-hormone hypothesis, testosterone is positively related to status-seeking behavior only when cortisol levels are low. Accordingly, such effects of testosterone should be absent if cortisol

concentrations are high (Mehta & Prasad, 2015). The dual-hormone hypothesis has also been linked to emotion recognition (Lausen et al., 2020) and empathy (Vongas et al., 2020). In turn, processing of facial emotions has been shown to be related to success in social interaction (see Osório et al., 2018). Similarly, better ability to recognize emotions has been linked to greater status-relevant outcomes, such as success in negotiations (Elfenbein et al., 2007), effective leadership (Rubin et al., 2005), and annual income (Momm et al., 2015). Therefore, it is likely that both emotion recognition and regulation are affected by the joint action of cortisol and testosterone.

In a systematic review considering sex hormones in relation to processing of facial expressions in females, Osório et al. (2018) reported that estrogen and progesterone significantly impact facial emotion processing. To date, there are no reviews on males. Several studies presented in the current review were discussed previously in a literature review on sex hormones and emotional processing of visual stimuli (Little, 2013). However, recent studies have revealed conflicting results. Therefore, an updated review of the literature is warranted. Additionally, a meta-analysis evaluating the links between cortisol and emotion recognition, empathy, and emotion regulation was published (Ji et al., 2021). However, many relevant studies were not included, partly due to the strict rules for inclusion in meta-analyses. Finally, previous literature reviews did not fully consider the complex interaction between cortisol and sex hormones while evaluating the ability to recognize and/or regulate emotions.

Here, we provided a review of studies evaluating the effects of both endogenous cortisol and sex hormones, together with exogenously administered substitutes (i.e., hormone gels, tablets) on emotion perception and regulation in males. In studies of endogenous hormones, many authors have evaluated the impact of basal hormone levels (e.g., participants provided saliva or blood samples before experiments), whereas others have investigated relationships with task-provoked changes in hormone levels (e.g., saliva/blood samples were collected both before and after experiments). We have also included relevant research involving transgender men (i.e., individuals assigned female at birth but with male gender identity). Because trans men often undergo testosterone treatment, findings from such studies might provide additional insights into the effects of sex hormones. Finally, it is important to highlight that sex hormones have both organizational and activational effects. The former refers to hormonal effects during sensitive developmental periods (i.e., pre- and perinatal, puberty) and the latter refers to post-pubertal effects of circulating hormones (Spielberg et al., 2019). As only a few studies have measured prenatal hormones directly, we included findings gathered using the 2D:4D ratio (i.e., the ratio of a second digit's (index finger) length divided by a fourth digit's (ring finger) length). The 2D:4D ratio is interpreted as an indicator of the balance of prenatal levels of testosterone and estrogens, such that high fetal testosterone and low fetal estrogen levels are linked to lower 2D:4D (for review: Breedlove, 2010; Manning et al., 2014). However, considering the lack of robust evidence of a relationship between the 2D:4D ratio and prenatal hormone levels (see Richards, 2017), we suggest that such results should be interpreted with caution. Hence, the aim of this review was to provide a thorough evaluation of the current findings linking sex and stress steroid hormones with emotion recognition and regulation in males.

The reviewed literature was searched in the PubMed and Scopus databases with the following terms in all fields (for PubMed) or in the title, abstract or keywords (for Scopus): *("glucocorticoid" OR "mineralocorticoid" OR "estrogen" OR "estradiol" OR "progesterone" OR "cortisol" OR "sex hormones" OR "testosterone" OR "androgen" OR "2d:4d" OR "2d4d" OR "digit ratio" OR "digit length" OR "steroid" OR "transgender") AND ("emotion regulation" OR "cognitive reappraisal" OR "reappraisal" OR*

"cognitive suppression" OR "emotion downregulation" OR "emotion upregulation" OR "emotion control" OR "emotion recognition" OR "facial expressions" OR "basic emotions" OR "rmet" OR "reading mind in eyes" OR "cognitive empathy" OR "social cognition" OR "prosody" OR "mentalizing"). All titles were screened. Studies not related to emotion recognition or regulation, animal studies, and studies investigating substances other than steroid hormones were excluded. The same criteria were examined while screening abstracts of remaining articles and only papers containing samples or subsamples of males were further reviewed. The references of selected articles were screened to include studies that were not found by the terms used. Only articles written in English and published in peer-reviewed journals until November 2023 were included. Although we are focusing specifically on cisgender males, many reported findings have come from studies involving mixed-sex samples. Therefore, we reviewed data from mixed-sex sample studies if measures to control for sex effects were applied, thus confirming the generalization of the effect to males.

2. Emotion recognition

Emotion recognition is the ability to understand the emotional state of another individual from an ensemble of sensory stimuli (Ferretti & Papaleo, 2019). This ability is important for predicting behavior, forming and maintaining social bonds (Lausen et al., 2020), and is related to better survival chances (Ferretti & Papaleo, 2019). Behavioral studies of emotion recognition use visual, auditory, or multimodal stimuli, and measure emotion recognition ability via accuracy and response time. Paradigms with static or dynamic images of facial expressions representing up to six basic emotions (i.e., anger, disgust, fear, happiness, sadness, and surprise) and requiring fast and accurate participants' decisions on which emotion was presented are common in such studies. Videos of body movements (e.g., Hauger et al., 2019) and recordings of vocal prosodies alone (e.g., Fujisawa & Shinohara, 2011) or in combination with facial expressions (e.g., Lausen et al., 2020) were also used. Another paradigm in emotion recognition studies is based on the reading the mind in the eye test (RMET). In the RMET, participants are instructed to infer actors' mental states from the eyes region as no other parts of the face are shown (Baron-Cohen et al., 2001). This task depicts mental states such as thoughts and intentions (e.g., serious, suspicious, flirtatious), which, compared to basic emotions, are considered to be more complex (Cassidy et al., 2021). In addition, there are more ecologically valid tasks with additional contextual information involving images (e.g. Wolf et al., 2015) or short movies (e.g., Vaskinn et al., 2020) of people in emotionally charged situations.

As the results from emotion recognition studies investigating basic emotions and more complex or context-related emotions might be interpreted differently, we described them in separate sections. In addition to behavioral emotion recognition research, we reviewed findings from studies investigating effects of sex hormones on the functioning of brain regions involved in the processing of facial expressions, such as the prefrontal cortex (PFC), inferior frontal gyrus and amygdala (Hadders-Algra, 2022), even when behavioral data were not collected or reported. We did not find any neuroimaging studies investigating emotion recognition-related brain structures in association with cortisol or the testosterone x cortisol interaction without behavioral data provided.

2.1. Links with sex hormones

2.1.1. Basic emotions

The most consistent associations have been observed between testosterone levels and the recognition of threat or dominance challenge related emotional expressions. For example, a positive relationship

between basal salivary testosterone levels and attention specifically to angry faces was demonstrated in the emotional Stroop task (van Honk et al., 1999), and in its masked version when angry faces were shown too briefly to be consciously perceived (in a mixed-sex sample, Wirth & Schultheiss, 2007). In a later study, testosterone was also shown to be associated with attention directed away from angry faces while using a dot-probe task (Wirth & Schultheiss, 2007). However, these findings are not contradictory. The authors argue that increased attention to angry faces in Stroop task may reflect an orientation toward signals of dominance challenge, whereas attentional bias to angry faces in a dot-probe task may reflect vigilance toward the threatening nature of dominance challenges (Wirth & Schultheiss, 2007).

Using an emotion recognition task, Derntl et al. (2009) reported shorter response times for fearful faces and stronger BOLD responses in the amygdala to fearful and angry faces. Moreover, these finding were related to the higher level of males' blood testosterone (Derntl et al., 2009). Similarly, a higher level of salivary testosterone was associated with heightened amygdala reactivity toward faces expressing anger and fear (Manuck et al., 2010). Moreover, the administration of transdermal testosterone was related to the decreases in males' preferred personal distance towards aggressive individuals (Wagels et al., 2017). Transdermal testosterone was also associated with heightened reactivity of the amygdala, hypothalamus, and periaqueductal gray to angry compared to neutral facial expressions (with no such effects for fearful or surprised expressions) (Goetz et al., 2014). Also, positive associations between testosterone treatment and amygdala activation (Beking et al., 2020) and amygdala-ventromedial PFC (vmPFC) co-activation (Grannis et al., 2021) were demonstrated in adolescent trans boys exposed to angry and fearful faces. Nevertheless, in contrast to the findings described before, Stanton et al. (2009) showed that males' salivary testosterone levels correlated negatively with the BOLD signal in the amygdala but positively with the BOLD signal in the vmPFC in response to angry but not neutral faces (Stanton et al., 2009). Clinical studies involving people with mental illnesses have yielded contradictory results. For example, both schizophrenia (Ji et al., 2015) and cocaine-dependence are associated with difficulties in processing facial expression (Ersche et al., 2015). Findings from patients with schizophrenia revealed that higher serum testosterone level was related to increased activity in the inferior frontal gyrus in response to angry faces, whereas such an association was absent in healthy males (Ji et al., 2015). In contrast, lower levels of serum testosterone mediated impaired facial anger recognition in cocaine-dependent males (Ersche et al., 2015). However, impaired recognition of fear from body movements was observed in anabolic-androgenic steroid (AAS) dependent individuals (Hauger et al., 2019).

In summary, studies reviewed thus far suggest that higher testosterone levels are related to better facial emotion recognition (Derntl et al., 2009; Ersche et al., 2015). They also suggest that testosterone is associated with greater attention (van Honk et al., 1999; Wirth & Schultheiss, 2007), greater amygdala activation (Beking et al., 2020; Derntl et al., 2009; Goetz et al., 2014; Manuck et al., 2010) (but see Stanton et al., 2009), and increased co-activation between the amygdala and vmPFC (Grannis et al., 2021) in response to threatening stimuli, such as angry and fearful faces. However, considering evidence from study with body movements, these effects may be absent if testosterone levels exceed the normal physiological range (Hauger et al., 2019).

There are some studies evaluating emotion recognition while combining multiple basic emotions (i.e., not evaluating anger or fear separately). Specifically, a study combining all basic emotions except surprise found that basal salivary testosterone of younger and older males did not predict the performance in a facial emotion recognition task (Grainger et al., 2021). However, the interpretation of the results of this study was further complicated as the performance in an emotion recognition task was at ceiling (> 85%) in both young and old adults. Another large sample (males, n = 282) study showed a small positive effect of testosterone in emotion-recognition accuracy. No testosterone effect was found

in recognition accuracy of specific emotions (Lausen et al., 2020). The testosterone level in this study was assessed from a mix of saliva samples collected before and after the emotion recognition task. Therefore, it is impossible to evaluate whether the positive relationship between emotion recognition accuracy and testosterone was determined by basal testosterone or by the rapid testosterone response to exposure to opposite-sex faces, which has been shown previously (Zilioli et al., 2014). Previous research showed that the differentiation between basal and task-induced levels of testosterone can be critical. For example, it has been shown that the social competition-induced increase in testosterone levels, but not the basal or post-task level of testosterone, was related to a better recognition of facial expressions (Vongas & Al Hajj, 2017). In contrast, an fMRI study on gender-affirming hormone treatment in transgender men revealed that a higher total blood testosterone level 6-10 months after treatment was associated with lower reactivity of the amygdala and anterior cingulate cortex (ACC) to facial expression of happiness, anger and surprise (Kiyar et al., 2022).

To our knowledge, there are no studies evaluating the direct links between prenatal testosterone levels and recognition of basic emotions. However, the results from a large sample of male children aged 8.5 years (n = 1718) indicated no relationship between the 2D:4D ratio and recognition of basic facial emotions (Barona et al., 2015). Nevertheless, a misattribution of facial expressions as angry, and poorer recognition of both sad and low intensity expressions (including happy, sad, angry, and fearful) were observed in 10% of male children with the lowest 2D:4D ratios (Barona et al., 2015). This suggests that the testosterone environment of males during early ontogenesis can affect facial emotion recognition later in life.

2.1.2. Complex emotions

The ability to correctly identify complex emotions (thoughts and feelings) from pictures of the eye region (RMET) correlated negatively with basal salivary testosterone in young (age ≈ 23 years) (Gamsakhurdashvili et al., 2021; Grainger et al., 2021) but positively in older (age ≈ 72 years) (Grainger et al., 2021) males. Considering that testosterone concentrations were significantly lower in older compared to younger males, it is possible that there is an inverted U-shape relationship between levels of testosterone and RMET performance, although this was not discussed by the study authors. Associations between high salivary testosterone levels and a decline in emotion recognition performance using the RMET were reported in a population of intimate partner violence perpetrators but not in control males (Romero-Martínez et al., 2016).

Only one study considered the organizational effects of testosterone by measuring testosterone levels directly from amniotic fluid (Chapman et al., 2006). This study revealed that fetal testosterone was negatively associated with the performance on the child version of the RMET in male children with an average age of 7.7 years. More have evaluated associations between the 2D:4D ratio as an indirect marker of prenatal testosterone exposure and RMET performance. These studies indicated no link between these variables in smaller (Blanchard & Lyons, 2010; Olsson et al., 2016) and larger samples investigated in the laboratory (males, n = 206, age ≈ 30 years) (Voracek & Dressler, 2006) or online (males, n = 995, age ≈ 35 years) (Hönekopp, 2012). Similarly, a study composed of two large sample placebo-controlled experiments (n = 241 and 400, age ≈ 23 years) did not show any significant relationship between transdermal testosterone or the 2D:4D ratio and the RMET performance (Nadler et al., 2019). We are aware of only one study involving males (n = 30, age ≈ 21 years) that revealed a positive relationship between lower 2D:4D ratios (high testosterone exposure) and RMET performance

(Carré et al., 2015). This study found a negative effect of transdermal testosterone on RMET performance among participants with low but not among those with higher 2D:4D ratios.

The basal salivary testosterone levels were not related to the ability of younger males to identify complex emotions embedded in a natural context using other tasks, such as the Multifaceted Empathy Test (MET) (Gamsakhurdashvili et al., 2021). They are, however, associated with poorer empathic accuracy in a mixed-sex sample when participants evaluated negatively-valenced videos of individuals discussing personal life events (Nitschke & Bartz, 2020). Also, a mixed-sex sample of AAS-dependent individuals showed an impaired ability to infer actors' mental states from movies (movies were used for the assessment of social cognition (MASC), Vaskinn et al., 2020). In contrast to these observations, transdermal testosterone-treated males showed fewer mistakes in answering cognitive empathy-related questions after watching personal stories than the placebo group (Puiu et al., 2022). Considered sex hormones other than testosterone, two studies did not show a relationship between exogenous estrogen and progesterone levels and the performance of the RMET or MET (Gamsakhurdashvili et al., 2021; Olsson et al., 2016).

In summary, positive (Puiu et al., 2022), negative (Carré et al., 2015; Gamsakhurdashvili et al., 2021; Nitschke & Bartz, 2020), and null (Gamsakhurdashvili et al., 2021; Nadler et al., 2019; Romero-Martínez et al., 2016) associations between testosterone and complex emotion recognition were reported. This discrepancy might be partly due to the different approaches, methodologies, and sample sizes used in the reviewed studies. Some contradictory findings between older and younger males (Gamsakhurdashvili et al., 2021; Grainger et al., 2021) suggest that age could be one critical factor modulating the interaction between sex hormones and social cognition, and should be taken more routinely into consideration. However, findings from studies involving only younger men are also polarized, with small sample sizes being among the possible explanations for the inconsistent findings (Nadler et al., 2019). In addition, most reviewed studies used RMET, which was designed mainly for individuals with mild deficits in social cognition and might not be sensitive enough to discern nuances in the whole range of the population (Voracek & Dressler, 2006; Zilioli et al., 2015). Furthermore, the validity of the RMET has been seriously questioned in a recent systematic scoping review (Higgins et al., 2024). Finally, the impact of prenatal testosterone on complex emotion recognition remains elusive as only one study measured testosterone levels in amniotic fluid (Chapman et al., 2006).

2.2. Links with cortisol

A greater ability to recognize threatening faces in males with higher testosterone levels corresponds with the idea that testosterone facilitates aggressive reactions in response to a social threat (Montoya et al., 2012). On the other hand, acute stress and increased cortisol levels might be related to both antisocial and prosocial outcomes (von Dawans et al., 2021). Stressed individuals might exhibit prosocial behavior, increased trust and social support seeking, which is regarded as a "tend and befriend" response (Taylor, 2006) (for more details about interactions between stress and "tend and befriend" model, see von Dawans et al., 2021). According to this model, stress-induced elevations in cortisol might be related to improved recognition of positive emotions, and impaired recognition of negative emotions (although links with cortisol were not evaluated, for effects of social stress on facial emotion recognition see Daudelin-Peltier et al., 2017; von Dawans et al., 2020). However, research on the relationship between cortisol levels and emotion recognition has revealed more complex associations.

2.2.1. Basic emotions

Only two studies investigating the link between basal cortisol levels and the recognition of basic emotions (Lausen et al., 2020; Weldon et al., 2015) were identified. One of these studies asked participants to recognize basic emotions as quickly and accurately as possible. Study results revealed a small positive effect of salivary cortisol in response time in males with no effect on accuracy (Lausen et al., 2020). The second study investigated if cortisol levels before or during the fMRI scan are related to processing of emotional information and did not find a link between basal salivary cortisol and emotion recognition accuracy in a mixed-sex sample (Weldon et al., 2015). However, this study showed that a higher level of cortisol before fMRI scanning was related to enhanced reactivity of the amygdala, hippocampus and subgenual anterior cingulate cortex during facial emotion recognition in contrast to the control task. These findings suggest that cortisol affects processing but not the recognition of facial emotions or it might be that emotion recognition task was not sensitive enough for cortisol effects to become present.

Another two studies evaluated emotion recognition following the Trier Social Stress Test (TSST) (Kirschbaum et al., 1993). The TSST, performed in virtual reality, decreased the response time, and increased the accuracy of the detection of both happy and angry facial expressions (presented in low, medium, high intensities). However, the stress-induced increase in salivary cortisol was not related to these improvements (Domes & Zimmer, 2019). Another study, investigating facial mimicry in mixed-sex sample, indicated that increased cortisol levels following the TSST were associated with reduced activity of the zygomaticus major muscle (involved in smiling) in response to happy faces (Nitschke et al., 2020). Unfortunately, neither emotion recognition accuracy nor response time were evaluated in this study.

In a recent fMRI study, a mixed-sex sample of adolescents first watched emotional faces and then performed a socially evaluated cold-pressor test (SECPT) (Roberts et al., 2022). This study revealed that a greater amygdala BOLD response to fearful faces was associated with a greater increase in salivary cortisol during the cold-pressor test, whereas baseline cortisol levels were not related to amygdala activation (Roberts et al., 2022). The authors suggested that the sensitivity of the HPA axis to stress might be related to the amygdala's sensitivity to emotional stimuli (Roberts et al., 2022). Moreover, a negative relationship between early life adversities and the recognition of fearful faces was reported in a mixed-sex sample (Lieslehto et al., 2017). This finding was interpreted by the authors as indicating that early adversities affect the sensitivity of the HPA axis through the impact on the functioning of glucocorticoid receptors, and could be associated with deficits in face processing (Lieslehto et al., 2017). Furthermore, the negative effect of early life adversity on the recognition of both basic and complex facial emotions was shown to be dependent on gene variants associated with higher HPA reactivity in combined-sex sample (Hartling et al., 2019).

2.2.2. Complex emotions

Several studies have investigated recognition of complex emotions in relation to TSST-induced stress and the elevation of cortisol levels in males (Nitschke et al., 2022; Smeets et al., 2009; Wolf et al., 2015). A high (vs. low) cortisol response to the TSST was related to greater accuracy in emotion recognition using movies for the assessment of social cognition (MASC) (Smeets et al., 2009). Similarly, higher stress-induced cortisol levels were related to greater empathetic accuracy, as assessed in two independent (between- and within-subject) studies using videos with actors expressing negative emotions (Nitschke et al., 2022). Contrary to the findings discussed above, no effect of TSST-evoked stress or cortisol

elevation on cognitive empathy was observed using the MET (Wolf et al., 2015) or RMET (Smeets et al., 2009).

2.2.3. Substances administration studies

Studies using the administration of hydrocortisone and/or fludrocortisone did not reveal an effect of these substances on emotion recognition (Chae et al., 2021; Duesenberg et al., 2016; Kukolja et al., 2008; Schultebraucks et al., 2016). This suggests the importance of natural hormonal release, or the possible role of other confounding factors. Recognition of sad and angry facial expressions in mixed-sex samples was not affected by administering either GC/MC receptors agonist hydrocortisone (Duesenberg et al., 2016) or fludrocortisone, which has an affinity for MC receptors approximately 15 times greater than that of GC receptors (Schultebraucks et al., 2016). Duesenberg et al. (2016) also did not reveal effects of hydrocortisone on MET performance. A recent study investigating the recognition of both basic and complex facial emotions by administering hydrocortisone also revealed no effect on the recognition of both basic and complex facial expressions (Chae et al., 2021). Similarly, the reaction time to happy and fearful faces was not affected by the administration of hydrocortisone in a mixed-sex sample (Kukolja et al., 2008).

Nevertheless, a recent study using an emotional dot-probe paradigm revealed that administration of hydrocortisone led attention away from sad faces, with no effect on happy faces (Metz et al., 2021). In contrast, the administration of fludrocortisone increased attentional bias toward sad faces with no effect on happy faces, compared to placebo (Schultebraucks et al., 2016). Although cortisol levels were diminished by fludrocortisone administration, cortisol itself was not associated with the attentional bias. Considering involvement of MC receptors in fast non-genomic actions and GR receptors in delayed genomic effects (Joëls et al., 2018), the authors of both studies suggested that a rapid stimulation of MC receptors is involved in modulation on selective attentional toward negative emotional stimuli (Metz et al., 2021; Schultebraucks et al., 2016).

Taken together, the findings suggest that emotion recognition might be affected specifically by stress-induced glucocorticoids but not by glucocorticoids in general (Nitschke et al., 2022). Moreover, as stress is followed by the release of a mix of hormones and neurotransmitters (Groeneweg et al., 2011), it might be that better emotion recognition following acute stress (Domes & Zimmer, 2019; Nitschke et al., 2022; Smeets et al., 2009; von Dawans et al., 2020) is affected by the complex interplay between neural and hormonal systems rather than by glucocorticoids alone.

However, the lack of effect of exogenous cortisol in the studies mentioned above might also be explained by differences in the pattern of hormone delivery. Specifically, single-administration studies did not maintain the nature of endogenous steroids to be released in a pulsatile pattern. The importance of such a pattern has been demonstrated in a study in which males underwent one of three treatment therapies for five days. All treatment conditions included the administration of the cortisol biosynthesis blocking agent metyrapone, and one of three hydrocortisone replacement therapies: (i) a continuous subcutaneous infusion providing a normal circadian rhythm, (ii) a pulsatile subcutaneous infusion providing both circadian and ultradian rhythms, and (iii) an oral treatment, involving three daily regimens, resulting in three pulses during the day and a low level at night (Kalafatakis et al., 2018). This study revealed a decrease in accuracy while evaluating negative facial expressions only in males treated with pulsatile hydrocortisone infusion. Moreover, this study used a dot-probe paradigm to reveal an attentional bias toward happy faces in males infused with hydrocortisone in a pulsatile pattern, and

attentional bias away from fearful faces in oral hydrocortisone-treated males. Hence, this study suggests that emotion recognition might be affected by corticosteroids if they are released in a natural pattern. A further study highlighted the importance of dose of exogenous glucocorticoids on the inhibition of emotional information processing (Taylor et al., 2011). This study showed that 10 mg but not 40 mg hydrocortisone elicited increased inhibition of angry faces relative to the placebo, suggesting a dose-dependent effect of exogenous cortisol. However, except for Kukolja et al. (2008) where 30 mg of hydrocortisone was used, all the abovementioned studies evaluating emotion recognition and the impact of hydrocortisone used doses of 10 mg and did not find significant effects. Finally, administration of 40 mg of hydrocortisone reduced preconscious attention (evaluated with a masked Stroop task) to fearful faces in males who reported higher levels of state anxiety (Putman et al., 2007). Meanwhile, administration of 40 mg but not 10 mg of hydrocortisone was related to increased attentional inhibition of happy faces in individuals from mixed-sex sample reporting higher levels of anxiety (Taylor et al., 2011). Hence, these two studies suggest an interplay between participant's psychological state and the effects of hormonal administration. In contrast, a basal level of salivary cortisol was associated with reduced preconscious attention to angry faces (masked Stroop task), with no link with trait anxiety in a mixed-sex sample (van Honk et al., 1998).

Although a pulsatile pattern of cortisol release (Kalafatakis et al., 2018) and treatment dose (Taylor et al., 2011) might be important, studies which administered hormones showed no effect of exogenous corticosteroids on emotion recognition (Chae et al., 2021; Duesenberg et al., 2016; Kukolja et al., 2008; Schultebraucks et al., 2016) while revealing their effects on attentional inhibition (Taylor et al., 2011), conscious (Kalafatakis et al., 2018; Metz et al., 2021; Schultebraucks et al., 2016) and preconscious attention (Putman et al., 2007). This suggests that corticosteroids might affect cognitive and affective neural pathways differently. Indeed, it was shown that emotional processing is increased and executive functions are suppressed by rapid non-genomic effects of cortisol (Joëls et al., 2018).

2.3. Dual-hormone hypothesis

Considering the dual-hormone hypothesis (Mehta & Josephs, 2010), the results to date are limited and inconsistent. A small but significant salivary testosterone association with higher accuracy and faster responses in basic emotion recognition task was found when the basal cortisol level was low but not when it was high (Lausen et al., 2020). However, relationships between salivary levels of testosterone, cortisol, and RMET performance were not revealed in two other studies with larger (n = 323, Zilioli et al., 2015) and smaller (n = 20, Romero-Martínez et al., 2016) samples. In addition, no effect of basal serum cortisol was observed in a study showing decreased personal distance to angry persons after testosterone administration (Wagels et al., 2017). However, it is important to consider the context of social status when dual-hormone effects are evaluated (Mehta & Prasad, 2015). These effects are expected to be present specifically in the context of social interactions such as competition or social evaluation. For example, one study revealed greater cortisol reactivity in response to the TSST in males with better emotion recognition abilities and higher testosterone levels (Bechtoldt & Schneider, 2016). The authors conclude that a better ability to recognize emotions puts people at risk of perceiving greater stress during social interactions, especially when individuals are motivated to seek status and social approval, which might be characteristic of high-testosterone individuals. Although this study did not assess dual-hormone effects, it revealed important interconnections between social context, testosterone, cortisol, and emotion recognition. Hence, considering that in the reviewed studies

participants were not manipulated to believe that performance on emotion recognition tasks would lead them to any status-related gains, it is not unexpected that dual-hormone effects were not present.

3. Emotion regulation

The ability to influence individuals' emotional experiences is known as emotion regulation (McRae & Gross, 2020). Many emotion regulation strategies have been investigated in different contexts, several of which have been applied in studies relevant to our review. Therefore, they are briefly introduced here. The two most often encountered strategies are cognitive reappraisal and distraction. Cognitive reappraisal involves reinterpreting or reevaluating an emotional situation. Accordingly, the intensity of a negative emotional response can be downregulated by reinterpreting situation to happen either in a positive context, or with a positive ending (e.g., Langer et al., 2023). Alternatively, participants might be asked to cognitively distance themselves from an emotional situation, by thinking of the situation as a photograph or scene produced by actors, and therefore not real (Kinner et al., 2014). In contrast, by reinterpreting a situation to have a disastrous outcome, or by putting oneself in the position of an observed scene, the intensity of a negative emotional response can be upregulated (e.g., Pan et al., 2023). During distraction, participants are asked to either shift their attention away from negative stimuli by thinking about neutral situation not related to seen stimuli (e.g., Langer et al., 2023), or they are provided with a distracting task overlaying an emotional stimulus (e.g., Sandner et al., 2021). Most of the reviewed studies instructed participants to reinterpret situations in a positive context or with a positive ending for reappraisal and to think about neutral situations for distraction strategies. Therefore, if not stated otherwise, we referred to these instructions when mentioning reappraisal or distraction. Other strategies included suppression (preventing the expression of an internal emotional state, e.g., by, keeping facial expression neutral to avoid showing disappointment), and rumination (recurrent direction of attention toward the causes and consequences of emotion e.g., by mentally re-playing negative experiences) (McRae & Gross, 2020).

In the reviewed studies, emotion regulation was evaluated using several different approaches: (i) the evaluation of the ability to use a specific strategy while performing a task involving different valence and arousal stimuli, (ii) the assessment of habitual use (trait) emotion regulation strategies evaluated using various self-report questionnaires, and (iii) the approach-avoidance paradigm in which participants were asked to approach or avoid stimuli by moving a joystick. In this review, all studies using the approach-avoidance paradigm used faces with happy or angry expressions where participants' automatic tendency is to approach happy and avoid angry faces, whereas execution of an opposite (approach angry and avoid happy faces) requires cognitive control which is reflected in longer reaction times (Kaldewaij et al., 2019a). Finally, several studies have evaluated the activity of different brain regions that are important for emotion regulation (Table 1) in relation to sex steroids and cortisol, therefore such studies were also included in the current review.

Table 1. Brain structures commonly investigated in a context of emotion regulation.

Brain structure	Function in emotion regulation
Amygdala	Encoding of emotional stimuli and exhibiting bias toward signals of potential threats (Ochsner et al., 2012).
Ventral Striatum	Encoding reward value of the stimulus (Ochsner et al., 2012).
Insula	Integration of sensory inputs to shape coherent representation of inner emotional states (Monachesi et al., 2023).

vmPFC	Integrating affective valuations of perceived stimuli in the current context (Ochsner et al., 2012).
vlPFC	Detecting salience and signaling the need for emotion regulation to dlPFC (Kohn et al., 2014).
dlPFC	Participating in response inhibition, executive and attentional control (Morawetz et al., 2020; Powers & LaBar, 2019).
dmPFC	Attribution of mental states and self-referential processing (Powers & LaBar, 2019).
dACC	Monitoring emotion regulation performance thus possibly helping to track how current regulation is changing emotional responses (Ochsner et al., 2012).
aPFC	Participating in social-emotion control over automatic actions (Kaldewaij et al., 2019a).

Note: vmPFC – ventromedial prefrontal cortex, vlPFC – ventrolateral prefrontal cortex, dlPFC – dorsolateral prefrontal cortex, dmPFC – dorsomedial prefrontal cortex, dACC – dorsal anterior cingulate cortex, aPFC – anterior prefrontal cortex.

3.1. Links with sex hormones

Existing neuroimaging studies suggested that frontal brain structures and the amygdala are influenced by gonadal hormones. Specifically, neural reactivity to threatening faces in the amygdala and orbitofrontal cortex correlated positively with testosterone concentration in males (see van Wingen et al., 2011, for review). Higher basal salivary testosterone levels were associated with lower activity at the border of the vlPFC and frontal pole in males (Volman et al., 2011) and with less recruitment of the aPFC in aggressive police recruits (Kaldewaij et al., 2019b) during an approach-avoidance task. Moreover, the results of these studies showed that lower testosterone levels were associated with stronger prefrontal cortex control over the amygdala (Kaldewaij et al., 2019b; Volman et al., 2011). Similarly, reduced connectivity between the dlPFC and amygdala during the resting state was observed in males who received transdermal testosterone compared to the placebo group (Votinov et al., 2020). Furthermore, there is evidence that default mode network (DMN), a system involved in emotion perception (Li et al., 2014), is also responsive to testosterone. An association between higher fetal testosterone level measured from amniotic fluid and reduced functional connectivity between the DMN subsystems was observed in adolescent males (Lombardo et al., 2020). Reduced resting-state connectivity between the amygdala and DMN was reported in AAS users compared to non-users and previous users (Westlye et al., 2017). Similarly, in comparison to non-users, long-term AAS users had larger amygdala volumes and decreased resting-state connectivity between the amygdala and other brain regions, including the dACC and insula (Kaufman et al., 2015).

In contrast, the strongest functional connectivity between the PFC (dlPFC and dACC) and amygdala during the control of provoked anger was observed in males with higher basal salivary testosterone and lower cortisol levels (Denson et al., 2013). The authors provided two possible explanations for these findings. Firstly, it might be that high-testosterone and low-cortisol individuals required greater recruitment of the PFC in response to amygdala activation, suggesting greater PFC control over a stronger subcortical response. Alternatively, it might be that high-testosterone and low-cortisol individuals had overall less sufficient PFC control over the amygdala, suggesting less efficient cognitive control mechanisms. The second explanation is supported by a study showing that testosterone administration reduced connectivity between the dlPFC and amygdala, even during the resting state (Votinov et al., 2020). Moreover, it is in line with evidence showing lower emotional control (measured

using the questionnaire Behavior Rating Inventory of Executive Function-Adult) in individuals with severe AAS dependence compared to AAS users with low dependence symptoms (Scarth et al., 2022). Denson et al. (2013) findings also correspond to studies showing positive associations between testosterone levels and amygdala reactivity to threatening faces (Derntl et al., 2009; Goetz et al., 2014; Manuck et al., 2010). However, they contradict previous results showing a reduced connectivity between the PFC and amygdala in males with higher testosterone levels during an approach-avoidance tasks (Kaldewaij et al., 2019b; Volman et al., 2011). Nevertheless, in approach-avoidance studies, participants were not explicitly instructed to regulate emotions, therefore less control by the PFC over the amygdala might be expected. Interestingly, mediation of higher salivary testosterone level on lower aPFC activity and aPFC-amygdala connectivity was shown in male psychopathic offenders but not in control males while performing an approach-avoidance task (Volman et al., 2016). This mediation by testosterone observed in psychopathic offenders supports the results gathered from aggressive police recruits (Kaldewaij et al., 2019b), suggesting that individual personality traits can act as mediators/modulators of testosterone effects. However, the lack of testosterone modulation over aPFC-amygdala connectivity in control males contrasted with the results of an earlier study by the same group (Volman et al., 2011). Volman et al. (2016) attributed this discrepancy to the older age, higher education, and lower anxiety of the participants in a later study.

Concerning the effects of sex hormones other than testosterone on emotion regulation in males, two studies administered pregnenolone (Sripada et al., 2013a) and dehydroepiandrosterone (DHEA) (Sripada et al., 2013b). The progesterone-derived neurosteroid pregnenolone is a precursor of allopregnanolone, whereas DHEA is a precursor of testosterone, and both are modulators of inhibitory GABA receptors (Schumacher et al., 2014; Soma et al., 2015). In these studies, emotion regulation was evaluated by showing facial expressions superimposed on pictures of buildings. Then, participants were asked to answer one of three questions: (i) what the gender of the shown face was, (ii) whether the scene in the background was indoor or outdoor, and (iii) how much they liked/disliked the shown face. Accordingly, (i) implicit emotional processing, (ii) attentional modulation and (iii) appraisal of emotional stimuli were measured (Sripada et al., 2013a). Administration of pregnenolone decreased the activity of the amygdala and insula (Sripada et al., 2013a), whereas administration of DHEA decreased activity in the amygdala, and increased activity in the rostral ACC (Sripada et al., 2013b) across all conditions and in response to all facial expressions (angry, fearful, neutral). Furthermore, administration of pregnenolone increased the BOLD signal in the dmPFC during face appraisal, as opposed to implicit emotion processing (Sripada et al., 2013a). These two studies revealed that the neuroactive precursors of the main sex steroids could also be considered when the interaction between sex hormones and emotion regulation abilities is evaluated.

3.2. Links with cortisol

An fMRI functional connectivity study demonstrated that cortisol impacts crosstalk between the medial PFC and amygdala even in the resting-state (Veer et al., 2012). Specifically, it was demonstrated that a higher basal level of salivary cortisol was associated with stronger negative connectivity between the amygdala and two regions of the mPFC (i.e., the perigenual ACC and medial frontal pole). Moreover, both fast and slow effects of glucocorticoids on emotion regulation-related brain activity and subjective evaluations were revealed by administering hydrocortisone (Henckens et al., 2010; Jentsch et al., 2019; Langer et al., 2022b; Pan et al., 2023). Administration of hydrocortisone rapidly (within 75 min) reduced the amygdala's response to emotional stimuli (Henckens et al., 2010). However, after 285 min,

desensitization remained only for positive stimuli and was accompanied by increased coupling between the mPFC and amygdala. It was also shown that hydrocortisone-treated males rated high-intensity negative images as less arousing than male controls when applying an emotion regulation strategy of distraction, and this effect remained stable in both 30 min and 90 min post-treatment time windows (Langer et al., 2022b). Similarly, hydrocortisone administration in a mixed-sex sample 90 min before task onset was associated with increased vlPFC regulatory activity during distraction and decreased emotion-related activity in the amygdala during reappraisal (Jentsch et al., 2019). Moreover, hydrocortisone-treated males reported less intense negative emotions than placebo-treated males (Jentsch et al., 2019). Furthermore, increased dmPFC activity in males was associated with 100 mg of hydrocortisone administered 110 min prior to the implicit emotion regulation task, which does not require purposeful effort to alter emotional experience (Ma et al., 2017).

The timing of cortisol effects (rapid vs. slow) was considered in a recent randomized and placebo controlled study involving a mixed-sex sample (Pan et al., 2023). In this study, participants received hydrocortisone or placebo 30 or 90 min prior to a cognitive reappraisal task which required down- and upregulation of negative emotions. The authors of the study showed that rapid cortisol effects (30 min post-treatment) impaired the effectiveness of reappraisal (both down- and upregulation) despite of an increased involvement of the dlPFC, suggesting a reduced capacity for the regulation of negative emotions (Pan et al., 2023). In contrast, the slow cortisol effects (90 min post-treatment) increased the effectiveness of reappraisal in modulating amygdala activation (i.e., decreasing activation during downregulation and/or increasing during upregulation). Taken together, the results of the abovementioned studies support the hypothesis of earlier cortisol-administrational studies suggesting that an increase in cortisol facilitates individuals' stress coping via the inhibition of task-irrelevant automatic emotional processing (see Putman & Roelofs, 2011, for a review).

The results from studies using the TSST indicate that stress-elevated salivary cortisol levels are positively related to the subjective success of reappraisal (Langer et al., 2020, 2022a) and distraction (Langer et al., 2022a). Furthermore, a rise in cortisol levels induced by a SECPT correlated positively with reduced subjective emotional arousal while using distraction (Langer et al., 2023). These findings were observed while using an approximately 25 min window between the onset of stress and the emotion regulation task, suggesting rapid non-genomic effects of cortisol. Furthermore, delayed genomic effects of cortisol on emotion regulation were suggested in a mixed-sex sample study, where effects of salivary cortisol were present 90 min after TSST induction (Langer et al., 2021). In this study, cortisol levels were related to higher valence and lower arousal ratings of negative stimuli during distraction but not reappraisal (Langer et al., 2021).

On the other hand, there are also studies reporting no relationships between acute stress and emotion regulation. One study showed no effect of acute psychosocial stress on reappraisal within 20-40 min after stress in a mixed-sex sample (Sandner et al., 2021). However, although the emotion regulation task was performed during the time-window when cortisol levels are expected to peak, the authors did not provide evaluations of relationships between cortisol levels and task performance. In another study, participants were instructed to distance themselves from the stimuli by reappraising the situation (Kinner et al., 2014). This study also did not show effects of SECPT on the down- or upregulation of negative emotions (Kinner et al., 2014). These two studies also investigated the effects of acute stress on distraction by asking participants if the math equation overlaying the emotional stimulus was correct. Sander et al. (2021) showed no effect of acute psychosocial stress. In contrast, Kinner et al. (2014)

reported that both acute psychosocial and physical stress were related to impaired effectiveness of distracting from negative emotional pictures (Kinner et al., 2014). This impairment remained significant even after controlling for increased salivary cortisol levels, suggesting the influence of stress-related factors other than cortisol (Kinner et al., 2014). It might be that physical stress during SECPT induces intense activation of the sympathetic nervous system, which in turn predominates HPA axis activity, and leads to less effective emotion regulation (Kinner et al., 2014; Sandner et al., 2021). In line with this idea, it was shown that administration of the hydrocortisone and the noradrenaline-reuptake inhibitor reboxetine was related to an amygdala response bias to negative emotional faces in a mixed-sex sample (Kukolja et al., 2008). Hence, interactions between the HPA axis and the sympathetic nervous system might lead to different effects of acute stress on emotional responses in general and on emotion regulation specifically.

Overall, the reviewed studies showed a relationship between cortisol levels and reduced amygdala reactivity (Henckens et al., 2010; Jentsch et al., 2019), positive associations between cortisol levels and subjective ratings of emotion regulation success (Langer et al., 2020, 2022a), lower intensity (Jentsch et al., 2019; Pan et al., 2023), lower arousal (Langer et al., 2021, 2022b, 2023), and higher valence ratings of negative stimuli (Langer et al., 2021). These findings are in line with the suggestion that corticosteroids contribute to the gradual downregulation of the salience network (which includes the amygdala), and upregulation of the executive network (which includes the dlPFC and dmPFC) (Hermans et al., 2014). It also corroborates a recent meta-analysis showing that cortisol levels are positively related to emotion control in males (Ji et al., 2021).

3.2.1. Reciprocal interactions between cortisol and emotion regulation

It is important to note that the association between cortisol levels and emotion regulation might be reciprocal. That is, cortisol may impact emotion regulation, and emotion regulation (or emotional intelligence in general) may modulate the cortisol response (Bechtoldt & Schneider, 2016). For example, participants with a steeper cortisol awakening response, and flattened diurnal cortisol slope reported greater habitual use of suppression strategy (Otto et al., 2018). In contrast, greater habitual reappraisal was associated with faster cortisol recovery after the TSST in one study (Lewis et al., 2018) but not in another (Krkovic et al., 2018). In the later study habitual use of rumination and catastrophizing predicted a reduced cortisol response to the TSST (Krkovic et al., 2018). Furthermore, reduced aPFC activity during an approach-avoidance task was associated with a subsequent increase in cortisol levels in response to the SECPT, suggesting a link between difficulty in emotion control and sensitivity to acute social stress (Kaldewaij et al., 2019a). The relationships between specific emotion regulation strategies and cortisol responses are often inconsistent, and there is a vast heterogeneity of applied methodologies (e.g., see Zoccola & Dickerson, 2012, for a review on rumination). However, this broader topic is not within the scope of the current literature review, therefore interested readers are directed to relevant systematic reviews and meta-analyses (Ji et al., 2021; Mikkelsen et al., 2021).

4. Discussion and future directions

The aim of the present review was to summarize the current knowledge on emotion recognition and regulation in males in relation to sex and stress steroids. Although there is heterogeneity in experimental designs, approaches, and results, some key findings can be discerned (Figure 2).

First, the findings of studies discussed in the current review suggest that individual differences (e.g., in personality traits) are important modulators of testosterone effects on the perception and regulation of

emotions (Kaldewaij et al., 2019b; Putman et al., 2007; Taylor et al., 2011; Volman et al., 2016). This observation is in line with previous studies showing links between testosterone and human social behaviors in the presence of specific personality traits such as dominance or impulsivity (for review: Carré & Archer, 2018; Carré & Robinson, 2020). Considering the importance of testosterone in status-seeking behaviors (Knight et al., 2020), it is possible that susceptibility to social norms, such as those related to masculinity, also modulates the effects of testosterone. Masculinity is a complex and dynamic construct, encompassing the feelings, attitudes, and behaviors that a society attributes to the biological aspects of being male (Berke et al., 2018). The prevailing norms of masculinity endorse males to control, restrict, or suppress their emotions, with the exception of anger (Berke et al., 2018). There is evidence that males' perception of masculinity shapes their expression and regulation of emotions and might determine the emergence of alexithymia (Berke et al., 2018). Moreover, violation of masculine norms might be perceived as a status-threat (Berke et al., 2018), thus motivating high-testosterone males to adopt behaviors that are perceived as masculine and hereby stick to maladaptive emotion regulation strategies.

These findings are supported by the reviewed neuroimaging studies. These studies revealed an association between testosterone levels and reduced coupling between prefrontal regions and the amygdala (Kaldewaij et al., 2019b; Volman et al., 2011; Votinov et al., 2020) suggesting that higher testosterone levels might impair the ability to top-down regulate emotions. However, this effect is not always the same. For example, connectivity between the prefrontal cortex and amygdala was increased in high-testosterone participants when they were instructed to control emotions in an anger-provoking context (Denson et al., 2013). Hence, it is likely that the inability to control emotions was perceived as a status threat for participants, thus enabling testosterone-modulated motivation to cognitively control emotions. Similarly, there is evidence that higher testosterone levels might be related to better emotion recognition in a competitive situation (Vongas & Al Hajj, 2017). Further research should investigate whether the induced (primed) belief that better ability to recognize and regulate emotions is an indicator of higher status would improve these abilities in males with high testosterone and low cortisol levels; this becomes particularly interesting when considering the positive effects of cortisol on emotion regulation (Jentsch et al., 2019; Langer et al., 2020, 2021, 2022a, 2022b, 2023; Pan et al., 2023). Furthermore, future studies could investigate whether the attribution of emotion recognition or adaptive emotion regulation strategies as masculine features impacts these abilities in males who are susceptible to masculine norms. It was shown that a reframed perception of masculinity helped males to seek psychological support to prevent suicide (Struszczyk et al., 2019). Therefore, it is likely that similar reframing could help to adjust their emotional behavior.

Second, threatening emotions, such as fear and anger, were better recognized (Derntl et al., 2009; Ersche et al., 2015), attracted more attention (van Honk et al., 1999; Wirth & Schultheiss, 2007), evoked greater amygdala reactivity (Beking et al., 2020; Derntl et al., 2009; Goetz et al., 2014; Manuck et al., 2010), showed stronger co-activation of the amygdala and vmPFC (Grannis et al., 2021), and enhanced PFC control over the amygdala response (Stanton et al., 2009) in males with higher testosterone levels. Together with findings showing a decreased personal distance to angry persons after testosterone administration (Wagels et al., 2017), these findings support the idea that testosterone facilitates dominance challenge (Carré & Olmstead, 2015; Wirth & Schultheiss, 2007). Although there are studies showing the effects of cortisol on attentional bias away from fearful (Putman et al., 2007) and angry faces (van Honk et al., 1998), and attentional inhibition of angry faces (Taylor et al., 2011), there are no studies evaluating these effects in the context of the dual-hormone hypothesis by directly measuring both testosterone and cortisol simultaneously in the same study. Together with the evaluation of personality traits, such studies might help to discern how males with different hormonal profiles are affected by threatening signals, thereby providing additional understanding of their psychological well-

being and emotional behavior. Although no evidence of interaction between testosterone and cortisol was found in studies using RMET (Romero-Martínez et al., 2016; Zilioli et al., 2015) or in a study investigating personal distance (Wagels et al., 2017), a small but significant effect supporting the dual-hormone hypothesis was found in a study of basic emotions (Lausen et al., 2020). However, it is important to note that the dual-hormone effect might be particularly present in more challenging social contexts, where participants believe that emotion recognition will lead to status gain.

Third, the present review showed that the associations between cortisol levels and basic emotion recognition were weak (Lausen et al., 2020), dependent on release type (Kalafatakis et al., 2018), or non-existent (Chae et al., 2021; Domes & Zimmer, 2019; Duesenberg et al., 2016; Kukolja et al., 2008; Schultebraucks et al., 2016; Weldon et al., 2015). On the other hand, studies showing (i) the effects of cortisol on attentional bias away from faces with negative expressions (Putman et al., 2007; Taylor et al., 2011; van Honk et al., 1999), (ii) reduced facial mimicry (Nitschke et al., 2020), and (iii) increased amygdala reactivity (Weldon et al., 2015) in response to emotional faces suggest the importance of cortisol in emotion processing. Moreover, because rapid cortisol stimulation might increase attentional bias toward negative stimuli (see Metz et al., 2021), the timing of cortisol activation seems essential, and therefore should be considered when the impact of cortisol on emotions and cognition is investigated.

Fourth, findings of testosterone and cortisol effects gained through paradigms of more complex emotions (evaluated using the RMET or other, more ecologically valid tasks) were equivocal. Some studies showed that higher cortisol levels were associated with increased recognition ability (Nitschke et al., 2022; Smeets et al., 2009), whereas other studies did not find any relationships (Smeets et al., 2009; Wolf et al., 2015). Inconsistencies were also found for the relationship between emotion recognition and testosterone with studies showing positive (Puiu et al., 2022), negative (Carré et al., 2015; Gamsakhurdashvili et al., 2021; Nitschke & Bartz, 2020), and no effects (Gamsakhurdashvili et al., 2021; Nadler et al., 2019; Romero-Martínez et al., 2016). Some of these inconsistencies might be explained by the different nature of the stimuli used. For example, there is evidence that visual contextual information affects early face processing (Righart & de Gelder, 2006), suggesting that performance differences between paradigms with and without contextual information might be expected. Furthermore, it is essential to note that paradigms with complex emotions differ from each other on the level of ecological validity. For example, as discussed by Smeets et al. (2009), the MASC task, which performance was affected by cortisol, is more ecologically valid than the RMET, which performance was not affected by cortisol. Therefore, there is a need for better standardized studies to ensure a more consistent and comparable evaluation of the impact of hormonal influence on the recognition of complex emotions.

Finally, the reviewed studies on emotion regulation showed that higher testosterone levels were associated with reduced coupling between prefrontal regions and the amygdala (Kaldewaij et al., 2019b; Volman et al., 2011; Votinov et al., 2020), whereas elevated cortisol levels were related to increased coupling between those structures (Henckens et al., 2010; Veer et al., 2012), increased prefrontal (Jentsch et al., 2019; Ma et al., 2017; Pan et al., 2023) and decreased amygdala activities (Jentsch et al., 2019). To our knowledge, there are no studies investigating the relationship between testosterone and the ability to implement emotion regulation strategies such as distraction or cognitive reappraisal. Future studies are needed to better understand the strength and direction of the relationships between testosterone and subjective evaluations of regulation success, valence, and arousal of seen stimuli.

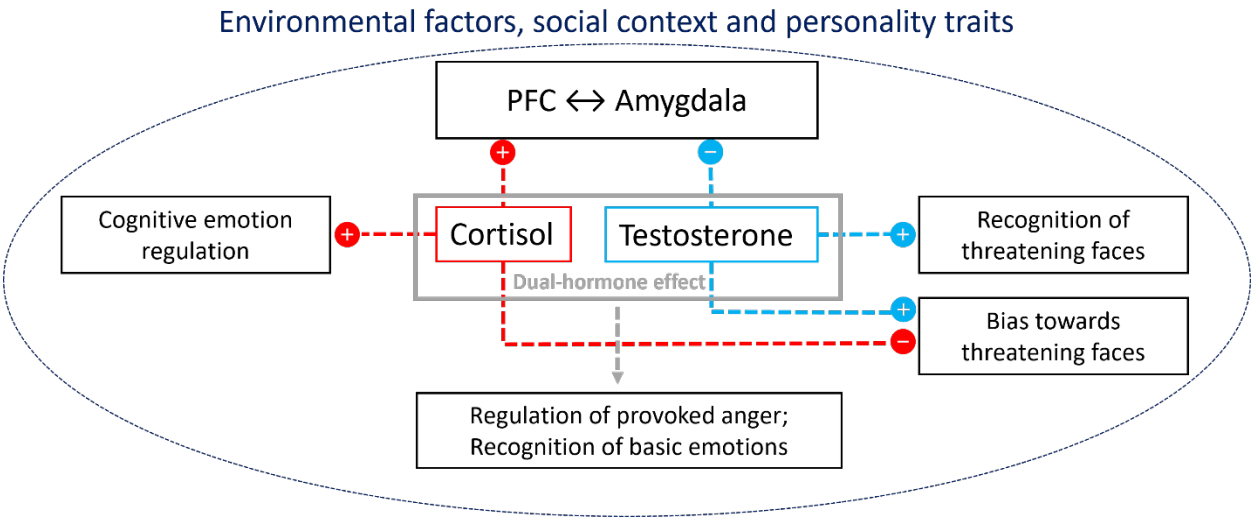

Figure 2. Schematic representation of testosterone and cortisol effects on emotion recognition and regulation in adult males. While the reviewed literature suggests that higher cortisol levels are related to better cognitive emotion regulation and reduced bias toward threatening faces, higher testosterone levels were associated with better recognition of and greater sensitivity to threatening faces. The dual-hormone hypothesis was present in the context of provoked anger regulation and recognition of basic emotions. During emotion regulation, connectivity between the prefrontal cortex (PFC) and amygdala was positively associated with cortisol levels and negatively with testosterone levels. Notably, these associations are also affected by different contextual factors and personality traits (represented outside the dashed oval line).

4.1. Conclusions

The reviewed literature suggested that higher testosterone levels in adult males are associated with sensitivity to and better recognition of threatening faces. Moreover, while cortisol levels were related to implicit emotional processing, but not the recognition of facial emotional expressions. The present review also suggests a negative effect of high testosterone but a positive effect of elevated cortisol on males' emotion regulation. However, the effects of testosterone and cortisol on emotion perception and regulation are not isolated but may interact with each other, and depend on individual differences in contextual, psychological, and social factors. Understanding these associations within a biopsychosocial approach could help to disentangle the exact roles of testosterone and cortisol in emotional behavior in males, thus providing clinical relevance for psychological well-being and increasing self-awareness. Future studies could investigate how endocrine factors are linked to emotion recognition and emotion regulation in situations when traditional masculinity norms are challenged. For example, when the use of adaptive cognitive emotion regulation strategies is endorsed as a masculine feature and is associated with higher social status. The findings of such studies might contribute to improving individuals' and society's health.

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