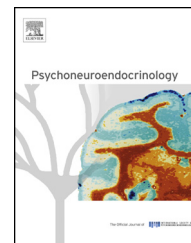




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Testosterone administration modulates moral judgments depending on second-to-fourth digit ratio

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Summary Moral judgment involves the interplay of emotions and social cognitions. The male sex-hormone testosterone might play a role in moral reasoning as males are more utilitarian than females. We investigated the role of testosterone in moral reasoning and social cooperation, which depend on right-hand's second-to-fourth (2D:4D) digit ratio, a proxy for prenatal sex-hormone (testosterone-versus-estradiol) priming. Here, in a placebo-controlled within-subjects design using 20 young females we show that 2D:4D predicts 44% of the variance in the effects of testosterone administration on moral judgment. Subjects who show an increase in utilitarian judgments following testosterone administration have significantly higher than average 2D:4D (relatively high prenatal estradiol priming), while subjects showing more deontological judgments following testosterone administration have near-significantly lower 2D:4D (relatively high prenatal testosterone priming). We argue that prenatally-organized differences in aromatase, i.e. conversion from testosterone to estradiol in the brain, might underlie these effects. Our findings suggest that early neurodevelopmental effects of sex steroids play a crucial role in the activational effects of hormones on moral reasoning later in life.

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1. Introduction

Moral judgment involves the complex interplay of emotions such as harm aversion and cognitions about what other people feel (Moll et al., 2002; Greene et al., 2004; Moll and de Oliveira-Souza, 2007). There is evidence suggesting that the neuroendocrine system, by way of the male

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sex-hormone testosterone plays a role in moral judgments. Males are more utilitarian than females in their moral decisions (Fumagalli et al., 2010; Youssef et al., 2012), and individuals with high salivary testosterone levels also make more utilitarian decisions (Carney and Mason, 2010). Crucially, utilitarian decisions are aimed at maximizing overall welfare ("the ends justify the means"), and are viewed as rational, whereas deontological decisions are the opposite; they are driven by emotion ("the means are more important than the ends") (Greene et al., 2001; Moll and de Oliveira-Souza, 2007). Testosterone therefore may facilitate instrumental over emotion-driven moral decision making.

Testosterone has indeed shown to be an important hormone in a range of human social cognitions and behaviors (Bos et al., 2012). Firstly, administration of testosterone reduces stress and fear in humans (Hermans et al., 2007; McCall and Singer, 2012; Bos et al., 2012), which is thought to underlie utilitarian moral decisions (Carney and Mason, 2010). Testosterone furthermore influences automatic affiliative behaviors, as administration of the hormone reduces facial mimicry, which is considered a measure of affective empathy (Hermans et al., 2006b). Moreover, on the social-cognitive level, testosterone influences social judgment; it decreases trustworthiness ratings of others (Bos et al., 2010) and importantly in the present respect, it decreases the ability to correctly identify complex emotions and feelings of others (i.e. cognitive empathy) (van Honk et al., 2011a). Importantly, this reduction of cognitive empathy by testosterone was strongly mediated by second-to-fourth finger length ratio (2D:4D); a proxy of prenatal sex-hormone (testosterone-versus-estradiol) priming (Lutchmaya et al., 2004; Zheng and Cohn, 2011). Only subjects with low 2D:4D, who are prenatally more strongly primed by testosterone, were substantially impaired in cognitive empathy after testosterone administration. Recently, we also showed increases in social cooperation after testosterone administration, but only in subjects with high 2D:4D, who are prenatally more strongly primed by estradiol (Zheng and Cohn, 2011; van Honk et al., 2012). Thus prenatal sex-hormone priming appears to modulate the effects of testosterone administration on social cognitions and behaviors later in life. In sum, empathic feelings, stressfulness and fearfulness are thought to play a role in moral reasoning and guide moral judgment (Young et al., 2007; Blair, 2007; Youssef et al., 2012; Starcke et al., 2011; Reniers et al., 2012), and testosterone administration influences all of these processes (Hermans et al., 2006b, 2007; van Honk et al., 2011a), partly depending on prenatal hormone priming (van Honk et al., 2011a).

In moral judgment tasks, subjects are confronted with scenarios of moral conflict, and they have to judge the moral permissibility of a harmful act. Prepotent negative affect such as harm aversion, but also higher-order cognitive ability such as the capacity to infer other people's feelings and the social consequences of moral dilemmas are important in this task (Haidt, 2007; Greene, 2007; Greene et al., 2009; Reniers et al., 2012). Testosterone might thus, by affecting prepotent negative responses and on a higher-order level by affecting cognitive empathy, influence the moral judgment process, but these effects might depend on prenatal exposure to the sex steroids. Therefore, in the present study we investigate the effects of testosterone administration on moral judgment. We hypothesize, on the basis of the sex differences and correlational data with testosterone levels

(Carney and Mason, 2010; Fumagalli et al., 2010) that testosterone administration increases utilitarian judgments, but that 2D:4D, the proxy of prenatal sex-hormone priming might mediate in these effects (van Honk et al., 2011a, 2012).

2. Methods

2.1. Subjects

Twenty healthy females (age range, 18–30) participated in this experiment that is approved by the local medical ethical committee (University Medical Center Utrecht). All participants were students at Utrecht University and were recruited through a participant database. Exclusion criteria were smoking, use of medication other than single-phase oral contraceptives, and history of medical, psychiatric or endocrine illness. All women used standard estrogen/progestagen oral contraceptives (containing ethinylestradiol and levonorgestrel).

2.2. Study design

Participants were tested in a randomized, double-blind, placebo-controlled, within-subjects design. Subjects were tested in groups of four and tables were separated by screens to guarantee privacy. The testosterone samples consisted of 0.5 mg of testosterone, 5 mg of the carrier cyclodextrine, 5 mg of ethanol, and 5 ml of water. The placebo samples were identical except for the omission of 0.5 mg of testosterone. Sublingual administration was used. Prior investigations into the pharmacokinetics of this exact testosterone administration in women showed that this method leads to a 10-fold increase in testosterone plasma levels which returns to baseline within 15 min and that behavioral effects peak at 4 h after intake (Tuiten et al., 2000). Multiple studies using this time interval and administration method have found behavioral, neural, and physiological effects of testosterone (van Honk et al., 2001, 2004, 2005; Hermans et al., 2006a, b). Therefore, in the current study the same interval of 4 h was applied. Furthermore, to minimize the influence of fluctuations due to diurnal hormonal and menstrual cycles, drug administration always took place in the morning and testing was restricted to the period wherein the participants took contraceptives.

2.3. Moral judgment task

The moral judgment task is based on previous work (Greene et al., 2001, 2004) and consists of impersonal and personal moral dilemmas. An example of a personal dilemma is the famous Trolley scenario: "A runaway trolley is heading down the tracks toward five workmen who will be killed if the trolley proceeds on its present course. You are on a footbridge over the tracks, in between the approaching trolley and the five workmen. Next to you on this footbridge is a stranger who happens to be very large. The only way to save the lives of the five workmen is to push this stranger off the bridge and onto the tracks below where his large body will stop the trolley. The stranger will die if you do this, but the five workmen will be saved." Twenty-four moral dilemmas were selected in order to make two versions of the moral

judgment task balanced on emotional intensity (Koenigs et al., 2007) and content, each version consisting of twelve dilemmas with six personal and six impersonal dilemmas. In personal dilemmas, such as the Trolley dilemma, the proposed action includes harm through direct physical contact (pushing the stranger) and in impersonal dilemmas harm is indirect (e.g., flipping a switch) (Greene et al., 2009). The personal dilemmas are further divided into dilemmas in which the death or harm of the victim is inevitable or evitable, which is an important factor in moral decision making (Greene et al., 2009; Huebner et al., 2011). An example of a moral dilemma where the proposed action involves evitable harm (i.e., harm to a person who would otherwise be spared) is the Trolley dilemma. An example of inevitable harm is the Crying Baby dilemma in which a group of people can be saved from an attack of soldiers by killing a crying baby. The baby threatens to reveal the hiding place of the group by crying loudly, and not killing the baby would lead to the death of everyone. Harm to the baby is in this case thus inevitable. Moral permissibility judgments are higher for actions that propose harm that is inevitable in comparison with evitable harm (Huebner et al., 2011). Subjects are asked to provide judgments of moral permissibility of the proposed action on each dilemma. Dilemmas were translated from English to Dutch, and then translated back from Dutch to English and checked for consistency by a native English speaker.

After reading the dilemma, subjects had to indicate on a visual analog scale from -100 to 0 to 100 how morally permissible she finds the proposed action (-100 is forbidden, 0 is permissible and 100 is obligatory). The moral dilemmas were self-directed, and thus required the subject imagining herself to be in the scenario.

2.4. Hormone and mood measurements

Baseline testosterone levels were measured from saliva on both days before testosterone or placebo administration. Mood was measured on both days before (morning) and after (noon) administration using a shortened version of the Profile of Mood States (POMS) questionnaire (Shacham, 1983), which consists of 6 subscales (depression, anxiety, fatigue, vigor, anger, tension) where subjects have to indicate on a visual analog scale (-100 up to 100) how they feel.

2.5. Digit ratio measurement

2D:4D was measured from an image scan of the right-hand by taking the length of the index and ring finger from the ventral proximal crease to the tip of the finger using an Adobe Photoshop measurement tool (Breedlove, 2010). An experienced rater who was blind to the experiment, measured 2D:4D twice with a time interval of several weeks. These two measurements were highly correlated ($r = .99$, $p < .0001$). The mean value of the two measurements was used for analysis.

2.6. Statistical analysis

Normality of the mean moral judgments was confirmed by Kolmogorov–Smirnov tests (all p 's $< .05$). To look for effects of testosterone administration, repeated measures ANOVAs were used with administration (testosterone, placebo) \times dilemma type (impersonal, evitable and inevitable) as within-subjects factors.

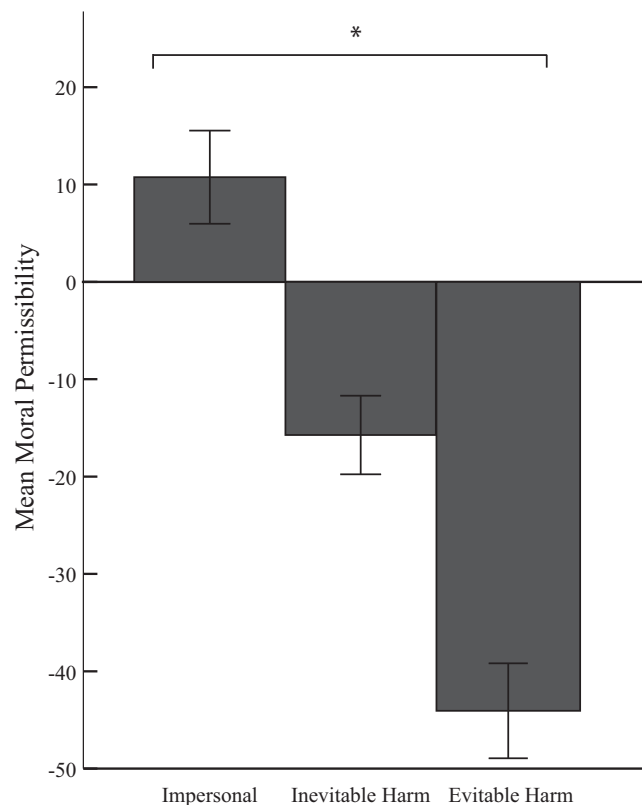


Figure 1 Main effect of dilemma type on moral permissibility ratings. Error bars indicate SEM. Asterisk indicates $p < .05$.

3. Results

3.1. Moral judgment task

Mean moral permissibility judgments did not differ between testosterone and placebo condition (testosterone: $M = -16.03$, $SD = 4.92$, placebo: $M = -16.66$, $SD = 4.25$) indicating that there was no significant main effect of testosterone administration ($F(1,19) = .017$, $p = .898$, $\eta_p^2 = .001$). There was a main effect for dilemma type ($F(2, 38) = 66.31$, $p < .001$, $\eta_p^2 = .78$) and post hoc comparisons showed that the actions proposed in impersonal dilemma types were judged as more morally permissible than dilemmas with inevitable harm and evitable harm, and dilemmas with inevitable harm were judged as more morally permissible than evitable harm (all p 's $< .001$, see Fig. 1). Importantly, the administration \times dilemma type interaction was not significant ($F(2,38) = .385$, $p = .683$, $\eta_p^2 = .02$).

To investigate if 2D:4D mediated in the effects of testosterone on moral judgments, we ran the original ANOVA with the continuous variable 2D:4D added as a covariate. This analysis showed a significant administration \times dilemma type interaction ($F(2,36) = 7.18$, $p = .002$, $\eta_p^2 = .29$) and crucially, a significant administration \times dilemma type \times 2D:4D interaction ($F(2,36) = 7.276$, $p = .002$, $\eta_p^2 = .29$). To further investigate this interaction we computed three separate repeated measures ANOVAs for the different dilemma types (impersonal, inevitable, evitable) with 2D:4D as a covariate which showed that the administration \times dilemma type \times 2D:4D interaction was driven by an administration \times 2D:4D interaction for the moral dilemmas involving inevitable harm ($F(1,18) = 14.47$, $p = .001$, $\eta_p^2 = .45$). No main effects of testosterone, or administration \times 2D:4D interactions were found on impersonal dilemmas ($F(1,18) = .000$, $p = .998$, $\eta_p^2 = .00$; $F(1,18) = .000$, $p = .996$, $\eta_p^2 = .00$) and on personal

dilemmas where harm is evitable ($F(1,18) = .008$, $p = .928$, $\eta_p^2 = .00$, $F(1,18) = .008$, $p = .929$, $\eta_p^2 = .00$).

As can be seen in Fig. 2 the direction of the testosterone administration \times 2D:4D interaction is such that 2D:4D predicts an increase in moral permissibility following testosterone relative to placebo ($r = .67$, $p = .001$). Therefore, in line with our previous studies (van Honk et al., 2011a, 2012), and to further specify this effect, we created groups of relatively high and low 2D:4D (indicative of low and high prenatal testosterone exposure respectively) based on median split. Non-parametric Wilcoxon tests showed that in the low 2D:4D group ($n = 10$) the decrease in moral permissibility judgments was not significant ($Z = -1.38$, $p = .169$) whereas in the high 2D:4D group ($n = 10$) the increase in moral permissibility judgments was marginally significant ($Z = -1.886$, $p = .059$).

From Fig. 2 it can also be observed that the type of effect that testosterone induces is either positive (an increase in moral permissibility, $n = 10$) or negative (a decrease in moral permissibility, $n = 10$). We normalized the individual 2D:4D and performed a non-parametric one-sample- t test (Wilcoxon signed rank test) separately for these groups. This test showed that the subjects showing an increase in utilitarian judgments have 2D:4D greater than the mean ($p = .037$), while the 2D:4D of subjects showing a decrease in utilitarian judgment after testosterone was marginally significant lower than the mean ($p = .059$, see Fig. 3).

3.2. Mood measurements

To investigate if testosterone administration affected subjects' self-reported mood, we conducted paired t -tests of mood measurements in placebo and testosterone condition. These tests showed no difference between mood measurements in the placebo and testosterone condition (all p 's $> .05$). To investigate if the effects of 2D:4D on

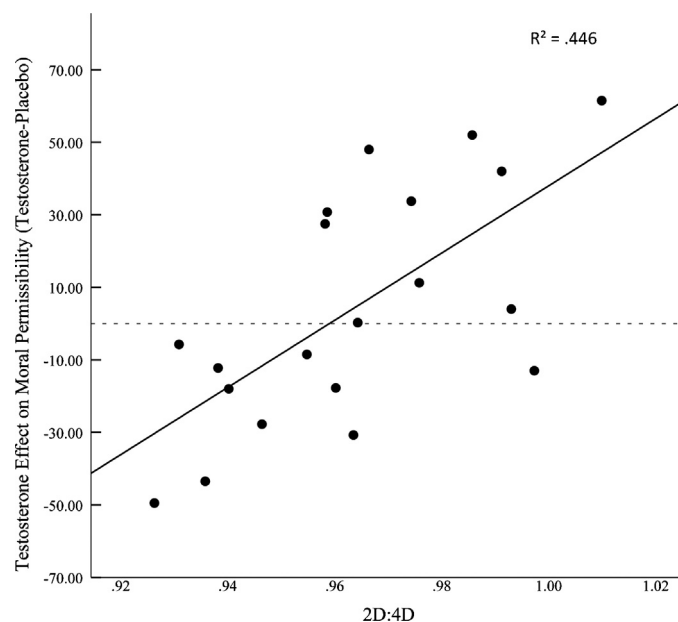


Figure 2 Scatterplot showing the individual 2D:4D measurements plotted against the effect of testosterone on moral permissibility judgments of dilemmas with inevitable harm (permissibility ratings in placebo condition subtracted from permissibility ratings in testosterone condition).

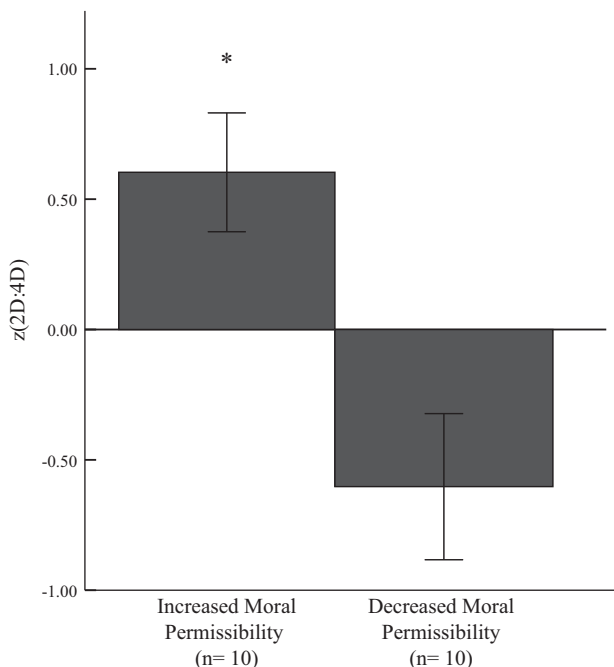


Figure 3 Subjects that show increased moral permissibility judgments after testosterone ($n = 10$) have above-average 2D:4D, and subjects showing decreased moral permissibility after testosterone ($n = 10$) have lower 2D:4D. Error bars indicate SEM. Asterisk indicates $p < .05$.

testosterone administration effects occur through differential effects of the hormone on subjective mood, we conducted the six ANOVAs on reported mood (anger, anxiety, vigor, tension, depression, fatigue) with 2D:4D as a covariate. 2D:4D did not mediate in the effects of testosterone on any of the subjective mood scales (all p 's $> .05$).

3.3. Hormone measurements

Saliva samples of one subject were missing and the sample of one subject in the placebo condition was out-of-normal range (higher than 1000 pmol/L); her data was excluded from the analysis. Testosterone levels were negatively skewed and therefore log transformed. Mean baseline testosterone levels did not differ between testosterone and placebo conditions (LOG [testosterone]: $M = 4.89$, $SD = .63$, $n = 19$, LOG[placebo]: $M = 4.89$, $SD = .60$, $n = 18$, $t(17) = -.799$, $p = .435$). Importantly for the present findings, baseline testosterone levels were not related to 2D:4D (all p 's $> .700$). Interestingly, testosterone levels were positively related to impersonal moral permissibility judgments ($\rho = .469$, $p = .050$, $n = 18$, see Fig. 4) but not to personal moral permissibility judgments on dilemmas involving inevitable harm ($\rho = .168$, $p = .505$) or evitable harm ($\rho = .333$, $p = .176$).

A repeated measures ANOVA on impersonal moral permissibility judgments with administration as within factor and baseline testosterone as a covariate showed that baseline testosterone levels did not predict the testosterone administration effect on impersonal moral judgments (all p 's $> .05$). To conclude, neither differences in baseline testosterone levels, nor differences in mood between the two conditions or two 2D:4D groups can account for the effects of testosterone administration reported above.

4. Discussion

We investigated the effects of testosterone administration on moral judgments, and whether these effects are mediated by prenatal sex-hormone priming. Three types of moral dilemmas were used: impersonal dilemmas and personal dilemmas with evitable and inevitable harm. Testosterone administration increased moral permissibility judgments on dilemmas involving inevitable harm in women with high 2D:4D, who are

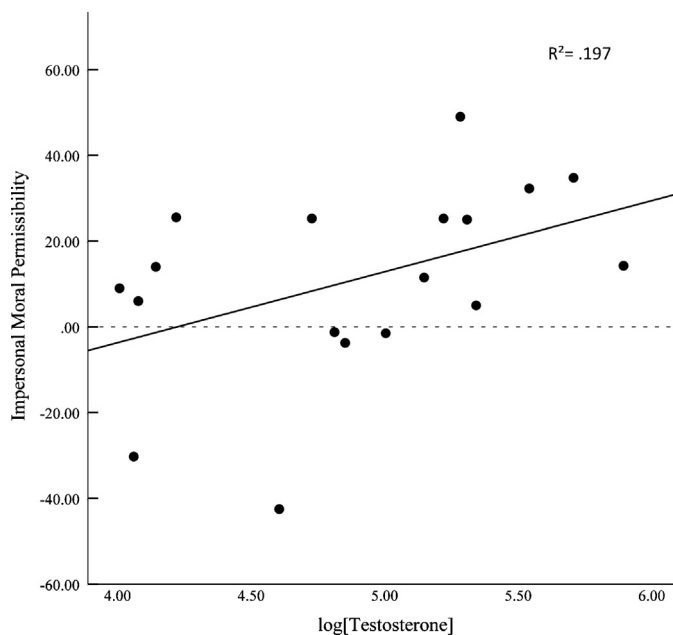


Fig. 4 Scatterplot showing the positive correlation between baseline testosterone levels and moral permissibility judgments (in the placebo condition).

prenatally more strongly primed by estradiol (Lutchmaya et al., 2004; Zheng and Cohn, 2011). This shift from deontological to utilitarian judgment bias in the subjects with relatively high 2D:4D suggests an increase in instrumental moral decision-making. These findings agree with correlational data showing that higher baseline testosterone levels relate to more utilitarian decisions (Carney and Mason, 2010), but similar to our recent effects of testosterone administration on social cooperation, they depend on 2D:4D as a mediating factor (van Honk et al., 2012).

As noted, testosterone reduces fearfulness, stress and affective empathy (Bos et al., 2012), and it selectively impairs cognitive empathy in women with low 2D:4D. This may explain differential effects of the administration in high and low 2D:4D groups. According to the dual-process theory, moral judgment starts with intuitive emotional responses such as harm aversion and empathy with the victim (Greene et al., 2001, 2004; Haidt, 2007). These prepotent emotional responses need to be instrumentally overridden in order to make utilitarian judgments (Greene et al., 2004). Support for this theory comes from patients with lesions to the ventromedial prefrontal cortex (VMPFC), who show emotional blunting and decreased empathy. However, logical reasoning and knowledge of social norms of these patients is preserved and they make more utilitarian judgments (Koenigs et al., 2007; Ciaramelli et al., 2007). Psychopaths, who have low anxiety levels and show impaired affective empathic ability, also make more utilitarian judgments (Young et al., 2012; Koenigs et al., 2012). In contrast, patients with autism spectrum disorders, a disorder marked by deficits in cognitive empathy, do not show increased utilitarian judgments (Zalla et al., 2011) and have been found to exaggerate moral blame for accidents (Moran et al., 2011), but see (Gleichgerrcht et al., 2012). Interestingly, pharmacological elevation of serotonin, a neurotransmitter that jointly with testosterone is involved in the regulation of aggression (Montoya et al., 2012), leads to an increase in deontological judgments of harms in personal dilemmas (Crockett et al., 2010). Thus testosterone and serotonin may have opposite effects on moral reasoning. Serotonin elevation might increase harm aversion (Crockett et al., 2010), thereby promoting deontological judgments, whereas testosterone administration might decrease harm aversion and promote utilitarian judgments. The contrasting effects of these neuromodulators on moral judgments would be in line with their contrasting effects on social aggression, since serotonin inhibits and testosterone facilitates aggression (Montoya et al., 2012).

Hence, in the high 2D:4D group the shift toward more utilitarian judgments after testosterone might result from reductions in fear and affective empathy, while cognitive empathic abilities are maintained (van Honk et al., 2011a). This also provides an explanation for why the effect of testosterone in the high 2D:4D group is on personal and not impersonal dilemmas, because in personal dilemmas the subject is put in direct confrontation with the to-be-sacrificed person and judgments about these actions might rely more on cognitive and empathic abilities. Within personal dilemmas, testosterone effects where only present on dilemmas involving inevitable harm. Our and previous data show that the proposed actions in these type of dilemmas are viewed as more permissible than dilemmas involving evitable harm, and thus intrinsically predispose toward utilitarian

responding (Huebner et al., 2011). Therefore, the responses to dilemmas with inevitable harm might be more sensitive to the effects of testosterone administration in subjects with high 2D:4D, causing a shift from deontological to utilitarian responding.

Testosterone administration thus may have facilitated instrumental moral judgments in subjects with high 2D:4D through its properties for lowering fear and stressfulness (Hermans et al., 2006a, 2007), decreasing affective empathy (Hermans et al., 2006b), but retaining cognitive empathy (van Honk et al., 2011a), which might decrease prepotent emotional arousal arising from the dilemma and increase the chance that instrumental cognitive processes override this. Accordingly, some of the effects we have shown in earlier studies (Hermans et al., 2006a, b, 2007) could be strongest in high 2D:4D subjects, but this needs to be tested in future research.

The present findings add to recent literature showing that testosterone can alter social decision-making (Eisenegger et al., 2010; van Honk et al., 2012). This could occur bottom-up, through altered prepotent affective responses, and top-down through altered cognitions about other people (Eisenegger et al., 2010, 2012), with the cognitive and emotional processes influencing and interacting with each other (Pessoa, 2008). A challenge for future testosterone studies is to combine cognitive and affective measures to gain more detailed insight in the workings of testosterone in social decision making.

Women with significantly higher than average 2D:4D made more utilitarian moral judgments after testosterone administration, and women who made more deontological moral judgments have near significantly lower 2D:4D. A neurobiological mechanism underlying this dissociation might involve the enzyme aromatase. Testosterone can act on the brain via its own androgen receptors, but also by way of estrogen receptors after conversion of testosterone to estradiol by the enzyme aromatase (Eisenegger et al., 2011; Bos et al., 2012). The availability of this enzyme differs between individuals (Sarachana et al., 2011). It is conceivable also with respect to the sex differences in testosterone, estradiol and aromatase, that subjects prenatally more strongly primed by estradiol convert more testosterone to estradiol in adulthood, and show effects mediated by estrogen receptors after testosterone administration. Contrariwise, subjects prenatally more strongly primed by testosterone may especially show effects of testosterone administration in adulthood which are mediated by androgen receptors (van Honk et al., 2012). Further research using administration of estradiol or testosterone with aromatase blockers is necessary to test this hypothesis (Eisenegger et al., 2012).

In the present study, we also show a positive relationship between endogenous testosterone, i.e. salivary testosterone levels, and moral permissibility judgments, but on impersonal moral dilemmas and not on personal dilemmas. These findings partly are in line with the results of Carney and Mason (2010), who show that females and males with high testosterone levels make more utilitarian moral decisions. However, these authors found this relationship exclusively on personal dilemmas while at present the effects of salivary testosterone are on impersonal dilemmas. The larger sample size, the inclusion of both males and females, and the use of one dilemma per category in the study of Carney and Mason

(2010) might be responsible for the diverging findings on salivary testosterone levels in the two studies.

Testosterone's binding sites in the brain show remarkable overlap with the key regions of the moral brain that have been found with neuroimaging. The moral brain seems to consist of VMPFC, dorsolateral prefrontal cortex, and sub-cortical regions such as the amygdala (Moll et al., 2005; Fumagalli and Priori, 2012). These regions contain androgen and estrogen receptors, especially on the amygdala (Osterlund et al., 2000; Bos et al., 2012), which also has high levels of the enzyme aromatase (Biegon et al., 2010). Prenatal sex-hormone priming by either testosterone or estradiol arguably results in different effects of testosterone administration in these brain regions, or on functional connectivity between these brain regions (van Honk et al., 2011b).

In summary, testosterone increases utilitarian moral judgments in women that are prenatally more primed by estradiol than testosterone. These results correspond to earlier research in animals which shows that early priming by sex hormones influences acute effects of testosterone on social behavior later in life (Phoenix et al., 1968; Thornton et al., 2009), and to our recent research in humans showing that acute effects of testosterone on social behavior depend on 2D:4D (van Honk et al., 2011a, 2012). Early neurodevelopmental effects of sex steroids also in humans thus seem to play a crucial role in the activational effects of hormones on social behavior in adulthood.

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Conflict of interest

None declared.

Contributors

JvH, GJW, DT, VB and WR designed research. GJW and DT performed data collection. ERM and DT did data analysis. All authors were involved in writing the manuscript.

References

- Biegon, A., Kim, S.W., Alexoff, D.L., Jayne, M., Carter, P., Hubbard, B., King, P., Logan, J., Muench, L., Pareto, D., Schlyer, D., Shea, C., Telang, F., Wang, G.J., Xu, Y., Fowler, J.S., 2010. Unique distribution of aromatase in the human brain: in vivo studies with PET and [N-methyl-11C]vorozole. *Synapse* 64, 801–807.
- Blair, R.J.R., 2007. The amygdala and ventromedial prefrontal cortex in morality and psychopathy. *Trends Cogn. Sci.* 11, 387–392.
- Bos, P.A., Panksepp, J., Bluthé, R.M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. *Front. Neuroendocrinol.* 33, 17–35.
- Bos, P.A., Terburg, D., van Honk, J., 2010. Testosterone decreases trust in socially naive humans. *Proc. Natl. Acad. Sci. U.S.A.* 107, 9991–9995.
- Breedlove, S.M., 2010. Minireview: organizational hypothesis: instances of the fingerpost. *Endocrinology* 151, 4116–4122.
- Carney, D.R., Mason, M.F., 2010. Decision making and testosterone: when the ends justify the means. *J. Exp. Soc. Psychol.* 46, 668–671.
- Ciaramelli, E., Muccioli, M., Ladavas, E., di Pellegrino, G., 2007. Selective deficit in personal moral judgment following damage to ventromedial prefrontal cortex. *Soc. Cogn. Affect* 2, 84–92.
- Crockett, M.J., Clark, L., Hauser, M.D., Robbins, T.W., 2010. Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *Proc. Natl. Acad. Sci. U.S.A.* 107, 17433–17438.
- Eisenegger, C., Haushofer, J., Fehr, E., 2011. The role of testosterone in social interaction. *Trends Cogn. Sci.* 15, 263–271.
- Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2010. Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature* 463, 356–359.
- Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2012. Eisenegger et al. reply. *Nature* 485, E5–E6.
- Fumagalli, M., Priori, A., 2012. Functional and clinical neuroanatomy of morality. *Brain* 135, 2006–2021.
- Fumagalli, M., Vergari, M., Pasqualetti, P., Marceglia, S., Mameli, F., Ferrucci, R., Mrakic-Sposta, S., Zago, S., Sartori, G., Pravettoni, G., Barbieri, S., Cappa, S., Priori, A., 2010. Brain switches utilitarian behavior: does gender make the difference? *PLoS ONE* 5, e8865.
- Gleichgerrcht, E., Torralva, T., Rattazzi, A., Marengo, V., Roca, M., Manes, F., 2012. Selective impairment of cognitive empathy for moral judgment in adults with high functioning autism. *Soc. Cogn. Affect* doi: 10.1093/scan/nss067.
- Greene, J.D., 2007. Why are VMPFC patients more utilitarian? A dual-process theory of moral judgment explains. *Trends Cogn. Sci.* 11, 322–323.
- Greene, J.D., Cushman, F.A., Stewart, L.E., Lowenberg, K., Nystrom, L.E., Cohen, J.D., 2009. Pushing moral buttons: the interaction between personal force and intention in moral judgment. *Cognition* 111, 364–371.
- Greene, J.D., Nystrom, L.E., Engell, A.D., Darley, J.M., Cohen, J.D., 2004. The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44, 389–400.
- Greene, J.D., Sommerville, R.B., Nystrom, L.E., Darley, J.M., Cohen, J.D., 2001. An fMRI investigation of emotional engagement in moral judgment. *Science* 293, 2105–2108.
- Haidt, J., 2007. The new synthesis in moral psychology. *Science* 316, 998–1001.
- Hermans, E.J., Putman, P., Baas, J., Koppeschaar, H., van Honk, J., 2006a. A single administration of testosterone reduces fear-potentiated startle in humans. *Biol. Psychiatry* 59, 872–874.
- Hermans, E.J., Putman, P., Baas, J.M., Geckis, N.M., Kenemans, J.L., van Honk, J., 2007. Exogenous testosterone attenuates the integrated central stress response in healthy young women. *Psychoneuroendocrinology* 32, 1052–1061.
- Hermans, E.J., Putman, P., van Honk, J., 2006b. Testosterone administration reduces empathetic behavior: a facial mimicry study. *Psychoneuroendocrinology* 31, 859–866.
- Huebner, B., Hauser, M.D., Pettit, P., 2011. How the source, inevitability and means of bringing about harm interact in folk-moral judgments. *Mind Lang.* 26, 210–233.
- Koenigs, M., Kruepke, M., Zeier, J., Newman, J.P., 2012. Utilitarian moral judgment in psychopathy. *Soc. Cogn. Affect* 7, 708–714.
- Koenigs, M., Young, L., Adolphs, R., Tranel, D., Cushman, F., Hauser, M., Damasio, A., 2007. Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature* 446, 908–911.

- Lutchmaya, S., Baroncohen, S., Raggatt, P., Knickmeyer, R., Manning, J., 2004. 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Hum. Dev.* 77, 23–28.
- McCall, C., Singer, T., 2012. The animal and human neuroendocrinology of social cognition, motivation and behavior. *Nat. Neurosci.* 15, 681–688.
- Moll, J., de Oliveira-Souza, R., 2007. Moral judgments, emotions and the utilitarian brain. *Trends Cogn. Sci.* 11, 319–321.
- Moll, J., de Oliveira-Souza, R., Bramati, I.E., Grafman, J., 2002. Functional networks in emotional moral and nonmoral social judgments. *Neuroimage* 16, 696–703.
- Moll, J., Zahn, R., de Oliveira-Souza, R., Krueger, F., Grafman, J., 2005. The neural basis of human moral cognition. *Nat. Rev. Neurosci.* 6, 799–809.
- Montoya, E.R., Terburg, D., Bos, P.A., van Honk, J., 2012. Testosterone, cortisol, and serotonin as key regulators of social aggression: a review and theoretical perspective. *Motiv. Emotion* 36, 65–73.
- Moran, M.M., Young, L.L., Saxe, R., Mei Lee, S., O'Young, D., Mavros, P.L., Gabrieli, J.D., 2011. Impaired theory of mind for moral judgment in high-functioning autism. *Proc. Natl. Acad. Sci. U.S.A.* 108, 2688–2692.
- Osterlund, M.K., Gustafsson, J.A., Keller, E., Hurd, Y.L., 2000. Estrogen receptor beta (ERbeta) messenger ribonucleic acid (mRNA) expression within the human forebrain: distinct distribution pattern to ERalpha mRNA. *J. Clin. Endocrinol. Metab.* 85, 3840–3846.
- Pessoa, L., 2008. On the relationship between emotion and cognition. *Nat. Rev. Neurosci.* 9, 148–158.
- Phoenix, C.H., Goy, R.W., Resko, J.A., 1968. Psychosexual Differentiation as a Function of Androgenic Stimulation. *Perspectives in Reproduction and Sexual Behavior*. Indiana Univ. Press, Bloomington, pp. 33–49.
- Reniers, R.L., Corcoran, R., Vollm, B.A., Mashru, A., Howard, R., Liddle, P.F., 2012. Moral decision-making, ToM, empathy and the default mode network. *Biol. Psychol.* 90, 202–210.
- Sarachana, T., Xu, M., Wu, R.S., Hu, V.W., 2011. Sex hormones in autism: androgens and estrogens differentially and reciprocally regulate RORA, a novel candidate gene for autism. *PLoS ONE* 6, e17116.
- Shacham, S., 1983. A shortened version of the profile of mood states. *J. Pers. Assess.* 47, 305–306.
- Starcke, K., Polzer, C., Wolf, O.T., Brand, M., 2011. Does stress alter everyday moral decision-making? *Psychoneuroendocrinology* 36, 210–219.
- Thornton, J., Zehr, J.L., Loose, M.D., 2009. Effects of prenatal androgens on rhesus monkeys: a model system to explore the organizational hypothesis in primates. *Horm. Behav.* 55, 633–645.
- Tuiten, A., Van Honk, J., Koppeschaar, H., Bernaards, C., Thijssen, J., Verbaten, R., 2000. Time course of effects of testosterone administration on sexual arousal in women. *Arch. Gen. Psychiatry* 57, 149–153.
- van Honk, J., Montoya, E.R., Bos, P.A., van Vugt, M., Terburg, D., 2012. New evidence on testosterone and cooperation. *Nature* 485, E4–E5.
- van Honk, J., Peper, J.S., Schutter, D.J., 2005. Testosterone reduces unconscious fear but not consciously experienced anxiety: implications for the disorders of fear and anxiety. *Biol. Psychiatry* 58, 218–225.
- van Honk, J., Schutter, D.J., Bos, P.A., Kruijt, A.W., Lentjes, E.G., Baron-Cohen, S., 2011a. Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proc. Natl. Acad. Sci. U.S.A.* 108, 3448–3452.
- van Honk, J., Schutter, D.J.L.G., Hermans, E.J., Putman, P., Tuiten, A., Koppeschaar, H., 2004. Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. *Psychoneuroendocrinology* 29, 937–943.
- van Honk, J., Terburg, D., Bos, P.A., 2011b. Further notes on testosterone as a social hormone. *Trends Cogn. Sci.* 15, 291–292.
- van Honk, J., Tuiten, A., Hermans, E.J., Putman, P., Koppeschaar, H., Thijssen, J., Verbaten, R., van Doornen, L., 2001. A single administration of testosterone induces cardiac accelerative responses to angry faces in healthy young women. *Behav. Neurosci.* 115, 238–242.
- Young, L., Cushman, F., Hauser, M., Saxe, R., 2007. The neural basis of the interaction between theory of mind and moral judgment. *Proc. Natl. Acad. Sci. U.S.A.* 104, 8235–8240.
- Young, L., Koenigs, M., Kruepke, M., Newman, J.P., 2012. Psychopathy increases perceived moral permissibility of accidents. *J. Abnorm. Psychol.* 121, 659–667.
- Youssef, F.F., Dookeeram, K., Basdeo, V., Francis, E., Doman, M., Mamed, D., Maloo, S., Degannes, J., Dobo, L., Ditshotlo, P., Legall, G., 2012. Stress alters personal moral decision making. *Psychoneuroendocrinology* 37, 491–498.
- Zalla, T., Barlassina, L., Buon, M., Leboyer, M., 2011. Moral judgment in adults with autism spectrum disorders. *Cognition* 121, 115–126.
- Zheng, Z., Cohn, M.J., 2011. Developmental basis of sexually dimorphic digit ratios. *Proc. Natl. Acad. Sci. U.S.A.* 108, 16289–16294.