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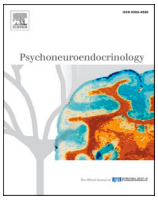

Variations in progesterone and estradiol across the menstrual cycle predict generosity toward socially close others

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ABSTRACT

The human tendency to share goods with others at personal costs declines across the perceived social distance to them, an observation termed *social discounting*. Cumulating evidence suggests that social preferences are influenced by the agent's neurohormonal state. Here we tested whether endogenous fluctuations in steroid hormone compositions across the menstrual cycle were associated with differences in generosity in a social discounting task. Adult healthy, normally-cycling, women made incentivized decisions between high selfish rewards for themselves and lower generous rewards for themselves but also for other individuals at variable social distances from their social environment. We determined participants' current levels of menstrual-cycle-dependent steroid hormones via salivary sampling. Results revealed that the increase in progesterone levels as well as the decrease in estradiol levels, but not changes in testosterone or cortisol, across the menstrual cycle, accounted for increased generosity specifically toward socially close others, but not toward remote strangers.

1. Introduction

Humans are social beings: we consider the wellbeing of others and we accept costs to help friends, family, or even socially remote strangers. Cumulating evidence suggests that the neurohormonal state of individuals can influence their social preferences and attitudes, often in a bi-directional fashion. For example, acute psychosocial stress in men increased generosity toward friends, family, and socially close others (Margittai et al., 2015), as well as unspecified, abstract others (von Dawans et al., 2012), possibly mediated by cortisol action (Margittai et al., 2018). By contrast, stress neurohormonal action has also been shown to induce spiteful punishment, weakened trust and reduced reciprocity (Steinbeis et al., 2015), as well as a diminished willingness to share resources (Schweda et al., 2020, 2019; Starcke et al., 2011; Steinbeis et al., 2015; Vinkers et al., 2013). Similar bi-directional effects on social preferences have been found for other hormones and peptides, such as testosterone (Boksem et al., 2013; Bos et al., 2010; Eisenegger et al., 2011; Kosfeld et al., 2005; Wu et al., 2019; Ou et al., 2021), oxytocin (De Dreu et al., 2010; Ma et al., 2015; Pornpattananangkul et al., 2017; Strang et al., 2017), vasopressin (Brunnlieb et al., 2016), and others.

Steroid hormones vary considerably across the female menstrual cycle. Despite large intersubjective variability, the menstrual cycle in adult healthy women is typically characterized by the menses phase, the follicular phase, and the luteal phase. While during menses both progesterone and estradiol levels are low, estradiol peaks and progesterone remains low in the follicular phase to facilitate ovulation, and a second, but lower peak of estradiol accompanied by a higher peak in progesterone define the luteal phase in preparation for potential pregnancy; if the egg has not been fertilized, both levels of progesterone and estradiol drop and a new menses occurs (Ecochard, 2000; Fehring et al., 2006; Hawkins and Matzuk, 2008; Mihm et al., 2011). Because pregnancy would put women in a relatively vulnerable state, mother and future offspring require social support and resource provision to increase chances for survival, as greater cooperative behavior would ensure reciprocated help and support in return (e.g. for allomaternal care after child birth). Thus, the clear rise in progesterone levels during the luteal phase to prepare for potential pregnancy (Holesh et al., 2021) has been hypothesized, evolutionarily, to boost proactive, unsolicited prosocial behavior in order to foster social alliances, support, and protection: accordingly, enhanced general social cognition has been tentatively linked to progesterone action (Barclay, 2012; Brown et al., 2009; Brown and Brown, 2006, 2015; Burkart et al., 2014, 2009). In other words, social preferences are expected to vary across the menstrual cycle with the variation in steroid hormone levels, specifically progesterone. The predicted progesterone-dependent prosociality might serve as an

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investment to guarantee social support in the long-run (i.e. to "profit back"; Windmann and Hein, 2018, p. 12), possibly mediated, among other things, by increasing reputation benefits (Hamilton, 2017a, 2017b).

However, to date, direct evidence for a menstrual-cycle-effect on social preferences is conflicting and ambivalent since prosocial behavior has been shown to both increase as well as decrease in the various phases of the menstrual cycle: while (Anderl et al., 2015) reported that cooperative behavior of women increased in their estimated follicular phase, (Stenstrom et al., 2018) found that women in their estimated luteal phase were more prone to allocate money to loved ones and anonymous others as a function of perceived social distance. In addition, neither study measured steroid hormones directly and objectively, but inferred the menstrual cycle state indirectly by the participants' self-assessment.

In the present study, we aimed to test the effect of endogenous steroid hormone fluctuations during normally cycling women on social preferences. We adopted and expanded the hypothesis that, in order to foster social alliances to seek social and material support in preparation of potential pregnancy, generosity toward others should increase during the luteal phase, when progesterone levels are high, relative to the follicular phase, when progesterone levels are low. More specifically, we reasoned that, in times of need in preparation for potential pregnancy and child support, it is more adaptive to focus costly befriending efforts on a delimited group of socially close others, such as family, romantic partners and close friends, from whom help can be realistically expected and reciprocated, than indiscriminately befriend everyone alike. We therefore refined our hypothesis and predicted a progesterone-related increase in generosity toward socially close others, but not necessarily toward socially distant strangers.

Social-distance-dependent generosity can be measured with so-called social discounting tasks (Jones and Rachlin, 2006; Sellitto et al., 2021; Strombach et al., 2015). Social discounting refers to the decrease in individuals' generosity toward others as a function of social distance between the individual and the recipient of help, i.e. how much the individual cares about the recipient. Here, we elicited social discounting in a task where female participants made a series of monetary decisions between higher selfish rewards for themselves and lower rewards for themselves paired with an equal reward to other people at different social distances from their social environment. The task was incentivized in such a way that not only the participant herself but also another person would receive money from one selected trial, if a generous choice had been made. We determined participants' steroid levels – progesterone, estradiol, testosterone, cortisol – via repeated saliva samples collection at the time of testing. We used the individual steroid levels as continuous independent variables, regardless of the self-reported menstrual cycle phase, to predict quantitative generosity parameters derived from the social discounting task. Based on the above premises, we expected increased generosity toward socially close others, but not toward socially distant strangers, with increased levels of progesterone, indicative of the luteal phase (Brown et al., 2009).

2. Materials and methods

2.1. Participants

A total of 109 young adult women (mean age = 23 years ± 4 SDs; range: 18–36 years), participated in the study. Sample size was determined using G*Power (Faul et al., 2007). Assuming a small-to-medium effect size $f^2 = 0.15$ (Margittai et al., 2018) for linear multiple regression, the sample size necessary to achieve a power of 0.95, given $\alpha = 0.05$, was $n = 89$. We eventually opted to collect data from 20 participants more, thus exceeding the minimum sample size requirement, to have a contingency for potential exclusions or other problems. Participants, recruited via flyers distributed at the university campus or via online social media platforms, were invited to the study only if meeting the following inclusion criteria, as measured via an online pre-screening questionnaire: regular menstrual cycles (i.e. within the 25–35 day range); no use of hormonal contraceptives for at least 6 months prior to beginning the experiment; a body mass index ≤ 30; smoking ≤ 5 cigarettes per day; drinking the equivalent of ≤ 3 glasses of wine per day. Additionally, participants had to report no physical or mental illnesses, no allergies, no use of medication or drugs, and not being under severe stress.

Participants were fluent in German, had not previously participated in studies from our team, and the majority of them were university students. 77% of participants reported a monthly net income between €0 and €499 and 23% between €500 and €999. 65% of participants reported to be single, 31% mentioned that they were currently in a long-term relationship, three participants said that they were married, and one participant said that she was divorced.

Before attending the experimental session, participants were instructed not to take any medication or alcohol, not to engage in sexual activities 24 h prior to participation, not to smoke or consume caffeinated drinks for 4 h prior to participation, not to eat or drink anything but water, to refrain from physical exercise, and not to chew gum or to brush teeth 2 h before the study. The compliance with these criteria was checked at the time of the experiment and took a few minutes, thus allowing participants to acclimate to the session environment and reduce initial stress. These criteria met previously published procedures involving salivary hormones collection (Margittai et al., 2018). If participants did not comply with one or more of such criteria, a new appointment was scheduled. The study was approved by the ethics committee of the Medical Faculty of the University Hospital Düsseldorf and conformed to the regulations of the Declaration of Helsinki. All participants gave written informed consent and received financial compensation for participation, ranging from €7.5 to €15.5, depending on their decisions in the task (see below).

2.2. Social discounting task

In this task (adapted from Sellitto et al., 2021; Strombach et al., 2015), participants were, first, asked to imagine people from their social environment, and rank-order them according to how close or how distant they felt to them, ranging from social distance 1 (the person socially closest to them) to 100 (a random stranger), where a person at rank 50 was described as a person that the subject had seen several times without knowing the name. Participants were then asked to select real persons located at social distances of 1, 5, 10, and 20, and to just imagine persons at social distance 50, and 100 (with no need of specifying the name and their social relationship), and they were encouraged to avoid thinking of people that they felt negatively toward and people they shared a bank account or household with. Social distance information was subsequently represented by a yellow icon on a ruler scale. The left-most icon, in purple, always represented the participant themselves at social distance zero (Fig. 1).

In the social discounting task, participants made repeated choices between a selfish option and a generous option involving one of the persons previously assigned to one of the social distance levels. The selfish option yielded a monetary reward to the participant between €75 and €155, and a zero-gain to the other person. The generous option always yielded a €75 gain to the participant and an equal €75 gain to the other person. Across trials, we manipulated the own-reward magnitude, ranging from €75 to €155 in steps of €10, and the social distance level of the other person, with social distance levels 1, 5, 10, 20, 50 and 100. Thus, the task consisted of 54 trials (nine own-reward magnitude levels x six social distance levels) that were presented in a pseudorandom order. In each trial, information about the social distance of the other person was always displayed on the ruler scale, and participants had unlimited time to make their decision. After the task, to check compliance with the instructions, participants were asked to report in more detail what type of relationship they had with each of the individuals assigned to the social distances 1, 5, 10, and 20. As SD 1, the 24% of participants

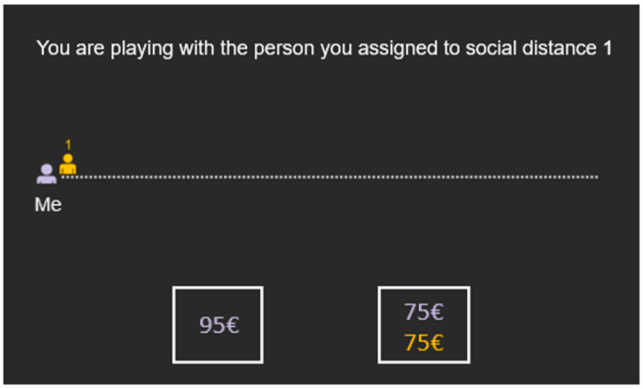

Fig. 1. Social discounting task. In this trial example, the participant (represented by the left-most purple icon) chooses between a selfish alternative of €95 and a generous alternative yielding an equal gain of €75 for the self and for the other person. The other person is represented by a yellow icon indicating her social distance (1 in this example).

indicated a friend, the 24% a sibling, the 23% a parent, the 23% their partner, 3 participants indicated someone they were in an open relationship with, 2 their fiancé(e), 1 a grandparent, 1 an uncle/aunt. As SD 5, the 46% of participants indicated a friend, the 17% a sibling, the 15% their partner, the 10% a parent, 4 participants indicated a grandparent, 3 an uncle/aunt, 2 a cousin, 1 a colleague, 1 a cohabitant, 1 someone she was in an open relationship with, 1 a business partner, 1 an 'other' (i.e. not included in the given options). As SD 10, the 43% of participants indicated a friend, the 11% a colleague, the 11% an "other", 10 participants indicated their partner, 8 a sibling, 7 a parent, 5 a cousin, 4 an uncle/aunt, 2 a grandparent, 2 an acquaintance, 1 their boss/superior. As SD 20, the 31% of participants indicated a friend, the 21% an acquaintance, the 12% someone they were in an open relationship with, the 11% their partner, the 10% a colleague, the 10% an "other", 7 participants indicated a sibling, 5 their boss/superior, 3 a parent, 3 a cousin, 1 a grandparent, 1 an uncle/aunt.

2.2.1. Incentivization procedure

The experiment was fully incentive compatible and participants were informed that one trial would be randomly selected for payment by means of a lottery and that the 10% of the monetary amount in the chosen trial would be paid out to self and other according to their decision in this trial. If the chosen trial involved a generous choice for someone at social distance 1, 5, 10, or 20, the €7.50 were sent to the respective person via cheque, whereas, if the trial involved someone at social distance 50 or 100, the €7.50 were given to a random person on university campus.

2.2.2. Data analysis

Following the procedure described in Strombach et al. (2015), we first determined, for each social distance level, the point at which a participant was indifferent between the selfish and the generous options via logistic regression. This indifference point describes the own-reward magnitude at which the probabilities of choosing the generous or selfish option are equal. We then computed the amount foregone as the own-reward magnitude at indifference point minus the €75 the participant would certainly get if she chose the generous option. The amount foregone was interpreted as a social premium the participant was willing to pay to bestow a financial benefit the other person. For example, if a participant was indifferent between €105 for herself (selfish option), and €75 for her and €75 for a person on social distance 10, she would be willing to forego €105 − €75 = €30 to grant €75 to the other person. The social premium can be construed as a proxy of the vicarious value the participant attaches to the other person receiving €75; in the above example, the vicarious value of the person on social distance 10 receiving €75 was, thus, equivalent to the social premium of €30.

We then fit, via non-linear least square fitting, the standard hyperbolic model (Jones and Rachlin, 2006)

$$v = \frac{V}{1 + k * SD}$$

to the individual social-distance-dependent indifference points, where parameter v refers to the social premium a subject is willing to pay so that another person on social distance SD would receive €75; thus, v is equivalent to the vicarious value that a participant places on €75 to the other person. V determines the height of the social discount function and it is commonly interpreted as the level of generosity toward socially close others. *k* describes the degree of discounting, which indicates the steepness of the decline in generosity across social distance. *k* does not only represent the vertical amplitude of the social discount curve, but it also reflects the asymmetry in the hyperbolic function's curvature, independent of its end-point. Therefore, although a change in V may be also indicative of a general upward/downward shift (*k*) of the curve, there are other reasons for a possible dissociation of V and *k* (e.g. difference in the steepness or asymmetry of the curve). Henceforth, the two parameters are treated and interpreted separately in the analyzes (for various examples see Margittai et al., 2018; Sellitto et al., 2021; Soutschek et al., 2016; Strang et al., 2017; Strombach et al., 2014; Vekaria et al., 2017; Wu et al., 2019).

Seven participants were excluded from these analyzes: for five participants, the hyperbolic model did not find a fitting solution; two participants were extreme outliers (+ 2 SDs) with respect to V and *k* parameters. For two participants who made only generous choices (i.e. they did not discount at all), V was set to 80 (i.e. maximum reward amount foregone = maximum selfish amount 155 − generous amount 75) and *k* was set to 0. For four participants who made only selfish choices (i.e. they discounted fully), both V and *k* were set to 0 (see Sellitto et al., 2021). Because of their natural positive skewedness, *k* values were log-transformed before being entered in the analyzes. We added + 1 to all *k* values to allow $k = 0$ values to be log-transformed.

2.3. Questionnaires

To exclude the possibility of spurious trait differences between participants, they completed several tests and self-report questionnaires to obtain trait measures: the Cognitive Reflection Test (CRT; Frederick, 2005), a measure of one's ability to override intuitive but incorrect responses to relatively simple computational problems by means of deliberate reasoning, which has been found to be affected by cortisol levels (Margittai et al., 2016), and the German version of the Social Desirability Scale (SDS-17; Stöber, 2001), a measure of the tendency to describe oneself with socially desirable attributes, which might affect responses at the social discounting task.

2.4. Procedure

To obtain a subjective, self-reported assessment of the current phase in the menstrual cycle in addition to the hormonal estimates (see below), participants were asked in the online pre-screening questionnaire to report the onset date of their last menses, the expected onset date of their next menses, and the average duration of their menstrual cycle. By means of forward or backward cycle counting, we calculated at which date ovulation was most likely to occur (or most likely had occurred). Our final sample consisted of participants with uniformly distributed self-reported menstrual cycle phases. Even though participants knew that information concerning their menstrual cycle was required to schedule the appointment for testing, they were unaware of our main study purposes. At the end of the testing session, we asked participants again to provide information about the first date of their last menses and the expected next menstrual onset. This allowed us to capture

unexpected irregularities (i.e. shorter or longer menses) and to adapt the participants' self-reported menstrual cycle phase.

To account for circadian fluctuations in hormone levels, all experimental sessions were run between 11:30 a.m. and 14:30 p.m., and lasted ~ 90 min. Upon arrival at the testing site, participants were asked several questions about their current level of stress, and whether they had followed the instructions concerning physical exercise, sexual and other activities (see above) prior to the experimental session. After reading and signing the consent form, the first saliva sample was collected (see below for salivary sampling). Then, participants completed the social discounting task and another task, i.e. a foraging task (adapted from Seinstra et al., 2018) that is not considered in the present manuscript, administered in counterbalanced order, separated by a second saliva sample collection. Afterwards, a third saliva sample was collected and then participants filled in the CRT, the SDS-17, and two other questionnaires, the Barratt Impulsiveness Scale (Patton et al., 1995) and the Behavioral Inhibition, Behavioral Activation and Affective Responses to Impending Reward and Punishment Scales (Carver and White, 1994) relevant to the foraging task only, all administered in counterbalanced order, and, finally, a short demographic questionnaire. At the end, a fourth saliva sample was collected, after which participants received their monetary compensation. Note that the order of administration of the two tasks did not affect our results (i.e. by including the task order as additional predictor in our main regression model).

Also note that we opted for multiple, redundant saliva samples collection to determine stable baseline measures of the four hormones (e.g. Fanson and Biro, 2019; Schweda et al., 2019). Because hormonal levels are highly time-dependent and dynamically change even over short time-scales, there is large interindividual variability across samples and individuals (e.g. Gamble et al., 2014). Collecting four temporally equidistant saliva samples covering the entire length of the testing session allowed us to have a more reliable baseline (average) measure of the levels of the four hormones while controlling for incidental unaccounted variability across samples. Furthermore, this redundant sampling procedure prevented participants' exclusion if one or more samples could not be analyzed.

2.4.1. Salivary sampling

To assess levels of progesterone, estradiol, testosterone, and cortisol, four saliva samples per participant were collected via passive drool (using SaliCaps from IBL International GmbH, Hamburg, Germany). All samples were frozen at − 20 °C until shipping (carried out by protecting the samples with dry ice) for analysis at Dresden LabService GmbH at the Technical University of Dresden (see also Schweda et al., 2019). The samples were analyzed using liquid chromatography coupled with tandem mass spectrometry (LC-MS/MS). The levels of each of the four steroid hormones were estimated from each saliva sample, thus resulting in four redundant measurements for each hormone; hormone levels were then averaged across samples for each participant, resulting in one value per hormone per participant. If hormone values were missing, e.g. due to too little saliva volume and/or non-detectability, the remaining values were averaged. Cortisol levels were converted from nmol/L to pg/ml following the standard immunoassay table of conversion. All hormonal raw data were log-transformed before statistical analyses.

To get insights into potential differences across the four measurements, we ran a series of analyses of variance (ANOVAs), one for each hormone, with measurement repetition as within-subject factor (Bonferroni corrected $\alpha = 0.0125$). We found that for progesterone, only the first measurement (3.02 ± 1.45 pg/ml) was significantly higher than the second (2.87 ± 1.48 pg/ml) ($p = 0.005$) but not different from the third (2.95 ± 1.56 pg/ml) and the fourth (2.96 ± 1.56 pg/ml), while the second, the third, and the fourth did not significantly differ from each other. For estradiol, no significant difference emerged across measurements (1: 1.34 ± 0.56 pg/ml; 2: 1.46 ± 0.52 pg/ml; 3: 1.40 ± 0.59 pg/ml; 4: 1.40 ± 0.60 pg/ml). For testosterone, the first measurement (2.35 ± 0.50 pg/ml) was significantly different from the second (2.22 ± 0.55 pg/ml), the third (2.23 ± 0.52 pg/ml), and the fourth (2.21 ± 0.51 pg/ml) (all ps ≤ 0.006), while the second, the third, and the fourth were nearly identical to each other. For cortisol, all paired comparisons between measurements were significant (1: 7.31 ± 0.72 pg/ml; 2: 7.08 ± 0.72 pg/ml; 3: 6.90 ± 0.69 pg/ml; 4: 6.80 ± 0.67 pg/ml; all ps ≤ 0.001), except the one between the third and the fourth, a result that is not surprising, considering that participants are typically stressed at the beginning of a testing session, and stress/cortisol levels decrease as the time passes. The differences in progesterone and testosterone are also typical, due to high pulsatility of sex hormones (e.g. Schweda et al., 2019; Veldhuis, 2008). Although we have no proper explanation why this was the case for the first measurement as compared to the following ones, it proves that one single measurement would have not constituted a reliable baseline. Thus, our procedure served well to capture the overall effect of hormone levels on prosocial behavior while controlling for incidental unaccounted variability.

3. Results

3.1. Hormones levels

Hormones raw levels, averaged across the four collected saliva samples per each participant, can be seen in Table 1.

In Fig. 2 participants are ordered by average log-levels of progesterone (low-to-high) to illustrate the relation between the level of progesterone to that of all other hormones. At a visual inspection, neither estradiol, nor testosterone, nor cortisol follow any clear correlative pattern relative to progesterone. Accordingly, correlation analyses revealed that the levels of none of the hormones correlated significantly with progesterone (estradiol: Pearson's $r = 0.11$, $p = 0.27$; testosterone: $r = 0.04$, $p = 0.69$; cortisol: $r = 0.17$, $p = 0.08$; two-tailed), and only a positive significant correlation between testosterone and cortisol emerged ($r = 0.37$, $p < 0.001$, Cohen's $d = 0.80$) (all remaining ps > 0.46).

Additionally, we found that age correlated positively with progesterone ($r = 0.34$, $p < 0.001$, Cohen's $d = 0.72$), but not with any of the other hormones (all ps > 0.35), suggesting that in our sample, although all women were in their pre-menopausal state, progesterone levels increased moderately with age (see Del Río et al., 2018; Farland et al., 2017). We therefore considered age as a potential independent predictor in the analyzes on social discounting parameters.

Afterwards, we ran a manipulation check and tested if there was any correspondence between progesterone levels – the only hormone with a clear low-to-high fluctuation from the follicular to the luteal phase – and the self-reported menstrual cycle phase by our participants, treated as dichotomous grouping variable. Please note that the allocation of participants to the respective cycle phase was purely based on their subjective self-report, not on any objective criterion. We used this classification for the mere purpose of the following exploratory analysis. A point-biserial correlation (self-reported follicular phase coded = 1; self-reported luteal phase coded = 2) showed that higher levels of progesterone corresponded to the self-reported luteal phase and vice versa ($r = 0.58$, $p < 0.001$, Cohen's $d = 1.42$). To further corroborate this finding, a t-test between the two groups revealed that progesterone levels were significantly higher in participants who self-reported to be in

Table 1
Hormones levels.

N = 109	mean ± SD	Range
progesterone	52.29 ± 73.48	2.52–349.00 pg/ml
estradiol	4.66 ± 2.09	0.82–11.13 pg/ml
testosterone	10.80 ± 4.98	2.25–27.95 pg/ml
cortisol	4.16 ± 3.49	0.81–21.70 nmol/L

Note. Hormones values are raw values. N: sample size; SD: standard deviation; pg/ml: picograms per milliliter; nmol/L: nanomoles per litre.

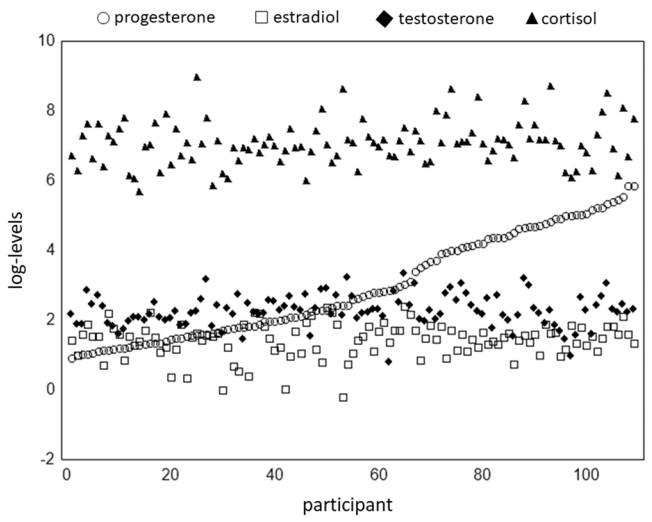

Fig. 2. Hormones log-levels (pg/ml). Participants ordered by mean progesterone log-levels, from low to high (x-axis). The log-levels of cortisol, testosterone and estradiol are shown in relation to the respective progesterone levels.

the luteal phase ($n = 61$, $M = 3.71 \pm 1.37$) than those who claimed to be in the follicular phase ($n = 48$, $M = 1.99 \pm 0.94$) ($t_{107} = -7.39$, $p < 0.001$, Cohen's $d = 1.46$), thus showing that the self-reported menstrual phase matched quite well with the objectively measured levels of progesterone. The menstrual cycle days of testing (ranging from 2 to 33; $M = 18$, $SD = 6.45$) also correlated positively with progesterone levels (Pearson's $r = 0.61$, $p < 0.001$, Cohen's $d = 1.54$), additionally ensuring that our recruitment protocol was successful in distributing progesterone levels (low-to-high) evenly across our sample.

3.2. Hormones and hyperbolic model

We ran multiple regression analyses with the V and the log-*k* parameters as dependent variables and the following independent predictors: the four hormones (progesterone, estradiol, testosterone, cortisol), their interaction terms (progesterone × estradiol, progesterone × testosterone, progesterone × cortisol, estradiol × testosterone, estradiol × cortisol, and testosterone × cortisol), as well as age to account for age-differences in progesterone. Hormonal levels were mean-centered before calculating interactions. Results showed that both progesterone levels (standardized ß coefficient = 0.29, $t = 2.56$, $p = 0.012$) and estradiol levels (ß = − 0.26, $t = -2.30$, $p = 0.024$) were significant predictors of the V parameter. No other significant result emerged, neither in this analysis nor in the one including the log-*k* as the dependent variable (see *Model 1*, Table 2 and Table 3 for full results). This suggests that, at increased levels of progesterone and decreased levels of estradiol, participants tended to be more generous toward socially close others, but there was no evidence to assume a hormone effect on generosity toward remote strangers (Fig. 3). Note that these findings could be replicated when including in the analysis only the first 89 participants collected (with replacement when exclusions occurred), i.e. the sample size determined by the power analysis, and when excluding age as predictor, supporting the robustness of our results.

For illustration of the social discount functions of participants with high- and low-levels of progesterone (median split of participants), refer to Fig. 4.

Collinearity diagnostics revealed an average variance inflation factor (VIF) = 1.32, SD = 0.17, suggesting that the variance in the social discounting parameters V and log-*k* explained by each predictor alone was not highly correlated with the variance explained by all others.

We also repeated the above regressions by additionally entering as independent predictors the marital status, which has been linked to different levels of steroid hormones (see Barrett et al., 2015), and monetary income, which in general can affect social discounting behavior. Results remained unchanged (see *Model 2*, Table 2 and Table 3 for full results).

The result of the effect of progesterone on V was expected, but, at the same time, the result on estradiol was not surprising either, considering that the luteal phase is typically characterized by a peak in estradiol much smaller than the one that is usually observed in the follicular phase.

3.3. Hormones and self-report measures

Neither CRT ($M = 0.98 \pm 1.10$ SDs; range: 0–3) nor SDS-17 ($M = 9.53 \pm 2.77$ SDs; range: 2–15) scores were predicted by any of the measured hormones (all $-0.14 <$ ßs < 0.15, all ps > 0.14). Additionally, neither the V nor the log-*k* parameters were predicted by any of these two trait scores (all $-0.12 <$ ßs < 0.04, all ps > 0.23). Thus, it is unlikely that our participants' prosocial behavior was mediated by putative changes in cognitive reflection ability and social desirability as a function of changes in endogenous steroid hormones level (see also Lazzaro et al., 2016).

Table 2
Regression analyses with the hyperbolic parameter V as dependent variable.

	Hyperbolic parameter V									
	Model 1					*Model 2*				
Predictors	B	CI	ß	t	p	B	CI	ß	t	p
Age	-1.25	[− 2.78, 0.29]	-0.17	-1.62	0.110	-1.63	[− 3.33, 0.07]	-0.22	-1.91	0.059
Progesterone	5.56	[1.24, 9.88]	0.29	2.56	0.012	5.01	[0.62, 9.41]	0.26	2.27	0.026
Estradiol	-14.64	[− 27.27, − 2.01]	-0.26	-2.30	0.024	-17.17	[− 30.28, − 4.07]	-0.30	-2.60	0.011
Testosterone	3.20	[− 10.44, 16.84]	0.05	0.47	0.642	3.31	[− 10.62, 17.24]	0.05	0.47	0.638
Cortisol	2.34	[− 7.61, 12.29]	0.05	0.47	0.641	1.80	[− 8.17, 11.77]	0.04	0.36	0.721
Prog × Estr	-7.07	[− 17.94, 3.80]	-0.15	-1.29	0.200	-8.47	[− 19.50, 2.57]	-0.18	-1.53	0.131
Prog × Test	4.08	[− 6.87, 15.03]	0.09	0.74	0.461	2.59	[− 8.56, 13.73]	0.06	0.46	0.645
Prog × Cort	2.80	[− 3.84, 9.45]	0.10	0.84	0.404	3.45	[− 3.33, 10.23]	0.12	1.01	0.314
Estr × Test	13.29	[− 12.18, 38.77]	0.11	1.04	0.303	14.10	[− 11.44, 39.64]	0.11	1.10	0.276
Estr × Cort	1.00	[− 16.58, 18.57]	0.01	0.11	0.910	0.72	[− 16.87, 18.30]	0.01	0.08	0.936
Test × Cort	-1.78	[− 24.56, 21.00]	-0.02	-0.16	0.877	-1.24	[− 24.15, 21.67]	-0.01	-1.11	0.915
Marital status						7.62	[− 2.86, 18.10]	0.16	1.45	0.152
Income						1.18	[− 13.34, 15.71]	0.02	0.16	0.872

Note. V is the hyperbolic parameter included as dependent variable. B is the unstandardized regression coefficient. CI is the 95% confidence interval for B. ß is the standardized regression coefficient. Prog = progesterone; Estr = estradiol; Test = testosterone; Cort = cortisol; x is the interaction term. *Model 1*: $R^2 = 0.16$, $F_{11,101} = 1.57$, $p = 0.12$. *Model 2*: $R^2 = 0.18$, $F_{13,101} = 1.49$, $p = 0.14$.

Table 3
Regression analyses with the hyperbolic parameter log-*k* as dependent variable.

	Hyperbolic parameter log-*k*									
	Model 1					*Model 2*				
Predictors	B	CI	ß	t	p	B	CI	ß	t	p
Age	0.01	[− 0.01, 0.01]	0.02	0.18	0.855	0.01	[− 0.01, 0.01]	0.02	0.16	0.877
Progesterone	0.01	[− 0.02, 0.02]	0.02	0.17	0.865	0.01	[− 0.02, 0.02]	0.02	0.13	0.898
Estradiol	-0.05	[− 0.12, 0.01]	-0.19	-1.67	0.099	-0.06	[− 0.12, 0.01]	-0.20	-1.68	0.097
Testosterone	0.03	[− 0.04, 0.10]	0.09	0.85	0.398	0.03	[− 0.04, 0.10]	0.10	0.90	0.371
Cortisol	0.01	[− 0.05, 0.05]	0.01	0.10	0.924	0.01	[− 0.05, 0.05]	0.01	0.08	0.940
Prog × Estr	0.01	[− 0.05, 0.06]	0.02	0.16	0.871	0.01	[− 0.05, 0.06]	0.01	0.10	0.922
Prog × Test	0.03	[− 0.03, 0.08]	0.13	1.03	0.305	0.03	[− 0.03, 0.08]	0.12	0.95	0.346
Prog × Cort	-0.01	[− 0.04, 0.02]	-0.07	-0.57	0.568	-0.01	[− 0.04, 0.03]	-0.07	-0.56	0.576
Estr × Test	-0.06	[− 0.19, 0.07]	-0.09	-0.90	0.373	-0.06	[− 0.19, 0.07]	-0.09	-0.89	0.376
Estr × Cort	-0.05	[− 0.14, 0.04]	-0.12	-1.10	0.274	-0.05	[− 0.14, 0.04]	-0.12	-1.09	0.279
Test × Cort	0.10	[− 0.01, 0.22]	0.20	1.79	0.076	0.11	[− 0.01, 0.22]	0.20	1.82	0.073
Marital status						0.01	[− 0.04, 0.06]	0.04	0.38	0.708
Income						-0.01	[− 0.09, 0.06]	-0.04	-0.31	0.757

Note. log-*k* is the hyperbolic parameter included as dependent variable. B is the unstandardized regression coefficient. CI is the 95% confidence interval for B. ß is the standardized regression coefficient. Prog = progesterone; Estr = estradiol; Test = testosterone; Cort = cortisol; x is the interaction term. *Model 1*: $R^2 = 0.10$, $F_{11,101} = 0.91$, $p = 0.53$. *Model 2*: $R^2 = 0.10$, $F_{13,101} = 0.78$, $p = 0.68$.

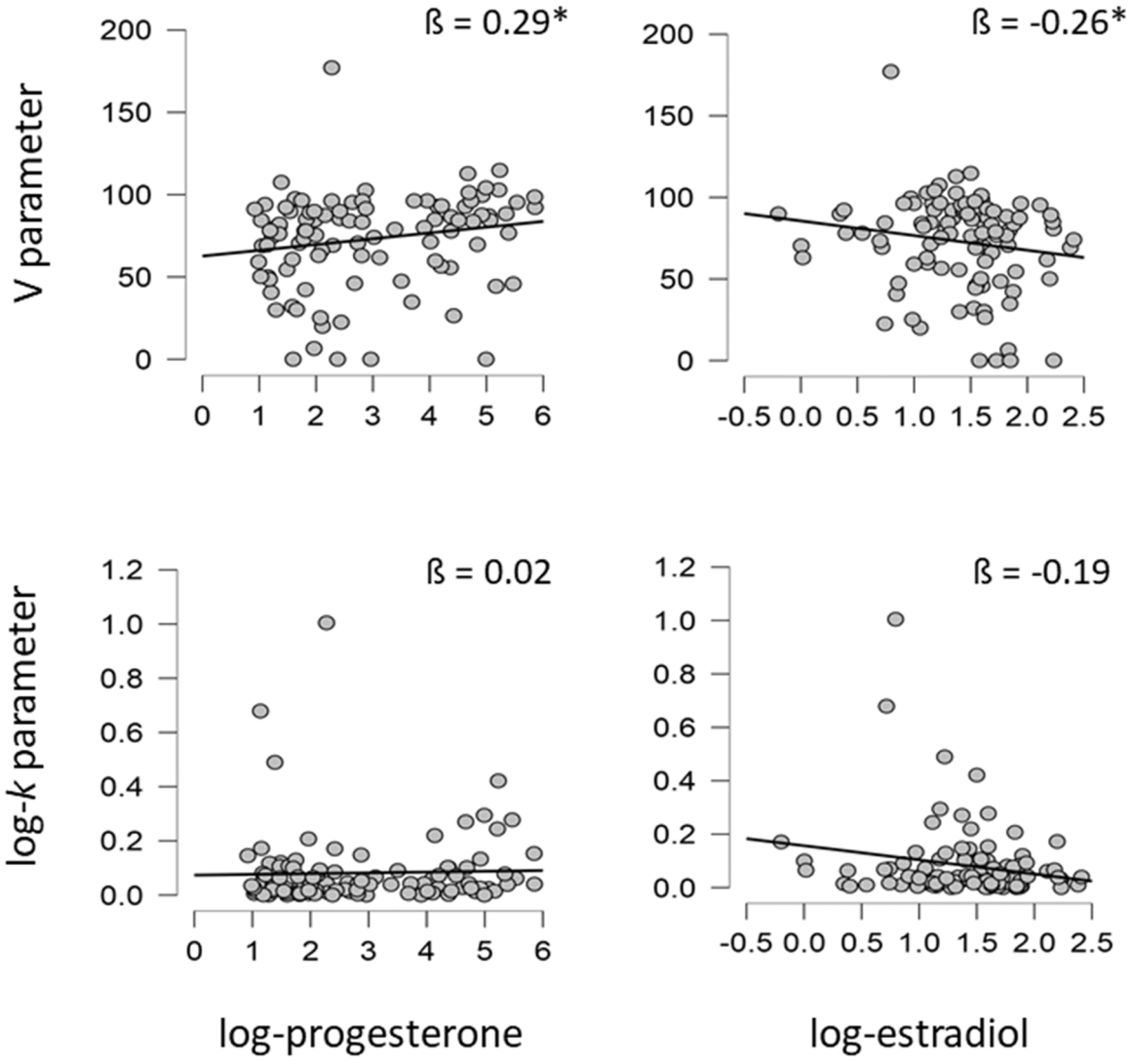

Fig. 3. Progesterone, estradiol, and the hyperbolic discount parameters V and log-*k*. The hyperbolic discount parameter V, an indicator of the level of generosity toward socially close others, was positively predicted by log-progesterone levels (top, left panel) and negatively predicted by log-estradiol (top, right panel). The hyperbolic discount parameter log-*k*, an indicator of the degree of discounting across social distances, was neither predicted by log-progesterone (bottom, left panel) nor by log-estradiol (bottom, right panel). ß = standardized regression coefficient; *$p < 0.05$.

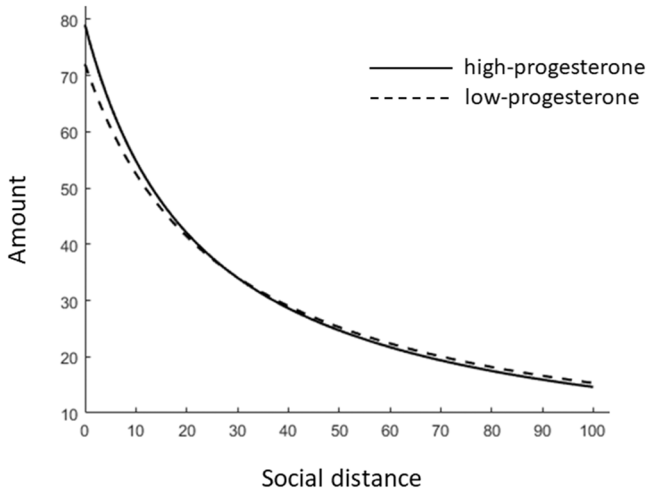

Fig. 4. Hyperbolic social discount functions. The figure illustrates the mean of the individual best-fitting hyperbolic functions, separately for high-progesterone (solid line) and low-progesterone (dashed line) participants. The y-axis refers to the amount foregone (i.e. the social distance-dependent reward amount that participants were willing to pay to increase the wealth of another person at a variable social distance by €75; see main text). The height of the social discounting curve is represented by the V parameter, an indicator of generosity at close social distances, the steepness of the social discounting curve is determined by the *k* parameter (see main text).

4. Discussion

In the present study, we tested the effect of endogenous steroid hormone fluctuations across the female menstrual cycle on prosocial preferences. Specifically, in an incentivized social discounting task, adult healthy female participants made a series of monetary choices between a selfish option, yielding a high reward for themselves, and a costly generous option, yielding a lower own-reward and an equal reward to other individuals at variable social distances from their social environment. In line with ample previous evidence (e.g. Margittai et al., 2018; Sellitto et al., 2021; Strombach et al., 2015), we found that the tendency to make costly generous choices declined across social distance between the participant and the other person. More importantly, we found that participants' generosity toward close others, but not remote strangers, grew with increasing levels of endogenous progesterone as well as decreased levels of endogenous estradiol. Neither testosterone, nor cortisol levels, nor their interactions with progesterone or estradiol, had any role on this effect.

High progesterone levels as well as low estradiol levels (i.e. lower than in the late follicular phase) coincide with the woman's body preparation for potential pregnancy (i.e. the luteal phase). Evolutionary accounts of female sex hormone effects on social preferences (e.g. Barclay, 2012; Brown et al., 2009; Brown and Brown, 2006, 2015; Burkart et al., 2014, 2009) predict that women should have increased tendencies to tend-and-befriend during this phase: since pregnancy would put them in a potentially vulnerable state, women should invest more into their social network to receive help, support, and protection in return. However, because help and protection can only be realistically expected from a delimited group of socially close others, such as partners, close friends and family, but not from remote strangers, it would be maladaptive to indiscriminately tend-and-befriend everyone alike; namely, costly efforts (i.e. increased generosity) during the luteal phase should be focused on a restricted group of socially close, but not remote others. Our findings are in line with these predictions. A supportive social network has fitness advantages after giving birth too, given the exceedingly high evolutionary costs of rearing and child care (e.g. Brown and Brown, 2006; Burkart et al., 2014, 2007; Sear and Mace, 2008). Interestingly, two recent studies offered initial insights into enhanced other-oriented motivations (e.g. monetary and umbilical cord donations, quitting smoking, trust) both during and after pregnancy, and, thus, into potential effects of pregnancy-related hormones on prosocial behavior (Bradstreet et al., 2012; Panasiti et al., 2020).

Note that in normal cycling women there are two peaks of estradiol at different phases in the menstrual cycle but only one peak of progesterone in the luteal phase, making progesterone the main sex hormone that clearly defines this phase relative to the follicular or other phases, as further evidenced by our participants' self-report measures. Therefore, our a priori hypotheses were about progesterone, and the estradiol effects were only discovered by chance. However, we do not consider our estradiol finding in contradiction to our theoretical grounding and, in acknowledging that the effect sizes of our results are comparably high for progesterone and estradiol, we offer post-hoc explanations for the role of estradiol in generosity toward socially close others, although only speculatively.

Cumulating evidence suggests that the neurohormonal state of individuals can influence social preferences (Margittai et al., 2015, 2018; Soutschek et al., 2017). Consistent with our finding that generosity increased with low-to-high fluctuation in progesterone (from the follicular to the luteal phase), previous evidence showed that progesterone is linked to increased maternal motivation and, more generally, to affiliation motives, i.e. the need for building positive bonding relations with others (e.g. Schultheiss et al., 2004), as well as increased sharing behavior (Strojny et al., 2021), social closeness (Brown et al., 2009), and social feedback sensitivity (Wang et al., 2021). Moreover, both endogenous and exogenous rise in progesterone have been found in relation to enhanced general social cognition, increased altruistic motivation, and suppression of self-interests, further supporting our conclusions (e.g. Brown et al., 2009; Brown and Brown, 2015; Duffy et al., 2017; Jones et al., 2005; Maner et al., 2010; Maner and Miller, 2014; Schultheiss et al., 2004; Strojny et al., 2021). In addition to this evidence, our social discounting task allowed us to detect differences between increased prosocial behavior toward close individuals and (relatively) stable prosocial attitude toward more remote individuals. At this point, we would like to note that, although our paradigm as well as the hyperbolic model and the parameters' interpretation have been widely used and are a convention in previous literature (e.g., Jones and Rachlin, 2006, 2009; Margittai et al., 2015, 2018; Sellitto et al., 2021; Soutschek et al., 2016; Strang et al., 2017; Strombach et al., 2014, 2015; Vekaria et al., 2017; Wu et al., 2019; Ou et al., 2021), one may argue that only the *k* parameter truly represents social discounting. *k* does indeed reflect the slope and steepness of the discount function at all social distances, i.e. including remote ones. However, importantly, the shape of the social discount function is as much determined by the *k* parameter as by the V parameter, which represents the height of the discount function. In our study, we found a correlation between progesterone and estradiol levels with the V, but not the *k* parameter. This might suggest that progesterone and estradiol levels correlated with generosity toward socially close others, as discussed above. Alternatively, though, this pattern of results might also be interpreted as evidence for a general upward slope of the social discount functions with progesterone and estradiol, suggesting a general, social-distance-independent increase in generosity toward everyone. However, the latter interpretation would imply that the steepness of the social discount functions would be identical across hormone levels – a conclusion that we cannot necessarily support considering that a null correlation between *k* and hormones cannot readily be interpreted as evidence for sameness. We are therefore somewhat hesitant to conclude a general upward shift of the social discount function with progesterone or estradiol, also in light of the absence of evidence for such a shift after visual inspection of the social discount functions in Fig. 4. We believe, instead, that the most parsimonious conclusion is that hormonal effects on social discounting are limited to the height of the discount function, that is, to generosity toward socially close others.

Concerning estradiol, to our knowledge, it has been so far mainly studied in association to frontal dopaminergic-dependent behaviors, e.g. reward responsiveness and future oriented behavior (Diekhof, 2015; Macoveanu et al., 2016; Reimers et al., 2014). Specifically, increased estradiol levels at mid-cycle, when fertility peaks, has been linked to decreased so-called "present-bias", i.e. the propensity to prefer immediate gratification (Smith et al., 2014), as well as to increased competition and reduced resource sharing during a dictator game (Necka et al., 2016), but also to mixed effects on trust (Zethraeus et al., 2009) and perceived fairness (Coenjaerts et al., 2021). While it is tempting to speculate that this evidence may lay the ground for our (exploratory) finding of a negative relation between estradiol levels and generosity during prosocial choice – i.e. reduced susceptibility toward self-gain –, we are cautious with our conclusions as most of the studies cited above either tested women during the periovulatory phase versus the menses or they manipulated hormonal levels artificially in postmenopausal participants.

Note that, as mentioned above, other-regarding behavior as well as the need for social support increases also post-partum, when progesterone and estradiol levels decrease, thus posing a challenge to our prediction. However, we argue that progesterone is clearly *not* the only determinant of prosociality. There are other neurohormonal factors that might more strongly influence self-interest suppression and maternal motivation post-partum than progesterone, e.g. prolactin, oxytocin, and their interaction with progesterone and estradiol, as well as several other neuropeptides (e.g. MacKinnon et al., 2018; Gómez-Carvajal et al., 2020; Russell et al., 2001). In addition, there are non-hormonal determinants, e.g. personality or social/cultural norm compliance, that might also shape other-regarding motivations post-partum beyond progesterone. However, we hesitate to make claims about hormones, non-hormonal factors, and social preferences during pregnancy or post-partum since we did not test pregnant women, or women who just gave birth; our hypotheses concern the preparation for potential pregnancy during normal ovulatory cycling.

One of the limitations of the present study is that participants were tested only once (either in the estimated luteal or in the estimated follicular phase). Considering that progesterone levels not only vary across the menstrual cycle, but also considerably between individuals (e.g. Marcinkowska and Holzleitner, 2020), our study cannot capture such differences. However, progesterone levels correlated highly with our participants' subjective self-report of menstrual cycle phase, providing tentative evidence that our hormonal measures were indeed valid markers of the menstrual cycle phase, and did not solely reflect potential variability between individuals. In addition, a within-subject, repeated-measures decision-making design that would capture within-subject hormone level variations would come with its own shortcomings since it cannot guarantee the independence of multiple exposure (e.g. Charness et al., 2012). In other words, participants tend to copy their own choice behavior when tested repeatedly, rendering their choices inflexible and insensitive to exogenous or endogenous moderating factors. Future investigation is needed to clarify whether participants with higher mean progesterone levels at the time of testing are generally more prosocial toward close others than participants with lower mean progesterone levels, independent of their current menstrual phase.

To date, the relation between gender/sex and prosocial behavior is relatively unclear, with mixed findings reported in the literature. While some studies showed that women are more prosocial than men in experimental games (e.g. Espinosa and Kovárík, 2015; Rand et al., 2016; Soutschek et al., 2017), others showed either opposite results (e.g. Eagly and Steffen, 1986) or no gender/sex differences in social decision tasks (e.g. Dorrough et al., 2021; Passarelli and Buchanan, 2020). It stands out, however, that many studies on the effect of hormones, or controlling for hormonal variations, on social preferences are done on male-only samples (with few exceptions, e.g. Anderl et al., 2015; Eisenegger et al., 2010; Schweda et al., 2019; Stenstrom et al., 2018; Strombach et al., 2016). The exclusion of women from such studies is usually justified by the necessity to overcome the variability in steroid hormone action associated with the menstrual cycle, and the variable (putative) effects of hormones on behavior – the very focus of the present study. However, in addition to the fact that studying female sex hormone effects on behavior is scientifically relevant, the practice of excluding women is methodologically problematic and unethical, as half of the population is excluded from data sampling. In addition, because societal policies are often informed by science, unawareness of female steroid hormone effects on social preferences, and putative sex-specificity of hormonal influences on behavior (Espinosa and Kovárík, 2015; Rand et al., 2016; Soutschek et al., 2017; Taylor et al., 2000), has potentially serious consequences on women's health and psychological wellbeing. Here, in line with the current debate on the inclusion of women in research and clinical trials (Clayton and Collins, 2014), we overcome such limitation by providing evidence that women's prosocial preferences can be influenced by the level of endogenous progesterone, as well as estradiol – i.e. menstrual cycle-related hormones –, thus opening for future investigation on the sex-specific effect of neurohormonal action on behavior. Future studies on the topic should also consider the inclusion of men as a control group to rendered this line of research even more comprehensive.

5. Conclusions

In summary, we have found that generosity toward relevant close others, but not toward remote strangers, increased as a function of increased progesterone as well as decreased estradiol levels across the menstrual cycle.

Authors statement

The authors declare no conflict of interest.

CRediT authorship contribution statement

M. S. and **T. K.** developed the study concept and contributed to the study design. **M. S.** performed data collection and data analysis. **M. S.** and **T. K.** interpreted the results and wrote the manuscript. All authors approved the final version of the manuscript for submission.

Data availability

Behavioral datasets have been supplied in Figshare (https://figshare.com/) under the https://doi.org/10.6084/m9.figshare.14269718.v1.

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