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Variability in ratings of trustworthiness across the menstrual cycle

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ABSTRACT

This study investigated how trusting behavior varies in naturally cycling women, as a function of sex and attractiveness of players in a trust game, at three distinct phases of the menstrual cycle. Women acted more cautiously in an investment game at the preovulatory phase, compared to the menstrual and the mid-luteal phase. Reduced willingness to trust in strangers was particularly expressed toward male players at this time. The increase of estradiol levels from menses to the preovulatory phase was negatively correlated with trust in attractive male other players, whereas the increase of progesterone levels from menses to the mid-luteal phase was positively associated with trust in unattractive female other players. No particular contribution of a single hormone level could be identified for the generally reduced willingness to trust in strangers in the preovulatory phase. Thus, the results emphasize the impact of the menstrual cycle on interpersonal trust, although the exact mode of hormonal action needs to be further investigated.

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1. Introduction

The ability to correctly judge other people's trustworthiness is of high ecological importance to individuals living in social groups. Therefore, it is thought to have been shaped by evolutionary pressures, and to have become embedded in the human congenital repertoire (Haselton and Ketelaar, 2005; De Dreu et al., 2011). Trusting behavior develops during ontogenesis through individual learning, and is triggered by external, social and situational contexts. A growing body of evidence demonstrates that interpersonal trust is also influenced by internal, biological factors, such as fluctuations in hormone levels (Frye, 2009). Especially, sex hormone receptors are widespread in the central nervous system (Stumpf and Sar, 1976), and these steroids have powerful neuromodulatory properties (Sherwin, 2003) and modulating effects on perceptive, motivational, and cognitive processes, including interpersonal trust (Frye, 2009). The hormonal modulation of interpersonal trust has been investigated extensively in social neuroscience, often by applying game theoretical approaches to empirically measure trust-related cognitive processes (e.g., Chang

et al., 2010; Hillebrandt et al., 2011; Unoka et al., 2009) and to examine hormonal effects on trusting behavior (Kosfeld et al., 2005; Baumgartner et al., 2008; Mikolajczak et al., 2010; Zak et al., 2005). One general conclusion from these studies is that the hormonal modulation of trust-related social cognitive processes seems to act on the regulation of agonistic and antagonistic, or activating and inhibiting processes. For instance, an inhibiting, or trust decreasing effect has been documented for the gonadal hormone testosterone: Bos et al. (2010) found significantly decreased judgments of trustworthiness in women after the application of 0.5 mg testosterone, compared to a placebo. This androgen also fluctuates in naturally cycling women and peaks in the late follicular phase (Sinha-Hikim et al., 1998). Therefore, Johnson and Breedlove (2010) postulated an evolutionary advantage for a testosterone modulated preovulatory decline in ratings of trustworthiness for women at risk of being overly trustful when evaluating strangers. However, this assumption has not been tested in naturally cycling women across the menstrual cycle. In general, very little is known about how the considerable hormone fluctuations, as they naturally occur in the course of the ovulatory cycle, affect interpersonal trust.

It is known from administration studies that hormone effects on human behavior depend on social and individual context conditions (Bartz et al., 2011; Bos et al., 2012a). For instance, the trust increasing effect of the neuropeptide oxytocin described in Kosfeld et al. (2005) was absent when research participants

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were interacting with a computational random generator, instead of with other people. Also, the trust decreasing effect of testosterone described in Bos et al. (2010) was not global, but was driven by the subgroup of participants with high baseline trust, that is to say, individuals with an increased likelihood of being betrayed. It can be assumed that steroid sex hormones have evolved neuromodulatory properties because they allow for flexible adaptations to social contexts. Such adaptations can, for example, be manifest in processing social (and, thus, mainly facial) cues (Jones et al., 2008). This assumption is backed-up by accumulating evidence from the social neurosciences: The gonadal hormone progesterone can bind to specific receptors in the brain, which accumulate in the amygdala. The amygdala is known to play a role in person perception and, thus, the ability to judge the trustworthiness of others (Adolphs, 2003). High levels of progesterone have also been found to be related to an increased sensitivity to facial cues carrying sources of threat or contagion (Conway et al., 2007), and accordingly, with a biased behavioral tendency toward avoidance as opposed to approach (Derntl et al., 2008). Such effects have been discussed as reflecting an adaptation to increased costs of social and physical threat or danger in pregnant women, in whom progesterone concentrations steadily increase.

Taken together, there is a gap in the literature concerning effects of endogenous sex hormones on interpersonal trust. The menstrual cycle builds an excellent model to study effects of naturally occurring hormone fluctuations on cognitive functioning. However, it also demands exact experimental planning and control of possible confounding factors. The present work is set out to close this gap, by investigating effects of alterations in the cycle-regulating hormone concentrations progesterone, estradiol, testosterone, luteinizing hormone (LH) and follicle stimulating hormone (FSH) on interpersonal trust. To this end, 33 naturally cycling women were tested at three distinct phases of the menstrual cycle in counterbalanced order. Testing of naturally cycling women was paralleled with testing of two same-aged control groups with stable hormone concentrations: A group of 33 women using a hormonal contraceptive (and therefore with suppressed endogenous hormone levels), and a group of 30 young men. We decided to use a combined game theoretical and social cue rating approach in order to assess the behavioral readiness to trust as a function of the type of interaction partner. As previous work has shown, hormone effects on trust do not seem to be global, but to be sensitive to, and to be calibrated by environmental factors (Delton et al., 2010; Bos et al., 2012b). We hypothesized that the readiness to trust in other individuals might be increased in the period of highest likelihood of conception preceding ovulation at mid-cycle, and that this readiness to trust might be decreased in the pregnancy-resembling mid-luteal period of the menstrual cycle, in which progesterone and estradiol concentrations peak in concert. We further assumed that these cycle-dependent alterations in trusting behavior might not be global, but might be expressed differently toward male and female, as well as toward rather attractive and rather unattractive individuals during the distinct periods. From an evolutionary perspective, it can be assumed that facilitated trust toward attractive males during the fertile preovulatory phase, as well as facilitated trust toward other females in the pregnancy-resembling luteal phase, would be adaptive (Gangestad and Thronhill, 2008; McKibbin and Shackelford, 2011). If fluctuations in gonadal sex hormones have activating effects on interpersonal trust, we expected this measure to be generally lower and less variable in women with suppressed endogenous hormone levels. If hormone fluctuations cause systematic changes in trusting variables in women, we expected no systematic changes of these variables in men across three testing sessions.

2. Methods

2.1. Participants and design

Participants were recruited via advertisements on campus of Ruhr-University Bochum, Germany, and were invited to attend three testing sessions. A monetary exchange experiment was conducted with three groups, using an intra-subject design. The first group consisted of 33 naturally cycling women who reported that they had not experienced any kind of hormonal intervention for at least 6 months prior to testing and had regular cycles ranging from 26 to 30 days. The second group consisted of 33 women who reported using a vaginal ring (Nuva® Ring) as a hormonal contraceptive for at least 6 months prior to testing. Because significant hormonal fluctuations were not expected in this group, these participants served as the control group for the naturally cycling women. Additionally, 30 young men were tested to control for general sex differences in ratings of trustworthiness.

For every naturally cycling woman, three test sessions that depended on when the menstrual cycle began were arranged according to reference values for progesterone and estradiol provided by Stricker et al. (2006). One test session took place during the menstrual phase (days 2–5), when the concentration of sex hormones is lowest. Another session was arranged between days 11 and 15 of the cycle, during the preovulatory LH-peak and the highest concentrations of estradiol and testosterone, and corrected for individual cycle length. Yet another session was scheduled for the mid-luteal phase (days 19–23) in order to have the women tested at their highest progesterone concentrations and the second surge of estradiol. The cycle phase in which women entered the testing series was counterbalanced, but the three sessions took place within the same or two consecutive cycles. Test sessions were organized in a similar way for the women using hormonal contraceptives, taking the day of applying a new vaginal ring as day 1. They were then scheduled for a test session between ring cycle days 2 and 5, followed by a session between ring cycle day 11–15 and one shortly before or directly after removing the ring between ring cycle days 19 and 23. For the male participants, test sessions were arranged with 8–10 days intervals. Individual test sessions were allocated randomly to the menstrual cycle phase sessions of the naturally cycling women, to control for test order effects. The time of day was held constant (either 9 a.m. or 1 p.m.) across all test sessions for each participant, to control for circadian variability in hormone release.

Anonymity was guaranteed at all times. The study protocol was approved by the ethics committee of the Ruhr-University Bochum, and all participants gave written, informed consent before participation. They were reimbursed for participation with a fixed charge and could earn some extra money, depending on their performance in the trust game.

2.2. Trust game

A modified version of the trust game described in Kosfeld et al. (2005) was used. In contrast to previous studies, natural hormone states were used in the current experiment, instead of administering hormones. Covering the individually distinct cycle phases requires testing participants separately, not with up to 12 persons in a room, as it is typically the case. In the version of the trust game used here, participants always assumed the position of the investor, and a black-and-white photo of a fictive trustee was presented on a computer screen, against a black background. The participants were told that the trustees were students from a South German university who had played the same game and whose responses had been recorded. Since they would receive the original answer of every trustee, the participants had to judge the trustworthiness of the other player by sending 0, 4, 8, or 12 money units (MU) of their initial endowment. Thus, if their judgment was faulty and they entrusted too much to a deceiving player, their overall payoff would decrease.

Pictures of the fictive trustees' faces (provided by an internal database of the Institute for Cognitive Neuroscience at Ruhr-University Bochum, Germany) had previously been judged for attractiveness on a seven-point Likert-scale by 30 female volunteers. Using the MathWorks™ software Matlab® (version 7.8.0) and the Biopsychology Toolbox (Rose et al., 2008), three parallel versions of the trust game were then constructed with five attractive and five unattractive male trustees, and five attractive and five unattractive female trustees, respectively. The games were programmed to present the 20 pictures in random order. The trustees' back transfers were held at a constant level of 40–60% of their payoff, so that all trustees were equally cooperative. If a participant invested, for instance, 8 MU in a given trustee, this amount was tripled and added to the other player's 12 MU initial endowment ((8 × 3) + 12 = 36). In this example, the computer randomly chose an amount between 14.4 and 21.6 MU and sent it back to the investor.

The actual experiment was preceded by six training trials, to reinforce the participant's impression of participating in a quasi-social interaction. This was achieved by presenting six faces from the middle of the attractiveness scale (three males and three females). A random event generator chose two of these six players to betray the participant's trust by not sending any MU back. The experimenter commented this and reinforced the participants to look for signs of trustworthiness before taking a decision. In the experimental game, the participants were alone in the experimental room, in order to control for bystander effects (Earley, 2010). They played 20 trials with one second inter-trial intervals. The total payoff was presented on the screen only after the last trial, and the participants immediately received their

payoff in Euros, rounded to increments of ten cents. Thus, if a participant had earned, for instance, 378 MU, she received 3.80 Euros (approx. USD 4.20). None of the participants expressed disbelief in the cover story, or showed discomfort at being deceived (for an evaluation of the use of deception in psychological research, see Christensen, 1988). However, in case that a participant would repetitively press the same answer key in all 20 trials, this was interpreted as disbelief in the cover story, or as insufficient motivation to play out the instructions well. Pressing the same answer key in every trial was therefore defined as exclusion criterion.

Participants' decisions were registered separately for every trustee. The total investment, as well as the investment in male versus female, attractive versus unattractive players, could thus be analyzed.

2.3. Hormone assays

Immediately after completing a test session, participants were accompanied to a medical practice on campus, where blood samples were taken and processed. Estradiol, progesterone, testosterone, LH, and FSH were determined by a solid-phase, competitive chemiluminescent enzyme immunoassay (Siemens Diagnostic GmbH, Munich, Germany). The intra- and interassay coefficients of variation for a low point of the standard curve were 3.1–7.9% and 4.1–7.8%, respectively. These hormone analyses served to confirm naturally cycling women's self-reported cycle phases. For the preovulatory phase, inclusion criteria were progesterone levels < 2.0 ng/ml, estradiol levels > 34 pg/ml, LH levels > 5 IU/l, and FSH levels > 4 IU/l. For the mid-luteal phase, inclusion criteria were progesterone > 2 ng/ml, and estradiol levels > 30 pg/ml. In addition, by means of SHBG determination, the use of hormonal contraceptives could be detected (as defined by SHBG levels > 120 nmol/l). For the hormonal contraceptives control group, it was considered that SHBG levels > 120 nmol/l would act as group inclusion criterion.

2.4. Data analyses

There is evidence that the total hormone concentration does not account best for the bioactive effects of gonadal hormones (Maguire and Mody, 2009), but rather that significant changes in hormone levels cause physiological, psychological or behavioral effects. Therefore, for all test sessions, the changes in hormone levels and behavioral measures were calculated and expressed in delta values (Δ).

The trust game exclusion criterion of invariant responses was accompanied by a potential bias toward overestimating the impact of contextual cues on trusting behavior. In order to control for this risk of misinterpretation, we compared the overall results of the corrected sample with results of a larger sample which included participant's responses with invariant responses.

All statistical analyses were calculated using PASW Statistics 18.0. To test the influence of cycle phase (or test session in men) on the investment in attractive and unattractive, male and female players, a repeated measures analysis of variances (ANOVA) was carried out with the within-subject factors 'cycle phase' (menses, preovulatory, mid-luteal), and 'player' (amount of MU invested in attractive/unattractive, male/female other players), and the between-subject factor 'group'. To test if hormone and trust levels were correlated, bivariate correlation analyses were computed.

3. Results

3.1. Hormone analyses

Valid measurement thresholds of the hormone assays were at 0.2 ng/ml for progesterone, 20 pg/ml for estradiol, 20 ng/dl for testosterone, and 0.1 U/l for LH and FSH. For cases of hormone concentrations below these thresholds, all values were placed at the threshold value minus 0.1.

In the group of naturally cycling women, nine out of 33 women did not meet the hormonal inclusion criteria (in seven women, the preovulatory phase was missed, and in two women, progesterone levels were too low for the mid-luteal phase). Another eight women did not complete all three testing sessions, due to schedule difficulties or technical error. 4 more women in this group had to be excluded from analysis because they had answered invariantly in the trust game in at least one of the test sessions. The remaining 12 women with three complete and valid sets of data in this group had a mean age of 23.92 years (S.D. = 2.4), and a mean average cycle length of 28.92 days (S.D. = 0.99).

From 33 tested contraceptive using women, four had to be excluded from analysis due to mismatch with the hormone inclusion criteria. Another five did not complete all three testing sessions due to schedule difficulties or technical error. Three more had to

be excluded because of invariant responses in the trust game. The remaining 21 women had a mean age of 23.29 years (S.D. = 2.41).

All of the 30 men completed three sessions and had hormone data in the male normal range. However, the rate of participants answering invariantly in the trust game was higher in the male control group, which is why nine participants had to be excluded from analyses. The remaining 21 men had a mean age of 24.95 years (S.D. = 4.44).

All hormone levels in the group of naturally cycling women were in the normal range for the corresponding cycle phase (Table 1). A repeated measures 3 (cycle phases) \times 5 (serum values of progesterone, estradiol, testosterone, LH, and FSH) ANOVA confirmed a significant cycle phase by hormone interaction, $F(8, 88) = 14.8$, $p < 0.001$. Expectedly, this interaction was not significant in men, $F(6, 114) = 0.94$, $p = 0.99$, and in women using hormonal contraceptives, $F(8, 136) = 1.04$, $p = 0.17$.

3.2. Trust game

The ANOVA with the large sample including all participants with valid hormone levels revealed a significant main effect of 'other players' ($F = 49.86$; $p = 0.00$; partial $\eta^2 = 0.41$). There was no main effect of test session ($F = 0.16$, $p = 0.85$ partial $\eta^2 = 0.00$); and the three groups did not differ significantly in overall investment across the three testing sessions, as indicated by the non-significant three-way interaction of test session \times 'other players' \times group ($F = 0.98$; $p = 0.46$; partial $\eta^2 = 0.03$). No other main effect or interaction reached significance (all p 's > 0.3). This pattern of results was not altered when the invariant responses exclusion criterion was applied: With a total $N = 54$, the main effect of other player was at $F = 51.68$; $p = 0.00$; partial $\eta^2 = 0.50$; and neither the main effect of test session ($F = 0.86$; $p = 0.43$; partial $\eta^2 = 0.02$), nor the three-fold interaction of test session \times 'other players' \times group ($F = 0.71$; $p = 0.75$; $\eta^2 = 0.03$) reached significance. Subsequent analyses are therefore reported only for the sample corrected for invariant responses in the trust game.¹

The absolute variance in overall investment across the three testing sessions was relatively large in naturally cycling women (mean investment at menses = 141.33 MU \pm 47.68, at mid-cycle = 130.67 MU \pm 51.23, at mid-luteal phase = 145.67 \pm 48.91), whereas the absolute overall variation in the control groups was only marginal (test session 1–3; women using hormonal contraceptives: 107.24 \pm 42.96, 113.71 \pm 37.39, 114.29 \pm 43.81; men: 123.43 \pm 47.89, 122.29 \pm 55.16, 121.9 \pm 40.31), we further investigated the effect of cycle phase in naturally cycling women in a separate 3 \times 4 ANOVA with cycle phase (menses, mid-cycle, mid-luteal) and 'other players' (male/female and attractive/unattractive) as within-subject factors. This ANOVA revealed a main effect of cycle phase ($F(2, 22) = 3.52$, $p = 0.047$, partial $\eta^2 = 0.242$), indicating that 24.2% of the variance in overall investment was explained by the factor cycle phase in this group. Irrespective of the particular other player, the investment was largest in the mid-luteal phase (test session 3). The investment in the menstrual phase (test session 1) was similar to the mid-luteal phase, but in the preovulatory phase (test session 2), overall investment was significantly reduced (Fig. 1). Although the absolute reduction of investment at the preovulatory phase was more pronounced in investment in male 'other players' than in female 'other players' (Fig. 2), the cycle phase \times player type interaction was statistically not significant, $F(6, 66) = 0.99$, $p = 0.44$.

¹ As in the global ANOVAs, the general pattern of results was not substantially altered in follow-up tests and correlation analyses when the larger sample was included.

Table 1

Hormone concentrations for naturally cycling women in the menstrual phase, the preovulatory phase, and the mid-luteal phase, compared to hormone concentrations of women using hormonal contraceptives and men.

Group	Cycle phase	Progesterone (ng/ml)		Estradiol (pg/ml)		Testosterone (ng/dl)		FSH (U/l)		LH (U/l)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Naturally cycling women (N = 12)	Menstrual	0.29	0.11	30.92	12.85	32.31	13.26	6.91	2.26	5.62	2.11
	Ovulation	0.67	0.99	89.66	34.46	46.22	17.72	6.10	1.44	9.49	3.15
	Mid-Luteal	6.61	2.50	94.26	34.56	33.59	11.16	3.42	1.19	6.79	5.80
Contraceptive women (N = 21)	T1	0.27	0.11	27.46	10.54	29.52	13.92	4.11	2.11	4.16	3.71
	T2	0.24	0.08	23.43	6.28	26.46	11.21	1.94	1.96	1.65	2.29
	T3	0.24	0.11	22.93	4.81	27.17	13.31	2.07	2.53	1.66	2.74
Men (N = 21)	T1	0.34	0.16	28.06	9.85	432.20	126.81	-	-	5.61	2.30
	T2	0.34	0.14	24.43	8.33	430.25	121.92	-	-	4.37	1.58
	T3	0.04	0.16	25.26	9.96	439.00	124.44	-	-	4.91	1.87

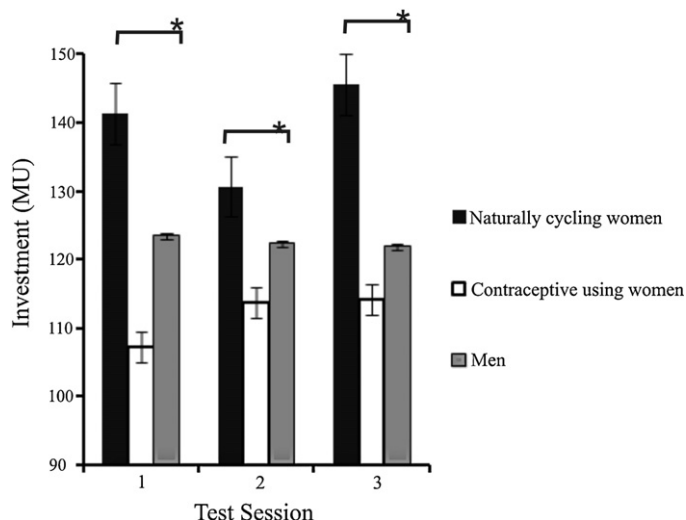


Fig. 1. Overall investment across three test sessions. While the overall investment was stable over three test sessions in women using hormonal contraceptives (white bars) and men (gray bars), it was significantly reduced at the preovulatory phase in naturally cycling women (black bars). Session number 1 = naturally cycling women's menstrual phase, number 2 = ovulatory phase, number 3 = mid-luteal phase. Order of sessions was counterbalanced across all participants. Error bars indicate standard error; asterisk indicates significant differences.

The variation in overall investment across the three test sessions was neither significant in hormonal contraceptive using women (main effect of test session, $F(2, 40) = 0.76, p = 0.47$), nor in men (main effect of test session, $F(2, 40) = 0.29, p = 0.97$), and the cycle

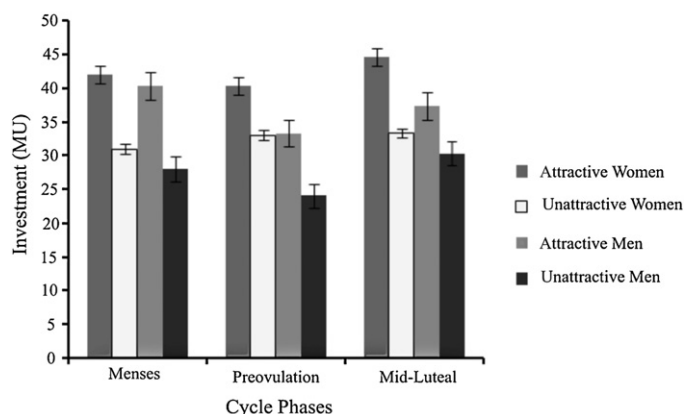


Fig. 2. Distribution of naturally cycling women's investment to four types of other players. The largest amount of MU was invested in attractive female players in all cycle phases. The investment in unattractive male players was particularly reduced in the preovulatory phase. Error bars indicate standard error.

phase \times player interaction was not significant in these groups (hormonal contraceptive using women: $F(2, 40) = 0.76, p = 0.91$; men: $F(2, 40) = 0.03, p = 0.73$).

To test if hormonal changes and alterations in trusting behavior were correlated in naturally cycling women, bivariate correlation analyses were computed. There was a significant relationship between progesterone ($r = 0.58; p = 0.047$) and estradiol ($r = 0.59; p = 0.043$) and the amount of MU invested in attractive female 'other players' in the menstrual phase. Furthermore, estradiol levels were positively correlated with the overall sum of investment (added up across all types of other players) in the preovulatory phase ($r = 0.59; p = 0.044$). The correlation between estradiol levels and sum of investment toward attractive male other players only narrowly missed significance in the preovulatory phase ($r = 0.58; p = 0.053$). The analysis of Δ -values revealed evidence that fits with the pattern of results from ANOVAs: the increase of estradiol from menses to preovulatory testing ($\Delta M-P$) was negatively correlated with the increase of investment toward attractive male other players during the same period ($r = -0.54; p = 0.068$), indicating that individuals with strong estradiol increase particularly reduced their investment in attractive men. Likewise, the increase of FSH from menses to the preovulatory phase was correlated with the reduction of investment in unattractive female other players ($r = -0.6; p = 0.039$). The increase of estradiol from menses to the mid-luteal phase ($\Delta M-L$) was associated with the reduction of investment in unattractive male other players ($r = -0.68; p = 0.016$). On the other hand, $\Delta M-L$ progesterone was strongly correlated with the increase of investment in unattractive female players ($r = 0.73; p = 0.007$). No significant associations of hormone/behavior changes were observed in the Δ -values between the preovulatory and the mid-luteal phase. Similarly, there was no evidence for a relationship between hormone levels and behavioral output in the investment game either in the group of women using Nuva® Rings, or in the group of men.

4. Discussion

This study provides the first direct evidence for a modulating effect of endogenous gonadal hormones on interpersonal trust in women, and can therefore be seen as the first attempt to close the gap in the literature concerning effects of endogenous sex hormones on interpersonal trust. We tested the hypothesis that young women dynamically adapt their trusting behavior according to their fertility status. Our modification of the trust game to the demands of menstrual cycle studies produced a valid measure of interpersonal trusting behavior: The vast majority of research participants took up the instructions well and adopted their ratings of trustworthiness according to their impression of the other player. In line with our hypothesis, we found that the readiness to trust in unknown other individuals systematically changed in naturally cycling women across three hormonally distinct phases of

the menstrual cycle, whereas no such systematic variation was evident in two control groups of women and men with stable hormone levels. The predicted direction of change was informed by recent knowledge about neuromodulatory properties of estradiol and progesterone, as well as by evolutionary psychology considerations: In naturally cycling women, we expected to find an increased willingness to trust in attractive male other players at the time of highest estradiol concentrations at mid-cycle; and a generally decreased willingness to trust in strangers at the time of highest progesterone concentrations in the mid-luteal phase. In fact, we observed a generally reduced investment, or less trustful interactions, in the most fertile mid-cycle phase, compared to the low-hormone menstrual and to the high-hormone mid-luteal phase. Although in our sample of naturally cycling women the cycle phase by other player interaction missed statistical significance, the reduction of trusting behavior was especially pronounced toward other male (attractive and unattractive) players.

Thus, overall, the preovulatory phase was associated with more conservative judgments of trustworthiness, which is in accordance with previous findings of reduced risk-taking (Bröder and Hohmann, 2003), increased sensitivity for signs of a man's potential sexual coerciveness (Garver-Apgar et al., 2007), and increased bias against outgroup members (Navarrete et al., 2009) in the fertile phase (but see Zethraeus et al., 2009). Furthermore, this pattern of results in accordance with the testosterone modulated preovulatory decline in ratings of trustworthiness postulated in Johnson and Breedlove (2010). Although we did not observe a direct link between endogenous testosterone levels and reduced trusting behavior in our sample, we plan to further investigate this potential link between high levels of baseline testosterone and reduced interpersonal trust in future studies.

If high levels of endogenous progestagens and estrogens (as in the mid-luteal phase of the menstrual cycle) are associated with facilitated trusting behavior, one would expect lower levels of trusting behavior in women with exogenously suppressed estrogen/progestagens levels. Despite the fact that the difference in overall investment between naturally cycling women and women using the NuvaRing missed statistical significance in our sample, the row data pointed into this expected direction. Future studies are needed to further investigate this potential association, because differential effects of endogenous and exogenous hormone effects on the CNS are only beginning to be investigated. In a recent research report about the neural mechanisms by which testosterone acts on interpersonal trust, both endogenous and exogenous levels of testosterone were assessed, and both were found to be correlated with increased amygdala activity during evaluation of untrustworthy faces (Bos et al., 2012b). Whether progestagens and estrogens produced naturally in the body, and their synthesized equivalents also affect central nervous activity in a concurrent manner remains an open question for now. Also the fact that we did not observe any significant hormone/behavior associations in men and in women using hormonal contraceptives, while other investigators have reported associations between, e.g. testosterone and behavioral factors which are associated with trusting behavior (for a review, see Stanton et al., 2011), emphasizes the need for more research on the relation between differing hormone levels and changed behavioral output in social contexts.

In naturally cycling women, the pattern of reduced interpersonal trust (revealed by ANOVAs) was not entirely matched by results from analysis of correlation between (changes in) total hormone concentrations and (changes in) our trust variable. For instance, based on the behavioral data one would expect strong negative correlations between estradiol (which peaks in the preovulatory phase) and the overall investment (which was lowest in the preovulatory phase). However, we observed moderate positive associations between estradiol concentrations and the overall

sum of investment in the preovulatory phase. Furthermore, there was only a trend for a negative association between the increase of estradiol from menses to preovulatory phase and the investment toward attractive male other players, indicating that women with steep estradiol increases particularly reduced their willingness to trust in attractive males at this time. A similar relation was observed in the difference in estradiol levels between menses and the mid-luteal phase, when the main estrogen typically reaches a second peak: women with steep estradiol increases particularly reduced their investment in unattractive male other players. The reduction of investment in unattractive female other players from menses to mid-cycle was associated with the increase of FSH during the same period. Thus, the gonadotropine can better account for the hypothesized behavioral adaptation than the gonadal steroid. Such seemingly inconsistent findings are indicative of two things: First, hormone effects which are inferred from menstrual cycle studies have to be interpreted with respect to the complexity of the hypothalamic–pituitary–gonadal (HPG)-axis, and can be caused by other factors than the total concentration of one single hormone of interest. Second, sex hormones probably do not directly modulate trusting behavior per se, but might be rather subtle and affecting implicitly driven aspects of social behavior. This may also explain why recent investigations of natural hormone fluctuations across the menstrual cycle have often failed to demonstrate a significant hormone/behavior relationship (e.g., Bowen et al., 2011; Farrelly, 2011; Hagemann et al., 2011). Such phenomena with expected small effect sizes are generally difficult to detect in low-powered menstrual cycle experimental designs. Because of high drop-out rates of 20–30% due to misclassification of cycle phases in menstrual cycle studies (Hampson, 1990; Hausmann, 2005; Bibawi et al., 1995; Voyer, 1996), replications of the menstrual cycle effect on trusting behavior will be needed in order to establish a well-grounded understanding of the interrelation of female sex hormones and interpersonal trusting behavior.

In conclusion, our data not only add to the growing body of evidence indicating that human social and emotional behavior is substantially influenced by hormones (Bos et al., 2012a), but also provide the first evidence that hormone fluctuations in the natural range are effectual to produce measurable changes in trusting behavior. Studying the effects of naturally occurring hormone effects on social cognitive processes is an important field of research within the psychoneuroendocrine domain. We provide evidence that endogenous gonadal steroids are involved in the regulation of interpersonal trust, but the exact hormonal mode of action remains to be determined. Nonetheless, our study might mark the starting point for future research to elucidate the nature of interpersonal behavioral adaptations as a function of fluctuating hormone levels.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biopsycho.2013.01.005>.

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