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# Estrogen modulates inhibition of return in healthy human females

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ABSTRACT

Estrogen has a key role in explaining gender differences in dopaminergic functioning. To date, previous studies on estrogen have focused on inhibitory output control, such as the intentional suppression of overt pre-potent actions, but whether input control is also modulated is an open question. For the first time, this study compared the ability to perform a cued target-detection task that measured inhibition of return (IOR), a reflexive inhibitory mechanism that delays attention from returning to a previously attended location, in young women ($n = 21$) across the three phases of their menstrual cycle (salivary estradiol and progesterone concentrations were assessed) and in young men ($n = 21$). Women showed more pronounced IOR effect in their follicular phase, which is associated with both higher estradiol levels and higher dopamine turnover rates, than in their luteal or menstruation phase. This increase in women's IOR in their follicular phase was also greater than the effect found for men at any of the three phases. Our results are consistent with the idea that estrogen promotes IOR. Given that the mechanism underlying IOR biases the cognitive system towards the intake of novel information, our findings suggest that when the estrogen level is high, women are biased towards cognitive flexibility rather than cognitive stability. We conclude that gender differences in inhibitory input control are variable and state-dependent but not structural.



## 1. Introduction

The gonadal steroid hormone estrogen does not only have a reproductive function, but also seems to modulate cognition. Several studies investigating cognitive performance during the menstrual cycle have shown that estrogen affects cognitive functions such as learning and working memory in both animal (Warren & Juraska, 1997) and human females (Gasbarri et al., 2008; Hampson, 1990a,b; Maki, Rich, & Rosenbaum, 2002). Consistent with this notion, studies assessing menopause or ovariectomy have revealed cognitive impairments in memory functions as consequence of the decline of the level of estrogen (Sherwin, 2002, 2005).

Growing evidence suggests that estrogen affects cognition through its neuromodular effect on the cholinergic (Norbury et al., 2007), the serotoninergic (Bethea, Lu, Gundlah, & Streicher, 2002), and the GABA system (Amin et al., 2006). However, the dopaminergic system seems to be particularly strongly affected by estrogen. After estrogen enters the brain, it is converted to cathecol estrogen, which is suspected to inhibit the catechol O-methyltransferase (Ball, Knuppen, Haupt, & Breuer, 1972), an enzyme responsible for the degradation of dopamine (DA). Moreover, the DA content of striatal tissue in mice is higher in females than in males (McDermott, Liu, & Dluzen, 1994) and DA turnover rates are higher during diestrus (rising estrogen level) than in estrus (low estrogen level) in rats (Fernandez-Ruiz, Hernandez, de Miguel, & Ramos, 1991). As pointed out by Czoty et al. (2009), receptor autoradiography studies have demonstrated that D2 receptor densities can increase in the presence of natural elevations in estrogen during the estrous cycle and after exogenous estrogen administration (Bazzett & Becker, 1994; Becker, 1999; Di Paolo, Falardeau, & Morissette, 1988; Pazos, Stoeckel, Hindelang, & Palacios, 1985; see Di Paolo, 1994). Consistent with this picture, other studies have pointed out that the follicular phase is related to enhancement in DA release associated by high levels of estrogen in rodents (Becker, Molenda, & Hummer, 2001; Dazzi et al., 2007; Di Paolo, Levesque, & Daigle, 1986; for review see Becker, 1999) and in monkeys (Czoty et al., 2009).

Previous studies on estrogen have focused on inhibitory *output* control, such as the intentional suppression of overt pre-potent actions. For example, a recent study by Colzato, Hertsig, van den Wildenberg, and Hommel (2010) showed that gender differences in inhibiting prepotent responses are restricted to the phase in women's menstrual cycle in which the estrogen level is particularly high—the follicular phase (FP)—while women do not differ from

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men in their luteal (LP) and menstrual phase (MP). In the present study, we investigated whether *input* control processes, specifically attentional selection, may also be affected. To examine this, we took advantage of the perhaps most reliable inhibitory phenomenon in human attention, the so-called inhibition of return (IOR) effect (Posner & Cohen, 1984), a reflexive inhibitory mechanism that delays attention from returning to a previously attended location. It is observed if people attend sequential displays or scan complex visual scenes (Klein, 1988) or other circumstances under which they move their attentional focus from one location or object to another location or object. Once a given location has been inspected and attention has moved to another location, the time needed to return to that previous location is increased—presumably to enhance the efficiency of attentional scanning by biasing attention away from irrelevant, old information and towards novel information (Klein, 1988).

Given the natural high level of estrogen in the FP is associated with increases in D2 receptor densities, there are a number of reasons suggesting that estrogen might impact IOR. For example, IOR is (a) eliminated after long-term intake of cocaine, which reduces D2 receptors densities (Colzato & Hommel, 2009), (b) reduced in Parkinson's patients, who suffer from a loss of nigrostriatal DA cells (Filoteo et al., 1997; Yamaguchi & Kobayashi, 1998), and (c) more pronounced in carriers of the 9-repeat allele of the DAT1 gene, associated with higher striatal DA levels than the 10-repeat allele (Colzato, Pratt, & Hommel, 2010). These studies converge onto the proposed crucial role of dopamine as the neurobiological mechanism underlying IOR (Poliakoff et al., 2003), and this transmitter is primarily targeted by estrogen.

The aim of the present study was twofold. The first goal was to determine whether estrogen can impact IOR. To test this, we compared the performance of young women in an IOR paradigm across different phases of their menstrual cycle. All three phases were considered: the FP, which is associated with the highest level of estrogen, the LP, and the MP. Given that estrogen is associated with higher DA turnover rates, if estrogen affects the DA functioning in driving inhibitory input control, we would expect more pronounced IOR in the FP (i.e., with the highest level of estrogen) than in the LP and MP.

The second goal of the study was to investigate whether women differ from men in inhibitory input control performance. As shown by Colzato, Hertsig, et al. (2010), it is possible that gender differences are restricted to a particular phase of the women's menstrual cycle, so we have conducted separate comparisons for the three phases of the cycle. Because estrogen modulates striatal DA activity in females, but not in males (McDermott et al., 1994), if estrogen affects the DA functioning in driving inhibitory control then we would expect gender differences to be most pronounced for women in their FP (which is associated with an elevated level of estrogen).

## 2. Experimental procedures

### 2.1. Participants

Twenty-one young healthy women, aged 18–30 (mean age 22.41 ± 3.3), mean IQ 113.8 ± 6.1, and twenty-one young healthy men, aged 18–30 (mean age 23.91 ± 2.9), mean IQ 114.6 ± 6.4, were compensated for their participation.

Women served in three experimental sessions held on three different days according to the phases of their menstrual cycle (menstruation, follicular, and luteal session). The menstruation session was held when the participants were in their first or second day of the menstrual cycle; the follicular session was held when participants were in their 9th–12th day (when the estradiol level is higher); the luteal session took place when participants were in their 17th–27th day. Men also served in three sessions separated by 10 days, so to match the corresponding time intervals between testing sessions in women. A randomized cross-over design with counterbalancing of the order of sessions was used to avoid training effects. In the female group, seven participants performed their first session in their menstruation phase, seven in their luteal phase, and seven in their follicular phase.

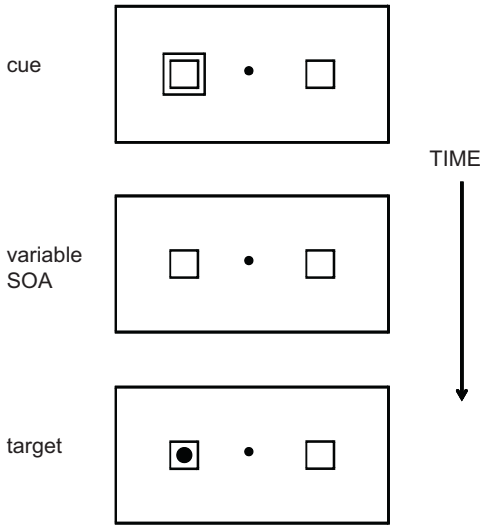


**Fig. 1.** Illustration of the sequence of events for a non-catch trial (SOA, stimulus-onset asynchrony).

Participants were all students from Leiden University and were recruited via ads posted on community bulletin boards and by word of mouth. Following Gasbarri et al. (2008) and Colzato, Hertsig, et al. (2010), participants were screened in accordance with the regularity of their menstruation cycle. We considered women with regular menstrual cycles who reported variations of less than eight days between her longest and shortest cycles. Our female participants had an average cycle length of 30 days (±1.5).

Following Elzinga and Roelofs (2005) and Colzato, Hertsig, et al. (2010), participants were selected with the Mini International Neuropsychiatric Interview (M.I.N.I.; Sheehan et al., 1998). The following exclusion criteria were applied: any form of oral contraceptive within the last 3 months, medication for chronic illness, neurological or psychiatric disorders, and substance abuse. To assess ovarian function and verify the cycle phase in women, non-invasive salivary measures of estradiol and progesterone were used. Following Gasbarri et al. (2008), we collected saliva samples for each experimental session, although we analyzed salivary estradiol and progesterone concentrations in the FP and LP and not in the MP.

All participants were tested individually and completed the IOR task and the intelligence test immediately after the collection of salivary samples. Written informed consent was obtained from all subjects; the protocol and the remuneration arrangements of 20 Euro was approved by the local ethical committee (Leiden University, Institute for Psychological Research).

### 2.2. Apparatus and stimuli

The experiment was controlled by a PC attached to a 17-in. monitor with a refresh rate of 100 Hz. The task was modeled after Castel, Chasteen, Scialfa, and Pratt (2003) and Colzato, Pratt, et al. (2010). The experiment took place in a dimly illuminated, sound attenuated room. Participants were seated 45 cm in front of a computer monitor. They were asked to fixate on a central cross (0.1° × 0.1°) and to make no eye movements during the experimental trials.

### 2.3. IOR task

The sequence of events is shown in Fig. 1. All stimuli were presented in white (77.0 cd/m$^2$) on a black background (0.5 cd/m$^2$). The initial display was presented for 1000 ms and consisted of two placeholder boxes located on the horizontal meridian to the left and right of the fixation point. The boxes were centered 5° from the fixation point and were 1° square. One of the boxes was then cued by outlining the perimeter for 50 ms. One of 5 randomly determined SOAs then followed the onset of the cue (50, 250, 750, 1000, 1500 ms). After the variable SOA, a target circle (0.78 cm) appeared in one of the two boxes (on 80% of the trials; the remaining 20% served as catch trials in which no target was presented). Participants were asked to respond to the target as quickly and as accurately as possible by pressing the space bar of the computer keyboard (regardless of the location of the target) and to remain fixated throughout each trial. The next trial began 500 ms later. The experiment consisted of 300 trials with cues and targets being equally likely to occur at the left and right locations.

### 2.4. IQ

Individual IQs were determined by means of a 30-min reasoning-based intelligence test (Raven Standard Progressive Matrices: SPM). The SPM assesses the

individual's ability to create perceptual relations and to reason by analogy independent of language and formal schooling; it is a standard, widely-used test to measure Spearman's g factor as well as fluid intelligence (Raven, Court, & Raven, 1988). Participants completed the SPM and subsequently performed on the behavioral task measuring IOR.

### 2.5. Immunoassay protocols

Salivary estradiol and progesterone concentrations were analyzed by an independent laboratory using commercially available immunoassay kits adopted for the analysis of salivary samples (DSL, Sinsheim, Germany). In contrast to venipuncture, this technique is non-invasive and provides accurate measures of estradiol and progesterone concentrations (Gandara, Leresche, & Mancl, 2007).

#### 2.5.1. Saliva sample collection

Subjects were asked to collect the saliva by passive drool into polypropylene tubes of 10 ml. For each experimental session, the saliva samples of all participants were collected at the same hour (14:00). Participants were asked to avoid alcohol consumption 24 h prior to sample collections, not eat within 60 min prior to sample collection, not brush teeth within the 3 h prior to sample collections, and wash mouth out with water 10 min prior to giving a sample. Following Gasbarri et al. (2008), and unlike in our recent publication (Colzato, Hertsig, et al., 2010), we collected saliva samples for all experimental session (i.e., all menstrual phases) but restricted the (rather expensive) analyses of salivary estradiol and progesterone concentrations to the FP and LP. The reason was that in women with a regular menstrual cycle, as our participants, the estradiol level in the MP is comparable to that in the FP while the progesterone level in the MP is comparable to that in the FP (Gandara et al., 2007).

#### 2.5.2. Saliva sample analysis

Saliva samples were analyzed with high sensitivity salivary estradiol or progesterone enzyme immunoassay kits from DSL laboratories (www.dslabs.com), using the exact procedure recommended by the company. The levels of estradiol or progesterone were computed by fitting the optical density reading of each saliva sample to obtain the standard curve. The minimal concentration of estradiol and progesterone that can be distinguished with this method is 1 pg/ml and 5 pg/ml, respectively.

### 2.6. Statistical analysis

First, to assess ovarian functioning in women and verify the cycle phase, statistical differences of estradiol and progesterone levels between cycle phases were analyzed by means of a repeated measures ANOVA with Cycle Phase (FP vs. LP) as within-subject factor. Independent samples *t*-tests were performed for analyses of age and IQ differences between men and women.

Second, the women's mean RTs and proportions of errors (PE) were analyzed by a repeated-measures $3 \times 2 \times 5$ ANOVAs with Cycle Phase (MP vs. FP vs. LP), and Trial Type (i.e., cued vs. uncued) and SOA (5 SOAs) as within-subject factor and order of phase as covariate (in order to account for possible order effect). Independent samples *t*-tests were performed for analyses of phase differences on mean RTs and PE of the IOR effect (calculated by subtracting the mean cued reaction time from the mean uncued reaction time) between men and women. Phase-specific comparisons between men and women were carried out between the corresponding subset of data from the women and an equivalent subset of data from men—so to equate the compared data sets in terms of the number of trials considered, practice level, variance, etc. This was achieved by creating dummy cycle phases in men by yoking every male participant to a female participant and assigning the corresponding phase of the female to him.

Third, in order to test whether the magnitude of the IOR effect is proportional to salivary estradiol and/or progesterone concentrations, three Pearson correlation coefficients were computed: (1) between the average hormone levels and the mean IOR effect across the three phases; (2) between hormone levels in the FP and the IOR effect in the FP; and (3) between the difference of hormone levels and the difference of the IOR effect in FP and LP. A significance level of $p < .05$ was adopted for all statistical tests and all reported *t*-test results refer to two-tailed testing.

## 3. Results

### 3.1. Participants

No significant group differences were obtained for age, $t(40) = 1.57$, $p = 0.12$ and intelligence, $t(40) = .32$, $p = 0.75$.

### 3.2. Hormonal levels

Estradiol and progesterone levels in participants in FP and LP were obtained by interpolation of data, utilizing a linear regression. The mean and standard errors of estradiol levels in FP and LP were $5.03 \pm 0.62$ pg/ml; and $3.19 \pm 0.25$ pg/ml, respectively. Repeated measures ANOVA showed a significant difference between cycle phases, $F(1,20) = 4.76$, $p < 0.05$, MSE = 7.418, $\eta^2 p = 0.192$.

The mean and standard errors of progesterone levels in FP and in LP were, $43.99 \pm 17.55$ pg/ml; and $118.72 \pm 68.30$ pg/ml, respectively. Repeated measures ANOVA showed a significant difference between cycle phases, $F(1,20) = 28.28$, $p < 0.0001$, MSE = 2073.249, $\eta^2 p = 0.586$.

These results indicate significantly higher levels of estradiol in the FP and progesterone in LP, as confirmation of normal ovarian functioning in our participants.

### 3.3. IOR task

Tables 1 and 2 provide an overview of the outcomes for RTs and proportion errors (PEs) at each stimulus-onset asynchrony (SOA) and as a function of the three phases, respectively. In women, RTs revealed a significant main effect of Trial Type, $F(1,20) = 115.29$, $p < 0.00001$, MSE = 673.45, $\eta^2 p = 0.85$; and of SOA, $F(4,80) = 15.18$, $p < 0.0001$, MSE = 942.16, $\eta^2 p = 0.43$. Trial Type was involved in two two-way interactions: with SOA, $F(4,80) = 7.47$, $p < 0.001$, MSE = 761.03, $\eta^2 p = 0.27$, indicating that the magnitude of the IOR effect is more pronounced with increasing SOAs, and with Phase, $F(2,40) = 3.45$, $p < 0.05$; MSE = 300.87, $\eta^2 p = 0.15$. Women showed a significant main effect of Trial Type, $F(1,20) = 61.74$, $p < .0001$, MSE = 124.208, $\eta^2 p = 0.75$; $F(1,20) = 46.08$, $p < .0001$, MSE = 76.012, $\eta^2 p = 0.69$; and $F(1,20) = 57.06$, $p < .0001$, MSE = 54.819, $\eta^2 p = 0.72$; for the FP, LP and MP, respectively. However, repeated measures ANOVA comparing the magnitudes of the IOR effect, $F(2,40) = 3.45$ $p < 0.05$, MSE = 300.87, $\eta^2 p = 0.15$, revealed that women showed a more pronounced IOR effect in the FP (−27 ms) than in the LP (−18 ms) and in the MP (−20 ms).

In men, RTs revealed a significant main effect of Trial Type, $F(1,20) = 115.29$, $p < 0.00001$, MSE = 673.45, $\eta^2 p = 0.85$; and of SOA, $F(4,80) = 15.18$, $p < 0.0001$, MSE = 942.16, $\eta^2 p = 0.43$. Trial Type was involved in a two-way interaction with SOA, $F(4,80) = 9.10$,

**Table 1**
Mean response latencies (in ms), error rates (in percent), and IOR effect (uncued–cued) at each stimulus-onset asynchrony (SOA) and averaged across menstrual phase for women and for men. Standard errors in parentheses.

| Variables (SD) | Women | | | | | Men | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| SOA | 50 | 250 | 750 | 1000 | 1500 | 50 | 250 | 750 | 1000 | 1500 |
| Cued | | | | | | | | | | |
| RT (ms) | 373 (9) | 358 (8) | 368 (8) | 361 (8) | 360 (9) | 359 (9) | 349 (8) | 353 (8) | 338 (8) | 335 (9) |
| Error rates (%) | 0.4 (0.2) | 1.1 (0.3) | 2.6 (0.5) | 3.4 (0.5) | 3.6 (0.7) | 0.5 (0.2) | 2.0 (0.3) | 2.8 (0.5) | 3.1 (0.6) | 3.7 (0.7) |
| Uncued | | | | | | | | | | |
| RT (ms) | 368 (8) | 338 (9) | 333 (9) | 325 (8) | 344 (9) | 355 (9) | 332 (9) | 318 (9) | 335 (8) | 322 (9) |
| Error rates (%) | 0.4 (0.1) | 1.3 (0.3) | 2.0 (0.5) | 3.2 (0.5) | 3.8 (0.7) | 0.4 (0.1) | 1.9 (0.3) | 2.8 (0.5) | 3.0 (0.5) | 3.9 (0.7) |
| IOR | | | | | | | | | | |
| RT (ms) | −8 | −30 | −42 | −38 | −22 | 5 | −12 | −39 | −34 | −23 |
| Error rates (%) | −0.1 | −0.2 | 0.1 | 0.4 | −0.6 | −0.1 | −0.2 | 0.1 | 0.1 | 0.9 |

**Table 2**
Mean response latencies (in ms), error rates (in percent), and IOR effect (uncued – cued) averaged across SOA for the follicular (FP), luteal (LP) and menstruation phase (MP) for women and for men (fictive). Standard errors in parentheses.

| Variables (SD) | Women | | | Men | | |
|---|---|---|---|---|---|---|
| Phase | FP | LP | MP | Dummy FP | Dummy LP | Dummy MP |
| Cued | | | | | | |
| RT (ms) | 361 (8) | 365 (9) | 366 (10) | 345 (8) | 347 (9) | 349 (10) |
| Error rates (%) | 1.9 (0.4) | 2.3 (0.5) | 2.4 (0.7) | 2.2 (0.3) | 2.3 (0.4) | 2.7 (0.4) |
| Uncued | | | | | | |
| RT (ms) | 334 (7) | 347 (10) | 346 (10) | 326 (7) | 328 (10) | 331 (10) |
| Error rates (%) | 2.1 (0.3) | 2.1 (0.4) | 2.3 (0.7) | 2.4 (0.4) | 2.7 (0.5) | 2.1 (0.4) |
| IOR | | | | | | |
| RT (ms) | −27 | −18 | −20 | −19 | −19 | −18 |
| Error rates (%) | −0.2 | 0.2 | 0.1 | −0.2 | −0.4 | 0.6 |

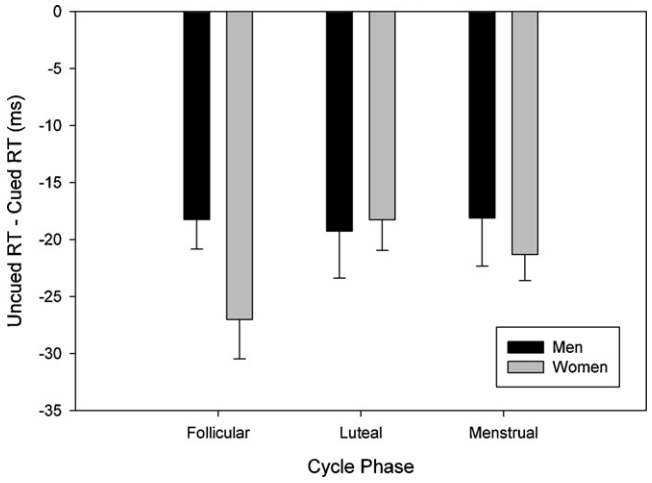


**Fig. 2.** Mean cueing effects (uncued reaction time, or RT, minus cued RT, averaged over SOA) as a function of follicular (FP), luteal (LP) and menstruation phase (MP) for women and for men (fictive). Error bars indicate standard errors of the mean.

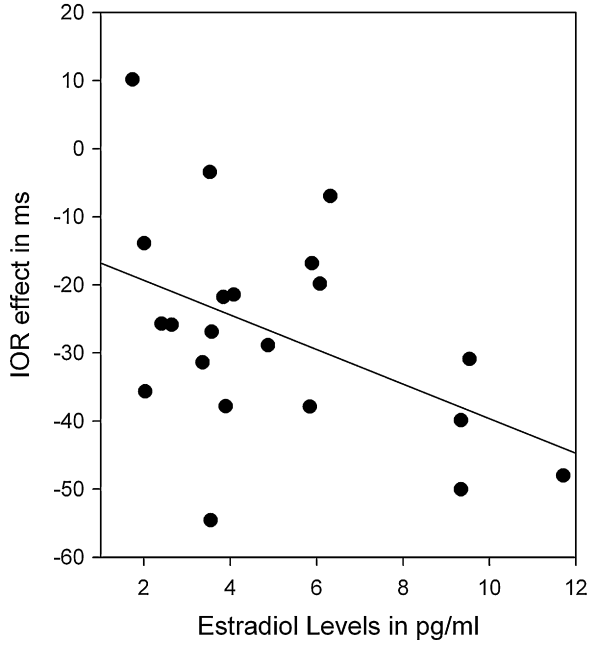


**Fig. 3.** Scatter diagram of estradiol levels (in pg/ml) in the FP against IOR effect (in ms) in the FP.

$p < 0.001$, MSE = 492.42, $\eta^2 p = 0.31$, longer SOAs were associated with more pronounced IOR effects. However, Trial Type did not interact with Phase, indicating that in men the magnitudes of the IOR effect did not vary across the dummy phases.

As expected, *t*-tests on magnitudes of the IOR effect (averaged over SOA) yielded a significant difference between men and women in FP, $t(40) = 2.041$, $p = 0.048$, but not in LP, $t(40) = 0.23$, $p = 0.840$, and MP, $t(40) = 0.67$, $p = 0.508$ (see Fig. 2). Moreover, in women, the individual magnitude of the IOR effect in the FP correlated significantly (and positively) with estradiol levels, $r(21) = -.456$, $p < .05$, but not with progesterone levels in the FP, $r(21) = .024$, $p = .91$; see Fig. 3. The correlations between the average IOR effect and estradiol and progesterone levels across the three phases and between the difference of hormone levels and the difference of the IOR effect in FP and LP, did not reach significance, $ps > .1$.

In the error analysis, SOA produced a main effect in both women, $F(4,80) = 13.26$, $p < 0.0001$, MSE = 18.068, $\eta^2 p = 0.34$, and men, $F(4,80) = 21.99$, $p < 0.0001$, MSE = 9.203, $\eta^2 p = 0.52$, indicating fewer errors at the shortest SOA. Phase was not involved in any significant effect.

## 4. Conclusions

Our findings show that the efficiency of inhibitory input control, as measured by an IOR task, varies across the menstrual cycle of healthy human females. In particular, women show an increased magnitude of the IOR effect in their FP (which is associated with higher levels of estradiol, higher DA turnover rates, and higher D2 receptor densities: Fernandez-Ruiz et al., 1991; Bazzett & Becker, 1994; see Di Paolo, 1994) than in the other two phases of their menstrual cycle. Interestingly, women showed a more pronounced IOR effect than men in the FP but not in the other two phases of their menstrual cycle. The two gender groups were matched for intelligence and age, with the latter being particularly important; while inhibitory control does not seem to be related to general intelligence (Logan, 1994), there is evidence that inhibitory processes decline throughout the adult life span (Castel et al., 2003; Logan, 1994; Williams, Ponesse, Schachar, Logan, & Tannock, 1999).

Our results are in line with the findings the estrogen modulates other inhibitory processes, as the intentional suppression of overt pre-potent actions (Colzato, Hertsig, et al., 2010). Correlational analyses revealed a significant positive association of estradiol level, but not of progesterone levels, with the magnitude of IOR. This finding confirms our expectation that estrogen, but not progesterone, was responsible for the observed changes in inhibitory control.

The present observations are consistent with the assumption of a crucial role of dopaminergic pathways in IOR, as suggested by Poliakoff et al. (2003). They are also in line with patients and drug studies showing a reduced IOR in the case of striatal dopaminergic hypoactivity (Colzato & Hommel, 2009; Couette,

Bachoud-Levi, Brugieres, Sieroff, & Bartolomeo, 2008; Filoteo et al., 1997; Yamaguchi & Kobayashi, 1998) and increased IOR in the case of enhanced striatal dopaminergic activity (Fillmore, Rush, & Abroms, 2005) and in DAT1 9-repeat carriers, which are associated with higher striatal DA levels than 10/10 homozygous (Colzato, Pratt, et al., 2010).

The variation of estrogen levels across the menstrual cycle may account for our observations of gender differences in IOR, suggesting that such differences are variable and state-dependent but not structural. These results are consistent with previous study by Colzato, Hertsig, et al. (2010) showing that gender differences in intentional suppression of overt pre-potent actions are restricted to a particular phase of the women's menstrual cycle. However, it is interesting to note that the direction of the effect in our previous study went in the opposite direction, with FP being associated with *less* efficient inhibitory output control. For one, this divergence of results supports the view that input and output control are independent and, thus, can be separated to at least some degree (Johnston, McCann, & Remington, 1995). For another, it is possible that individual differences modulate findings of that sort. Very recently, Jacobs and D'Esposito (2011) suggested that inconsistent results from studies on WM (and, perhaps, other control functions, like inhibitory control) might reflect a dependency of the interplay between estrogen and cognitive processes on baseline DA, which varies considerably across individuals. Indeed, the authors showed that the direction of the effect of the impact of estrogen on WM depends on indices of baseline DA (as genetic variability associated with the COMT $Val^{158}$Met genotype).

The present findings also raise the question whether estrogen may modulate other cognitive control functions, such as "updating" (and monitoring of) working memory (WM) representations and cognitive flexibility (Miyake et al., 2000). Interestingly, previous studies have demonstrated the impact of the menstrual cycle on implicit memory (Maki et al., 2002) and working memory (Gasbarri et al., 2008), but whether these effects reflect an effect of the maintenance component of WM or an effect of/on memory-control functions is still an open question.

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## Conflicts of interest

All authors declare that they have no conflicts of interests.

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