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Relationships between ovarian hormone concentrations and mental rotations performance in naturally-cycling women

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ABSTRACT

Circulating gonadal hormones have been linked to variation in the structure and function of the adult human brain, raising the question of how cognition is affected by sex hormones in adulthood. The impacts of progestogens and estrogens are of special interest due to the widespread use of hormone supplementation. Multiple studies have analyzed relationships between ovarian hormones and mental rotation performance, one of the largest known cognitive sex differences; however, results are conflicting. These discrepancies are likely due in part to modest sample sizes and reliance on self-report measures to assess menstrual cycle phase. The present study aimed to clarify the impact of progestogens and estrogens on visuospatial cognition by relating mental rotation task performance to salivary hormone concentrations. Across two studies totaling 528 naturally-cycling premenopausal women, an internal meta-analysis suggested a small, positive effect of within-subjects changes in progesterone on MRT performance (estimate = 0.44, $p = 0.014$), though this result should be interpreted with caution given multiple statistical analyses. Between-subjects differences and within-subject changes in estradiol did not significantly predict MRT. These results shed light on the potential cognitive effects of endogenous and exogenous hormone action, and the proximate mechanisms modulating spatial cognition.

1. Introduction

Circulating gonadal hormones influence the structure and function of the adult primate brain in areas beyond those implicated directly in reproduction (Morrison, 2008). Mapping of estrogen and progesterone receptors in the brains of non-human primates and rodents has revealed receptor expression in regions such as the amygdala, hippocampus, cingulate cortex, midbrain raphe nuclei, central gray matter, and prefrontal cortex (McEwen, 2001). This distribution throughout the brain suggests that ovarian hormones may modulate cognitive sex differences, as well as changes in cognition across the menstrual cycle.

One of the largest known cognitive sex differences is the ability to visualize the rotation of an object around its axis (Miller and Halpern, 2014), with men outperforming women in mental rotation tests (MRT) by approximately 0.6 standard deviations (Jansen and Heil, 2010). A large body of research in humans and non-human animal models suggests that sex differences in spatial cognition result, at least in part, from organizing effects of androgen on the developing brain (Collaer and Hines, 2020; Puts et al., 2008; Shirazi et al., 2020). Although some studies have reported effects of testosterone administration on aspects of spatial cognition in small samples (Aleman et al., 2004; Pintzka et al., 2016), neither individual differences (Griksiene and Ruksenas, 2011; Puts et al., 2010; Shirazi et al., 2020; Wharton et al., 2008) nor intra-individual fluctuations (Griksiene et al., 2019; Puts et al., 2010; Silverman et al., 1999) in testosterone concentrations appear to predict mental rotations performance in healthy young adult women or men.

Some evidence suggests that MRT performance fluctuates across menstrual cycle phases (e.g., Hampson, 1990; but see e.g. Griksiene and Ruksenas, 2011), suggesting modulation by progesterone and/or estradiol (reviewed in Poromaa and Gingnell, 2014). However, studies exploring this possibility present conflicting results (Griksiene and Ruksenas, 2011; Hampson et al., 2014; Noreika et al., 2014; Zhu et al.,

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2015), and differ in whether the design is between-subjects (e.g., Griksiene et al., 2019), within-subjects (e.g. Zhu et al., 2015), or both (e.g., Courvoisier et al., 2013). The few studies that have simultaneously evaluated between- and within-subjects effects have involved small samples (e.g., Courvoisier et al., 2013, n women = 7), which cannot provide reliable estimates of population effects (Gangestad et al., 2016).

Due to methodological limitations in previous investigations and the considerable variability in past results, we utilized data from two previously completed studies to investigate both interindividual and intraindividual effects of progesterone and estradiol on MRT. Specifically, in our combined sample of 528 premenopausal, naturally-cycling women, we tested whether average ovarian hormone levels predicted differences in MRT between subjects, and whether intraindividual fluctuations in these hormones predicted changes in MRT across two study sessions.

2. Methods

2.1. Study 1 recruitment, procedure, and hormone quantification

Participants from Pennsylvania State University (n = 353; mean age: 19.98, SE = 0.17) were recruited via radio, Craigslist, newspaper advertisements, posts on social media sites, the psychology department subject pool, and emails on university research volunteer list-servs. This study was approved by the university institutional review board. All participants met the inclusion criteria of being fluent in English and having naturally occurring menstrual cycles without exogenous hormonal supplementation. Though participants between the ages of 18 and 61 participated in the broader study that produced these data, we restrict our analyses here to those younger than 45, excluding women (n = 16) who could potentially be perimenopausal (see Shirazi et al., 2019). The inclusion of all women regardless of age did not meaningfully affect our results, and model summaries utilizing data from the full sample are presented in the electronic supplementary material (ESM). Participants received monetary compensation or course credit and provided informed consent. Participants were tested between 09:00 and 12:00 to minimize effects of diurnal changes in estradiol (Bao et al., 2003). Participants were then invited to return for a second, identical testing session at the same time of day (within 1 h) as the first session. Sessions were scheduled according to an aim of the broader study of which the present study is a part and were scheduled irrespective of cycle day with the requirement that the second session was completed between 1 and 3 months after the first session (mean length between sessions: 58.45 days, SE = 0.78). Participants completed all tasks and questionnaires at private workstations in the laboratory and provided one saliva sample via passive drool before testing and one saliva sample after testing. To minimize the influence of pulsatile hormone secretory patterns, the two samples were combined by aliquoting 0.5 mL from each into a third tube after each session, then stored on ice before being frozen at −20 °C until compositional analysis.

Samples were analyzed at the Nipissing University Biomarkers Lab (Nipissing University, North Bay, Ontario). All samples were assayed in duplicate using commercially available enzyme immunoassay kits purchased from DRG International. Sensitivity for the progesterone assay was 3.8 pg/mL. Intra- and inter-assay CVs were 14% and 12%, respectively. Samples were also assayed for estradiol; however, because of limitations in estradiol quantification using enzyme immunoassays (Rosner et al., 2013), models including estradiol as a predictor for Study 1 are presented as ESM.

2.2. Study 2 recruitment, procedure, and hormone quantification

Participants from Michigan State University (n = 191; 122 singletons, 33 twin pairs, 1 sister trio; mean age: 19.53, SE = 0.08) were recruited via email and letters as part of a larger study involving siblings approved by the university institutional review board. All participants were students who met the inclusion criteria of English fluency and having naturally occurring menstrual cycles without exogenous hormonal supplementation. All participants provided informed consent. Participants reported the date of onset of their last menstrual bleed and their average cycle length. These variables were used to schedule participants for one laboratory session within one day of estimated peak follicular estradiol production, and for one laboratory session within two days of estimated peak luteal progesterone production using the methods of Puts (2006) to identify these days (see also Puts et al., 2013). Session order (follicular or luteal first) was counterbalanced across participants (mean length between sessions: 14.02 days, SE = 0.42). Because counting-based methods are imprecise and prone to error (see Gangestad et al., 2016) and because the primary aim of this study was to investigate endocrine factors that may predict within- and between-subjects variation in MRT, we present analyses with hormone levels, rather than cycle phase, as predictors. To prevent time of day from confounding results, both sessions occurred between 1:00 and 4:00 for all participants, and for each participant, both sessions occurred within an hour of the same time of day. Participants provided one saliva sample via passive drool. Samples were stored in sodium azide-coated polystyrene tubes and kept upright at room temperature for 18–24 h to allow mucins to settle. Each tube was then frozen at −20 °C until compositional analysis.

Samples were analyzed by the Neuroendocrinology Assay Laboratory at the University of Western Ontario, Canada. Progesterone and estradiol concentrations were quantified via radioimmunoassay with Coat-A-Count assay kit (Diagnostic Products Corporation, Los Angeles, CA) and 125I Ultra-Sensitive E2 RIA DSL-4800 kit (Diagnostic Systems Laboratories, Webster, TX), respectively, modified for use with saliva (Hampson et al., 2014). Each sample was assayed twice, and then averaged for analyses. Assay sensitivities were 0.65 pg/mL and 5 pg/mL, and intra-assay CVs were 5.1% and 10.7%, for estradiol and progesterone, respectively. Mean hormone values (and standard errors) are displayed in Table 1. Session numbers correspond to the order in which sessions were completed. Change (Δ) values reflect the absolute value of differences between first and second session values.

2.3. Mental rotation task

For both studies, mental rotation abilities were evaluated via the Mental Rotation Test originally described by Vandenberg and Kuse (1978). A fully automated 3-D Mental Rotation Task (MRT) was administered to participants via computer. For each item in the MRT, a 3-dimensional block figure is depicted with a 2-dimensional line drawing, and participants are asked to identify the block figure after it has been rotated in space (Fig. 1). For each item, a target block figure was shown on the left, followed by four similar figures on the right. Two of the figures on the right are rotated images of the target, while the others are rotated mirror images. Participants are asked to identify both of the images identical to the target. An item was scored as having been answered correctly only if the participant identified both correct images,

Table 1
Means (and standard errors) for participant ages, hormone values, and mental rotation task (MRT) scores.

	Study 1	Study 2
Age	19.98 (0.17)	19.53 (0.08)
Progesterone pg/mL, session 1	44.69 (2.86)	81.6 (5.36)
Progesterone pg/mL, session 2	45.94 (7.06)	67.35 (4.5)
Δ Progesterone	37.20 (5.43)	56.48 (5.68)
Estradiol pg/mL, session 1		2.05 (0.08)
Estradiol pg/mL, session 2		1.5 (0.06)
Δ Estradiol		0.87 (0.06)
MRT no. correct, session 1	7.37 (0.21)	10.25 (0.33)
MRT no. correct, session 2	8.98 (0.47)	12.7 (0.39)
Δ MRT	2.88 (0.28)	3.44 (0.19)

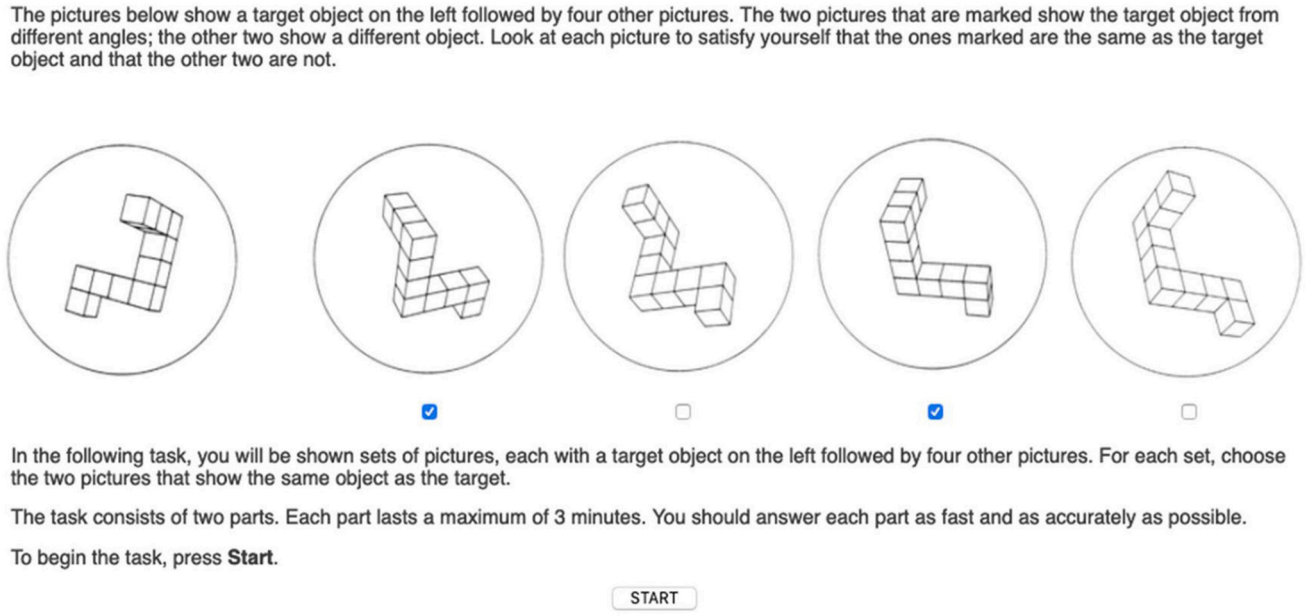

Fig. 1. Example stimuli from the mental rotations test administered in Studies 1 and 2.

which eliminates the need to adjust for guessing. A total of 20 items were presented in two 3-minute blocks of 10 questions for a maximum score of 20 points.

2.4. Data analysis

Data were analyzed using random intercept multilevel models (using maximum likelihood estimation) with an unstructured covariance structure using the nlme package in R, nesting observations within participants. Age, sexual orientation, race, and session (to control for practice effects) were entered as covariates in all analyses. Both progesterone and estradiol (and their interaction) were included as hormonal predictors for Study 2, while progesterone was the sole hormonal predictor for models using Study 1 data. Models from Study 1 including estradiol as a predictor are presented in the ESM.

Our first models tested the effect of between-subjects differences in progesterone on MRT performance, using data from all participants irrespective of the number of sessions completed. Our second models included data from participants who had valid data for both test sessions, and evaluated terms indexing both between-subject differences and within-subject changes in progesterone. We analyzed data from Study 1 and Study 2 separately, and then performed an internal meta-analysis using R's metafor package. To facilitate comparisons of effect sizes across studies, all models used for this meta-analysis included progesterone, and not estradiol, as the sole hormonal predictor. Results from a meta-analysis of models including both progesterone and estradiol as predictors are presented as ESM. All models used for meta-analysis were random effects models, which allow for moderators of effect size such as differences in experimental design and in covariates across studies (Grimbos et al., 2010; Hunter and Schmidt, 2000), rather than fixed effects models, which assume homogeneity across studies. Random effects models are thus appropriate for the analysis of effect sizes from studies wherein moderators may influence effects across studies, as in the case of the studies described in the present manuscript.

3. Results

3.1. Between-subject analyses

In the model using data from all women in Study 1 ($n = 353$) to assess whether between-subject differences in progesterone predicted differences in MRT, the effect of progesterone was not significant ($p = 0.803$, ESM Table 1). Analysis of this same model, with the inclusion of estradiol as a predictor, using Study 2 data ($n = 191$) yielded a significant positive effect of progesterone on MRT scores ($p = 0.014$, ESM Table 1), no effect of estradiol ($p = 0.415$), and no significant interaction between progesterone and estradiol ($p = 0.848$). The effect of progesterone was not significant in our internal meta-analysis (estimate = 0.27, $p = 0.216$, Fig. 2). These results were not modulated by the inclusion or exclusion of estradiol as a predictor (ESM Table 2).

3.2. Within-subject analyses

Within-subject analyses included model terms for both between- and within-subjects effects of progesterone, and for Study 2, these effects for estradiol. In Study 1 ($n = 92$), the within-subjects effect of progesterone was positive but not statistically significant ($p = 0.380$, ESM Table 3). The between-subjects effect of progesterone was not significant ($p = 0.233$). In the analysis using Study 2 data ($n = 166$), the effect of within-subjects progesterone was positive and statistically significant (estimate = 0.49, $p = 0.030$, ESM Table 3). When including this within-subjects term, the effect of between-subjects progesterone was no longer significant ($p = 0.545$). Neither the between- nor within-subjects effect of estradiol was statistically significant ($p = 0.620$ and $p = 0.596$, respectively). Interactions of between-subjects progesterone and estradiol terms ($p = 0.735$) and within-subjects progesterone and estradiol terms ($p = 0.928$) were not statistically significant. The effect of within-subjects progesterone was significant in our internal meta-analysis (estimate = 0.44, $p = 0.014$, Fig. 2). These results were not modulated by the inclusion or exclusion of estradiol as a predictor (ESM Table 4).

4. Discussion

Prior research investigating relationships between circulating ovarian hormones and MRT has been inconclusive, potentially due to small sample sizes and other methodological limitations. In the present work, we sought to elucidate the relationship between ovarian hormones and MRT using, to our knowledge, the largest combined sample in which such relationships have been investigated. In general, we found little evidence that ovarian hormones predicted mental rotation

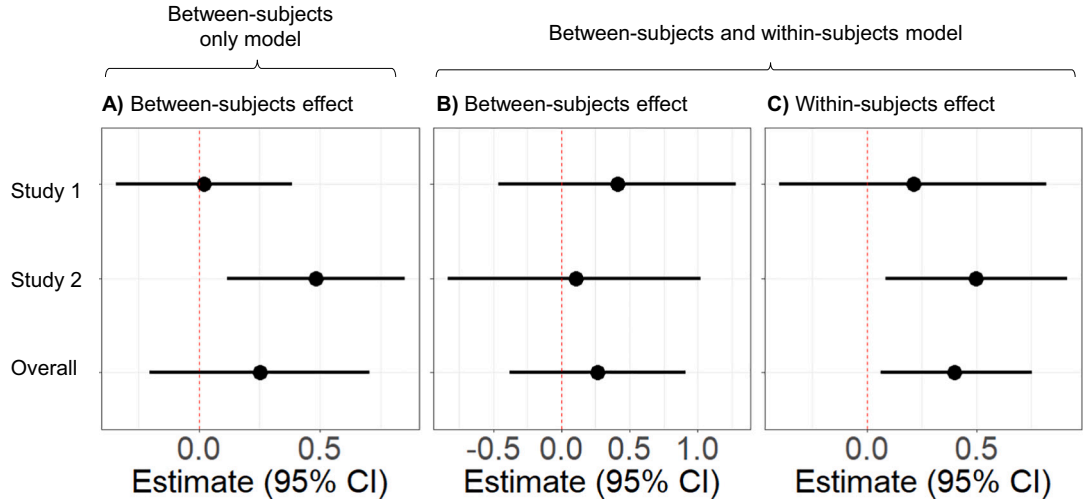

Fig. 2. Estimates (and 95% CI) for the effect of progesterone across Study 1, Study 2, and the internal meta-analysis in models estimating between-subjects effects only (panel A), and models estimating both between- and within-subjects effects (panels B and C).

performance either at between- or within-subjects levels in normally-cycling young women, with the exception of a positive within-subjects effect of progesterone in Study 2 and a non-significant association in the same direction in Study 1. Meta-analysis across Studies 1 and 2 indicated a modest positive within-subjects effect of progesterone, suggesting that high levels of progesterone, as seen in the luteal phase, are associated with improved mental rotations performance. Given the multiple statistical tests that we conducted, however, this effect should be treated cautiously. Progesterone did not predict MRT performance between-subjects when controlling for within-subjects changes in progesterone. Similarly, neither between-subjects differences nor within-subjects changes in estradiol predicted MRT performance. These findings add to accumulating evidence that circulating hormone concentrations do not mediate the differences seen in spatial cognition between young men and women (Griksiene et al., 2019; Puts et al., 2010; Silverman et al., 1999), potentially pointing to organizational effects.

Several factors promote confidence in the present results. First, the present study employed a considerably larger sample size than previous studies, in terms of both participants and total samples analyzed. Second, the methodology of measuring ovarian hormones from saliva was more reliable than previous studies that estimated these from self-reported menstrual cycle phase and better suited to investigating the proximate mechanisms modulating putative relationships between menstrual cycle phase and MRT. Third, by using nested models, we could simultaneously evaluate both between-subjects and within-subjects effects, whereas most previous studies with sufficient power have evaluated between-subjects effects only.

Our results are particularly salient in the context of hormone supplementation, which is employed as treatments for conditions like menopause and endometriosis, and more commonly as contraceptives that suppress endogenous hormone production and ovulation. Understanding hormonal influences on affect, cognition, and behavior is necessary to better inform women choosing among contraceptive types and may also guide our study of changes in these phenotypes as women transition between physiological states (e.g., pregnancy) associated with dramatically different hormonal milieus.

As both samples were largely comprised of college-aged women, it is unknown whether our findings can be extended to other groups, though our pattern of results was similar when expanding the age range in Study 1 to include women 45 and older. Comparability across studies 1 and 2 is potentially hindered by the differences in sampling protocols. For example, session scheduling in Study 2 was specifically designed to target high and low progesterone phases, and it is possible that the larger changes in progesterone observed across sessions in Study 2 (Table 1) contributed to the stronger association between within-subject changes in progesterone and changes in MRT performance observed in Study 2 compared to Study 1. Future work assessing the association between effect sizes and sample density, and other experimental design-related characteristics, is necessary to understand variability in the effect sizes of hormones' activational effects. We also assessed MRT using a single task; though it is the most commonly used MRT task in prior cycle phase work (Poromaa and Gingnell, 2014), the examination of several different MRT tasks simultaneously would increase confidence in any observed effects.

Taken together, our results suggest that high levels of progesterone, characteristic of the luteal phase, may be associated with small increases in mental rotation performance within individual participants. Future work should employ denser sampling schedules, which would allow for testing time-lagged effects, and for better estimating both between- and within-subjects terms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2020.104886.

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