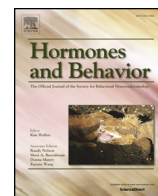


Contents lists available at [ScienceDirect](http://ScienceDirect.com)

# Hormones and Behavior

journal homepage: [www.elsevier.com/locate/yhbeh](http://www.elsevier.com/locate/yhbeh)

Regular article

## Switching between forest and trees: Opposite relationship of progesterone and testosterone to global–local processing

Belinda Pletzer<sup>a,b,c,d,\*</sup>, Ourania Petasis<sup>a,b</sup>, Larry Cahill<sup>a,b</sup><sup>a</sup> Department of Neurobiology & Behavior, University of California, Irvine, USA<sup>b</sup> Center for Neurobiology of Learning & Memory, University of California, Irvine, USA<sup>c</sup> Department of Psychology, University of Salzburg, Austria<sup>d</sup> Center for Cognitive Neuroscience, University of Salzburg, Austria

### ARTICLE INFO

#### Article history:

Received 14 February 2014

Revised 13 May 2014

Accepted 15 May 2014

Available online 27 May 2014

#### Keywords:

Sex hormones

Sex differences

Menstrual cycle

Attention

Global–local processing

Hemispheric asymmetries

### ABSTRACT

Sex differences in attentional selection of global and local components of stimuli have been hypothesized to underlie sex differences in cognitive strategy choice. A Navon figure paradigm was employed in 32 men, 41 naturally cycling women (22 follicular, 19 luteal) and 19 users of oral contraceptives (OCs) containing first to third generation progestins in their active pill phase. Participants were first asked to detect targets at any level (divided attention) and then at either the global or the local level only (focused attention). In the focused attention condition, luteal women showed reduced global advantage (i.e. faster responses to global vs. local targets) compared to men, follicular women and OC users. Accordingly, global advantage during the focused attention condition related significantly positively to testosterone levels and significantly negatively to progesterone, but not estradiol levels in a multiple regression model including all naturally cycling women and men. Interference (i.e. delayed rejection of stimuli displaying targets at the non-attended level) was significantly enhanced in OC users as compared to naturally cycling women and related positively to testosterone levels in all naturally cycling women and men. Remarkably, when analyzed separately for each group, the relationship of testosterone to global advantage and interference was reversed in women during their luteal phase as opposed to men and women during their follicular phase. As global processing is lateralized to the right and local processing to the left hemisphere, we speculate that these effects stem from a testosterone-mediated enhancement of right-hemisphere functioning as well as progesterone-mediated inter-hemispheric decoupling.

© 2014 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

### Introduction

Most stimuli we are exposed to in everyday life are hierarchical, i.e. consisting of a global structure that is made up of local parts, like a forest of trees. The processing of global and local structures is traditionally assessed through attention tasks using hierarchical stimuli, typically letters (Navon, 1977). Participants are usually asked to detect targets at either the global or the local level, while ignoring the other level (focused attention paradigm). Alternatively participants may be asked to detect a target at any level (divided attention paradigm). From experiments with these stimuli, the concept of global precedence was developed (Navon, 1977, 1981).

Global precedence is established as:

- (1) Global advantage: reactions to global targets are faster than reactions to local targets.

- (2) Global-to-local interference: when asked to accept only local targets, rejection of non-targets is faster than rejection of global targets.
- (3) Absence of local-to-global interference: when asked to accept only global targets, rejection of local targets is equally fast as rejection of non-targets.

However, the view of global precedence as a universal phenomenon has to be questioned based on the sex difference literature.

Sex differences have been observed most robustly in spatial tasks like mental rotation and navigation, where men usually outperform women (see Andreano and Cahill, 2009 for a review; see Silverman et al., 2007 for a cross-cultural study; see Voyer et al., 1995 for a meta-analysis). These differences have been associated with differential processing of global/holistic and local/detail information between the sexes. For example men tend to use a more holistic approach in mental rotation tasks (Pena et al., 2008; Rilea, 2008), focus on distal landmarks and use allocentric coordinates in navigation tasks (Galea and Kimura, 1993; Lawton, 1994, 2001; Lawton et al., 1996). Women, on the other

\* Corresponding author at: Department of Psychology, University of Salzburg, Hellbrunnerstr. 34, 5020 Salzburg, Austria.

E-mail address: [Belinda.Pletzer@sbg.ac.at](mailto:Belinda.Pletzer@sbg.ac.at) (B. Pletzer).

hand use a more segmentary strategy in mental rotation and focus on local landmarks and use egocentric coordinates in navigation. It has been demonstrated that men outperform women in both real world and 2D-matrix navigation, when the use of allocentric coordinates is encouraged, whereas women outperform men, when the use of egocentric coordinates is encouraged (Saucier et al., 2002b). The same authors were furthermore able to demonstrate that performance with allocentric, but not egocentric coordinates was related to mental rotation performance. These results lead to two important conclusions concerning global–local processing. First, men appear to be superior in the processing of global/holistic information, while women appear to be superior in the processing of local/detail information. Consequently, in spatial navigation sex differences are attributable to the use of different strategies. Indeed it has been demonstrated that sex differences in virtual navigation decline with the availability of local landmark information (Andersen et al., 2012). Second, global processing is beneficial for spatial tasks. Using global processing, men outperform women in navigation whenever local processing is impossible due to the lack of landmark information. Furthermore, the global processing strategy (use of allocentric coordinates) is related to mental rotation performance. Thus, the male superiority in mental rotation can be explained by their superiority in the processing of global stimulus aspects.

A preference for global/holistic information in men and local/detail information in women has also been observed in tasks eliciting sex differences in favor of women, like number comparison and emotional memory retrieval. Men compare multi-digit numbers holistically (Pletzer et al., 2013) and tend to remember the gist of an emotional story (Cahill and van Stegeren, 2003; Cahill et al., 2004), while women compare numbers in a decomposed fashion (i.e. decades and units separately) and remember the details of an emotional story.

However, few studies reporting inconsistent results have investigated sex differences in the processing of hierarchical stimuli (Kimchi et al., 2009; Razumnikova and Vol'f, 2011; Roalf et al., 2006). Using hierarchical letter stimuli, it has been demonstrated that women show local advantage in stimuli evoking no advantage in men using a divided attention paradigm (Roalf et al., 2006), while men show global advantage in stimuli evoking no advantage in women using a focused attention paradigm (Razumnikova and Vol'f, 2011). However, Kimchi et al. (2009) were unable to detect sex differences in global advantage using hierarchical stimuli made of lines and shapes. Several task-related factors may have contributed to these inconsistent results.

First, there appear to be inconsistencies between studies using hierarchical letter (Razumnikova and Vol'f, 2011; Roalf et al., 2006) vs. shape stimuli (Kimchi et al., 2009). Visual-hemifield, EEG and fMRI data suggest that global information is preferably processed in the right hemisphere, while local information is preferably processed in the left hemisphere for letter stimuli (e.g. Fink et al., 1996; Robertson and Lamb, 1991). Also, verbal information is preferably processed in the left hemisphere, while non-verbal object information is preferably processed in the right hemisphere (see e.g. Kinsbourne, 1970 for a review). Therefore, verbal information (letters) could facilitate local processing, while object information (shapes) could facilitate global processing.

Second, the reported studies used different stimulus spacings and inconsistencies may arise from a lack of control for the spacing of local elements. It has been demonstrated that global advantage declines with increasing sparsity of the stimuli (Martin, 1979). However, it remains unclear whether the dynamics of adapting to different spacings are the same for men and women. As women show higher cognitive flexibility (Mekarski et al., 1996; Muller et al., 2007), global advantage may increase faster with decreasing sparsity in women than in men. Therefore stimuli with dense spacing may fail to elicit significant sex differences. If the spacing becomes larger than the local elements themselves, the local elements may no longer be perceived as part of a global structure, but as independent global structures. Therefore, sex

differences in global–local processing should be least confounded with cognitive flexibility, when spacing equals the size of the local elements.

Third, there appear to be inconsistencies between studies employing a divided attention paradigm (Roalf et al., 2006) vs. a focused attention paradigm (Kimchi et al., 2009). A divided attention paradigm requires the processing of both global and local levels, while a focused attention paradigm allows participants to focus on processing of one level. However, if there are sex differences in global–local processing, men and women may not be equally comfortable with those levels. Furthermore, men and women may differ in their flexibility of switching between levels during divided attention or inhibiting information of the level, they were not instructed to attend during focused attention. Sex differences in cognitive flexibility and cognitive control favoring women have been reported previously (Chapple et al., 2010; Mekarski et al., 1996; Muller et al., 2007).

Importantly, however, none of these studies controlled for the hormonal status of participants, i.e. menstrual cycle phase or hormonal contraceptive use.

First, several studies suggest that sex differences in spatial abilities are related to testosterone (see e.g. Martin et al., 2007 for a review). Particularly, testosterone relates positively to performance in mental rotation (e.g. Hooven et al., 2004; Levine et al., 2001; Silverman et al., 1999; Vuoksimaa et al., 2012) (but see Puts et al., 2010) and spatial navigation tasks (Burkitt et al., 2007; Saucier et al., 2002a). The question however, whether testosterone relates to the use of global vs. local strategies has to our best knowledge not been investigated so far. It has been suggested though, that (early) testosterone levels relate to both structural lateralization and functional lateralization in favor of the right hemisphere (see Toga and Thompson, 2003 for a review). Given the right-hemispheric dominance for global information (e.g. Fink et al., 1996; Robertson and Lamb, 1991) and the reported link between spatial performance and global processing, we hypothesize that testosterone relates positively to global advantage during the processing of hierarchical stimuli.

Second, spatial abilities vary also over the menstrual cycle, suggesting a role of estradiol and/or progesterone. Generally, women score better on spatial tasks during their low-hormone follicular phase than during their high-hormone luteal phase (Hampson, 1990; Hausmann et al., 2000; McCormick and Teillon, 2001; Schoning et al., 2007). If spatial performance is indeed dependent on global processing, these results suggest increased global and reduced local processing during the follicular phase as opposed to the luteal phase. Consequently, sex differences in global advantage may be stronger and hence easier to detect, when a majority of women participate during their luteal phase. While menstrual cycle phase has been demonstrated to influence global and local processing in number comparison (Pletzer et al., 2013) and emotional memory (Nielsen et al., 2011, 2013), evidence from hierarchical stimuli is still lacking.

Third, oral hormonal contraceptives contain varying doses of ethinyl estradiol and synthetic progestins, and hence may exert estrogenic, progestogenic and androgenic or anti-androgenic effects. Consequently, we seek to explore, whether OC users differ in their processing of hierarchical stimuli from naturally cycling women.

The present study aims to address whether hormonal status of women and sex hormone levels relate to global–local processing in a traditional Navon paradigm systematically varying stimulus materials and attention conditions. We specifically hypothesize that women during their luteal phase show significantly lower global advantage global-to-local interference than men, women during their follicular phase and women on OC. We expect testosterone to relate positively to global advantage and seek to explore, whether estradiol or progesterone relates to global advantage. The effects of hormonal status on global-to-local interference and local-to-global interference and their relationship to sex hormone levels will be explored.

## Materials & methods

### Participants

Forty men (mean age  $\pm$  SD = 20.72  $\pm$  2.72 years), 63 naturally cycling women (mean age  $\pm$  SD = 19.95  $\pm$  1.63 years) and 35 women using oral hormonal contraceptives (OC; mean age  $\pm$  SD = 20.06  $\pm$  1.59 years) participated in the study. Age ranged from 18 to 31 years and did not differ significantly between groups ( $F_{(2,135)} = 1.95$ ,  $p = 0.15$ ). All participants were US college students and received course credit for their participation. All participants gave their signed written consent to participate in the study. The study was approved by the local ethical board. According to self-reports, subjects were not currently on medication and had no psychological, neurological or endocrine disorders. All participants were right-handed. Two of the naturally cycling women, two OC-users and three men reported occasional smoking (2–7 cigarettes per week). All other participants were non-smokers.

Only participants with a regular menstrual cycle between 21 and 35 days were included in the naturally cycling group. These inclusion criteria were set based on the observations on cycle phase length by [Fehring et al. \(2006\)](#). Mean cycle length  $\pm$  SD was 29.50  $\pm$  3.28 days. Naturally cycling women were divided into a follicular (before ovulation) and a luteal (after ovulation) group. Based on the data reported by [Fehring et al. \(2006\)](#), ovulation was assumed 14 days before the onset of the next period. It was estimated by participants' self-reports of the onset of their last period and average cycle length. Women were allocated to the follicular group if their self-reported cycle day was before the time-point of ovulation and their progesterone level lay below the group median of 100 pg/ml. Women were allocated to the luteal group if their self-reported cycle day was after the time-point of ovulation and their progesterone level lay above the group median of 100 pg/ml. According to those criteria, 15 naturally cycling women had to be excluded. 25 women were allocated to the follicular group (mean cycle day  $\pm$  SD: 9.16  $\pm$  5.22) and 23 women to the luteal group (mean cycle day  $\pm$  SD: 24.05  $\pm$  7.02). Only three of the women included in the follicular group had estradiol levels slightly above the group median of 2.90 pg/ml.

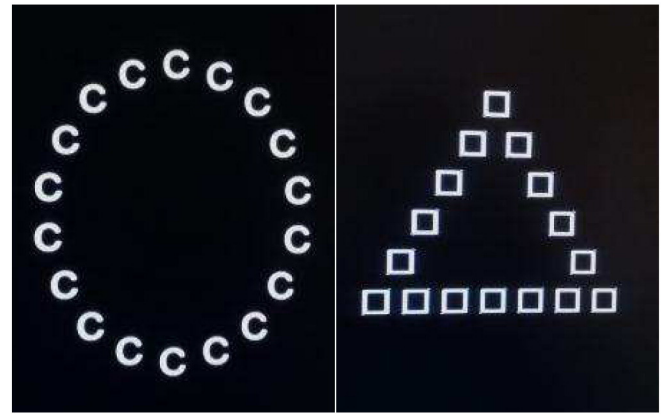
On the day of testing, ten OC users were in their placebo phase. As placebo pills do not contain synthetic hormones, they were excluded from further analysis. The other 25 OC users were in their active pill phase and remained for data analysis. All OC users were on pills containing androgenically active ([Sitruk-Ware, 2006](#)) first (norethindrone acetate – 6 subjects), second (levonorgestrel – 8 subjects) or third generation progestins (norgestimat, desogestrel – 11 subjects).

### Navon task

Global and local processing was assessed using traditional Navon stimuli ([Navon, 1977](#)), which consist of a large global form made up of small local forms of the same type (i.e. large letters of small letters and large shapes of small shapes, see [Fig. 1](#)).

Navon stimuli were constructed from (a) the letters “O”, “C”, “D”, “U” and “V”, and (b) the shapes “triangle” (T), “square” (S), “circle” (C), “hexagon” (H) and “pentagon” (P). None of the letters/shapes used contained an element of fixation to avoid facilitation of local processing, as suggested by [Navon \(2003\)](#). Spacing equaled approximately the size of the local letters/shapes themselves, which was approximately 7% of the global letters/shapes.<sup>1</sup>

There are 20 possible letter stimuli combinations: Oc, Od, Ou, Ov, Co, Cd, Cu, Cv, Do, Dc, Du, Dv, Uo, Uc, Ud, Uv, Vo, Vc, Vd, and Vu, and 20 possible shape stimuli combinations: Ts, Tc, Th, Tp, St, Sc, Sh, Sp, Ct, Cs, Ch, Cp, Ht, Hs, Hc, Hp, Pt, Ps, Pc, and Ph. Upper case letters represent the global letter/shape, and lower case letters represent the local letter/



**Fig. 1.** Example stimuli made of letters (left) and shapes (right).

shape. Combinations presenting the same letter/shape at the global and local levels were excluded (e.g. Oo, Tt) in order to clearly determine whether there was a preference for one level over the other.

Two targets were randomly selected for each participant, and stimuli with targets at both levels were also excluded from presentation. For example, if the selected targets in the letter trial were “O” and “D”, the combinations Do and Od were never presented, thus leaving 18 combinations of letters/shapes for presentation, 6 of which contain a target at the global level and 6 contain a target at the local level.

In one run, these combinations were presented 3 times in randomized order, i.e. 54 stimuli total, 18 each with a target at the global level, target at the local level or no target. Stimuli were presented for 150 ms, preceded by a fixation cross at the center of the screen for 500 ms and followed by an inter-stimulus interval (ISI) of 1500 ms.

In the divided attention condition, participants completed one run and were asked to respond with the left mouse key (YES) whenever a target appeared at any level, either global or local, and the right mouse key (NO) otherwise. Thus, two thirds of the stimuli in this condition did require a left mouse response and one third a right mouse response.

In the focused attention condition, participants completed two runs. In one run they were asked to respond with the left mouse key only if a target appeared at the global level and the right mouse key otherwise. In the other run they were asked to respond with the left mouse key only if a target appeared at the local level and the right mouse key otherwise. Thus, one third of stimuli in this condition did require a left mouse response and two thirds a right mouse response.

Designs using two targets have been successfully employed previously during both divided and focused attention ([Hubner et al., 2007](#); [Muller-Oehring et al., 2007](#); [Volberg and Hubner, 2004](#)). The divided attention condition does not allow for a decision about which letter has been seen, but requires the identification of a target, as both levels need to be attended (compare e.g. [Plaisted et al., 1999](#); [Roalf et al., 2006](#)). In order to compare performance between the divided and focused attention conditions, the same paradigm was employed with focused attention. While the proportion of the left and right responses differed between divided and focused attention conditions, the number of global targets and local targets requiring a left response remained constant to further ensure the comparability of global advantage effects (see [Analyses](#)) between attention conditions.

Stimuli were presented using Presentation software and participants responded with their right hand. Reaction times over correctly solved items (RTs) and error rates (ERs) were recorded.

Data of 21 participants (8 men, 3 follicular women, 4 luteal women, 6 OC users) had to be excluded due to the following problems with either the letter or the shape stimuli or both: (i) 6 participants failed (<15% correct responses) to respond with the left key to local targets in the divided attention condition, while correctly responding to global

<sup>1</sup> Note that two other spacing conditions were also investigated, but are not the focus of this manuscript.

targets and no-targets. This suggests that they misunderstood the instructions for the divided attention condition and directed their attention only to the global level. While this may have been caused by an extreme global bias, the number of correctly solved items was too low to calculate a reliable RT mean. (ii) 6 participants failed (<15% correct responses) to respond with the right key to local targets in the global condition. This suggests that they misinterpreted the instructions for the divided attention condition. While again, this may have been caused by an extreme local bias, the number of correctly solved items was too low to calculate a reliable RT mean. (iii) 2 participants failed (<15% correct responses) to press a key in response to no-targets and (iv) 6 participants did not perform above chance in any category (50% correct responses). The number of participants excluded did not differ between groups ( $\chi^2 = 3.18$ ,  $p = 0.36$ ). Thus, 32 men, 22 follicular women, 19 luteal women and 19 OC users were included in the analysis of the Navon paradigm.

To ensure task reliability for this sample, Cronbach's alpha and split-half reliability using the odd-even method were assessed over RT to the first 14 correctly solved items in each category. For letter stimuli, Cronbach's alpha ranged from 0.83 to 0.87 and split-half reliability from 0.87 to 0.91. For shape stimuli, Cronbach's alpha ranged from 0.80 to 0.91 and split-half reliability from 0.86 to 0.92. Hence, task reliability was good to excellent for the current sample.

### Procedure

Participants arrived at the lab between 9:00 am and 11:00 am and were asked to rinse their mouth with water to remove any particles before saliva sampling. They read and signed the consent form and completed a health questionnaire. Before the actual experiment they completed training trials on both letter and shape stimuli. Participants were trained in the divided attention condition to avoid any possible priming effects of the training on the actual experiment. Priming effects of and on global and local processing have been reported in a variety of areas (see e.g. Forster and Dannenberg, 2010 for an extensive review). Each training trial started off with a slow presentation frequency to allow participants to get used to the stimuli and ended with the presentation frequency of the actual experiment to allow them to get used to the speed as well. Then, all participants completed both the letter and the shape experiments. About half of the participants completed the letter experiment first; the other half completed the shape experiment first. Participants, who received letters first in the experiment, also received letters first in the training, and participants, who received shapes first in the experiment, also received shapes first in the training. Participants started with the divided attention condition for both letters and shapes to avoid any priming effects of the focused attention condition on the divided attention condition. In the focused attention condition about half of the participants were first asked to respond to global targets only (GL); the other half were first asked to respond to local targets only (LG). Participants who received the GL order with letters also received the GL order with shapes, and participants who received the LG order with letters also received the LG order with shapes to ensure comparability of the effects.

Participants gave their first saliva sample after the training trial. The second saliva sample was taken between the letter and shape experiments and the last saliva sample was taken at the end of the experiment. Saliva samples were collected using the passive drool method.

### Sex hormones

Sex hormone levels were quantified from saliva samples using Salimetrics assay kits for progesterone (sensitivity: 5 pg/ml), 17 $\beta$ -estradiol (sensitivity: 0.1 pg/ml) and testosterone (sensitivity: 1.0 pg/ml). For the assessment of steroid hormones, saliva sampling is preferable over blood sampling, because it is non-invasive, not stressful to the participants and the assessment is less complicated by the

presence of specific and non-specific binding proteins. Analysis of sex hormone levels was restricted to men and naturally cycling women, because OCs contain a variety of synthetic progestins at varying concentrations with varying binding affinities to progesterone, estradiol and testosterone receptors. Consequently, the levels assessed by the assay kit may not necessarily reflect the levels of endogenous hormones or the levels of biologically active hormones present. Until hormone assessment, saliva samples were stored at  $-20^\circ\text{C}$  and centrifuged two times at 3000 rpm for 15 min and 10 min, respectively. As recommended by the Salimetrics assay instructions, for each participant the level of each hormone was calculated as the mean over the values assessed in three samples that were collected over the course of the experiment (see Procedure). The value for each sample was determined as the mean over duplicate measurements to ensure reliability of the assessment. Due to CVs higher than 25% between duplicate samples 6 progesterone values, 4 estradiol values and 2 testosterone values were excluded from the analysis.

### Analyses

The global advantage effect, in the divided and focused attention conditions as well as interference effects on reaction times were calculated as standardized contrasts (compare Zhang, 2010), i.e. difference in mean reaction times divided by the standard deviation, for each participant before entering group analysis.<sup>2</sup> Global advantage refers to the difference in RT between YES-responses to local targets and YES-responses to global targets. Global-to-local interference refers to the difference in RT between NO-responses to global targets and NO-responses to stimuli containing no targets in the local condition. Local-to-global interference refers to the difference in RT between NO-responses to local targets and NO-responses to stimuli containing no targets in the global condition. All effects were tested for significance towards zero using one-sample t-tests. The effects were compared between groups and task conditions using repeated measures ANOVAs and related to sex-hormone levels using multiple regression analyses. Inferential statistics are described in detail in the Results section and linked to the specific hypotheses derived in the Introduction.

## Results

### Hormone levels

To confirm that men and naturally cycling women during their follicular and luteal phases showed the expected hormone profiles (compare Table 1), progesterone, estradiol and testosterone levels were compared between men, follicular women and luteal women using one-way ANOVAs (all  $F_{(2,66)} > 9.64$ , all  $p < 0.001$ , all  $\eta^2 > 0.21$ ). Post-hoc Tukey's tests revealed that progesterone and estradiol levels were significantly higher in luteal women compared to men and follicular women (all  $p_{\text{post-hoc}} < 0.008$ , all  $d > 1.00$ ). Follicular women and men did not differ significantly in their estradiol and progesterone levels (both  $p_{\text{post-hoc}} > 0.50$ , both  $d < 0.32$ ). Testosterone levels were significantly higher in men than the female groups (both  $p_{\text{post-hoc}} < 0.001$ , both  $d > 2.55$ ). Follicular and luteal women did not differ in their testosterone levels ( $p_{\text{post-hoc}} = 0.85$ ,  $d = 0.33$ ).

### Global advantage

To test, whether over all participants, reactions to global targets were significantly faster than reactions to local targets, one-sample t-tests were performed comparing the global advantage effects for

<sup>2</sup> Note that unstandardized contrasts, i.e. traditional mean RT differences, did yield the same results for global advantage (compare Section Global advantage). Interference effects (compare Section Interference) did not differ significantly between groups and were not related to sex hormone levels using unstandardized contrasts.

**Table 1**  
Hormone levels.

	Estradiol [pg/ml]	Progesterone [pg/ml]	Testosterone [pg/ml]
Men	2.16 ± 0.76	65.22 ± 44.64	150.42 ± 47.03***
Follicular	2.41 ± 0.80	53.92 ± 27.61	56.88 ± 15.41
Luteal	3.19 ± 0.76##	159.88 ± 34.67###	62.97 ± 21.54

Significantly larger than in follicular women and men: ##p < 0.01 and ###p < 0.001. Significantly larger than in both female groups: \*\*\*p < 0.001.

the divided and focused attention conditions with letter and shape materials to zero. With letter stimuli, reactions to global targets were significantly faster than reactions to local targets for both attention conditions (both  $t_{(91)} > 2.56$ , both  $p < 0.05$ , both  $d > 0.26$ ). With shape stimuli, reactions to global targets were significantly faster than reactions to local targets ( $t_{(91)} = 2.90$ ,  $p < 0.01$ ,  $d = 0.30$ ) in the focused attention condition. In the divided attention condition however, reactions to local targets were by trend faster than reactions to global targets ( $t_{(91)} = -1.81$ ,  $p = 0.07$ ,  $d = 0.19$ ).

In order to address, whether global advantage was reduced in women during their luteal phase as opposed to men, follicular women and OC users, a  $2 \times 2 \times 4$ -repeated measures ANOVA was performed on global advantage effects including the within-subjects factors 'stimulus material' (letters, shapes) and 'attention condition' (divided, focused) and the between subjects factor 'group' (men, follicular, luteal, OC) (compare Fig. 2).

**Task effects**

We observed, significant main effects of stimulus material ( $F_{(1,88)} = 11.75$ ,  $p = 0.001$ ,  $\eta^2 = 0.12$ ) and attention condition ( $F_{(1,88)} = 17.77$ ,  $p < 0.001$ ,  $\eta^2 = 0.17$ ). Global advantage was significantly larger for letter stimuli than for shape stimuli and for the focused attention condition than for the divided attention condition. Stimulus material and attention condition did not interact with each other ( $F_{(1,88)} = 0.32$ ,  $p = 0.58$ ,  $\eta^2 = 0.004$ ).

**Group differences**

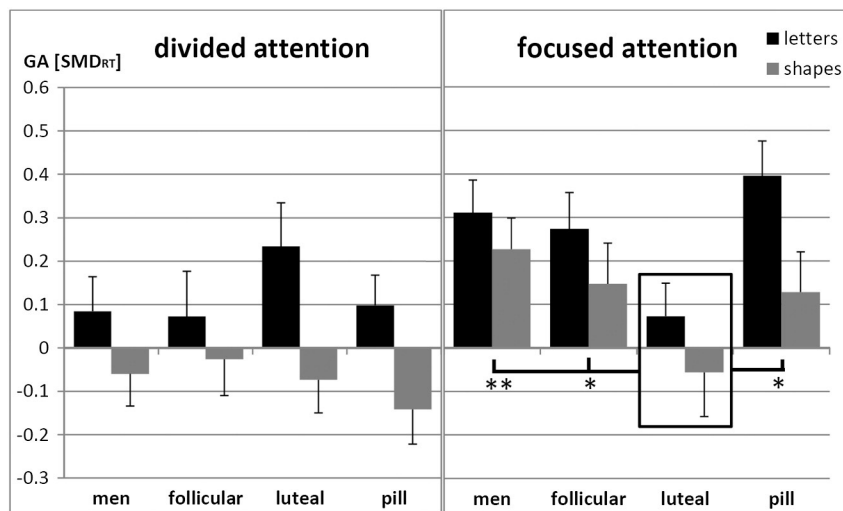
There was no significant main effect of group ( $F_{(3,88)} = 0.75$ ,  $p = 0.52$ ,  $\eta^2 = 0.03$ ) and group did not interact with stimulus material ( $F_{(3,88)} = 0.51$ ,  $p = 0.68$ ,  $\eta^2 = 0.02$ ). However, we observed a significant interaction of group  $\times$  attention condition ( $F_{(3,88)} = 4.01$ ,  $p = 0.01$ ,  $\eta^2 = 0.12$ ), suggesting that group affected global advantage differentially in the different attention conditions.

To further resolve this interaction, we ran separate  $2 \times 4$  ANOVAs with 'stimulus material' as within-subjects and group as between-subjects factor for the divided and focused attention conditions. There was no significant main effect of group in the divided attention condition ( $F_{(3,88)} = 0.49$ ,  $p = 0.69$ ,  $\eta^2 = 0.02$ ), indicating that global advantage during divided attention did not differ significantly between groups. However, a significant main effect of group was observed in the focused attention condition ( $F_{(3,88)} = 3.20$ ,  $p < 0.05$ ,  $\eta^2 = 0.10$ ). A Dunnett's post-hoc test comparing luteal women to all other groups, confirmed that luteal women showed significantly lower global advantage than men ( $p_{\text{post-hoc}} < 0.01$ ,  $d = 0.44$ ), as well as follicular women ( $p_{\text{post-hoc}} < 0.05$ ,  $d = 0.34$ ) and OC users ( $p_{\text{post-hoc}} < 0.05$ ,  $d = 0.35$ ) in the focused attention condition. One-sample t-tests confirmed, that global advantage in the focused attention condition did not differ significantly from zero in luteal women (both  $|t_{(18)}| < 0.73$ , both  $p > 0.47$ , both  $d < 0.20$ ). Additionally, a Tukey's post-hoc test was performed in order to explore, whether global advantage differed further between men, follicular women and OC-users. No significant mean differences were observed between those groups (all  $p_{\text{post-hoc}} > 0.90$ , all  $d < 0.09$ ).

**Relation to sex hormones**

To evaluate the relationship of sex hormones to global advantage in the focused attention condition, i.e. the condition for which group differences were observed, the global advantage effects were averaged over letters and shapes for the focused attention condition. Testosterone, estradiol, and progesterone were entered as independent variables into multiple regression models with global advantage in the focused attention condition as dependent variable. As no hormone levels were available for OC users, these analyses were restricted to men and naturally cycling women. Furthermore, as the hormonal profile differs between men, follicular women and luteal women, the regression model was run not only for the total sample (without OC users), but also for each group separately.

Global advantage in the focused attention condition was significantly related to sex hormone levels (Table 2). In the total sample, testosterone significantly positively related to global advantage during focused attention (compare Fig. 3). The higher the testosterone levels the stronger was the global advantage effect in the focused attention condition. The positive relationship of global advantage to testosterone was confirmed for men and follicular women. However for luteal women, a significant negative relationship between testosterone and global advantage during focused attention was observed. Regression coefficients for testosterone observed in luteal women were significantly different



**Fig. 2.** Global advantage (GA) for the different conditions in men (n = 32), naturally cycling women (22 follicular, 19 luteal) and oral contraceptive (OC) users (n = 19). GA is significantly smaller for shapes than for letters. GA is significantly smaller for divided attention than for focused attention. In the focused attention condition, GA is significantly smaller in luteal women compared to follicular women, men and OC users. SMDRT = standardized mean difference in reaction time. \*p < 0.05, \*\*p < 0.01.

**Table 2**  
Results of regression analyses for global advantage.

Predictors	Total sample <sup>a</sup>		Men		Follicular		Luteal	
	$\beta$	t	$\beta$	t	$\beta$	t	$\beta$	T
Estradiol	0.07	0.50	0.25	0.90	0.04	0.20	-0.01	-0.04
Progesterone	-0.31	-2.14*	-0.36	-1.27	-0.29	-1.32	-0.49	-2.17*
Testosterone	0.31	2.65**	0.38	2.03*	0.47	2.17*	-0.59	-2.74**
Model summary	R	F	R	F	R	F	R	F
	0.43	4.69**	0.42	1.74	0.49	1.85	0.71	4.10*

<sup>a</sup> Without OC users, \* $p < 0.05$ , \*\* $p < 0.01$ .

from coefficients observed in men and follicular women according to Fisher's Z transformation (both  $Z > 3.45$ , both  $p < 0.001$ ).

Furthermore, progesterone was significantly negatively, while estradiol was not related to global advantage during focused attention. The higher the progesterone level the weaker was the global advantage effect in the focused attention condition (compare Fig. 3). The negative relationship between progesterone and global advantage was found in all three groups, although, due to reduced sample sizes, it did only reach significance in luteal women. The three groups did not differ in their regression coefficients for progesterone (all  $Z < 0.70$ , all  $p > 0.24$ ).

### Interference

Over all participants, we observed significant global-to-local interference, but also significant local-to-global interference for both letter and shape stimuli as revealed by one-sample t-test comparing interference effects to zero (all  $t_{(91)} > 2.01$ , all  $p < 0.05$ , all  $d > 0.21$ ).

To explore, whether the hormonal status of participants did also affect interference effects, a  $2 \times 2 \times 4$  repeated-measures ANOVA was performed on the interference effects with 'stimulus material' (letter, shapes) and 'direction' (global-to-local, local-to-global) as within-subjects factors and group as between subjects factor (compare Fig. 4).

### General effects

Significant main effects of stimulus material ( $F_{(1,88)} = 4.38$ ,  $p < 0.05$ ,  $\eta^2 = 0.05$ ) and direction ( $F_{(1,88)} = 6.03$ ,  $p < 0.02$ ,  $\eta^2 = 0.06$ ) were observed, but there was no interaction of stimulus material with direction ( $F_{(1,88)} = 0.05$ ,  $p = 0.83$ ,  $\eta^2 = 0.001$ ). Both global-to-local interference and local-to-global interference were stronger for letter stimuli than for shape stimuli. As expected, global-to-local interference was stronger than local-to-global interference for both letter and shape stimuli.

### Group differences

There was a significant main effect of group ( $F_{(3,88)} = 3.24$ ,  $p < 0.05$ ,  $\eta^2 = 0.10$ ). A post-hoc Tukey's test revealed that compared to OC-users,

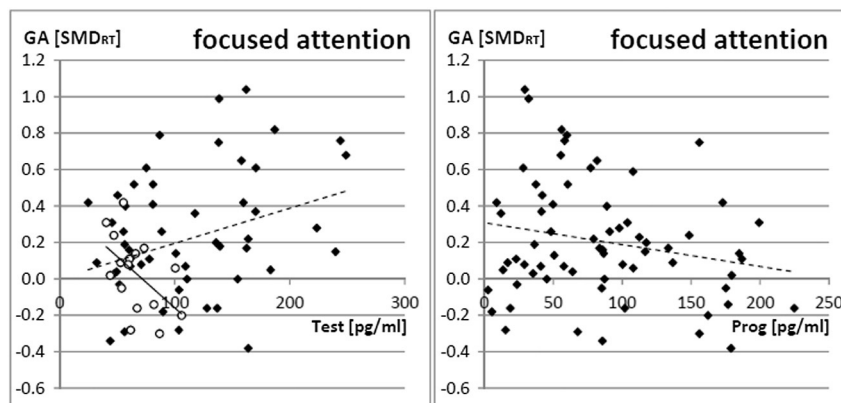
interference was significantly lower in luteal women ( $p_{\text{post-hoc}} < 0.05$ ,  $d = 1.02$ ) and by trend lower in follicular women ( $p_{\text{post-hoc}} = 0.07$ ,  $d = 0.79$ ). Follicular and luteal women did not differ in their interference effects ( $p_{\text{post-hoc}} = 0.96$ ,  $d = 0.17$ ) and men did not differ from any of the female groups (all  $p_{\text{post-hoc}} > 0.22$ , all  $d > 0.58$ ). Group did not interact with stimulus material ( $F_{(3,88)} = 0.87$ ,  $p = 0.46$ ,  $\eta^2 = 0.03$ ) and also not with direction ( $F_{(3,88)} = 0.96$ ,  $p = 0.83$ ,  $\eta^2 = 0.03$ ). Consequently, both global-to-local interference and local-to-global interference were lower in luteal women than the other groups and higher in OC users than the other groups.

### Correlation with sex hormones

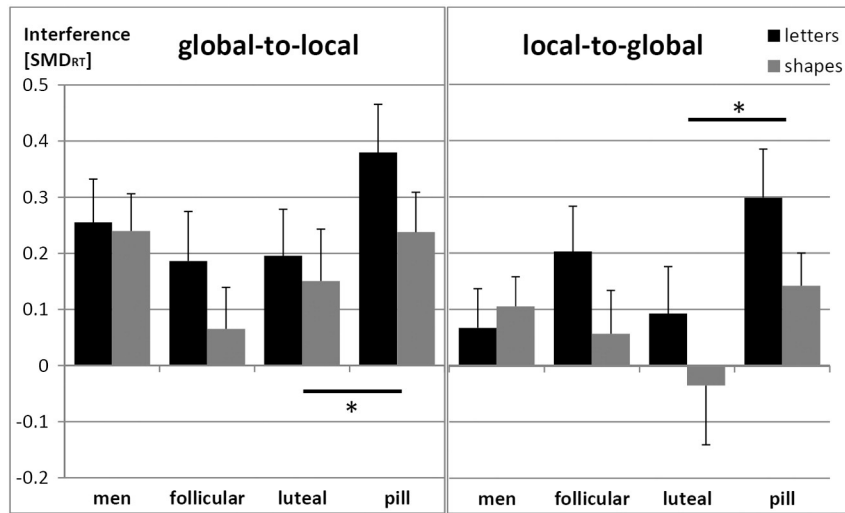
To evaluate the relationship of sex hormones to interference, global-to-local and local-to-global interference effects were averaged over the letters and shapes conditions. Testosterone, estradiol, and progesterone were entered as independent variables into multiple regression models with dependent variables global-to-local interference and local-to-global interference. As no hormone levels were available for OC users, these analyses were restricted to men and naturally cycling women. Furthermore, as the hormonal profile differs between men, follicular women and luteal women, the regression model was run not only for the total sample (without OC users), but also for each group separately.

Global-to-local interference was significantly related to sex hormone levels in the total sample (Table 3). Testosterone was significantly positively related global-to-local interference. The higher the testosterone level, the stronger was the global-to-local interference effect (compare Fig. 5). This relationship was confirmed in men and follicular women, but was absent in luteal women. Regression coefficients for testosterone did however not differ between luteal women and men or follicular women (both  $Z < 1.32$ , both  $p > 0.18$ ) in the analysis of global-to-local interference.

Local-to-global interference was not related to sex hormones in the total sample or in men and follicular women (compare Fig. 5). In luteal women however, local-to-global interference was significantly negatively related to testosterone (Table 3). The higher the testosterone



**Fig. 3.** Relationship of testosterone (Test) and progesterone (Prog) to global advantage during focused attention in men and naturally cycling women. Global advantage (GA) during focused attention relates positively to testosterone and negatively to progesterone in all participants (black rhomboids, dotted line). In luteal women (white circles, solid line), the relationship of testosterone to global advantage is reversed.  $SMD_{RT}$  = standardized mean difference in reaction time.



**Fig. 4.** Interference effects in men (n = 32), naturally cycling women (22 follicular, 19 luteal) and oral contraceptive (OC) users (n = 19). Interference is significantly smaller for shapes than for letters. Global-to-local interference is stronger than local-to-global interference. Naturally cycling women in their luteal phase show less interference than OC users. SMD<sub>RT</sub> = standardized mean difference in reaction time. \*p < 0.05.

level, the weaker was the local-to-global interference effect in luteal women. Regression coefficients for testosterone were significantly more negative in luteal women compared to men and follicular women (both Z > 1.96, both p < 0.05) in the analysis of local-to-global interference.

Progesterone and estradiol were not related to global-to-local or local-to-global interference in the total sample or any group.

**Discussion**

We employed a Navon paradigm in men and women controlling for OC use and menstrual cycle phase. Attention condition (divided vs. focused) and stimulus material (letters vs. shapes) were included as possible modulatory factors. We hypothesized reduced global advantage in women during their luteal phase as opposed to men, women during their follicular phase and users of OC containing androgenic progestins. We suspected a negative relationship of global advantage with testosterone and aimed to differentiate whether estradiol or progesterone best accounted for possible changes over the menstrual cycle.

As predicted, global advantage was reduced in naturally cycling women during their luteal phase compared to men, naturally cycling women during their follicular phase and OC users. There were no differences in global advantage between men, follicular women and OC users. These findings are in good accordance with findings of enhanced detail

memory in women during their luteal phase (Nielsen et al., 2013) and previous findings of more local strategy use in women compared to men as observed in navigation (Galea and Kimura, 1993; Lawton, 1994, 2001; Lawton et al., 1996) and number comparison (Pletzer et al., 2013, 2014).

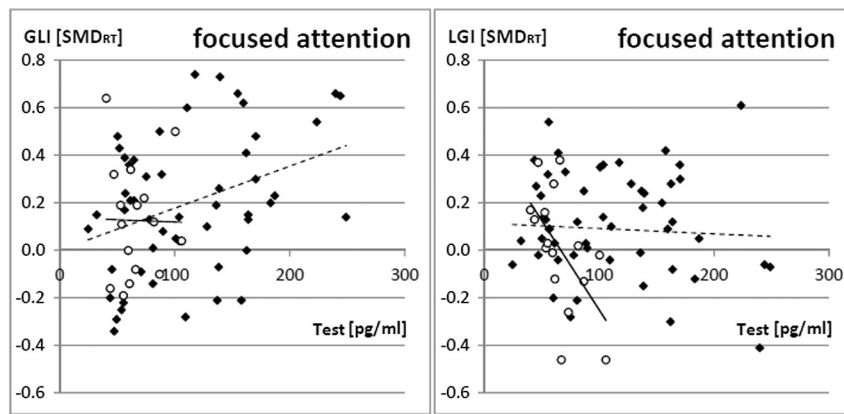
The finding of enhanced global advantage in OC users compares to previous findings of enhanced spatial performance (Wharton et al., 2008), reduced detail memory (Nielsen et al., 2011) and altered brain activation patterns (Pletzer et al., 2014) in OC users. Thus, our study adds to the increasing evidence that studies comparing men and women may fail to detect significant differences without controlling for hormonal contraceptive use. We do note however, that due to the between-subjects design, pre-existing differences between OC users and naturally cycling women could not be controlled for.

As expected, global advantage (during the focused attention condition), as well as global-to-local interference, were positively related to salivary testosterone levels. Remarkably, in women during their luteal phase, global advantage was not positively, but negatively related to testosterone levels. Also, in women during their luteal phase, testosterone levels were not positively related to global-to-local interference, but negatively to local-to-global interference. Apparently, menstrual cycle phase did not only affect global–local processing, but also how it related to sex hormone levels, in particular, testosterone levels. One speculative explanation may be provided by the higher affinity of the enzyme 5α-

**Table 3**  
Results of regression analyses for interference effects.

Global-to-local	Total sample <sup>a</sup>		Men		Follicular		Luteal	
	β	t	β	T	β	t	β	t
Predictors								
Estradiol	0.05	0.30	0.11	0.38	−0.03	−0.14	0.07	0.22
Progesterone	0.05	0.34	0.04	0.15	−0.26	−1.15	0.16	0.51
Testosterone	0.35	2.88**	0.35	1.86~	0.42	1.88~	0.00	−0.01
Model summary	R	F	R	F	R	F	R	F
	0.35	2.80*	0.40	1.53	0.43	1.38	0.20	0.16
Local-to-global	Total sample <sup>a</sup>		Men		Follicular		Luteal	
	β	t	β	T	β	t	β	t
Predictors								
Estradiol	−0.13	−0.81	−0.03	−0.11	−0.30	−1.28	0.12	0.49
Progesterone	−0.06	−0.37	0.14	0.46	0.31	1.33	−0.27	−1.06
Testosterone	−0.08	−0.64	−0.15	−0.71	−0.04	−0.19	−0.64	−2.65*
Model summary	R	F	R	F	R	F	R	F
	0.18	0.70	0.17	0.24	0.36	0.91	0.62	2.48

<sup>a</sup> Without OC users, \*p < 0.05, \*\*p < 0.01, ~p < 0.10.



**Fig. 5.** Relationship of testosterone (Test) to interference effects in men and naturally cycling women. Testosterone relates positively to global-to-local interference (GLI) and not to local-to-global interference (LGI) in all participants (black rhomboids, dotted line). In women during their luteal phase (white circles, solid line), testosterone is not related to GLI and significantly negatively to LGI.  $SMD_{RT}$  = standardized mean difference in reaction time.

dehydrogenase for progesterone compared to testosterone (Wright et al., 1983).  $5\alpha$ -dehydrogenase converts testosterone into the physiologically more active dihydro-testosterone. In the presence of high progesterone levels, less testosterone is converted, resulting in higher levels of testosterone that are physiologically less active. Regression results in single groups should however be interpreted with care, as they may have suffered from insufficient statistical power.

Furthermore a negative relationship was observed between global advantage and progesterone, but not estradiol levels for the focused attention condition. The relationship to progesterone was particularly strong during the luteal cycle phase. Thus, the menstrual cycle-dependent differences in global advantage during focused attention were likely attributable to progesterone, but not estradiol. Thus, a previously suggested estradiol-dependent reduction of right-hemisphere functioning during the luteal phase (Hampson, 1990) is unlikely to account for menstrual cycle-dependent changes. One possible explanation for the reduction of global advantage during the luteal phase however, is provided by menstrual cycle dependent changes in hemispheric asymmetries.

Lateralization of brain functions has been related to inter-hemispheric inhibition, i.e. an inhibitory influence of the hemisphere dominant in a task on the non-dominant hemisphere (Chiarello and Maxfield, 1996). While global processing is lateralized to the right hemisphere, local processing is lateralized to the left hemisphere (Fink et al., 1996; Robertson and Lamb, 1991). Therefore, a global advantage suggests that the inhibitory influence of the right on the left hemisphere during global processing is stronger than the inhibitory influence of the left on the right hemisphere during local processing. It is possible, that a general right hemisphere dominance as observed in attention tasks (Heilman et al., 1983), can account for this fact. Thus, the right-hemispheric dominance in attention tasks superimposes on the left-right dichotomization of global-local processing. Consequently, the size of the global advantage effect may depend on inter-hemispheric inhibition. While the relation of global advantage to inter-hemispheric communication has to our best knowledge not been tested directly before, it has been demonstrated that global-to-local interference, another indicator of global precedence, was absent in commissurotomy patients (Robertson et al., 1993). Thus, it is important to note that in the present study global advantage during focused attention was significantly related to global-to-local interference ( $r = 0.24$ ,  $p < 0.05$ ). Also, a reduction in global advantage (e.g. during the luteal phase or with shape stimuli) was always accompanied by reduced interference.

Importantly, hemispheric asymmetries are less pronounced in women than in men (see Renteria, 2012 for a review), and particularly reduced during the luteal cycle phase (Hausmann and Gunturkun, 2000). This reduction has been attributed to a progesterone-mediated reduction in inter-hemispheric inhibition (Hausmann and Gunturkun,

2000). Consequently, the observed progesterone-mediated reduction of global advantage during the luteal phase may result from a progesterone mediated reduction of inter-hemispheric inhibition during global-local processing. Note that interference was also lowest during the luteal phase, however not modulated significantly by progesterone levels. While recent studies do also suggest a role of estradiol in inter-hemispheric communication (Hausmann and Gunturkun, 2000; Hausmann et al., 2013; Weis and Hausmann, 2010; Weis et al., 2008), no association between estradiol and global advantage or interference has been observed in the present study.

Global processing has previously been associated with positive mood (Gasper and Clore, 2002; Rowe et al., 2007), which is reduced during the luteal cycle phase (Backstrom et al., 2003). However, the relationship between mood and steroid hormones, particularly progesterone is still discussed controversially and both positive and negative effects have been reported (Schwartz et al., 2012). If our findings are associated with sex hormone dependent mood changes, they may have important implications not only for cognitive, but also for emotional processing. In line with this assumption, processing of gist and detail information in an emotional memory task has been related to hormonal status of participants (Nielsen et al., 2011).

Turning to the modulatory effects of task factors, it is important to note that the group differences in global advantage and its relation to sex hormones were independent of stimulus material, underscoring the universality of the effect. However, contrary to our assumption that letter stimuli might facilitate local processing, global advantage and also interference in both directions were stronger for letter stimuli than for shape stimuli. One important difference between letter and shape stimuli that may have contributed to this finding is symmetry, which has been found to reduce inter-hemispheric communication (Brybaert, 1994, 2004). While most letter stimuli are asymmetrical, shape stimuli are symmetrical. Furthermore, while letter stimuli have a verbal and shape stimuli a visuo-spatial nature, the recognition of both forms does not per se require verbal or spatial manipulations. On the other hand, stimulus material has been demonstrated to modulate the lateralization of global processing to the right and local processing to the left hemisphere. Some studies find that with shape or object material, lateralization is reduced or even reversed (Fink et al., 1997; Keita and Bedoin, 2011). As our previous argument speculatively linked the size of the global advantage effect to the right-hemisphere advantage in attention, these findings may explain the reduced global advantage in shape stimuli observed in the present study. If global aspects are not processed selectively in the right hemisphere, a right-hemisphere advantage in attention would result in reduced global advantage.

However, contrary to its universality across stimulus materials, global advantage was only related to hormonal status and sex hormone levels in the focused attention condition, not in the divided attention



condition. Furthermore, global advantage was in general smaller during divided attention than during focused attention. We do however interpret this latter comparison carefully, as the proportion of targets participants had to respond unavoidably differed between the divided and focused attention conditions.

Studies directly comparing divided and focused attention tasks in global and local processing are rare and mostly conducted in clinical populations. Supporting our finding of reduced global advantage in divided compared to focused attention, autistic children show local precedence in a divided attention task, but global precedence in a focused attention task (Plaisted et al., 1999). Also patients with visuo-spatial neglect were particularly impaired in global processing during a divided, but not during a focused attention task (Lux et al., 2006).

We suspect important differences in inter-hemispheric communication between the divided and the focused attention condition. During divided attention global and local levels need to be processed simultaneously, which is done most efficiently in different hemispheres. However, since any target requires a response, neither level needs to be suppressed, i.e. there is no need for inter-hemispheric inhibition. During focused attention however, responses to targets at the non-instructed level need to be inhibited, i.e. inter-hemispheric inhibition is necessary. If global advantage is indeed related to inter-hemispheric inhibition, a stronger global advantage is to be expected during focused attention than during divided attention. Furthermore, progesterone should only affect global advantage negatively in conditions involving inter-hemispheric inhibition, i.e. during the focused, but not during the divided attention condition. Both predictions are in line with results of the present study.

In summary, the present study was the first to investigate the hormonal modulation of global–local processing in a traditional Navon paradigm. During the luteal cycle phase, when progesterone levels were elevated, global advantage was significantly reduced and the relationship of global advantage and interference to testosterone levels was altered. Since the attentional selection of global and local stimulus aspects seems to underlie a variety of sex differences in cognition and emotion, our results indicate that the differential processing of global and local information may be one simple principle underlying not only sex dependent, but more importantly also menstrual cycle dependent behavioral changes. As the present study did not involve visual-hemifield manipulations the link to hemispheric asymmetries in global–local processing remains speculative. However, if the lateralization of brain functions does indeed contribute to our findings, hemispheric asymmetries in global and local processing may influence brain function and behavior to a higher degree than has so far been recognized. Thereby, progesterone may act, at least in part as a switch between the hemispheres counteracting testosterone and allowing women to see the trees in the forest during their luteal cycle phase.

## Acknowledgments

This project was funded by NIMH grant 575082LC supporting Larry Cahill and Schrödinger fellowship J3165–G17 of the Austrian Science Fund supporting Belinda Pletzer. We thank Rachel Tong, Annie Hu and Azadeeh Gohardaz for their help with data collection and Nicole Ertman, Nicole Ferree and Shawn Niensens for their help with hormone assessment and their advice. Furthermore, we acknowledge all participants for their time and willingness to contribute to this study.

## References

Andersen, N.E., Dahmani, L., Konishi, K., Bohbot, V.D., 2012. Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiol. Learn Mem.* 97 (1), 81–89.

Andreano, J.M., Cahill, L., 2009. Sex influences on the neurobiology of learning and memory. *Learn. Mem.* 16, 248–266.

Backstrom, T., Andreen, L., Birzniece, V., Bjorn, I., Johansson, I.M., Nordenstam-Haghjo, M., Nyberg, S., Sundstrom-Poromaa, I., Wahlstrom, G., Wang, M.D., Zhu, D., 2003. The role

of hormones and hormonal treatments in premenstrual syndrome. *Cns Drugs* 17, 325–342.

Brybaert, M., 1994. Interhemispheric-transfer and the processing of foveally presented stimuli. *Behav. Brain Res.* 64, 151–161.

Brybaert, M., 2004. The importance of interhemispheric transfer for foveal vision: a factor that has been overlooked in theories of visual word recognition and object perception. *Brain Lang.* 88, 259–267.

Burkitt, J., Widman, D., Saucier, D.M., 2007. Evidence for the influence of testosterone on the performance of spatial navigation in a virtual water maze in women but not in men. *Horm. Behav.* 51, 649–654.

Cahill, L., van Stegeren, A., 2003. Sex-related impairment of memory for emotional events with beta-adrenergic blockade. *Neurobiol. Learn. Mem.* 79, 81–88.

Cahill, L., Gorski, L., Belcher, A., Huynh, Q., 2004. The influence of sex versus sex-related traits on long-term memory for gist and detail from an emotional story. *Conscious. Cogn.* 13, 391–400.

Chapple, C.L., Vaske, J., Hope, T.L., 2010. Sex differences in the causes of self-control: an examination of mediation, moderation, and gendered etiologies. *J. Crime Justice* 38, 1122–1131.

Chiarello, C., Maxfield, L., 1996. Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. *Brain Cogn.* 30, 81–108.

Fehring, R.J., Schneider, M., Raviele, K., 2006. Variability in the phases of the menstrual cycle. *J. Obstet. Gynecol. Neonatal.* 35, 376–384.

Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1996. Where in the brain does visual attention select the forest and the trees? *Nature* 382, 626–628.

Fink, G.R., Marshall, J.C., Halligan, P.W., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1997. Hemispheric specialization for global and local processing: the effect of stimulus category. *Proceedings. Biol. Sci. R. Soc.* 264, 487–494.

Forster, J., Dannenberg, L., 2010. GLOMO(sys): a systems account of global versus local processing. *Psychol. Inq.* 21, 175–197.

Galea, L.A.M., Kimura, D., 1993. Sex-differences in route-learning. *Personal. Individ. Differ.* 14, 53–65.

Gasper, K., Clore, G.L., 2002. Attending to the big picture: mood and global versus local processing of visual information. *Psychol. Sci.* 13, 34–40.

Hampson, E., 1990. Variations in sex-related cognitive-abilities across the menstrual-cycle. *Brain Cogn.* 14, 26–43.

Hausmann, M., Gunturkun, O., 2000. Steroid fluctuations modify functional cerebral asymmetries: the hypothesis of progesterone-mediated interhemispheric decoupling. *Neuropsychologia* 38, 1362–1374.

Hausmann, M., Slabbekoorn, D., Van Goozen, S.H.M., Cohen-Kettenis, P.T., Gunturkun, O., 2000. Sex hormones affect spatial abilities during the menstrual cycle. *Behav. Neurosci.* 114, 1245–1250.

Hausmann, M., Hamm, J.P., Waldie, K.E., Kirk, I.J., 2013. Sex hormonal modulation of inter-hemispheric transfer time. *Neuropsychologia* 51, 1734–1741.

Heilman, K.M., Watson, R.T., Bower, D., Valenstein, E., 1983. Right-hemisphere dominance for attention. *Rev. Neurol.* 139, 15–17.

Hooven, C.K., Chabris, C.F., Ellison, P.T., Kosslyn, S.M., 2004. The relationship of male testosterone to components of mental rotation. *Neuropsychologia* 42, 782–790.

Hubner, R., Volberg, G., Studer, T., 2007. Hemispheric differences for global/local processing in divided attention tasks: further evidence for the integration theory. *Percept. Psychophys.* 69, 413–421.

Keita, L., Bedoin, N., 2011. Hemispheric asymmetries in hierarchical stimulus processing are modulated by stimulus categories and their predictability. *Laterality* 16, 333–355.

Kimchi, R., Amishav, R., Sulitzeanu-Kenan, A., 2009. Gender differences in global–local perception? Evidence from orientation and shape judgments. *Acta Psychol.* 130, 64–71.

Kinsbourne, M., 1970. The cerebral basis of lateral asymmetries in attention. *Acta Psychol. (Amst)* 33, 193–201.

Lawton, C.A., 1994. Gender differences in way-finding strategies – relationship to spatial ability and spatial anxiety. *Sex Roles* 30, 765–779.

Lawton, C.A., 2001. Gender and regional differences in spatial referents used in direction giving. *Sex Roles* 44, 321–337.

Lawton, C.A., Charleston, S.I., Zieles, A.S., 1996. Individual- and gender-related differences in indoor wayfinding. *Environ. Behav.* 28, 204–219.

Levine, A., Kramer, J.H., Brizendine, L., 2001. Testosterone is related to speed of mental rotation in older, healthy men. *Arch. Clin. Neuropsychol.* 16, 860–861.

Lux, S., Thimm, M., Marshall, J.C., Fink, G.R., 2006. Directed and divided attention during hierarchical processing in patients with visuo-spatial neglect and matched healthy volunteers. *Neuropsychologia* 44, 436–444.

Martin, M., 1979. Local and global processing – role of sparsity. *Mem. Cogn.* 7, 476–484.

Martin, D.M., Wittert, G., Burns, N.R., 2007. Gonadal steroids and visuo-spatial abilities in adult males: implications for generalized age-related cognitive decline. *Aging Male* 10, 17–29.

McCormick, C.M., Teillon, S.M., 2001. Menstrual cycle variation in spatial ability: relation to salivary cortisol levels. *Horm. Behav.* 39, 29–38.

Mekarski, J.E., Cutmore, T.R.H., Suboski, W., 1996. Gender differences during processing of the Stroop task. *Percept. Mot. Skills* 83, 563–568.

Muller, J., Dreisbach, G., Brocke, B., Lesch, K.P., Strobel, A., Goschke, T., 2007. Dopamine and cognitive control: the influence of spontaneous eyeblink rate, DRD4 exon III polymorphism and gender on flexibility in set-shifting. *Brain Res.* 1131, 155–162.

Muller-Oehring, E.M., Schulte, T., Raassi, C., Pfefferbaum, A., Sullivan, E.V., 2007. Local–global interference is modulated by age, sex and anterior corpus callosum size. *Brain Res.* 1142, 189–205.

Navon, D., 1977. Forest before trees – precedence of global features in visual-perception. *Cogn. Psychol.* 9, 353–383.

- Navon, D., 1981. The forest revisited – more on global precedence. *Psychol. Res. Psychol. Forsch.* 43, 1–32.
- Navon, D., 2003. What does a compound letter tell the psychologist's mind? *Acta Psychol.* 114, 273–309.
- Nielsen, S.E., Ertman, N., Lakhani, Y.S., Cahill, L., 2011. Hormonal contraception usage is associated with altered memory for an emotional story. *Neurobiol. Learn. Mem.* 96, 378–384.
- Nielsen, S.E., Segal, S.K., Worden, I.V., Yim, I.S., Cahill, L., 2013. Hormonal contraception use alters stress responses and emotional memory. *Biol. Psychol.* 92, 257–266.
- Pena, D., Contreras, M.J., Shih, P.C., Santacreu, J., 2008. Solution strategies as possible explanations of individual and sex differences in a dynamic spatial task. *Acta Psychol.* 128, 1–14.
- Plaisted, K., Swettenham, J., Rees, L., 1999. Children with autism show local precedence in a divided attention task and global precedence in a selective attention task. *J. Child Psychol. Psychiatry* 40, 733–742.
- Pletzer, B., Kronbichler, M., Nuerk, H.C., Kerschbaum, H., 2013. Sex differences in the processing of global vs. local stimulus aspects in a two-digit number comparison task – an fMRI study. *Plos One* 8.
- Pletzer, B., Kronbichler, M., Nuerk, H.C., Kerschbaum, H., 2014. Hormonal contraceptives masculinize brain activation patterns in the absence of behavioral changes in two numerical tasks. *Brain Res.* 1348, 55–62.
- Puts, D.A., Cardenas, R.A., Bailey, D.H., Burriss, R.P., Jordan, C.L., Breedlove, S.M., 2010. Salivary testosterone does not predict mental rotation performance in men or women. *Horm. Behav.* 58, 282–289.
- Razumnikova, O.M., Vol'f, N.V., 2011. Selection of visual hierarchical stimuli between global and local aspects in men and women. *Fiziol. Cheloveka* 37, 14–19.
- Renteria, M.E., 2012. Cerebral asymmetry: a quantitative, multifactorial, and plastic brain phenotype. *Twin Res.* 15, 401–413.
- Rilea, S.L., 2008. A lateralization of function approach to sex differences in spatial ability: a reexamination. *Brain Cogn.* 67, 168–182.
- Roalf, D., Lowery, N., Turetsky, B.J., 2006. Behavioral and physiological findings of gender differences in global–local visual processing. *Brain Cogn.* 60, 32–42.
- Robertson, L.C., Lamb, M.R., 1991. Neuropsychological contributions to theories of part/whole organization. *Cogn. Psychol.* 23, 299–330.
- Robertson, L.C., Lamb, M.R., Zaidel, E., 1993. Interhemispheric relations in processing hierarchical patterns: evidence from normal and commissurotomy subjects. *Neuropsychology* 7, 325–342.
- Rowe, G., Hirsh, J.B., Anderson, A.K., 2007. Positive affect increases the breadth of attentional selection. *Proc. Natl. Acad. Sci. U. S. A.* 104, 383–388.
- Saucier, D., MacFadden, A., Elias, L., Bell, S., 2002a. Sex differences in real-world navigation may relate to disorientation and endogenous testosterone levels. *J. Cogn. Neurosci.* 105–105.
- Saucier, D.M., Green, S.M., Leason, J., MacFadden, A., Bell, S., Elias, L.J., 2002b. Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behav. Neurosci.* 116, 403–410.
- Schoning, S., Engelen, A., Kugel, H., Schafer, S., Schiffbauer, H., Zwitserlood, P., Pletziger, E., Beizai, P., Kersting, A., Ohrmann, P., Greb, R.R., Lehmann, W., Heindel, W., Arolt, V., Konrad, C., 2007. Functional anatomy of visuo-spatial working memory during mental rotation is influenced by sex, menstrual cycle, and sex steroid hormones. *Neuropsychologia* 45, 3203–3214.
- Schwartz, D.H., Romans, S.E., Meiyappan, S., De Souza, M.J., Einstein, G., 2012. The role of ovarian steroid hormones in mood. *Horm. Behav.* 62, 448–454.
- Silverman, I., Kastuk, D., Choi, J., Phillips, K., 1999. Testosterone levels and spatial ability in men. *Psychoneuroendocrinology* 24, 813–822.
- Silverman, I., Choi, J., Peters, M., 2007. The Hunter–Gatherer theory of sex differences in spatial abilities: data from 40 countries. *Arch. Sex. Behav.* 36, 261–268.
- Sitruk-Ware, R., 2006. New progestagens for contraceptive use. *Hum. Reprod. Update* 12, 169–178.
- Toga, A.W., Thompson, P.M., 2003. Mapping brain asymmetry. *Nat. Rev. Neurosci.* 4, 37–48.
- Volberg, G., Hubner, R., 2004. On the role of response conflicts and stimulus position for hemispheric differences in global/local processing: an ERP study. *Neuropsychologia* 42, 1805–1813.
- Voyer, D., Voyer, S., Bryden, M.P., 1995. Magnitude of sex-differences in spatial abilities – a metaanalysis and consideration of critical variables. *Psychol. Bull.* 117, 250–270.
- Vuoksima, E., Kaprio, J., Eriksson, C.J.P., Rose, R.J., 2012. Pubertal testosterone predicts mental rotation performance of young adult males. *Psychoneuroendocrinology* 37, 1791–1800.
- Weis, S., Hausmann, M., 2010. Sex hormones: modulators of interhemispheric inhibition in the human brain. *Neuroscientist* 16, 132–138.
- Weis, S., Hausmann, M., Stoffers, B., Vohn, R., Kellermann, T., Sturm, W., 2008. Estradiol modulates functional brain organization during the menstrual cycle: an analysis of interhemispheric inhibition. *J. Neurosci.* 28, 13401–13410.
- Wharton, W., Hirshman, E., Merritt, P., Doyle, L., Paris, S., Gleason, C., 2008. Oral contraceptives and androgenicity: influences on visuospatial task performance in younger individuals. *Exp. Clin. Psychopharmacol.* 16, 156–164.
- Wright, F., Giacomini, M., Riahi, M., Mowszowicz, I., 1983. Antihormone activity of progesterone and progestins. In: Bardin, C.W., Milgröm, E., Mauvais-Jarvis, P. (Eds.), *Progesterone and Progestins*. Raven Press, pp. 121–134.
- Zhang, X., 2010. Contrast variable potentially providing a consistent interpretation to effect sizes. *J. Biom. Biostat.* 1.