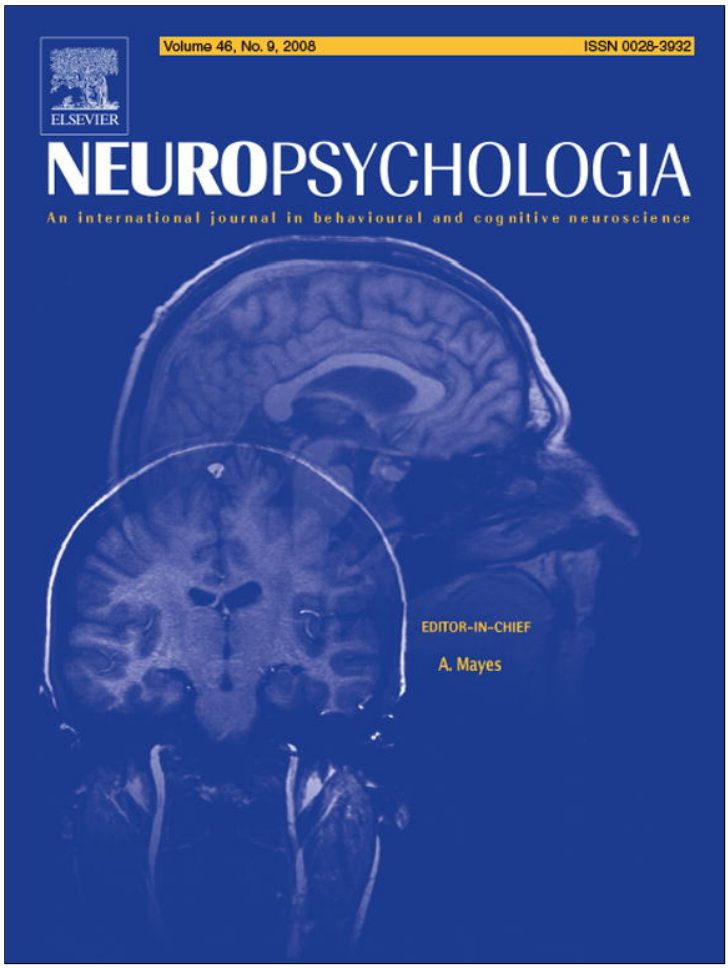

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Interhemispheric interaction during the menstrual cycle

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ABSTRACT

Fluctuating levels of sex hormones and high levels of progesterone (P), in particular, have been suggested to reduce interhemispheric inhibition. The present study focuses on hormone-dependent modulation of interhemispheric integration. In two versions of the Banich–Belger task, participants were asked to match letters according to their physical (e.g., A vs. A) and semantic identity (e.g., A vs. a). Matches were presented either within or across visual half-fields. Moreover, a simple reaction-time task (Poffenberger task) that is assumed to estimate interhemispheric transfer time (IHTT) was used. Seventeen normally cycling women were tested during low P menses and high P midluteal phase. Saliva levels of P were analysed using chemiluminescence assays. Fifteen postmenopausal women performed the same tasks in corresponding time intervals. Additionally, 28 younger male controls were tested once. In agreement with previous results, the more demanding (semantic) interhemispheric-integration task revealed a typical across-field advantage (AFA) for all three groups. However, in normally cycling women, the AFA was significantly reduced during menses. IHTT did not change across the cycle phases. The results indicate that interhemispheric integration fluctuates across the menstrual cycle and is reduced during menses. During the luteal phase, however, the AFA is increased, suggesting that accompanying hormonal conditions favour an efficient interhemispheric integration. We conclude that transcallosal mechanisms involved in interhemispheric integration are profoundly altered when sex hormones are permanently reduced as in men and postmenopausal women. This difference enables an efficient interhemispheric integration without modulatory effects of P.

1. Introduction

Sex hormones are capable to change the functional cerebral organization by organizing and activating effects (Wisniewski, 1998). The effects of sex hormones have been particularly investigated in normally cycling women because their endogenous hormone levels fluctuate dramatically across the menstrual cycle. Although contradictions exist (e.g., Chiarello, McMahon, & Schaefer, 1989; Compton & Levine, 1997), the majority of studies testing women during different cycle phases reported cycle-dependent fluctuations in functional cerebral asymmetries (FCAs) (Bibawi, Cherry, & Hellige, 1995; Hausmann, Becker, Gather, & Güntürkün, 2002; Hausmann & Güntürkün, 2000; Heister, Landis, Regard, & Schroeder-Heister, 1989; McCourt, Mark, Radonovich, Willison, & Freeman, 1997; Mead & Hampson, 1997; Rode, Wagner, & Güntürkün, 1995; Sanders & Wenmoth, 1998). Some of these studies suggest that it is especially the left hemisphere which is affected by sex-hormone-related changes across the menstrual cycle (e.g., Bibawi et al., 1995; Hampson, 1990a; Hampson, 1990b), while others propose the opposite, and suggest that the right hemisphere is particularly sensitive for hormonal fluctuations (e.g., Sanders & Wenmoth, 1998).

A different approach has been proposed by others (Hausmann & Güntürkün, 2000) who hypothesized that the interaction between both hemispheres is affected by the activating effects of sex hormones. This idea is based on the assumption that interhemispheric interaction that takes place as interhemispheric inhibition between homotopic structures is a fundamental prerequisite for the manifestation of FCAs (e.g., Chiarello & Maxfield, 1996). Specifically, the hypothesis of progesterone-modulated interhemispheric decoupling (Hausmann & Güntürkün, 2000) assumes that high levels of progesterone (P) and its metabolites attenuate interhemispheric inhibition by decreasing glutamatergic callosal synaptic efficiency. This then leads to a functional decoupling of both hemispheres which finally results in reduced FCAs when P-levels are high. In these studies, the typical left-hemispheric superiority in word matching as well as the right-hemispheric advantage in polygon matching and face discrimination was reduced during the midluteal phase (Hausmann et al., 2002; Hausmann & Güntürkün, 2000), suggesting that a sex-hormones-related reduction of FCAs is relatively task-independent.

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Although the hypothesis of P-modulated interhemispheric decoupling (Hausmann et al., 2002; Hausmann & Güntürkün, 2000) refers to a specific process of interhemispheric inhibition and hence, may only account for P-related changes of FCAs, the general idea that sex hormones affect interhemispheric interaction has received some support from studies using tasks which cannot be performed without interhemispheric crosstalk. For example, during the midluteal phase, Hausmann (2005) found a reduced hand-use difference in a visual line-bisection task which has been assumed to be affected by transcallosal interactions. The reduced hand-use difference has been suggested to reflect transcallosal spreading activation from the line-bisection bias-dominating right hemisphere to the left hemisphere, controlling the left and right hand, respectively. In this study, the reduced hand-use difference was mainly related to high estradiol (E) levels. Even though this task provides a rather indirect measure of interhemispheric interaction, these findings suggest that different transcallosal processes might be differentially affected by E and P.

The first direct physiological support of the idea that gonadal hormones affect interhemispheric interactions comes from a recent study (Hausmann et al., 2006) using transcranial magnetic stimulation (TMS). Hausmann et al. (2006) examined transcallosal motor inhibition in normally cycling women during menses, follicular, and midluteal cycle phase. The results revealed a negative relationship between transcallosal inhibition and E- and P-levels during the follicular and luteal phase, respectively, which underlines their neuromodulatory properties on glutamatergic and GABAergic neurons. Since motor functions have been shown to be asymmetrically organized in the brain, these findings can be interpreted in terms of the hypothesis of P-modulated interhemispheric decoupling (Hausmann et al., 2002; Hausmann & Güntürkün, 2000) according to which a P-related reduction of interhemispheric inhibition should result in a more bilateral organization of motor functions (*see* Hausmann et al., 2006 *for details*).

A different aspect of interhemispheric interaction has been considered by Compton, Costello, & Diepold (2004) who investigated whether sex hormones modulate interhemispheric integration in women during the menstrual cycle. The authors used a prominent paradigm by Banich and Belger (1990) which can hardly be performed without an integration of information between the hemispheres (e.g., Zaidel, 1995). In the Banich–Belger task, individuals must decide whether a target item matches either one of two probes. If the target and matching probe are positioned in the same visual half-field (VHF, within-field trials), and hence directed to the same hemisphere, no interhemispheric interaction is required to make the decision. In contrast, on across-field trials, the target and matching probe are directed to different hemispheres. Thus, the brain must integrate the information across hemispheres to identify the match. To this end, both hemispheres must be able to actively participate without being inhibited by the other side. Thus, the Banich and Belger task measures the ability for bihemispheric activation and integration of information across hemispheres by comparing bi-hemisphere processing to within-hemisphere processing. It has been shown that across-field integration allowing for a division of labour between the hemispheres enhances performance when task complexity increases (across-field advantage, AFA), but impedes performance on less demanding tasks (Banich & Belger, 1990). Compton et al. (2004) used a more complex version of the Banich–Belger task in which normally cycling women were required to determine whether two letters had the same name (e.g., "A" and "a"). Since a match decision in this task cannot be made on physical characteristics alone, it requires the transformation of letters into their semantic code. This is considerably more demanding and hence should produce an advantage in performance when the two hemispheres must communicate (AFA).

It is important to note that the type of interhemispheric interaction required by the Banich and Belger task deviates from the previously used perceptual asymmetry experiments. The Banich–Belger task requires a bihemispheric activation and interhemispheric integration and thus both hemispheres contribute to the output. In contrast, the perceptual asymmetry tasks employed by Hausmann and Güntürkün require an inhibitory coupling to achieve meta-control of the dominant side during task performance (only one hemisphere dominates the output) (Chiarello & Maxfield, 1996). Referring to the hypothesis of progesterone-mediated interhemispheric decoupling, Compton et al. (2004) expected a P-related reduction in AFA during the midluteal phase compared to menses, which is based on interhemispheric decoupling. Given the view presented above, this is not necessarily the case. One might also hypothesize that P leads to a greater integration between the hemispheres due to less interhemispheric inhibition. In fact, behavioural data did not reveal any hormonal effects on interhemispheric integration (Compton et al., 2004). The authors concluded that P might modulate interhemispheric inhibition but not interhemispheric integration.

As stated above, task difficulty seems to be an important factor in tasks that require interhemispheric integration. The AFA is particularly present when the benefit of interhemispheric integration is sufficient to overweigh its costs, a situation that is usually given on highly demanding across-field trials (Weissman, Banich, & Puente, 2000). In contrast, on less demanding across-field trials the benefit of interhemispheric integration is too small to outweigh the costs leading to no or even a negative AFA, indicating a within-field advantage. Thus, regardless whether the AFA is positive or negative, it reflects the efficiency of interhemispheric integration relative to intrahemispheric processing. Since it has been shown that the relative efficiency of interhemispheric processing gradually changes as a function of task difficulty (Weissman & Banich, 2000), the present study investigates the influence of task difficulty on cycle-related changes in AFA. Normally cycling women were tested during the midluteal and the menstrual phase in a less and a more demanding version of the Banich–Belger paradigm, the physical- and name-identity task, respectively. Given that interhemispheric integration indeed changes across the menstrual cycle, it seems likely that sex hormones mainly affect interhemispheric processes on a higher processing level. Thus, we hypothesize that menstrual cycle-related fluctuations in AFA are particularly pronounced in the more demanding name-identity task.

Men and postmenopausal women not taking any hormonal replacements were used as controls. Due to stable and low P-levels in postmenopausal women, we predict the AFA to be relatively stable across time and similar to the AFA in men and women during menses.

Additionally, we used a simple reaction-time task (Poffenberger task) to investigate whether interhemispheric transfer times fluctuate across the menstrual cycle. In this task, participants must respond to visual stimuli presented either in the left (LVF) or right visual field (RVF) with the right and the left hand. The crossed–uncrossed difference (CUD), in which median RT under the two uncrossed conditions (stimuli presented in the VHF ipsilateral to the responding hand) is subtracted from median RT under the crossed conditions (stimuli presented in the VHF opposite to the responding hand), can be used as an estimate of IHTT (Poffenberger, 1912). Compared to the Banich–Belger task, the Poffenberger task was assumed to be the least demanding task since it only requires a transfer of visuo-motor information. A recent study has shown sex differences in IHTT as measured by event-related potentials (Moes, Brown, & Minnema, 2007). Specifically, this study found more symmetric and shorter overall IHTTs in females than in males. Up to now, no study has inves-

tigated whether sex hormones affect IHTT across the menstrual cycle.

2. Method

2.1. Participants

Twenty normally cycling women with a mean age of 24.9 years (S.D. = 5.42, age range: 20–40), and a regular menstrual cycle between 25 and 30 days participated in the present study. Additionally, 15 postmenopausal women with a mean age of 58.7 years (S.D. = 5.79, age range: 48–68) who had their last menses at least 1 year before testing, and 28 younger men with a mean age of 26.3 years (S.D. = 4.15, age range: 18–36) were investigated. All participants were right handed as determined with the Edinburgh Inventory (Oldfield, 1971). The asymmetry-index provided by this test is calculated as $((R-L)/(R+L)) \times 100$, resulting in values between −100 (consistent left-handedness) and +100 (consistent right-handedness). The mean handedness score for normally cycling women was 93.8 (S.D. = 7.05; range: 80.0–100), 83.4 (S.D. = 26.19; range: 10.0–100) for the postmenopausal women,[1] and 68.2 (S.D. = 25.16; range: 25.0–100) for men.

Female participants who had used hormonal contraceptives/replacements or any other medication during the last 6 months which could affect the central nervous system were excluded. All participants had normal or corrected to normal visual acuity. They were naïve for the experimental hypotheses. All participants were recruited by announcements, and were paid for their participation.

2.2. Procedure

Sex-hormone-related effects on interhemispheric integration and interhemispheric transfer time were investigated with two versions of the Banich–Belger task, and the Poffenberger task, respectively. Normally cycling women were tested twice, once during the menstrual phase (cycle days 1–2) and once during the midluteal phase (cycle days 18–23), to yield the largest differences in P-levels. Before the first experimental session, normally cycling women were informed about the general procedure and data were collected about the individual length of their menstrual cycle. All women agreed to inform us about the first day of their next cycle. The individual cycle length was taken into account when planning the appointments for the experiments. To control for repeated-measures effects, women were tested in a balanced order, starting during menses or the midluteal phase. Normally cycling women were tested within one or two consecutive cycles.

Postmenopausal women were tested twice in corresponding time intervals of about two weeks. Before and after each session, a saliva sample was collected from all female participants. Saliva P-levels were determined with Chemiluminescence assay (CLIA) by an independent professional hormone laboratory, with commercially available hormone assays. Male controls were tested only once. For the analyses of interhemispheric integration (Banich–Belger task), five male participants had to be excluded because they performed only one task condition. For the analyses of interhemispheric transfer times (Poffenberger task), one male had to be excluded because he did not finish the task.

2.3. Interhemispheric integration (Banich–Belger task)

The interhemispheric-integration task was identical to that used by Banich and Belger (1990). Participants were asked to fixate a cross in the middle of the screen. Then, an array of three stimuli arranged in "V" formation was presented around a central fixation cross. The top two stimuli were always two different uppercase letters, one on either side of the fixation cross. These letters were presented 2.8° of visual angle lateral from the midline and 1.4° visual angle above fixation cross. A third letter was centred 1.4° visual angle below the fixation point and 1.4° visual angle either to the right or left of the centre. In the less demanding physical-identity task, the third letter was an uppercase letter, and participants were asked to indicate whether the bottom letter was the same as either of the top two letters. In the more demanding name-identity task, the bottom letter was a lowercase letter, and participants determined whether this had the same name as either of the top two letters. Letter stimuli were A, B, E, G, H, Q, R, T, and, in the name-identity task, their lowercase equivalents. Each trials started by presentation of a fixation cross for 200 ms, followed by a stimulus array for 200 ms and then by an inter-trial interval of randomized length between 500 and 2000 ms in which responses were recorded. Both tasks comprised of 224 trials divided into four blocks of 56 trials each with brief breaks between blocks. The participants responded with either the right or left index finger on alternating blocks. The order of hand use was balanced between subjects. Prior to each task, participants performed 28 practice trials which were excluded from the analyses. Within each block, half of the trials were match trials and half were mismatch trials. Half of the match trials were within-field matches and the other half were across-field matches. Within both types of matches, the bottom letter appeared equally often in the RVF and LVF. Median reaction times (RTs) of only correct trials and accuracy were used as dependent variables. For RT and accuracy only match trials were analysed, because mismatch trials cannot be categorized as across- or within-field trials.

2.4. Interhemispheric transfer time (Poffenberger task)

The Poffenberger task used in the present study was identical to Corballis (2002). The stimuli were filled circular disks, 0.86° visual angle, placed 2.5° visual angle either to the left or right of a central fixation cross, or simultaneously on both sides. Responses were made with the index finger of either the right or the left hand on a keyboard placed at the participant's midline. The stimuli were presented in two blocks of 100 trials per each hand with a brief break after 50 trials. On a given block of trials, participants used the same hand. The order of response hand was balanced between participants. Within each block, there were 30 trials in which the disks were presented in the LVF, 30 in which they were in the RVF, 30 in which stimuli were presented simultaneously in both VHF (bilateral), and 10 "catch trials" in which no stimulus was presented. Catch trials and trials with simultaneous stimulus presentation were not analysed. At the beginning of each trial a fixation cross appeared in the middle of the screen followed by two consecutive stimuli presented for 135 ms, with inter-stimulus intervals of 300, 400, 500, 600, or 700 ms. Each of the five intervals was paired six times with each stimulus configuration. Participants were instructed to press the response key as quickly as possible when they detected the stimulus, but refrain from responding if no stimulus appeared. The experiment started by placing the head of a seated participant to a chin rest at a distance of 57 cm from a monitor. Participants were instructed to keep their head and body still during the whole test. Median RT for the left and right hand on stimulus presentation in LVF and RVF were recorded. IHTT was estimated by calculating the difference of median RTs in the crossed and uncrossed conditions (CUD).

2.5. Mood questionnaire

To control for potential cycle-dependent variations in mood, a German mood scale (Befindlichkeits-Skala, BFS, Zerssen, 1976) was applied to all normally cycling women before each test session. BFS mood scores can range between 0 (euphoric) and 56 (extremely depressive). To avoid confounding effects of strong variations in mood between the two sessions which can influence performance on interhemispheric integration (Compton & Mintzer, 2001), normally cycling women who showed a difference of more than 25 points between cycle phases were excluded from further analyses.

In postmenopausal women, potential variations in mood between sessions were measured with the State-Trait-Cheerfulness-inventory (STCI-S18; Ruch, Köhler, & van Thriel, 1997). The STCI-S18 measures three different concepts of mood: cheerfulness, seriousness, and bad mood. Each concept included six items. Written response was given on a 4-point rating-scale (strongly disagree, 1; moderately disagree, 2; moderately agree, 3; and strongly agree, 4).

3. Results

3.1. Mood scales

Since cycle-dependent fluctuations in mood can affect interhemispheric processes (Compton & Mintzer, 2001), German mood scales were applied. Three normally cycling women were excluded from further analysis, because their BFS mood scores differed largely (≥25 point) between cycle phases. For the remaining 17 normally cycling women, a paired *t*-test revealed no significant difference in mood between menses ($M = 13.5$, S.D. = 8.02) and the midluteal phase ($M = 16.0$, S.D. = 7.46), $t(16) = 1.53$, n.s. Similarly, mood scores did not differ between normally cycling women tested during menses ($M = 10.3$, S.D. = 4.71) and midluteal phase ($M = 16.3$, S.D. = 7.28), $t(15) = 2.01$, n.s., when only the first session was taken into account (between-participants analysis). For postmenopausal women, mood scores did not differ between test sessions 1 and 2. In neither of the three STCI-S18 subscales (Ruch et al., 1997) paired *t*-tests revealed significant differences in mood between sessions: cheerfulness ($t(14) = -0.47$, n.s.), seriousness ($t(14) = -0.37$, n.s.), and bad mood ($t(14) = -0.53$, n.s.).

3.2. Hormone assay

For normally cycling women, the mean P-level was 38.6 pg/ml (S.D. = 22.72, range: 10.0–89.0 pg/ml) in the menstrual phase and

[1] All statistical analyses including postmenopausal women were additionally performed with LQ as a covariate because of participants' large variability in right-handedness. Since the pattern of results was not affected, these data are not reported.

Table 1
Mean reaction time (in ms ± S.E.M.) of normally cycling women in the Banich–Belger task (within-participants analysis) as a function of Cycle phase (menses, luteal), Task (physical-identity, name-identity), and Trial type (within-field, across-field) and AFA (in ms ± S.E.M.) in the physical-identity task (AFA PI), the name-identity task (AFA NI), and across both tasks (AFA)

Phase	Menstrual			Luteal		
Task	Within	Across	AFA	Within	Across	AFA
Physical ID	384 ± 20.5	399 ± 22.2	−15.1 ± 8.79	378 ± 19.2	380 ± 19.6	−1.6 ± 8.16
Name ID	557 ± 29.9	549 ± 29.4	7.1 ± 17.31	552 ± 30.2	499 ± 29.0	52.9 ± 13.10***
Total	470 ± 19.2	474 ± 19.1	−4.0 ± 9.96	465 ± 23.0	439 ± 22.2	25.6 ± 7.62**

*Marks simple effects between trial types per cycle phase with ***$p \leq 0.001$; **$p \leq 0.01$.

Table 2
Mean reaction time (in ms ± S.E.M.) of normally cycling women in the Banich–Belger task (between-participants analysis) as a function of Cycle phase (menses, luteal), Task (physical-identity, name-identity), and Trial type (within-field, across-field) and AFA (in ms ± S.E.M.) in the physical-identity task (AFA PI), the name-identity task (AFA NI), and across both tasks (AFA)

Phase	Menstrual			Luteal		
Task	Within	Across	AFA	Within	Across	AFA
Physical ID	378 ± 30.6	392 ± 31.7	−13.8 ± 11.09	365 ± 28.8	361 ± 29.9	3.6 ± 5.08
Name ID	482 ± 45.7	483 ± 38.8	−0.8 ± 16.64	538 ± 43.1	472 ± 36.6	65.9 ± 17.69**
Total	430 ± 33.1	437 ± 29.7	−7.3 ± 13.21	451 ± 31.3	416 ± 28.0	34.7 ± 8.99**

*Marks simple effects between trial types per cycle phase with **$p \leq 0.01$.

193.6 pg/ml (S.D. = 147.44, range: 14.5–514.0 pg/ml) in the midluteal phase. A paired *t*-test revealed this difference in mean P-levels to be significant, $t(16) = 4.77$, $p < 0.0001$. For postmenopausal women, the mean P-level did not significantly differ between session 1, 42.7 pg/ml (S.D. = 24.88, range: 14.0–92.0) and session 2, 34.4 pg/ml (S.D. = 25.37, range: 9.0–111.0), $t(14) = 1.08$, n.s.

3.3. Interhemispheric integration (Banich–Belger task)

3.3.1. Normally cycling women

Median RTs were subjected to a $2 \times 2 \times 2 \times 2$ analysis of variance (ANOVA) with repeated measures, with Cycle phase (menses, luteal), Task (physical-identity, name-identity), Trial type (within-field, across-field), and VHF (LVF, RVF) as within-participants factors. AFA was calculated as the difference between trial types (AFA: within-field RT minus across-field RT). The ANOVA revealed a significant main effect of Task, $F(1,16) = 47.33$, $p < 0.0001$, $\eta^2 = 0.75$, with faster response times in the physical- than name-identity task. The Task by Trial type interaction was also significant, $F(1,16) = 8.10$, $p < 0.05$, $\eta^2 = 0.34$, indicating an advantage on across-field trials (mean ± S.E.M.: $M = 524 \pm 24.0$ ms) compared to within-field trials ($M = 554 \pm 24.4$ ms) in the more demanding name-identity task but not in the physical-identity task (across-field trials: $M = 389 \pm 18.8$ ms; within-field trials: $M = 381 \pm 16.6$ ms). Moreover, there was a significant Cycle phase by Trial type interaction, $F(1,16) = 7.30$, $p < 0.05$, $\eta^2 = 0.31$ (see Table 1).

Alpha-adjusted post hoc paired *t*-tests (see Table 1) revealed a significant difference between trial types in the luteal phase. Midluteal RTs on across-field trials were significantly reduced compared to within-field trials, $t(16) = 3.36$, $p < 0.01$. The effect of Trial type during the menstrual phase did not approach significance ($t(16) = -.40$, n.s). Simple comparisons between the two cycle phases per trial type, however, did not reveal significant differences either in within-field trials ($t(16) = -.23$, n.s.) or across-field trials ($t(16) = -1.64$, n.s.).

Although the 2-way interaction was mainly driven by the name-identity task, the 3-way interaction did not approach significance ($F(1,16) = 2.21$, n.s.). Neither the main effect of Cycle phase nor any other interaction with Cycle phase approached significance, all $F < 3.68$, n.s.

The results were virtually identical when Cycle phase was treated as a between-participants factor. In this analysis, only data of the first session were included. However, in contrast to the within-participants design, the Cycle phase × Task × Trial type interaction was significant ($F(1,15) = 5.00$, $p < 0.05$, $\eta^2 = 0.25$, see Table 2). Alpha-adjusted post hoc paired *t*-tests (Table 2) revealed a significant difference between trial types in the name-identity task during the midluteal phase ($t(8) = 3.73$, $p < 0.01$) but not during menses ($t(7) = -.05$, n.s.). An unpaired *t*-test, revealed the luteal and menstrual AFA in the name-identity task to be significantly different, $t(15) = 2.72$, $p < 0.05$ (Fig. 1). In agreement to the within-participants analysis, neither the main effect of Cycle phase nor any other interaction with Cycle phase approached significance, all $F < 0.08$, n.s.

The corresponding $2 \times 2 \times 2 \times 2$ ANOVA for accuracy (within-participants analysis) revealed a main effect of Task, indicating a higher performance in the physical- than name-identity task ($F(1,16) = 5.86$, $p < 0.05$, $\eta^2 = 0.27$). Neither the main effect of Cycle phase nor any interaction with Cycle phase approached significance, all $F < 1.83$, n.s.

In the between-participants analysis of accuracy, only the Cycle phase × VHF interaction was significant ($F(1,15) = 18.67$, $p < 0.01$, $\eta^2 = 0.55$). During the luteal phase, the number of correct responses on stimuli presented in the LVF was higher than to stimuli pre-

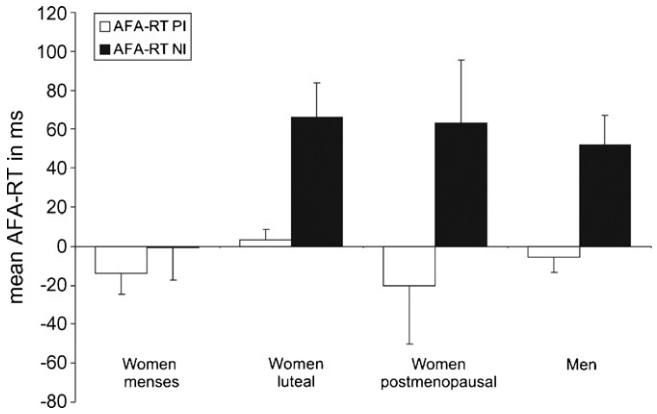

Fig. 1. Mean AFA in ms (±S.E.M.) in normally cycling women during menses and the luteal phase (between-participants analysis), postmenopausal women (session 1), and men in the physical-identity task (white bars) and name-identity task (black bars).

sented in the RVF (LVF: $M = 93.2 \pm 1.9\%$; RVF: $M = 91.2 \pm 1.8\%$). The inverted pattern was evident for women during menses (LVF: $M = 88.7 \pm 3.4\%$; RVF: $M = 91.3 \pm 2.8\%$). No other main effect or interaction approached significance, all $F < 2.64$, n.s.

3.3.2. Postmenopausal women

The median RTs on matching trials of postmenopausal women were subjected to a $2 \times 2 \times 2 \times 2$ ANOVA with Session (sessions 1 and 2), Task, Trial type, and VHF as within-participants factors. Overall, postmenopausal women showed a better performance in session 2 than session 1, resulting in a significant main effect of Session ($F(1,14) = 8.65$, $p < 0.05$, $\eta^2 = 0.38$). As indicated by the significant main effect of Task ($F(1,14) = 96.94$, $p < 0.0001$, $\eta^2 = 0.87$), RTs were faster in the physical- than name-identity task. This effect did significantly interact with Trial type ($F(1,14) = 10.22$, $p < 0.01$, $\eta^2 = 0.42$). Alpha-adjusted post hoc paired t-tests revealed a significant Trial type effect only in the name-identity task ($t(14) = 2.62$, $p < 0.05$), not in the physical-identity task ($t(14) = -0.23$, n.s.). All interaction with Session did not approach significance (all $F < 2.92$, n.s.). Descriptive statistics are shown in Table 3.

The analysis of the accuracies revealed a significant main effect of Task with higher performances in the physical- than name-identity task ($F(1,14) = 14.18$, $p < 0.01$, $\eta^2 = 0.50$). This effect did not interact with Trial type and/or Session (all $F < 0.09$, n.s.).

3.4. Interhemispheric transfer time (Poffenberger task)

3.4.1. Normally cycling women

The $2 \times 2 \times 2$ ANOVA with repeated measures with Cycle phase, Hand-use (right hand, left hand), and VHF as within-participants factors did not reveal any significance (all $F < 3.5$, n.s.). Response time differences between uncrossed- and crossed trials did not significantly differ between menses (CUD = 4.9 ± 4.84 ms) and midluteal phase (CUD = 4.8 ± 5.57 ms), $t(16) = -.02$, n.s. Similarly, no significant effects were found in the between-participants analysis (all $F < 2.58$, n.s.).

3.4.2. Postmenopausal women

Median RTs were subjected to a $2 \times 2 \times 2$ ANOVA with repeated measures, with Session, Hand-use, and VHF as within-participants factors. Neither the main effects of Session, Hand-use, or VHF nor any interaction between these factors approached significance (all $F < 4.5$, n.s.). The crossed–uncrossed difference did not change significantly between session 1 (CUD = 8.9 ± 3.61 ms) and session 2 (CUD = 5.5 ± 5.07 ms), $t(14) = 0.66$, n.s.

3.5. Sex differences in interhemisperhic integration (Banich–Belger task)

When response times in the Banich–Belger task of normally cycling women during the midluteal phase were compared to those of male controls, neither the main effect of Sex nor any interaction with Sex was significant (all $F < 1.48$; n.s.). Similarly to women during the luteal phase (see Table 1), male controls showed a significant difference between within- and across-field trials (overall AFA = 23.4 ± 9.70 ms; $t(22) = 2.41$, $p < 0.05$). This effect was particularly pronounced in the more demanding name-identity task (AFA = 52.0 ± 15.12 ms, $t(22) = 3.44$, $p < 0.01$) and was virtually identical to that of normally cycling women during the midluteal phase (see Table 1). Although the effect of Trial type was significant in men but not in women during menses (see Table 1), the comparison between these two groups did not reveal a significant interaction between Sex and Trial type ($F(1,38) = 3.72$, $p < 0.07$). The difference between AFA in men and women during menses was also not significant ($t(38) = 1.91$; $p < 0.06$). Neither the main effect of Sex nor any other interaction with Sex approached significance (all $F < 1.48$; n.s.).

The comparison between postmenopausal women (session 1) and men revealed faster responses in males ($F(1,36) = 29.50$, $p < 0.001$, $\eta^2 = 0.45$). Moreover, the interaction between Sex and Task was significant ($F(1,36) = 4.76$, $p < 0.05$, $\eta^2 = 0.12$) which suggests that an increase of response times in the more demanding semantic task was more evident in postmenopausal women than in men. No other interaction with Sex was significant (all $F < 2.73$, n.s.). AFA in the name-identity task was virtually identical in both groups (postmenopausal women: AFA = 63.4 ± 32.23 ms), $t(36) = -.36$, n.s.

3.6. Sex differences in interhemispheric transfer time (Poffenberger task)

Comparing the overall response times of women during the midluteal phase with those of men, the main effect of Sex was significant ($F(1,42) = 6.78$, $p < 0.05$, $\eta^2 = 0.14$). Men revealed faster responses than women during the luteal phase. However, the CUD did not differ between women during the luteal phase (CUD = 4.8 ± 5.57 ms) and men (CUD = 4.0 ± 1.85 ms), $t(42) = -.16$, n.s.. No other interaction with Sex approached significance (all $F < 1.13$, n.s.). Comparing response times of women during menses and men, again only the main effect of Sex was significant ($F(1,42) = 6.31$, $p < 0.05$, $\eta^2 = 0.13$) with faster responses in men. All other interactions with Sex were not significant, $F < 1.26$, n.s. The CUD in men was virtually identical to the CUD in women during menses (CUD = 4.9 ± 4.84 ms, $t(42) = -.21$, n.s.).

The comparison between postmenopausal women at session 1 and men revealed a significant main effect of Sex with faster responses in men than in postmenopausal women ($F(1,40) = 26.05$, $p < 0.0001$, $\eta^2 = 0.39$). Moreover, the main effect of VHF ($F(1,40) = 4.71$, $p < 0.05$, $\eta^2 = 0.11$) and the interaction between hand use and VHF ($F(1,40) = 12.45$, $p < 0.01$, $\eta^2 = 0.24$) were significant. Participants responded particularly faster on stimuli presented in RVF than LVF. This pattern was especially pronounced when the right hand was used. Although CUDs in postmenopausal women (CUD = 8.9 ± 3.61 ms) were slightly larger than in men (CUD = 4.0 ± 1.85 ms), this difference did not approach significance ($t(40) = 1.36$, n.s.).

3.7. Relationships between progesterone and interhemispheric tasks

In view of the significant interaction between Cycle phase and Trial type in interhemispheric integration (Banich–Belger task), P-

Table 3
Mean reaction time in ms ± S.E.M. of postmenopausal women in the Banich–Belger task as a function of Session (sessions 1 and 2), Task (physical-identity, name-identity), and Trial type (within-field, across-field) and AFA (in ms ± S.E.M.) in the physical-identity task (AFA PI), the name-identity task (AFA NI), and across both tasks (AFA)

Session	Session 1			Session 2		
Task	Within	Across	AFA	Within	Across	AFA
Physical ID	712 ± 66.2	732 ± 51.0	−20.0 ± 30.23	672 ± 68.3	663 ± 51.3	9.2 ± 21.99
Name ID	962 ± 84.5	899 ± 66.3	63.4 ± 32.23	864 ± 54.0	789 ± 50.9	74.8 ± 28.83*
Total	837 ± 74.0	815 ± 56.7	21.7 ± 29.05	768 ± 58.7	726 ± 50.1	42.0 ± 20.23

*Marks simple effects between trial types per session with $^{*}p \leq 0.05$.

levels were expected to be significantly related to AFA. However, P-levels were not significantly related to AFA, neither when normally cycling women from both cycle phases (session 1) were included in the analysis ($r = 0.18$, $n = 17$, n.s.) nor when the correlation was restricted to women in the luteal phase (sessions 1 and 2) ($r = -.18$, $n = 17$, n.s.). Moreover, P-levels were not significantly related to RTs and accuracies on within- and across-field trials (all $r < \pm 0.43$, n.s.). The relationship between P-levels and CUD (Poffenberger task) was also not significant (all $r < \pm 0.24$, n.s.).

Finally, we analysed the relationship between AFA and CUD. Although the correlation between both measures of interhemispheric interaction was always positive, it did not approach significance. This insignificant effect was found for AFA based on the physical and name-identity task and was present for all participating groups (all $r < 0.27$, n.s.).

4. Discussion

In line with previous findings (Banich & Belger, 1990; Weissman et al., 2000), the results of the present study support the idea that interhemispheric integration becomes advantageous with increasing task demands. Men, normally cycling women, and postmenopausal women revealed an AFA in the more demanding name-identity task but not in the less demanding physical-identity task. Moreover, the present study revealed the first evidence for cycle-dependent fluctuations in interhemispheric integration. Normally cycling women during the luteal phase showed a strong AFA for the more demanding name-identity task, in particular, a finding which was significant in the between-participants analysis. In contrast to our predictions, the AFA of normally cycling women during the luteal phase was virtually identical to that of age-matched men and postmenopausal women who showed a robust AFA in both testing sessions. However, no advantage of interhemispheric integration was found in normally cycling women during menses. The results suggest that in younger women, the menstrual cycle and concomitant changes in sex-hormone levels are related to dynamic changes in interhemispheric integration. Interactions across the hemispheres seem to be differently organized in postmenopausal women. Here, a stable hormonal environment with low gonadal hormones seems to promote a stable interhemispheric integration. Although men of the present study were tested only once, we assume the AFA of men to be similarly stable as it is in postmenopausal women because both groups have comparably low and stable sex hormone-levels.

The present finding is in contrast to a previous study (Compton et al., 2004) which did not find cycle-related fluctuations in interhemispheric integration. The conflicting finding cannot simply be explained by the fact that Compton et al. (2004) used only the name-identity task. Both studies were also similar with respect to participants' age and selected cycle phases. However, normally cycling women in Compton et al. (2004) and the present study differed substantially in the participants' hormonal status. Participants' mean luteal P-level in Compton et al. (2004) was approximately twice as high as the mean P-level during menses, whereas in the present study, luteal P-levels were about five times higher than during menses. Moreover, in Compton et al.'s study, normally cycling women showed higher P-levels during menses (72.8 pg/ml) than the present study (38.59 pg/ml), whereas P-levels were lower during the midluteal phase (131.0 pg/ml) than those reported here (193.55 pg/ml). If cycle-related fluctuations in hormone levels are indeed related to a cycle-dependent modulation of interhemispheric integration, the present study is more likely to find significant effects. It should be noted, however, that P itself was unrelated to interhemispheric integration in both studies. This might indicate that these effects are not directly mediated by sex hormones. An alternative hormonal explanation might be that cycle-related fluctuations in interhemispheric integration, as measured by the Banich–Belger task, are affected by sex hormones other than P but also increase during the midluteal phase, e.g., E and/or P-metabolites. Although there is evidence that P-levels are related to other interhemispheric processes, i.e. interhemispheric inhibition (Hausmann et al., 2002; Hausmann & Güntürkün, 2000; Hausmann et al., 2006), it is rather unlikely that such an inhibition is also involved in interhemispheric integration.

The key finding that only normally cycling women during menses did not show a strong AFA clarifies two different but intertwined aspects, namely the nature of interhemispheric interactions, and the difference between cycle-related effects in younger women on one side, and men and postmenopausal women on the other. We will discuss these two points separately.

4.1. The nature of interhemispheric interactions

Interhemispheric inhibition refers to mechanisms that suppress a concurrent processing in the opposite hemisphere by activation of GABAergic interneurons in homotopic areas (Toyama & Matsunami, 1976; Toyama, Tokashiki, & Matsunami, 1969). This inhibitory coupling between hemispheres can take place at a very early level of cortical processing (Bergert, Windmann, & Güntürkün, 2006), possibly already between the occipital cortices (Miniussi, Girelli, & Marzi, 1998). As a result, one hemisphere dominates the task. In contrast, interhemispheric integration involves parallel processing in both hemispheres by activating common resources, probably mainly at later processing stages (Mohr, Landgrebe, & Schweinberger, 2002). It requires a more decoupled interhemispheric state that allows both sides to independently process the relevant stimuli. Although the mechanisms underlying the AFA are not fully clear, it has been suggested that it does not simply reflect a processing load division effect but rather a reduction of mutual interference between hemispheres during perceptual processing (e.g., Sohn, Liederman, & Tippens Reinitz, 1996).

Our findings suggest that different interhemispheric processes are differentially affected by sex-hormonal fluctuations across the menstrual cycle. Tasks that mainly rely on interhemispheric inhibition seem to be affected by P (and E), and thus modulate FCAs (Hausmann et al., 2002; Hausmann & Güntürkün, 2000; Hausmann et al., 2006). Tasks which require a bihemispheric activation of common resources with a subsequent integration are also affected by the menstrual cycle, without P being directly relevant.

IHTT seems not to be affected by the menstrual cycle and cycle-related hormonal changes, at least when measured behaviourally. The present study showed that CUD in the Poffenberger task as an estimate of IHTT did not fluctuate across the menstrual cycle and did not differ between men and women, regardless which cycle phase was taken into account. However, due to the fact that sex differences in IHTT can be measured by event-related potentials (Moes et al., 2007), it seems possible that CUD based on response times is not sensitive enough to detect sex and sex-hormonal effects. This assumption is also supported by the non-significant overall difference between crossed and uncrossed trials, suggesting that CUDs as measured by the Poffenberger task do not provide a reliable estimate of IHTT.

4.2. Sex- and age-specific differences of interhemispheric interactions

Previous perceptual asymmetry studies focusing on cycle-related fluctuation in FCAs have shown that men, postmenopausal women, and normally cycling women during menses show simi-

lar asymmetry patterns, probably because their levels of relevant sex hormones, i.e., P and E, are similarly low (Hausmann et al., 2002; Hausmann & Güntürkün, 2000). Only few studies that did not use interhemispheric-inhibition tasks suggest a more male-like functional cerebral organization in women during the luteal phase rather than for women during menses (e.g., McCourt et al., 1997). This is similar to the present study which also found virtually identical results in women during the luteal phase and in men. The enhanced interhemispheric integration in women during the luteal phase suggests that high levels of sex hormones, others than P, might temporally optimize parallel processing in tasks that demand interhemispheric integration.

However, why did postmenopausal women and men show a robust AFA although they reveal low sex-hormone levels, comparable to those of women during menses? To understand this paradoxical finding it is important to stress the profound effect of sex hormones, such as E and P, on many aspects of neuronal processing, ranging from synaptic adjustments up to neurotrophic factors that alter cellular morphology. The low level of these hormones in men and their loss in postmenopausal women requires a difference in neural functional architecture, including interhemispheric interactions. These neural differences are by far not understood.

In older adults, several neuromorphological changes have been shown with increasing age (e.g., Sowell et al., 2003), including changes in frontal and parieto-occipital brain regions which are known to be critical for visual letter processing and interhemispheric integration (e.g., Pollmann, Zaidel, & von Cramon, 2003; Puce, Allison, Asgari, Gore, & McCarthy, 1996). In contrast, age-related changes in corpus callosum morphology seem to be relatively small, particularly in older women (Cowell, Allen, Zalatimo, & Denenberg, 1992; Dubb, Gur, Avants, & Gee, 2003; Sullivan, Rosenbloom, Desmond, & Pfefferbaum, 2001). Thus, given that the costs associated with communication between the hemispheres are virtually the same in women during menses and postmenopausal women, we are inclined to believe that an AFA in the latter group occurred in part because the relative performance on within-field trials vs. across-field trials was reduced due to an age-related decline.

This assumption is in line with the idea that additional recruitment of brain areas via callosal pathways serves as a compensatory mechanism to counteract age-related deficits in cognitive functions (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002). It has been shown that older adults relative to younger adults benefit more from interhemispheric interaction even when task demands are relatively low (Banich & Brown, 2000; Reuter-Lorenz et al., 2000). A greater bilateral involvement with increasing age was also reported in several neuroimaging studies showing bilateral activity in frontal and parietal sites in older adults but a more lateralized activity in younger adults (e.g., Cabeza et al., 2002; Reuter-Lorenz & Stanczak, 2000). Thus, according to the present results, it seems reasonable to assume that different neuronal conditions in younger and postmenopausal women ensure an effective interhemispheric integration, particularly when the task becomes more demanding.

5. Summary

In summary, the present study provides the first evidence that the AFA in the Banich–Belger task changes dynamically in women across the menstrual cycle, whereas it remains relatively stable in postmenopausal women without HRT. Although no relationship between P-levels and interhemispheric integration was found, modulating effects of E or other cycle-related hormones cannot be ruled out. However, IHTT, estimated by response time CUDs, was not affected by the menstrual cycle, and thus seems not to be under sex-hormonal control.

The idea that the interhemispheric crosstalk is hormonally affected and fluctuates across the menstrual cycle is based on the hypothesis of P-modulated interhemispheric decoupling, referring to interhemispheric inhibition (Hausmann et al., 2002; Hausmann & Güntürkün, 2000). The present study focuses on a complementary interhemispheric process that requires bihemispheric processing with subsequent interhemispheric integration. Thus, the present study importantly extends the theory of Hausmann and Güntürkün by clarifying two aspects:

1. In normally cycling women, the hormonal condition during menses is associated with increases in interhemispheric coupling via inhibition, and subsequently enhances FCAs. However, this hormonal state concomitantly decreases the AFA in the Banich–Belger task. During the luteal phase, interhemispheric inhibition is reduced, resulting in low FCAs and a condition that favours bihemispheric processing and thus, increases AFAs.
2. The system of bihemispheric activation is profoundly altered when gonadal steroid hormones, such as E and P, are drastically reduced, as in men and postmenopausal women. We assume that permanently low levels of such important neuroactive agents are accompanied by a different architecture of interhemispheric communication that is presently not properly understood. This different architecture ensures successful interhemispheric integration without the modulatory effects of sex hormones.

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