Brain and Cognition 80 (2012) 214–222

Contents lists available at SciVerse ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Salivary progesterone is associated with reduced coherence of attentional, cognitive, and motivational systems

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ARTICLE INFO

Article history:
Accepted 28 July 2012
Available online 22 August 2012

Keywords:
Attention networks
Gonadal steroids
Motivation
Referential competence
Personal goals
Implicit motives
Hemispheric function

ABSTRACT

The present study tested whether the hypothesis that high levels of progesterone (P) have a decoupling effect on the function of the brain hemispheres (Hausmann & Gunturkun, 2000) also extends to attentional functions, referential connections between verbal and nonverbal representations and the degree to which implicit motivational needs match a person's explicit goal commitments. Participants (28 women on oral contraceptives, 14 naturally cycling women, 50 men) completed the Lateralized Attention Network Task (Greene et al., 2008), a measure of the alerting, orienting, and conflict-resolution functions of attention for each hemisphere; a measure of referential competence (i.e., the ability to quickly name nonverbal information); a measure of the implicit motives power, achievement, and affiliation; and a content-matched personal goal inventory. In addition, they provided a saliva sample that was assayed for P and cortisol (C). Higher levels of P were associated with lower interhemispheric correlations for alerting and orienting, but with a higher correlation of conflict-resolution performance. Higher P was also associated with longer interhemispheric transfer time, lower congruence between implicit motives and explicit goal commitments and, after controlling for C, with lower referential competence. These results suggest that (a) P is associated with the degree to which attentional functions are correlated between hemispheres, although in a different direction for more posterior (alerting and orienting: decoupling) than for more anterior functions (conflict resolution: coupling), (b) that high P is associated with other indicators of reduced functional coherence between cognitive systems (longer interhemispheric transfer time, lower referential competence), and (c) that high P is also associated with low coherence between implicit and explicit motivational systems.

1. Introduction

Steroid hormones play a key role for a diverse range of cognitive functions and social behavior, both through their lasting effects on the organization of the nervous system during development and through reversible, activating effects on the brain throughout life (e.g., Hampson, 2002; Williams, 2002). The steroid progesterone (P) is secreted by the ovaries and adrenals and exerts its activating effects both directly and through its neuroactive metabolites (e.g., allopregnanolone). One of the pathways through which P influences cognition, emotion, and behavior is by binding to the gammaminobutyric acid (GABA) receptor, which has an inhibitory effect on neural signal transmission (Majewska, Harrison, Schwartz, Barker, & Paul, 1986; Paul & Purdy, 1992). Through GABA receptor activation, P and its metabolites can have widespread attenuating effects on neural transmission as manifested in P-dependent reduction of alertness, emotionality, and learning and memory (for a review, see Wirth, 2011). In the present research, we explore P-mediated reductions in neural transmission by looking at variations in interhemispheric coherence of attentional functions, integration of nonverbal and verbal information processing, and, as a downstream consequence of such integration, alignment of implicit and explicit motivational systems. In doing so, we also examine the role of oral contraceptive (OC) use, gender, and cortisol, whose levels covary with P, in the association of P with these markers of functional coherence.

1.1. Progesterone and interhemispheric decoupling

Evidence for a P-associated loss of functional coupling between brain areas comes from research by Hausmann and Gunturkun (2000), who studied the role of variations in P in the lateralization of cognitive functions. Functions that are typically lateralized in men, such as verbal functions (left hemisphere, LH) or visuospatial functions (right hemisphere, RH), have turned out to be less lateralized in women, who also show greater variability in lateralization. Hausmann and Gunturkun (2000) identified menstrual cycle stage and the concomitant changes in P as a key determinant of

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http://dx.doi.org/10.1016/j.bandc.2012.07.001

functional lateralization. Women tested in the low-P menstrual phase of the cycle show the typical pattern of lateralization also observed in men, whereas women tested in the luteal, high-P phase show considerably less lateralization. Hausmann and Gunturkun explain these observations as follows: Homotopic areas (i.e., areas with similar locations) in the hemispheres are connected through callosal fibers, and these callosal connections allow the hemispheres to interact such that when an area in one hemisphere is active, function of the homotopic area in the other hemisphere is inhibited (Cook, 1984). This gives rise to lateralization effects of functions that can be more easily executed by one hemisphere than by two hemispheres in tandem. However, high levels of P, through GABA-receptor-mediated inhibition of signal transmission, reduce callosal communication and thereby allow the normally suppressed hemisphere to execute the function, too. The result is a loss of lateralization as assessed by the performance difference between LH and RH, because now the same task can be processed similarly well by both hemispheres. Hausmann and Gunturkun (2000) termed this effect *P-mediated interhemispheric decoupling*.

Across several studies, Hausmann and colleagues found replicable evidence in support of the interhemispheric-decoupling hypothesis. Individuals high in P showed less hemispheric differences on tasks for which lateralization is typically found, such as classifying words and non-words (LH advantage) or judging the identity of figural drawings (RH advantage), whereas individuals low in P did show a lateralization effect (e.g., Hausmann & Gunturkun, 2000; Hausmann, Becker, Gather, & Gunturkun, 2002; but see Compton, Costello, & Diepold, 2004, for a failure to replicate). However, this research did not address the issue of whether P-mediated interhemispheric decoupling can also be documented for cognitive functions that are less lateralized than the processing of verbal or figural material but which might nevertheless depend on callosal communication for optimal efficiency. Indeed, interhemispheric (de)coupling should be difficult to document as long as hemispheric-difference scores, which yield values around 0 for non-lateralized functions, are used to test the hypothesis, as was done by Hausmann and colleagues. The present research therefore addresses the issue of P-mediated interhemispheric decoupling by examining the role of P in the *correlation* of the attentional functions alerting, orienting, and conflict resolution assessed in the two hemispheres. As past research has shown (e.g., Juarez & Corsi-Cabrera, 1995), this represents a viable alternative approach to studying interhemispheric interaction and documenting sex-dependent differences in interhemispheric coupling.

1.2. Progesterone and referential processing between verbal and nonverbal systems

In addition to testing a role of P in interhemispheric decoupling, we also explore whether P attenuates the functional coherence of referential processing between verbal and nonverbal systems (see Paivio, 1986), a process that is not only interesting from a multiple-systems perspective on cognition, but also represents a key mechanism for the integration of motivational systems (see next section). In a liberal sense, testing effects of P on referential processing represents an extension of the interhemispheric-decoupling hypothesis, because many key verbal functions are located in the LH, whereas nonverbal processing, particularly in terms of gestalt-like, holistic cognition, is more efficiently performed by the RH, and naming objects therefore requires efficient functional connectivity between separate and independent processing modules (Paivio, 1986). Most research on the role of P in cognitive processes has focused on verbal processing or object-related processing per se (e.g., Hausmann et al., 2002), but research on the functional integration of verbal and nonverbal processing, such as in object-naming tasks, is lacking. An exception is a study by Derntl, Kryspin-Exner, Fernbach, Moser, and Habel (2008). These authors had women name the emotions displayed on face photographs. Derntl et al. found that women in the high-P luteal phase of the menstrual cycle were less likely to correctly name the emotion displayed. Further analyses revealed that this effect was specific to P, because higher P was associated with a lower ability to find the correct verbal labels for facial expressions of emotion, and this effect held even when variations in estradiol levels were controlled for. It remains an open question whether the effects observed by Derntl et al. are specific to retrieving verbal labels for facial expressions or whether they represent a more general attenuation of referential connections between nonverbal and verbal codes.

In the present study we therefore include a measure of color-naming as a test of basic referential connections between object recognition and verbal representations, termed *referential competence* (RC; Bucci, 1984; Schultheiss & Strasser, 2012). Color naming requires functional connections between RH occipital areas, which are involved in color perception (Barnett, 2008), and LH language areas, which are involved in verbal labeling, via the posterior part of the callosum (e.g., Beauvois & Saillant, 1985; Geschwind & Fusillo, 1966). Assuming that the interhemispheric-decoupling hypothesis of P also extends to functional connections between non-homotopic brain areas (see Weis, Hausmann, Stoffers, & Sturm, 2011), we expect higher levels of P to be associated with impaired color-naming ability and thus low RC.

1.3. Progesterone and incongruence between implicit and explicit motivational systems

Extending on the hemispheric-decoupling hypothesis and the impaired naming ability hypothesized to be associated with high P, we also speculate that P may be associated with incongruence between nonverbally represented (i.e., implicit) and verbally represented (i.e., explicit) motivational needs. Research on human motivation has accumulated evidence for the existence of two independent systems that regulate behavior (McClelland, Koestner, & Weinberger, 1989; Schultheiss, 2008; Schultheiss & Brunstein, 2010). One operates at the conscious, explicit level by setting and pursuing verbally represented goals, the other operates at the unconscious, implicit level through the pursuit of natural incentives such as dominance and affiliative contact. Motivation theorists assume that the explicit system is rooted in the brain's capacity to represent desired end states symbolically and to devise complex plans for their attainment (i.e., functions the LH excels at), whereas the implicit system is based on affect and the processing of nonverbal information in the service of need satisfaction (McClelland et al., 1989; Rolls, 2005; Schultheiss, 2008).

Measures of implicit and explicit motivational strivings consistently show correlations in the very low positive range ($r \sim .10$), attesting to the independence of the two systems (e.g., Spangler, 1992). Researchers have started to explore the antecedents, correlates, and consequences of discrepancies between implicit and explicit motivational strivings by using absolute difference scores between implicit motive and explicit goal measures to quantify the degree of motivational incongruence for a given individual (e.g., Schultheiss, Patalakh, Rawolle, Liening, & MacInnes, 2011). Consistent with the notion that independence between implicit and explicit forms of motivation is due to their differential association with nonverbal vs. verbal information processing, Schultheiss et al. (2011) found in three studies that individuals with impaired referential connections between verbal and nonverbal codes, as assessed through their response speed on a color-naming task, also had more motivational incongruence across different domains of motivation. Based on these observations, we propose that the degree of motivational congruence could represent the degree of functional coupling between distinct, presumably lateralized (see McClelland, 1986), brain modules and thus be sensitive to variations in P. We therefore expected higher levels of P to be associated not only with less RC, but as a consequence also with more motivational incongruence.

1.4. Overview of the present study

To summarize, the present study tests the hypothesis that high P is linked to cognitive indicators of interhemispheric decoupling and is associated with impaired referential processing between verbal and nonverbal codes and, as a consequence, with high incongruence between implicit and explicit motivation measures. We assessed P in saliva samples obtained from naturally cycling (NC) women, women using OCs, and men. Interhemispheric coupling of attentional functions was assessed with the Lateralized Attention Network Test (LANT; Greene et al., 2008), a measure of the efficiency of alerting, orienting, and conflict resolution in response to stimuli presented in the left and right visual fields (LVF and RVF) and thus to the RH and the LH. It is based on the Attention Network Test by Fan, McCandliss, Sommer, Raz, and Posner (2002) and has acceptable to good convergent validity with this measure. More importantly, LANT scores for the three attentional functions are positively correlated between hemispheres (*r*s between .32 and .74; see Greene et al., 2008), suggesting a substantial degree of interhemispheric coupling of attentional processes. In keeping with the hemispheric-decoupling hypothesis, we expected higher P to be related to smaller correlations and hence less interhemispheric coupling. The LANT also allowed us to explore whether this prediction holds for all three attention networks equally. The three attentional functions follow a posterior–anterior gradient, with alerting and orienting rooted in the more posterior brain areas of thalamus and parietal cortex, respectively, and conflict resolution depending on the anterior cingulate cortex (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). On the LANT, the hand with which participants respond varies independently of the visual field in which a stimulus is presented. This allowed us to also calculate an interhemispheric transmission time index (the crossed-uncrossed difference, or CUD; see Iacoboni & Zaidel, 2000). CUD scores represent the response time difference between trials on which both stimulus processing and response generation occur ipsilaterally and trials on which they occur contralaterally. It is viewed as an index of the relative efficiency with which information is exchanged between hemispheres and thus constitutes an additional measure of interhemispheric coupling (Iacoboni & Zaidel, 2000).

Referential processing was assessed with a color-naming/word-reading task used to measure RC and validated in previous studies (Bucci, 1984; Schultheiss et al., 2011). We expected higher P to be associated with longer color-naming latencies, relative to word-reading latencies.

Participants' implicit motives were assessed with a Picture Story Exercise (PSE; McClelland et al., 1989), a well-validated method for measuring the motivational needs for achievement, affiliation, and power. Explicit goal strivings were assessed with a personal goal inventory (Brunstein, Schultheiss, & Grässmann, 1998) on which participants first listed goals for the domains of achievement, affiliation, and power and then rated their commitment to each goal. Calculation of absolute difference scores between standardized implicit motive and explicit goal commitment scores provided us with an estimate of the degree to which implicit and explicit motivational systems were incongruent. We expected higher P to be associated with higher motivational incongruence across all three domains tested (i.e., achievement, affiliation, and power).

Finally, we also measured cortisol (C), whose levels are highly correlated with P, as a possible confounding variable in this study (see Wirth, Meier, Fredrickson, & Schultheiss, 2007). Both P and C are produced by the adrenals during stress, and stress-related C increases are known to impair some cognitive functions. We therefore aimed to show that the hypothesized decoupling effects are specific to P and not a spurious side effect of stress-related C increases.

2. Method

2.1. Participants and design

One-hundred-six students at Friedrich-Alexander University, Erlangen, Germany, participated in a cross-sectional study on "attention and performance" for payment of €15 (findings for referential competence and motivational congruence in this larger sample have been reported as Study 3 in Schultheiss et al. (2011)). Data collection sessions (120 min) were scheduled between 9 am and 6 pm on weekdays. Of the initial sample, 92 participants (42 women, 50 men; mean age 23 years) had complete data for salivary hormones, the LANT, the RC task, the PSE, and the personal goal inventory and reported to have normal color vision. Four participants self-identified as preferring the use of the left hand for most everyday activities. Twenty-eight women self-identified as OC users, the rest ($n = 14$) were NC women. Participant group (men, NC women, OC women) constituted a quasiexperimental factor and was not significantly associated with age or handedness.

2.2. Salivary hormone assessment

Saliva samples were collected and processed according to the recommendations given by Schultheiss and Stanton (2009). All hormone assays were conducted using solid-phase Coat-A-Count ^{125}I radioimmunoassays for P (TKPG) and C (TKCO) provided by Siemens Healthcare Diagnostics GmbH (Eschborn, Germany), following validated protocols for the assessment of salivary P and C (Schultheiss, Dargel, & Rohde, 2003; Wirth, Welsh, & Schultheiss, 2006; a 24-h preincubation at room temperature was added in both cases). Interassay reliability was evaluated for P by including samples from male and female in-house saliva pools in each assay, intraassay reliability was determined in participants' samples, and recovery was assessed with CON6 control samples (Siemens Healthcare Diagnostics), appropriately diluted for salivary hormone levels. According to validation data supplied by the manufacturer, none of the assays cross-reacts with estrogens and gestagens contained in oral contraceptives. For P, interassay CV was 0.94% for luteal-phase female saliva (75 pg/mL) and 1.49% for male saliva (48 pg/mL), intraassay CV was 11.83%, and analytical sensitivity (B0–3 *SD*) was <2 pg/mL. For diluted control samples, analytical recovery was 113% for low (20 pg/mL) and 110.5% for high concentrations (100 pg/mL). For C, intraassay CV was 7.43%, and analytical sensitivity (B0–3 *SD*) was 0.12 ng/mL. For a low-concentration (1.5 ng/mL) control sample, analytical recovery was 96.7%.

2.3. Lateralized attention network task

We assessed hemispheric contributions to the alerting, orienting, and conflict-resolution components of attention with the LANT (Greene et al., 2008). On a LANT trial, participants have to indicate by key press whether a target stimulus is an arrow pointing up or down. Assessment of the alerting function is achieved by presenting a cue that precedes the target stimulus by a fixed interval on some trials. Faster responses on cued than on uncued trials index more efficient alerting. Orienting is assessed by presenting the cue either in the same spatial location as the subsequent target (valid trials) or in another spatial location (invalid trials). Faster responses on validly cued than on invalidly cued trials index more efficient orienting. Assessment of executive attention is achieved by presenting the target arrow either in a context of congruent flankers (e.g., a downward arrow flanked by other downward arrows) or incongruent flankers (e.g., a downward arrow flanked by upward arrows). Slower responses on incongruent trials than on congruent trials index less efficient conflict resolution.

Lateralized assessment of attentional functions was achieved by presenting targets and spatial cues in the LVF and RVF, about 1.15° of visual angle to the left or to the right of a central fixation cross. Cues were presented for 100 ms, followed by a 400 ms pause and a 170 ms presentation of a target/flanker compound stimulus. Response time (RT) registration started with the onset of this compound stimulus and lasted for 2000 ms. Intertrial intervals varied between 400 and 1600 ms. Participants first completed a block of practice trials and received feedback whenever they responded incorrectly (“Wrong key!”) or did not respond for 2000 ms (“Faster!”). After 20 mandatory practice trials, practice commenced as soon as participants had correctly completed another 38 consecutive trials or a maximum of 250 additional practice trials.

During actual testing, participants first completed a block of 48 trials with one hand (the one they had not used during practice), using index and middle fingers to press buttons for upward or downward arrows on a response pad. Then they switched to the other hand for the second block of 48 trials. Which hand participants started with was balanced across individuals. No feedback was given on test trials.

Across both testing blocks, trials represented a 4 (no cue, central cue, left cue, right cue) × 3 (congruent flankers, incongruent flankers, neutral flankers) × 2 (LVF, RVF) × 2 (upward vs. downward arrow) × 2 (left vs. right hand) factorial design, with the first three factors varied randomly within hand blocks. After removing incorrect response trials and implausibly short (<230 ms) or excessively long (>2000 ms) RTs (4.3% of all data), RTs were averaged across levels of the last two factors for all analyses.

To derive three attentional network scores for each hemisphere, we followed the procedures outlined by Greene et al. (2008) and Fan et al. (2002) and compared the performance of one condition to an appropriate reference condition for each visual hemifield. The operational definitions of the efficiencies of the three attentional networks for subsequent analyses were calculated to produce a positive score in each case. For the LH (RVF): Alerting = $RT_{\text{no cue}} - RT_{\text{right cue}}$; Orienting = $RT_{\text{right invalid cue}} - RT_{\text{right valid cue}}$; Conflict resolution = $RT_{\text{right incongruent}} - RT_{\text{right congruent}}$. And correspondingly for the RH (LVF): Alerting = $RT_{\text{no cue}} - RT_{\text{left cue}}$; Orienting = $RT_{\text{left invalid cue}} - RT_{\text{left valid cue}}$; Conflict resolution = $RT_{\text{left incongruent}} - RT_{\text{left congruent}}$. Note that with this type of calculation, larger positive scores indicate more efficient alerting and orienting, but less efficient conflict resolution (i.e., shielding against irrelevant information).

2.4. Referential competence

RC was assessed with the color-naming task described in Schultheiss et al. (2011). In brief, participants completed eight blocks, with each block featuring 24 trials, resulting from a 4 (colors: red, green, blue, yellow) × 2 (stimulus type: color word, color patch) × 3 (repetitions) factorial. Words (“red”, “blue”, “green”, “yellow”) were printed in 90-point Arial with black color. Color patches (in red, blue, green, yellow) were sized at 5 cm × 5 cm, with pure color hues. Participants were instructed to read the words or name the colors presented on the screen as quickly and accurately as possible. On each trial, RT was determined by measuring the time lag between stimulus onset and onset of the voice response. After discarding very short (RTs < 250 ms) and excessively long response latencies (RTs > 1500 ms; 1.3% of all data), we calculated overall RTs separately for color naming and word reading by averaging RTs across levels of the factors color and repetitions and across all blocks and then derived an overall referential competence score by dividing the difference between color naming and word reading latencies through their sum. Lower scores on this measure represent quicker color naming and thus higher referential competence. According to Schultheiss et al. (2011), RT differences between color naming and word reading are consistent across blocks within the task (Cronbach’s alphas: .74 to .90) and stable for a retest interval of 2 weeks (r = .80).

2.5. Implicit motives

Participants worked on the 6-picture PSE described by Pang and Schultheiss (2005), following standard instructions for computer administration described in Schultheiss and Pang (2007). Stories were later coded for imagery related to power (e.g., controlling, impressing, convincing others), achievement (e.g., unique accomplishments or doing a task well), and affiliation (e.g., dialog or expression of friendly feelings towards others) by two trained scorers using Winter’s (1994) *Manual for Scoring Motive Imagery in Running Text*. Scorers had previously exceeded 85% inter-scorer agreement on calibration materials prescored by an expert that are contained in the manual. Interrater reliability (Pearson correlations of each participant’s raw motive score) was satisfactory, with .79 for power, .74 for achievement, and .86 for affiliation. PSE protocol length (M = 605 words, SD = 152 words) was significantly correlated with participants’ overall motive scores for power (M = 4.49, SD = 2.39), r = .45, achievement (M = 5.06, SD = 2.59), r = .45, and affiliation (M = 6.54, SD = 2.76), r = .41, all ps < .0001. Following Winter’s (1994) recommendation, we corrected for the influence of protocol length by multiplying total motive raw scores with 1000 and dividing the product by the total word count.

2.6. Personal goals

Participants’ personal goals within the domains of power, achievement, and affiliation were assessed with Brunstein et al’s (1998) personal goal inventory. After being told that “personal goals refer to the objectives, plans, and projects that you have pursued lately and that you intend to work on in the near future,” participants were asked to list one goal for each of three striving areas: (a) “striving for affiliation and friendly social contacts” (affiliation), (b) “striving for achievement and mastery experiences” (achievement) and (c) “striving for independence, social influence, and self-reliance” (power). Each striving area was illustrated by a number of examples adopted from pilot work. All participants listed and assigned one goal to each of the three striving areas. Subsequently, they rated each goal on a 4-item scale assessing their goal commitment (e.g., “I fully identify myself with this goal”). The response scale ranged from 1 (*disagree strongly*) to 5 (*agree strongly*). To obtain goal commitment scores for each goal domain, we averaged the 4 item scores within each domain. Coefficient alphas for the 4-item commitments scales were .75 (affiliation), .76 (achievement) and .86 (power). Mean (SD) goal commitment was 3.84 (0.80) for affiliation, 3.99 (0.76) for achievement, and 3.74 (0.81) for power.

2.7. Procedure and equipment

Participants worked on this fixed task sequence: PSE, LANT, personal goal assessment, saliva collection, color-naming task, and biographical data. These tasks were interspersed with other tasks and questionnaires not related to the results we report here. All tasks and questionnaires were programmed in Inquisit 3 (Millisecond Software, Seattle, Washington, USA) and presented on personal computers running Windows XP with 22-in. LCD monitors (refresh rate: 60 Hz). Participants' responses were measured via PC keyboard (PSE, biographical data), microphone and voice key (referential competence), and a Cedrus Corporation (San Pedro, CA, USA) RB-830 response pad (LANT). Participants were seated at computer desks, approximately 70 cm from the screen.

3. Results

3.1. Descriptive statistics

Table 1 provides descriptive statistics for the LANT by function and visual half-fields (VHF). Lateralized attention scores did not vary as a function of participant group in a repeated-measures analysis with VHF and attentional function as within-subjects factors, *Fs* < 1.95. Table 2 provides descriptive statistics and correlations for hormone and coherence measures, broken down by participant group. Because P and C were not normally distributed, we subjected them to a log transformation and based all inferential statistics on these transformed values.

3.2. Effects of group status and time of day

Salivary P levels for men and women were well within the range established in a multicenter study using similar assay protocols (Sufi et al., 1985). Although OC women tended to have lower levels of P (see Table 2), the effect of participant group on P levels did not become significant, $F(2, 89) = 2.92$, $p > .05$. However, when we tested OC women against the combined group of men and NC women, the former group had significantly lower P levels than the latter, $F(1, 90) = 5.62$, $p = .02$. Participant group did not have significant effects on C, which was strongly correlated with P, or any of the coherence measures described below, *ps* > .05. Time of day was negatively associated with levels of P, $r = -.19$, $p = .07$, and C, $r = -.55$, $p < .0000001$. Controlling for time of day did not substantially alter any of the analyses involving hormone measures and we therefore will not consider this variable in the following. The same applies to handedness.

3.3. P and LANT hemifield score correlations

Performance on the LANT LVF and RVF tests was correlated for alerting, $r = .45$, $p = .000008$, orienting, $r = .47$, $p = .000002$, and conflict resolution, $r = .32$, $p = .002$. To test whether P moderated these correlations, and thus the degree to which attentional processes were coupled between hemispheres, we ran a series of regressions with RVF LANT scores as dependent variables, LVF LANT scores, P, and their interaction as predictors, and pill use as a covariate to control for the overlap between this variable and P. For all three types of attention, P significantly moderated the effect of LVF performance on RVF performance, and thus the strength of the interhemispheric correlation, although in different directions (pill use did not significantly moderate this effect). For alerting and orienting, the regression weights for the interaction were negative ($B = -0.440$, $SE = 0.151$, $t(87) = -2.90$, $p = .005$ and $B = -0.241$, $SE = 0.108$, $t(87) = -2.24$, $p = .005$), but for conflict resolution *B* was positive ($B = 0.433$, $SE = 0.143$, $t(87) = 3.02$, $p = .003$), suggest-

Table 1

Descriptive statistics for LANT difference scores (in ms) in LVF/RH and RVF/LH and correlations (correlations for sample without OC women in parentheses, $n = 64$) between LVF and RVF scores, broken down by progesterone level (Md = 18 pg/mL).

	LVF/RH		RVF/LH		Progesterone	
	M	*SD*	*M*	*SD*	Low (<Md) $r_{LVF/RVF}$	High (⩾Md) $r_{LVF/RVF}$
Alerting	62.13	32.74	58.48	38.44	$.60^{***}$ ($.63^{***}$)	.20 (.28)
Orienting	53.59	41.75	57.66	38.20	$.59^{***}$ ($.53^{**}$)	$.36^{*}$ (.24)
Conflict resolution	57.05	31.42	63.76	39.65	.19 (.18)	$.43^{**}$ ($.47^{*}$)

[*] $p < .05$.

[**] $p < .005$.

[***] $p < .00005$.

Table 2

Descriptive statistics and intercorrelations for the main variables (below diagonal: entire sample, $N = 92$; above diagonal: men and NC women, $n = 64$). Correlations involving hormone measures were calculated with log-transformed hormone levels.

	Men		NC women		OC women		1	2	3	4	5	6
	M	*SD*	*M*	*SD*	*M*	*SD*						
1. Progesterone (pg/mL)	24.37	13.42	28.90	31.87	18.77	16.55	–	$.56^{***}$	.20	$.22^{H}$	.09	$.26^{*}$
2. Cortisol (ng/mL)	2.35	1.64	1.58	0.86	2.09	1.37	$.51^{***}$	–	.10	.00	−.16	.06
3. HANDI	−0.67	30.65	4.71	42.43	0.15	31.93	$.21^{*}$	.04	–	.15	$.23^{H}$	.08
4. CUD	2.37	18.53	−6.05	12.33	−0.42	14.14	$.21^{*}$	.03	.01	–	.16	−.05
5. Referential competence[a]	0.090	0.034	0.097	0.025	0.094	0.041	.14	−.16	$.23^{*}$	$.18^{H}$	–	$.24^{*}$
6. Motivational incongruence	0.30	0.31	0.37	0.28	0.40	0.29	$.25^{*}$	.03	.13	−.15	$.21^{*}$	–

Note: HANDI: hemispheric attentional network decoupling index (0.5× [|alerting difference score| + |orienting difference score|] − |conflict-resolution difference score|). CUD: crossed-uncrossed difference (0.5× [left hand/RVF RT + right hand/LVF RT] – 0.5× [left hand/LVF RT + right hand/RVF RT]).

[a] Higher numeric values denote larger differences between color naming and word reading and thus lower referential competence.

[H] $p < .10$.

[*] $p < .05$.

[***] $p < .00005$.

ing that P's effect on interhemispheric coupling of attention was different for the former two functions than for the latter. When we controlled in addition for C in these analyses, all interactions remained significant; when we replaced P with C in the regressions, none of the interactions involving C became significant. Thus, the observed moderation effects of P on interhemispheric attentional-network (de)coupling were specific to P.

To follow up on our results, we split the sample at the P median (18 pg/mL; 18 men in the low-P group, 32 men in the high-P group) into two equally sized groups and calculated LVF/RVF correlation coefficients separately for each group for each attentional function. As shown in Table 1, low-P individuals showed strong coupling of performance for the more posterior functions alerting and orienting, but not for the more anterior conflict resolution function, whereas the opposite pattern emerged for high-P individuals: they showed stronger interhemispheric coupling of the conflict resolution function, but less coupling for alerting and orienting. Means for LVF and RVF did not differ significantly for any of the three attentional function measures.

To capture this complex pattern of interhemispheric attentional-network couplings in one measure that could also be related to other indicators of functional coherence, we created an overall hemispheric attentional network decoupling index (HANDI) as follows: We first calculated absolute difference scores between LVF and RVF scores for each attention task that represent the degree to which hemispheres diverged in their performance on the task and then derived an overall HANDI score by subtracting conflict resolution difference scores from averaged alerting and orienting difference scores. Thus, higher scores capture greater decoupling of alerting and orienting functions relative to conflict resolution. As shown in Table 2 (lower triangle) and depicted in Fig. 1, higher P was associated with higher HANDI scores. This effect remained robust ($p < .05$) when we controlled for differences in C.

3.4. P and interhemispheric transfer time

To test effects of P on interhemispheric transfer time, we averaged all LANT latencies (values in ms) separately for left hand/LVF ($M = 521$, $SD = 63$), left hand/RVF ($M = 527$, $SD = 66$), right hand/LVF ($M = 511$, $SD = 64$), and right hand/RVF ($M = 516$, $SD = 66$) trials and entered these variables into a repeated-measures analysis with response hand (left, right) and visual field (left, right) as within-subjects factors and P as between-subjects factor. The hand × visual field interaction was significant, $F(1, 90) = 3.96$, $p = .049$, indicating that participants were slightly faster responding to trials in which stimulus perception and response execution occurred ipsilaterally (uncrossed: $M = 518.89$ ms) than to trials in which stimulus perception and response execution occurred contralaterally (crossed: $M = 519.13$ ms). In addition, the P × hand × visual field interaction was significant, $F(1, 90) = 4.29$, $p = .04$. To follow up on this effect, we calculated a CUD index of interhemispheric transfer time, which captured the hand × visual field interaction, by subtracting uncrossed-trial mean latencies from crossed-trial mean latencies and correlated the resulting scores with P. As shown in the lower triangle of Table 2 and in Fig. 1, higher levels of P were associated with higher CUD scores, indicating that high-P individuals, in comparison to low-P individuals, had longer interhemispheric transfer times.

3.5. P and referential competence

Higher P tended to be associated with longer color-naming latencies and thus lower referential competence, although nonsignificantly so (see Table 2). When we regressed referential competence on P and C simultaneously, thus controlling for the large variance overlap between these variables, both hormones had significant unique effects on referential competence, although in different directions: P was positively associated, $B = 0.015$, $SE = 0.006$, $t(89) = 2.46$, $p = .02$, whereas C was negatively associated with larger color-naming/word-reading differences and hence lower RC, $B = -0.019$, $SE = 0.007$, $t(89) = -2.57$, $p = .01$. These effects are depicted in Fig. 2.

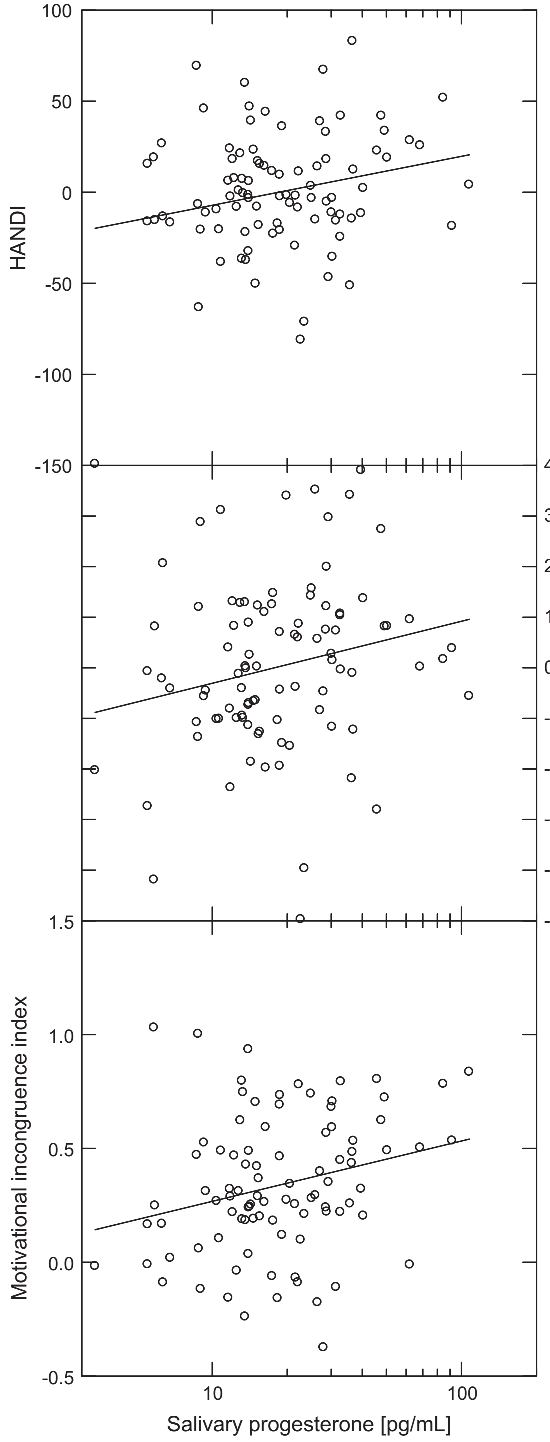

Fig. 1. Scatterplots with fitted regression lines of the association between salivary progesterone and hemispheric attentional network decoupling index (HANDI, upper panel), crossed-uncrossed difference (CUD) scores (middle panel), and motivational incongruence index (lower panel).

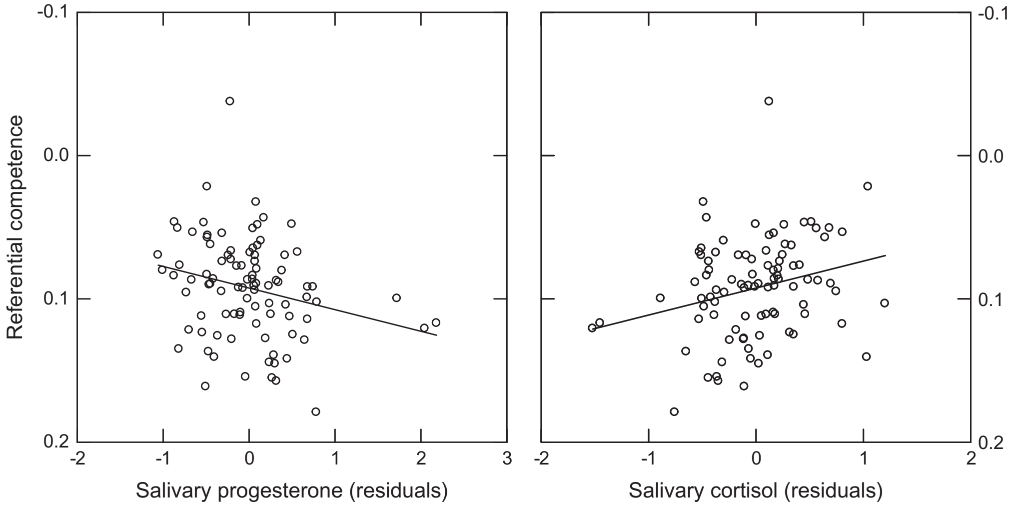

Fig. 2. Scatterplots with fitted regression lines of the association between referential competence and salivary progesterone (P), residualized for cortisol (C, left panel), and salivary C, residualized for P (right panel). Because lower scores signify better referential competence, the y axis has been reversed. If the individual with referential competence scores <0 (indicating faster color naming than word reading) is removed, correlations remain robust for residualized P ($r = .25$, $p = .02$) and residualized C ($r = -.27$, $p = .009$).

3.6. P and motivational congruence

To create a motivational incongruence index, we followed the procedure described by Schultheiss et al. (2011) and first transformed implicit motives and goal commitment scores into z scores to convert them to a common metric. Next, we created, separately for the domains of power, achievement, and affiliation, absolute motive-goal incongruence scores according to the formula: log (0.5 + |motive − goal commitment|). The log transformation brought the resulting incongruence scores into closer alignment with a normal distribution. Higher levels on these incongruence scores thus indicate a greater mismatch between implicit motives and explicit goal commitments, regardless of whether incongruence is the result of implicit motives exceeding or falling short of levels on the explicit goal measures. When we subjected the three incongruence scores to a GLM with motivational domain (power, achievement, affiliation) as within-subjects factor and P as between-subjects predictor, only the effect of P was significant, $F(1, 90) = 6.14$, $p = .02$. We therefore created an overall motivational incongruence score by averaging the three domain incongruence scores. As shown in the lower triangle of Table 2 and in Fig. 1, higher levels of P were associated with greater motivational incongruence.

3.7. Additional analyses

To ensure that the use of OCs did not bias results, we repeated all correlation, regression, and GLM analyses with OC women excluded from the sample. The same pattern of P × LVF on RVF interactions emerged for the three LANT measures and, as a consequence, the correlations for low and high P groups, split at the median of the reduced sample, did not change (see Table 1). As Table 2 (upper triangle) shows, effect sizes and directions for associations between P and coherence measures did not substantially change and statistical reliability was preserved in most cases, despite the smaller size of the subsample ($n = 64$). Likewise, the unique effects of P and C on referential competence remained significant, $ps < .08$. We also tested whether men, NC women, and OC women differed on C, HANDI, CUD, and motivational incongruence, but univariate ANOVAs did not become significant, $ps > .05$. Participant gender did not moderate the regression effects of P × LVF on RVF scores, the effect of P on motivational congruence, RC, or CUD, all $ps > .10$. Thus, the effects of P on our measures do not reflect mere gender differences.

4. Discussion

As predicted by the interhemispheric-decoupling hypothesis (Hausmann & Gunturkun, 2000), salivary P was associated with the degree to which performance measures of the attentional functions alerting, orienting, and conflict resolution correlated between hemispheres. Consistent with the hypothesis, higher P was linked to lower interhemispheric correlations for alerting and orienting, two functions located in posterior and subcortical brain networks. Contrary to the hypothesis, however, we found higher P to be associated with a *higher* interhemispheric correlation for conflict resolution, a function that depends on prefrontal brain functions, particularly those of the anterior cingulate. While this finding generally supports the notion that P levels influence interhemispheric interaction, it also suggests that this influence is not homogenous. Whether P has a coupling or decoupling effect may depend on specific functional networks and, perhaps, the location of this network on an anterior–posterior continuum of callosal connections.

We suggest two reasons for why our finding of coupling functions of P (in addition to decoupling functions) diverges from earlier observations by Hausmann and colleagues. First, these authors typically studied functions such as letter recognition and figural-features matching that recruited more posterior brain networks such as parietal and temporal areas. Our finding of a hemispheric decoupling effect of P for posterior attention functions is consistent with these findings. However, earlier studies rarely examined tasks that recruit frontal functions, like the conflict-resolution component of the LANT does, and therefore a coupling effect of P may have gone unnoticed so far (cf. Hochman, Eviatar, Barnea, Zaaroor, & Zaidel, 2011). Indeed, there is some evidence from electroencephalography studies that activation of GABA receptors, to which P binds, decreases interhemispheric correlation in most power bands, but also increases it in others (see Ugalde, Del Rio-Portilla, Juarez, Roldan, Guevara, & Corsi-Cabrera, 1998). Further research is needed to determine if P is causally involved in the interhemispheric coupling of conflict resolution (and perhaps other frontal functions) and, if so, through which mechanism.

Second, in their studies on the interhemispheric-decoupling hypothesis, Hausmann and colleagues relied on a strategy that tested effects of P on difference scores that reflected the degree to which a cognitive function is lateralized. These authors interpreted difference scores near 0, reflecting an absence of lateralization of usually lateralized functions (such as word recognition, figure matching, and face discrimination; e.g., Hausmann & Gunturkun, 2000; Hausmann et al., 2002), as an indicator of interhemispheric decoupling. In contrast, we examined the degree to which performance for the same type of task, presented to the two hemispheres, was correlated between hemispheres, with weaker correlations signifying less interhemispheric coupling of a given function. In other words, whereas Hausmann and colleagues used *mean performance differences* between hemispheres as a criterion, we used the *covariation of performance* between hemispheres as an indicator of interhemispheric coupling and decoupling. We contend that our strategy provides a more stringent test of the interhemispheric decoupling hypothesis, because the meaning and interpretation of mean score differences between hemispheres is not straightforward: performance between hemispheres can be highly correlated even if the mean score of performance differences between hemispheres is exactly zero and, vice versa, a mean score indicating a strong lateralization of performance does not automatically imply that performance between hemispheres is (negatively) correlated (as argued by Hausmann & Gunturkun (2000)), which would indicate interhemispheric coupling.

In contrast to earlier studies that have failed to find an association between P and interhemispheric transfer time as a measure of interhemispheric interaction (e.g., Bayer & Hausmann, 2009), higher levels of P were linked to longer interhemispheric transfer times in the present study, perhaps owing to the larger sample size and resulting higher test power of our study relative to earlier studies. Alternatively, differences in findings can also be due to differences in the tasks employed: whereas Bayer and Hausmann (2009) used a CUD measure which requires participants only to respond, with either the left or the right hand, to simple stimuli presented in the LVF or RVF, we calculated a CUD score based on the LANT task which required participants to make decisions about the type of target stimulus shown as well as dealing with predictive and flanker stimuli. Our CUD measure was therefore based on a more demanding task, making it more dependent on efficient interhemispheric functional integration and thus more vulnerable to high levels of P than the original, less demanding CUD measure (see Banich, 2004).

RC was reliably associated with P once the large overlap between P and C was controlled for. Higher levels of P were linked to less referential competence (i.e., relatively longer color naming than word reading latencies), suggesting less efficient connections between nonverbal processing of color in the visual system and naming functions of the language cortex. Notably, low RC was also associated with HANDI and CUD scores indicative of less interhemispheric coupling. This finding is consistent with neuropsychological cases of color anomia in which an inability to correctly name colors was associated with severed posterior callosal pathways between the RH visual system and the LH language system (Beauvois & Saillant, 1985; Geschwind & Fusillo, 1966). Thus, like the HANDI and CUD indices, our measure of referential competence may reflect the efficiency with which information is exchanged between the hemispheres. It is presently unclear why C, after holding P constant, was associated with *high* referential competence. We tentatively explain this finding with the fact that C and performance on many cognitive tasks have a curvilinear relationship, with higher levels of C being associated with better performance up to a certain point, after which further increases in C are related to impaired performance (Williams, 2002). Participants were not exposed to acute stressors that would have raised C beyond this critical level in the present study, and this may be the reason why we did not see C-related impairments of cognitive functions in any measured variable, including referential competence. More generally, however, the finding of differential predictive validity of P and C despite the large correlation between these variables reinforces the necessity to measure and control for one hormone while testing for effects of the other (see also Wirth et al., 2007). Otherwise, effects of the stress hormone C cannot be disentangled from those of the gonadal steroid hormone P.

The present study also explored for the first time whether a role for P in reduced coherence can be documented for phenomena beyond the domain of cognitive tasks. Consistent with our hypothesis that congruence between implicit motives and explicit goals depends on functional coherence between nonverbal and verbal behavior-regulating systems, we found low P to be associated with higher congruence between implicit and explicit motive measures across the domains of power, achievement, and affiliation.

A limiting factor for the interpretation of our findings is the correlational design of our study. While results are consistent with the hypothesis of a causal effect of P on indicators of reduced coherence, we cannot rule out other interpretations of our findings, such as an effect of cognition on hormone levels (e.g., Kim, 2008), a reciprocal relationship between hormones and behavioral variables (e.g., Mazur, 1985), or effects of other variables on both P and cognitive and motivational markers of coherence. With regard to the latter possibility, we could rule out variations in C, which is metabolized from P and whose levels are strongly correlated with P, as an alternative explanation for the effects we observed. We could also rule out gender, OC use, or time of day as potential confounds or moderators, which suggests that our observations are specifically related to circulating P levels, but not more distal background factors that influence both P and a host of other variables. We did not measure and test for variations in estradiol, which has also been implicated in interhemispheric decoupling (e.g., Bayer & Hausmann, 2009; but see Derntl et al., 2008). As already mentioned, experimental manipulation of P levels and also studies on naturally occurring temporal changes in P levels (such as over the course of the menstrual cycle) will provide opportunities for disentangling the issue of causality further. Finally, although gender and OC use did not significantly moderate associations of P with attention, CUD, RC, or motivational incongruence in the present study, future research should specifically target larger subsamples of OC and NC women as well as men to provide more sensitive tests of whether gender and particularly OCs, which alter the body's endogenous P secretion through the addition of exogenous hormones, represent background variables that moderate the more proximal effects of circulating P on cognitive and motivational functions.

To conclude, the present study provides evidence in support of a role for P in reduced coherence by showing that P is associated with: (a) the degree to which attentional functions are correlated across hemispheres (with P attenuating correlations for posterior functions and increasing the correlation for an anterior function), (b) slower interhemispheric transfer time, (c) impaired referential competence, as reflected in longer color-naming latencies relative to word reading latencies, and (d) incongruence between participants' implicit motives and explicit goal commitments.

Acknowledgement

We thank Michelle M. Wirth for helpful suggestions on a previous draft of this paper.

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