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

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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.

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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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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