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Hormonal correlates of paternal responsiveness in new and expectant fathers

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Abstract

Little is known about the physiological and behavioral changes that expectant fathers undergo prior to the birth of their babies. We measured hormone concentrations and responses to infant stimuli in expectant and new fathers living with their partners to determine whether men can experience changes that parallel the dramatic shifts seen in pregnant women. We obtained two blood samples from couples at one of four times before or after the birth of their babies. After the first sample, the couples were exposed to auditory, visual, and olfactory cues from newborn infants (test of situational reactivity). Men and women had similar stage-specific differences in hormone levels, including higher concentrations of prolactin and cortisol in the period just before the births and lower postnatal concentrations of sex steroids (testosterone or estradiol). Men with more pregnancy (couvade) symptoms and men who were most affected by the infant reactivity test had higher prolactin levels and greater post-test reduction in testosterone. Hormone concentrations were correlated between partners. This pattern of hormonal change in men and other paternal mammals, and its absence in nonpaternal species, suggests that hormones may play a role in priming males to provide care for young.

Keywords: Paternal/parental responsiveness; Couvade syndrome; Prolactin; Estradiol; Cortisol; Testosterone

Effective parental care is critical to infant survival in all mammalian species. Lactation ensures a central nurturant role for females, but in a few mammalian species, including our own, paternal care also can increase offspring survival (Wynne-Edwards and Lisk, 1989; Hewlett, 1992; Hurtado and Hill, 1992; Gubernick et al., 1993). Pre- and postnatal hormonal changes are clearly involved in the rapid onset of mammalian maternal behavior at birth

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(Rosenblatt et al., 1988; Bridges and Ronsheim, 1990; McCarthy et al., 1994), but little is known about comparable changes in males.

Men show marked individual (Belsky et al., 1991) and cultural variation (Barry and Paxson, 1971) in the expression of paternal care. Men had moderate to high levels of contact with infants in about 40% of cultures in a cross-cultural survey (Barry and Paxson, 1971), and they are most paternal when couple intimacy is high (Whiting and Whiting, 1975; Broude, 1983; Belsky et al., 1991). Male (couvade) pregnancy symptoms also are more common in cultures with paternal care and high levels of couple intimacy, and these symptoms may reflect socially induced physiological changes that prepare men for fatherhood (Elwood and Mason, 1994). Because successful adoption occurs, we know that humans can bond to children without experiencing the hormonal changes of pregnancy. However, close contact with the pregnant partner may induce hormonal changes that enhance and accelerate the onset of paternal responsiveness in some men, as has been found in nonhuman animal studies.

Males of other paternal mammals are also variable in their expression of paternal care (Gubernick et al., 1994; Roberts et al., 1998; Storey and Snow, 1987; Storey et al., 1994 compared to Oliveras and Novak, 1986). Interactions with mates and young facilitate parental behavior in male mammals (Elwood, 1977, 1986; Brown, 1986; Gubernick and Alberts, 1989; Storey and Walsh, 1994; Storey and Joyce, 1995), but not all males respond in the same way to particular social experiences (Perrigo et al., 1991; Gubernick et al., 1994). For example, some males of the naturally paternal California mouse (*Peromyscus californicus*) become paternal during their mates' pregnancies, whereas the rest only become paternal after their pups are born (Gubernick et al., 1994). This variation in expression and onset of paternal responsiveness may persist because the reproductive value of paternal care changes with ecological context. Male care increases offspring survival under some conditions (e.g., by providing warmth at low temperatures, Gubernick et al., 1994; or by assisting with the births, Jones and Wynne-Edwards, in press), whereas providing care would not offset the costs of lost mating opportunities under other conditions. The individual variability in the social cues that trigger paternal behavior may lead us to the view that hormones are not involved in the expression of parental behavior in male mammals. An alternate, but as yet untested, hypothesis is that hormonal changes promote the onset of paternal behavior, but that individual males are more variable in the social experiences that induce these hormonal changes.

Exposure to pups makes male rats paternal without significantly changing their hormone levels (Brown and Moger, 1983; Samuels and Bridges, 1983; Tate-Ostroff and Bridges, 1985), findings that discouraged research on the hormonal basis of mammalian paternal care. However, rats are not naturally paternal, and we now realize that attention should be focused on naturally paternal species (which comprise less than 10% of all mammalian species). Males of rodent, primate, and canid species with paternal care show perinatal increases in prolactin (Gubernick and Nelson, 1989; Kreeger et al., 1991; Ziegler et al., 1996; Brown et al., 1995; Reburn and Wynne-Edwards, 1999) or higher prolactin levels during infant contact (Dixson and George, 1982). Prolactin increases prior to the onset of parental behavior in male and female birds (Silver, 1978) as well as male (Ziegler et al., 1996; Brown, et al., 1995) and female mammals (Fleming and Corter, 1988; Bridges and Ronsheim, 1990; McCarthy et al., 1994; Fleming et al., 1997). In male birds and mammals, this increase in prolactin occurs around the same time that testosterone concentrations decrease (Silver, 1978;

Ball, 1991; Brown et al., 1995; Reburn and Wynne-Edwards, 1999). Cortisol, another hormone that increases in late pregnancy, has been linked to mother-infant attachment (Fleming and Corter, 1988; Fleming et al., 1997). Cortisol is higher just before birth in males of the paternal species of dwarf hamster, but not in a closely related nonpaternal species, e.g., *Phodopus* spp (Reburn and Wynne-Edwards, 1999).

The consistent pattern of hormonal changes in paternal animals, and its absence in nonpaternal ones, supports the need for investigation in our own frequently paternal species. Based on hormonal data for women and for males of naturally biparental mammals, we predicted that hormone changes in men would start prior to the birth of their children and continue into the postnatal period. Further, we predicted that individual variation in hormone levels would be related to the incidence of male pregnancy (couvade) symptoms and to the men's responsiveness to infant cues. Finally, we took a second blood sample 30 minutes after the first sample to determine whether there were stage-specific changes in hormonal responsiveness to the infant cues. We predicted that the magnitude of this change, which we called situational reactivity, would increase close to the birth.

1. Methods

1.1. Subjects

Thirty-four couples were recruited from prenatal classes at the Grace General Hospital in St. John's, Canada. Thirty-one couples provided blood samples at one of four times either before or after the birth of their babies. Repeated samples were taken from the other three couples to confirm that the group differences were a good reflection of the stage-specific changes seen in couples sampled only once. Two couples were tested once each before and after their babies were born, and both their prenatal and postnatal samples were used in the analysis. One couple provided 10 samples between 45 days before the birth and 33 days after, including samples in labor and at 14h postpartum; and only their first prenatal (−45 days) and first postnatal (+9 days) samples were used. Thus, our group sizes for the purposes of analyses were: Early Prenatal ($N = 12$ between 16 and 35 weeks of the 40-week pregnancy); Late Prenatal ($N = 8$ in the last 3 weeks before the birth), Early Postnatal ($N = 9$ within 3 weeks after the birth), and Late Postnatal ($N = 8$ when the babies were between 4 and 7 weeks old).

All but three of the couples were first-time parents. Data from the three couples tested for their second baby were included in the analysis after confirming that they did not differ from the rest of their respective groups.

1.2. Procedure

Prenatal instructors allowed us to describe our research at the end of their classes. We told each group that we were interested in hormonal changes in fathers, as well as in mothers, and we wanted to determine whether these hormonal changes and changes in physical and emotional symptoms played a role in preparing men for fatherhood. No incentives were offered for participation in the study. A sign-up sheet was passed around at the end of class and the volunteer rate was approximately 10%. Volunteers were called later and asked if they still wanted to participate; if so, we scheduled an appointment time. All volunteers were of European descent and were between 25 and 40 years of age.

All testing was conducted between 16:00 and 20:00 hours so that diurnal rhythms in hormone concentrations would be held constant (Boyar et al., 1975; Miyatake et al., 1980; Diaz et al., 1989; Genazzani et al., 1992; Simoni et al., 1992). Late afternoon and early evenings are times when levels of all these hormones are low and relatively stable (i.e., prolactin levels are most variable at night); thus, this time was chosen partly to minimize variation among couples.

Couples were tested either in their own homes or in the home-like setting of the breastfeeding clinic. First, we reviewed the test procedure with each couple. They then signed a consent form approved by the Human Investigation Committee of Memorial University. Our technician took a 5-ml venipuncture blood sample from the man and then from the woman. A second sample was taken from each person about 30 minutes later so that we could examine short-term hormonal changes in response to external stimuli (infant cues), which we called a test of situational reactivity. We chose a 30-minute time interval between samples because hormone levels have been shown to be affected by social stimuli well within that period [e.g., women's prolactin increases during the first 30 minutes of a nursing bout (Howie et al., 1980; Glasier et al., 1984; Stern et al., 1986; Stallings et al., 1996); and men's testosterone increases after competitive interactions (Booth et al., 1989) or sexual stimulation (Stoleru et al., 1993)].

1.3. Situational reactivity test

After providing the first sample, couples were asked to sit in comfortable chairs and each was asked to hold a soft-bodied doll on their shoulders. The doll was wrapped in a receiving blanket that had been worn by a newborn within the past 24 hours. Fathers in the postpartum groups held their newborn child and the mother held the doll. We then played a 6-minute tape of newborn cries previously recorded from the neonatal unit, followed by a 5-minute video sequence from the film "Breast is Best" (produced by Video Vital for the Baby Friendly Hospital Initiative for the Norwegian Board of Health) in which a couple greets their newborn and the newborn struggles to nurse for the first time. We were interested in both changes over time relative to the birth and changes in how baby stimuli affected short-term hormonal responses. We considered the first sample as the "unstimulated" estimate of hormone concentrations and the difference between the samples as a measure of "situational reactivity" in response to the test situation. Because all subjects were tested with the infant stimuli, we can only address questions about whether there were stage differences in degree of reactivity to our test situation. The experimenter talked to the couples for the rest of the 30-minute period between samples, with the conversation focused mainly on baby and parent issues. The experimenter also noted when or whether either member of the couple spontaneously put down the doll that they had been asked to place on their shoulders, and, if so, when that occurred.

Couples completed a two-page questionnaire on their pregnancy symptoms and responses to our baby stimuli after they provided the second blood sample. Couples were asked to complete a checklist of pregnancy symptoms about themselves and about their partners. Symptoms on the checklist were weight gain, nausea, increase in appetite, fatigue, decrease in appetite, weight loss, and emotional changes. Men reporting two or more pregnancy symptoms were classified as having couvade syndrome (Masoni et al., 1994). The checklist of responses to baby cries included "content, irritated, excited, anxious, concerned, want to comfort baby" and "other" (which they were asked to specify). Couples were asked to specify the degree of stress resulting from the sampling, using a five-point scale that ranged from "no stress" to "very high stress."

1.4. Statistical procedures

When the O'Brien's test for unequal variance was significant (all hormones for women and testosterone for men), results were compared using a Welch statistic analysis of variance (ANOVA) with adjusted degrees of freedom for the F-test (means weighted by the reciprocal of sample variances on the group means; SAS Institute, Cary, NC, U.S.A.). Post hoc comparisons between groups used a Student's t-statistic (for analyses with unequal variances) and Neuman-Keuls for standard ANOVAs. Pearson product moment correlation coefficients were used to examine relationships among hormone levels. Multiple regression was used to determine the role of time to birth in the hormone associations within couples.

1.5. Hormone assays

Blood samples were centrifuged after the test session. The serum was removed and frozen until it was analyzed for prolactin and cortisol for both parents, as well as for testosterone in the men and estradiol in the women. Hormonal assays were performed in the Biochemistry Laboratory of the Health Sciences Centre of Memorial University. Prolactin in each sample was measured by fluoroimmunoassay (AutoDELPHIA Prolactin kit, Wallec, Gaithersburg, MD, U.S.A.) and ranged from 3.5 to 13.0 μg/L in the men, within the normal range of values for males between 19 and 57 years of age. The lowest levels in the women were between 2.6 and 6.8 μg/L for three non-nursing women in the Late Postnatal group, which are within the range for nonpregnant women cited in the kit instructions. The higher prolactin values for pregnant and parturient women (highest 232 μg/L) are similar to those found in previous studies (Fleming and Corter, 1988). Cortisol in each sample was measured by fluoroimmunoassay (Tdx/TDxFLx Cortisol Assay System, Abbott Laboratories, Morgan Hill, CA) in unextracted serum and ranged from 40 for both sexes up to 520 nmol/L for the men and 1,760 nmol/L for the women. The lower end of values lies well within the normal range for humans and the higher values for third trimester women are similar to those found by Fleming and Corter (1988). All men with high levels of cortisol were in the Late Prenatal or Early Postnatal groups. Estradiol was measured by fluroimmunoassay (AutoDELPHIA Estradiol kit) and ranged from nondetectable ($<$0.05 nmol/L) in some parturient women to a high of 89 nmol/L for one third-trimester woman (assay kit range for third-trimester women is 20 to 130 nmol/L). Testosterone was measured by radioimmunoassay (Coat-a-Count Free Testosterone, DAC Corp, Los Angeles, CA, U.S.A.) and ranged from 19 to 90 pmol/L, falling in the middle of the range of the assay and within the normal range of values for males between 20 and 49 years of age. Intra- and interassay variabilities were $<$5% with each of these methods.

One man's cortisol level apparently rose by more than 300% from sample 1 to sample 2, which was taken 30 minutes later. Because decreases were observed in all but three other men (who averaged a 30% increase), we assumed a measurement error had occurred and deleted all the cortisol data for this man.

2. Results

2.1. Possible stress effects

Both cortisol and prolactin increase in some stressful situations in humans, which is a potential problem in this study (Jeffcoate et al., 1986; Farrace et al., 1996; Harlow et al., 1996). However, links between prolactin and stress have not been found in other studies (Pearce et al., 1980), and not all stress studies find correlations between concentrations of the two hormones (Leino et al., 1995; Hetz et al., 1996).

We took several steps to minimize, or hold constant, stress responses that might make it difficult to interpret the hormone results. First, the between-subjects design (different couples tested at each stage, except for three couples) prevented us from confounding stage of pregnancy with number of times tested (if stress levels were reduced at each test). The first blood sample was taken within 10 minutes of meeting with the couple to keep the time course of any stress response constant across couples. We found no relationship between hormone levels and the subjective stress level reported by the couples or judged by the technician taking the samples.

We found that cortisol-prolactin associations differed among stage-specific groups, but the pattern was very similar for the men and women. There was a significant positive correlation between cortisol and prolactin in the Early Prenatal group for both men (Pearson's $r = .77, p < .01$) and women ($r = .58, p < .05$), but no other significant correlations in the other groups (although both sexes show a near significant relationship at the Early Postnatal stage). Similarly, it is of interest to note that the woman who provided 10 blood samples showed increasing prolactin and cortisol levels between 6 weeks (45 days) and 3 weeks (21 days) before the birth, but showed decreases in prolactin and increases in cortisol in the last 3 weeks of the pregnancy. During labor, both the man and the woman showed substantial increases in cortisol compared to 5 days earlier (increased by 76% for the man and 102% for the woman). Prolactin levels dropped in the same period (decreased by 24% and 57%, respectively, Table 1). It appears that, as in previous literature, prolactin and cortisol sometimes change together and sometimes do not.

2.2. Stage-specific differences in hormone concentrations

2.2.1. Prolactin

Prolactin levels in women differed among stages (all analyses reported are for first samples, $F_{3,16.6} = 14.7, p < .0001$, Fig. 1a). Women in the Late Prenatal group had higher prolactin levels than women in all other stages ($p < .05$, Fig. 1a), and women in the Early Prenatal Group had higher levels than women in the Late Postnatal group ($p < .05$). In contrast with women, there were no significant differences among stages in men's prolactin levels with the three-week cutoff for the end of the Early Postnatal stage used in the other analyses ($F_{3,16.6} = 1.86, p < .10$, Fig. 1d). However, there appears to be a shorter time course in the prolactin recovery in the postnatal period in comparison with the men's other hormones that resulted in

Table 1
Hormone levels in the late prenatal and late postnatal periods for the couple tested ten times

	Man			Woman		
Test Time	Testosterone (pmol/L)	Prolactin (μg/L)	Cortisol (nmol/L)	Estradiol (nmol/L)	Prolactin (μg/L)	Cortisol (nmol/L)
−45 days	42	5.4	105	25.8	116	556
−35 days	53	4.0	222	29.8	112	796
−28 days	47	5.0	221	28.8	130	820
−21 days	27	6.1	184	31.8	177	947
−12 days	36	4.8	232	30.7	143	841
−5 days	47	4.2	225	31.7	122	853
Labor	45	3.2	398	30.3	53	1730
14 hours postpartum	60	2.8	204	1.9	87	894
+9 days	41	3.3	296	0.1	93	459
+33 days	47	3.6	223	<.05	141	149

marked differences within the Early Postnatal group. Blood samples taken within 2 weeks after the birth had significantly lower levels of prolactin (mean 4.7 ± 0.5 μg/L, $n = 5$) than blood sampled in the third week after the birth (mean 8.5 ± 0.5, $t_7 = 4.6, p < .01, n = 4$, levels more like those in the late Postnatal group). Using 2 weeks as the cutoff for the Early Postnatal group substantially reduces the within-group variability for the two postnatal groups. With a 2-week cutoff, the stage differences in prolactin levels were significantly different ($F_{3,33} = 3.79, p < .05$) with men in the Late Prenatal group having higher prolactin levels than men in the Early Prenatal group and in the Early Postnatal group ($p < .05$).

2.2.2. Cortisol

Cortisol levels differed among stages for both women ($F_{3,14.1} = 22.1, p < .0001$, Fig. 1b) and men ($F_{3,35} = 3.62, p < .05$, Fig. 1e), with the highest levels found in the Late Prenatal Stage. For women, cortisol levels in the Late Prenatal group were higher than for all other groups ($p < .05$, Fig. 1b), and they were higher in the Early Prenatal group than in either postnatal group ($p < .05$). For men, the Late Prenatal group had higher cortisol levels than the Early Prenatal group and the Late Postnatal group ($P < .05$, Fig. 1e).

2.2.3. Steroid hormones

In women, estradiol showed the largest changes among stages of any of the hormones ($F_{3,13.2} = 45.1, p < .0001$, Fig. 1c). Estradiol levels were significantly higher in the Late Prenatal group than in any other group, and the Early Prenatal group was higher than either postnatal group ($ps < .05$, Fig. 1c). In men, testosterone differed among stages ($F_{3,17.7} = 5.3, p < .01$, Fig. 1f), with levels in the Early Postnatal group lower than those in the Late Prenatal group ($p < .01$, Fig 1f).

2.2.4. Within-couple changes

In three couples tested once before and once after the birth, men showed a decrease in testosterone (all one-tailed paired, $t_2 = 4.3, p < .05$) and women showed a decrease in estradiol ($t_2 = 2.95, p < .05$) from the prenatal to the postnatal period (Table 2). All three women and two of the three men showed postnatal declines in prolactin and cortisol.

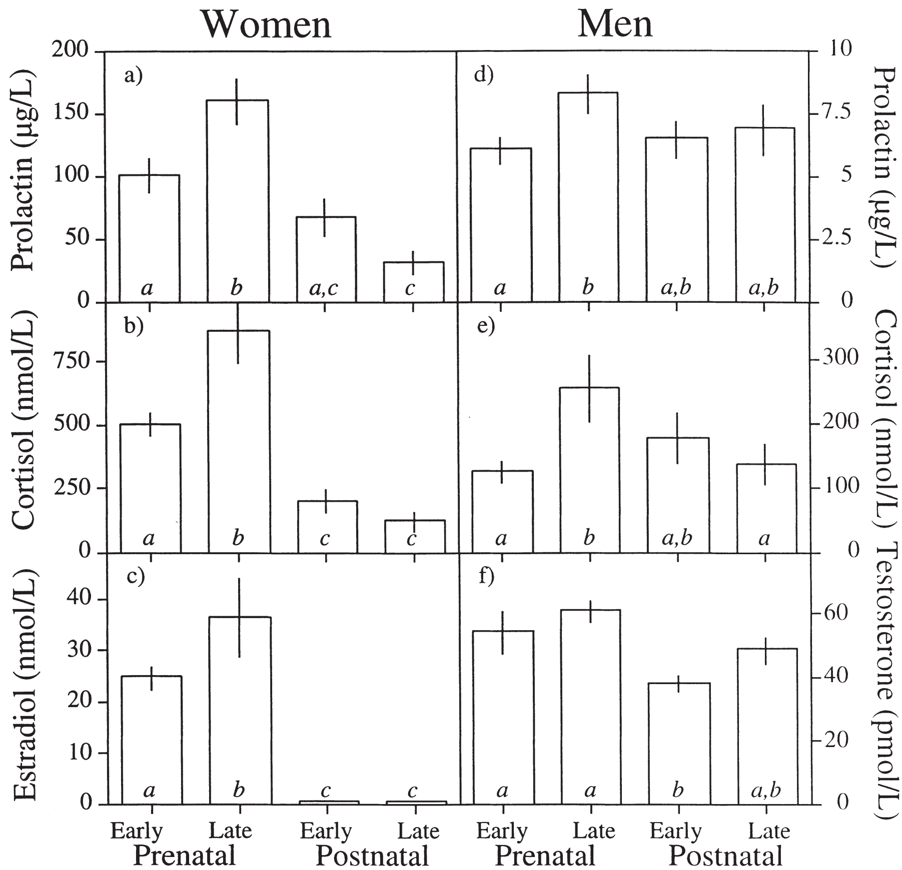

Fig. 1. Sample 1 concentrations (±SE) of hormones for women (a) prolactin, (b) cortisol, and (c) estradiol, and for men (d) prolactin, (e) cortisol, and (f) testosterone tested during the Early Prenatal period ($n = 12$), Late Prenatal period ($n = 8$), Early Postnatal period ($n = 9$), and Late Postnatal period ($n = 8$). Different letters on the bars indicate significant group differences relative to the Early Prenatal Group.

Data from the one couple sampled 10 times helped to pinpoint when the hormonal changes occurred (Table 1). Both the man and the women showed a pronounced elevation in cortisol during labor. The woman's estradiol level dropped within 14 hours after the birth. The man's testosterone rose within 1 day of the birth but then dropped by 9 days postpartum. Prolactin levels were lowest for both members of the couple in the peripartum period.

2.3. Situational reactivity: changes in hormone concentrations over a 30-minute period

Overall, there was a significant decrease from sample 1 to sample 2 for men and women for both prolactin (paired *t*-tests, men, $t_{36} = 3.3, p < .01$; women, $t_{33} = 1.7, p < .05$) and cortisol (men, $t_{35} = 5.1, p < .001$; women, $t_{33} = 2.6; p < .05$).

We predicted that the magnitude of short-term change between samples would vary with reproductive stage, a measure we called "situational reactivity." Situational reactivity indicates a change in the magnitude of response to salient environmental stimuli, which may be

Table 2
Mean (± SE) of hormone levels in the Late Prenatal period (8.0 ± 1.0 days before birth) and Early Postnatal period (9.7 ± 3.7 days after birth) for the three couples tested before and after their babies were born

	Men		Women	
	Late Prenatal	Early Postnatal	Late Prenatal	Early Postnatal
Prolactin (μg/L)	6.6 (1.2)	5.5 (1.0)	140.3 (19.7)	67.1 (13.1)*
Cortisol (nmol/L)	260.0 (58.9)	199.3 (74.8)	683.7 (100.6)	336.3 (64.6)*
Testosterone (pmol/L)	57.0 (5.5)	46.7 (6.3)*	—	—
Estradiol (nmol/L)	—	—	44.5 (14.5)	0.13 (0.02)*

*Significant paired t-test, $p < .05$.

due to elevations in the baseline levels as well as to a greater impact of emotional stimuli. Situational reactivity (mean change from sample 1 to sample 2) changed in the immediate perinatal period for men's testosterone ($F_{3,33} = 3.70, p < .05$) and men's cortisol ($F_{3,33} = 6.1, p < .01$). Cortisol decreases were greater between samples in the Late Prenatal group, and testosterone increases were greater in the Early Postnatal group than at other stages (ps $< .05$, Fig. 2).

Higher baseline levels of cortisol were associated with greater situational reactivity, particularly in the men (all groups significant, overall $r = .80, p < .01$; range of correlation coefficients in individual groups, 0.50 to 0.93). Women's baseline levels of cortisol showed a weaker relationship with situational reactivity (overall, $r = .40, p < .05$, range of correlation coefficients, 0.19 to 0.57).

There were some significant within-group positive correlations between the baseline levels of other hormones and their situational reactivities (e.g., testosterone, $r = .47$ and prolactin $r = .46$ for men in the combined prenatal groups; prolactin, $r = .82$, for women in the Late Postnatal group), but the cortisol relationship for the men was the most consistent across groups. Prenatal estradiol was the only hormone to show a negative relationship; higher estradiol levels were associated with lower situational reactivity ($r = -.87, p < .01$).

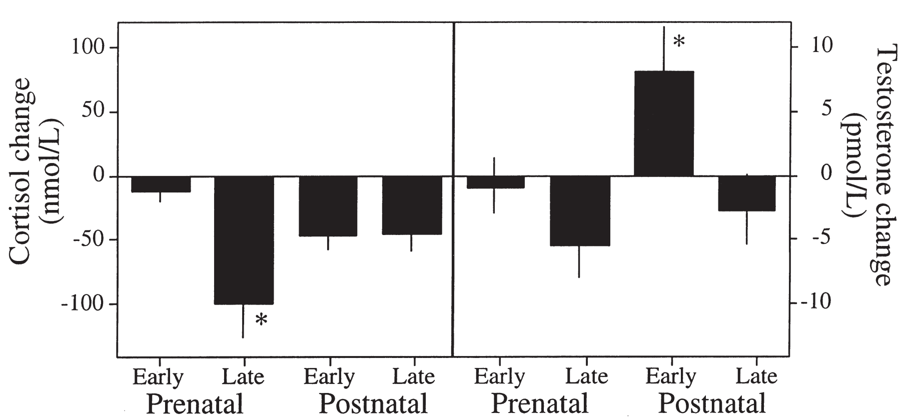

Fig. 2. Situational reactivity or the mean change (±SE) in hormone concentrations from sample 1 (before exposure to infant stimuli) and to sample 2 (30 minutes later, after exposure; negative values indicate that sample 2 was lower than sample 1) for men's cortisol (left panel) and men's testosterone (right). Asterisk indicates a significant difference, based on post hoc tests, $p < .05$.

Women who reported feeling concern on hearing the baby cry showed a greater cortisol decrease than women who did not (prenatal women only, concerned, -68.3 ± 11.7, $n = 6$; not concerned, -24.2 ± 24.0, $n = 11$, $t_{15} = 2.2$, $p < .05$), which supports the hypothesis that individual differences in reactivity are linked to responsiveness to our test stimuli.

2.4. Relation of behavioral and emotional measures to hormone levels

Men in the combined prenatal and postnatal groups who reported feeling concerned in response to the baby cries had higher average prolactin levels (7.4 ± 0.5 μg/L, $n = 16$) than other men (5.7 ± 0.5 μg/L, $n = 17$, $t_{31} = 2.4$, $p < .05$, also significant for both the first and second samples considered separately). Also, men who felt concerned or wanted to comfort the baby had a significantly different pattern of testosterone change than men not reporting these feelings. Testosterone levels in the combined pre- and postnatal groups decreased for the more concerned men (-2.6 ± 1.4 pmol/L, $n = 24$) compared to less responsive men (less concerned, 4.4 ± 3.6 pmol/L, $n = 9$, $t_{31} = 2.7$, $p < .05$).

Some men in the prenatal groups removed the doll from their shoulders before the end of the 30-minute interval between samples (men in the postnatal groups were holding their own babies and none removed the baby so were not included in this particular comparison). Men who held the doll on their shoulders for the full interval had lower testosterone concentrations (44.5 ± 5.2, $n = 12$) and their prolactin concentrations showed a significantly larger situational response ($-12.5\% \pm 0.05$) than men who laid the doll down during the test interval (testosterone, 73.6 ± 5.5, $t_{16} = 3.5$, $p < .01$; prolactin response, $0.04\% \pm 0.04$, $t_{16} = 1.9$, $p < .05$, $n = 6$).

2.5. Relation of couvade symptoms to hormone concentrations

Men with two or more pregnancy symptoms [used as a definition of couvade syndrome (Masoni et al., 1994)] had higher average prolactin levels (7.2 ± 0.5 μg/L, $n = 20$) than men with fewer than two symptoms (5.6 ± 0.4 μg/L, $n = 14$, $t_{32} = 2.3$, $p < .05$). For the two prenatal groups combined (but not for all couples), men with two or more symptoms showed a greater situational testosterone response (-5.7 ± 2.1 pmol/L, $n = 9$) than men with fewer symptoms (1.27 ± 2.2 pmol/L, $n = 11$, $t_{18} = 2.2$, $p < .05$). Similarly, partners of men with two or more symptoms had higher prolactin and cortisol levels than partners of men with fewer symptoms (men have two or more symptoms: women's prolactin, 147.6 ± 16.0 μg/L; fewer symptoms, 88.1 ± 10.9 μg/L; $t_{15} = 2.99$, $p < .01$; women's cortisol when men have two or more symptoms, 711.7 ± 94.6 nmol/L; fewer symptoms 453.7 ± 60.7 nmol/L, $t_{15} = 2.2$, $p < .05$).

The nonhuman literature, as well as our couvade data and situational reactivity data, suggests that an inverse correlation between testosterone and prolactin is related to paternal responsiveness. Testosterone levels showed a significant negative correlation with prolactin only in the Early Prenatal group ($r = -.61$, $p < .05$). Men in the Early Prenatal group with higher prolactin showed larger situational testosterone responses than men with lower prolactin ($r = 0.59$, $n = 12$, $p < .05$) and men with higher testosterone showed smaller prolactin responses than men with lower testosterone ($r = -.84$, $p < .01$).

2.6. Evidence that hormonal status was related between partners

Men whose partners reported feeling concerned about the baby cries had a larger cortisol response (-59.8 ± 13.4 nmol/L, $n = 16$) and prolactin response (-1.06 ± 0.3 μg/L) than men whose partners did not report concern (cortisol, $n = 15$, -17.4 ± 8.7 nmol/L, $t_{29} = 2.6$; prolactin, $n = 16$, -0.01 ± 0.03 μg/L, $t_{30} = 2.76, p < .01$).

There were no significant correlations between partners' hormone levels for the combined four prenatal and postnatal groups. There were, however, hormone relationships within the four groups (Table 3). Levels of all three female hormones were positively correlated with both the men's cortisol levels and the magnitude of the men's cortisol response in the situational reactivity test (Table 3). The similarity in the pattern of correlations for men's cortisol and change in cortisol reflects the high positive correlation for the two measures (overall: $r = .80, p < .01$) as discussed in the situational reactivity section earlier. In contrast, women's cortisol responses did not show a consistent relationship to their partners' baseline hormone levels (Table 3).

Female hormone levels were higher as the birth approached in the prenatal couples (estradiol, $r = -.51$; cortisol, $-.55, p < .05$; prolactin $r = -.67, p < .01, n = 17$). There were no significant correlations among the men, except for that between the magnitude of change in cortisol in the reactivity test and the number of days to birth ($r = -.51, p < .05, n = 19$), such that cortisol response was greater as the birth approached in the prenatal groups.

Multiple regression analyses and partial correlations were used to further examine whether female hormone levels were linked to the timing of physiological changes associated with the birth process and male hormones were linked to female hormones. Using days before birth as the independent variable, we found a significant relationship in all women for hormones and days until birth ($F = 3.78, p < .01$) with first sample estradiol levels ($t = 3.9$,

Table 3
Correlations (Pearson's r) for women's first sample hormone levels and (a) men's cortisol and (b) men's change in cortisol and (c) between men's baseline hormone levels and women's change in cortisol

	Prenatal Groups			Postnatal Groups		
	Early (N = 12)	Late (N = 8)	Combined (N = 20)	Early (N = 9)	Late (N = 8)	Combined (N = 17)
a. Men's cortisol						
Women's estradiol	−0.36	0.67	0.53*	−0.31	0.37	−0.03
Women's prolactin	−0.34	0.74*	0.68†	0.12	0.02	0.20
Women's cortisol	0.53	−0.41	0.44*	−0.14	0.86†	0.41
b. Men's change in cortisol						
Women's estradiol	−0.12	0.64	0.62†	0.09	0.50*	0.10
Women's prolactin	0.63*[a]	0.76*	0.77†	−0.33	−0.08	−0.19
Women's cortisol	0.18	−0.09	0.47*	−0.04	0.85†	0.36
c. Women's change in cortisol						
Men's testosterone	−0.30	0.32	−0.13	0.32	−0.02	0.04
Men's prolactin	0.08	0.68*	0.32	−0.09	−0.13	−0.19
Men's cortisol	0.60*	0.20	0.29	0.06	−0.07	0.06

[a]Positive correlation indicates that change is greater when hormone levels are higher.
*$p < .05$; †$p < .01$.

$p < .01$) and reactivity test changes in estradiol levels ($t = 3.2, p < .01$) as the significant dependent variables. The prepartum hormone levels in women were also significant ($F = 8.9, p < .01$) with baseline prolactin, baseline cortisol, and change in prolactin being the significant dependent variables ($t = 3.2, 3.1$, and 3.45, respectively, $p < .05$). There were no significant relationships between days until birth and hormone levels for all men or for men tested before their babies were born. Similarly, holding days until birth constant decreased the correlation coefficients for the women's hormones in the prenatal groups but had no effects on either women in the postnatal groups or men in either the pre- or postnatal groups.

In summary, women's hormone levels are correlated with time remaining before the birth, whereas the men's hormones are generally related to the women's levels and not to the time before birth.

3. Discussion

Men experienced significant pre-, peri-, or postnatal changes in each of the three hormones measured, with patterns of change parallelling those found in women in this and other studies (Fleming and Corter, 1988; Fleming et al., 1997). Our results suggest that hormonal reactivity to social stimuli is also an important component of stage and individual differences in hormone-behavior dynamics, although these changes have not been the focus of as much research as the absolute hormone concentrations (but see Wingfield et al., 1990; Castro and Matt, 1997). Hormone correlations between partners suggest that communication within couples is related to the physiological changes the men experience.

Lower levels of testosterone may be associated with men becoming more paternal in the early postnatal period. Testosterone levels were 33% lower in Early Postnatal fathers than for men in the Late Prenatal group, corresponding to the first time the men would be able to interact with their infants. In addition to the low baseline level, the Early Postnatal group was the only one to show an increase in testosterone from sample 1 to sample 2 of the reactivity test, which may represent a challenge response (as in Wingfield et al., 1990) involved in mobilizing physiological responses to protect the baby in these new fathers.

Links between testosterone and response to our test stimuli support the idea that lower testosterone is associated with greater paternal responsiveness. Men with lower testosterone held our test dolls longer. Furthermore, men who were more responsive to infant cues had lower testosterone concentrations or a greater decrease in testosterone from sample 1 to sample 2 of the reactivity test. This decrease in testosterone at the onset of parental behavior occurs in other paternal mammals (Brown et al., 1995; Reburn and Wynne-Edwards, 1999) and is widespread in paternal birds (Feder et al., 1977; Silver, 1978; Wingfield and Farner, 1993). Testosterone implants have been shown to decrease paternal feeding rates in male birds, primarily because males increase the time they spend in competitive activities (Hegner and Wingfield, 1987; Ketterson and Nolan, 1992). Increases in testosterone in men have also been associated with successful competitive behavior (reviewed in Mazur and Booth, 1998). Thus, it appears that the testosterone decrease in the postnatal period may enhance paternal responsiveness in men by reducing their tendencies to engage in incompatible non-nurturing behaviors.

Estradiol levels peaked in the Late Prenatal group as in previous studies (Fleming and Carter, 1988; Fleming et al., 1997). Estradiol is important for priming mammalian maternal behavior (Rosenblatt et al., 1988) and levels of estradiol in pregnant pigtail macaques (*Macaca nemestrina*) correlate with responsiveness to infants (Maestripieri and Zehr, 1998). We found little evidence of a relationship between estradiol concentrations and responsiveness to infant cues. However, this probably reflects the fact that we sampled primarily in the last trimester when estradiol levels and responsiveness were already at high levels.

Prolactin levels were higher for both men and women in the Late Prenatal group than in the Early Prenatal group. Prolactin levels also were higher in men showing greater responsiveness to baby cries and in men reporting more pregnancy (couvade) symptoms. All of these results were consistent with the known roles of these hormones in the parental responses of male mammals (Gubernick and Nelson, 1989; Kreeger et al., 1991; Ziegler et al., 1996; Brown et al., 1995; Reburn and Wynne-Edwards, 1999; Dixson and George, 1982), including the only two other paternal primates that have been tested (Ziegler et al., 1996; Dixson and George, 1982).

Prolactin increased between pairing and early lactation in a highly paternal hamster (*Phodopus campbelli*) and before the birth in a closely related, but opportunistically paternal, hamster (*P. sungorus*, Reburn and Wynne-Edwards, 1999). Prolactin has been closely linked to the onset of paternal behavior in birds (Silver, 1978; Ball, 1991) and prolactin administration within the central nervous system enhances paternal behavior in ring doves (*Streptopelia risoria*, Buntin et al., 1991). In all studies of biparental male mammals, except for the California mouse (Gubernick and Nelson, 1989), male levels were lower than females, but the stage-specific differences relative to parturition were similar. Thus, we argue, as in other studies, it is the pattern of change, not the absolute levels, that is important. Taken together, our results and those for other paternal species support a role for increasing prolactin and decreasing testosterone in paternal responsiveness.

Cortisol levels increased just before the births and decreased in the postnatal period for both men and women. Cortisol levels were twice as high in the Late Prenatal group relative to the Early Prenatal group, and both partners in the couple sampled in labor showed a further 75% increase in cortisol in labor relative to late pregnancy. In women, cortisol is elevated before birth (Fleming and Corter, 1988; Fleming et al., 1997), and it is involved in the onset of labor (McLean et al., 1995; Karalis et al., 1996). Cortisol levels in women have been linked to maternal affiliative behaviors toward infants. New mothers with higher cortisol levels were more attracted to infant odors and were better able to discriminate their own infant's odors than new mothers with lower cortisol levels (Fleming et al., 1997). In nonhuman mammals, glucocorticoids are involved in the establishment of social bonds in mated pairs (Carter and Altemus, 1997) and may sensitize females to stimuli involved in maternal imprinting (bonding to the infant) peripartum (Leon, 1992). The similar temporal pattern in the men suggests that cortisol increases in late pregnancy and during labor may help new fathers focus on and become attached to their newborns. Thus, the high baseline cortisol levels in the Late Prenatal group may indicate heightened glucocorticoid responses to stress, whereas the larger decrease after exposure to baby stimuli may reflect greater sensitivity to infant cues. This decrease in cortisol may be mediated by increased levels of oxytocin, a hormone involved in social bonding (Carter and Altemus, 1997).

Men reporting more pregnancy (couvade) symptoms had higher levels of prolactin and a significantly greater drop in testosterone in their second samples than men reporting fewer symptoms. These findings support the hypothesis that couvade symptoms reflect physiological changes in men in preparation for fatherhood (Elwood and Mason, 1994). The cross-cultural perspective suggests that the closeness of the two parents around the time of the birth is related to whether men experience couvade symptoms (Elwood and Mason, 1994) and whether they show high levels of paternal involvement (Barry and Paxson, 1971; Whiting and Whiting, 1975; Broude, 1983; Elwood and Mason, 1994). When men experience these couvade symptoms and changes in responses to babies, they may be also be signaling their partners about their intention or ability to invest in the new baby (Symons discussed in Churchwell, in press).

The relation between the women's hormone levels and both their partners' hormone levels and number of symptoms suggests a link between prenatal intimacy and the development of paternal responsiveness. That women's hormone levels were highly correlated with days remaining before the birth indicates that women's hormones were closely tied to the physiological processes of pregnancy. In contrast, the strongest correlations for the men's hormones were with their partners' hormone levels, not with time remaining until birth, suggesting that the men's responses were influenced by their partners. This suggestion needs to be tested more carefully by examining changes in pregnant women and the fathers of their babies who are not living together. In men, as in other paternal mammals, prolonged contact with the pregnant partner may be important for changes in paternal responsiveness. Pheromonal communication (olfaction) between partners may be involved, as it has been shown that such cues can influence endocrine status in humans, particularly where close social bonds are maintained (Stern and McClintock, 1998; Weller et al., 1995).

Thus, in this first attempt to identify a hormonal basis for paternal behavior in men, we found strong parallels to the peripartum changes that are known to be involved in mammalian maternal care. While still far from a functional proof of hormonal involvement in paternal behavior, these data nevertheless suggest that men exposed to appropriate stimuli undergo hormonal changes around the birth of their child that may facilitate the expression of paternal behavior.

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