Published in final edited form as:

Horm Behav. 2016 January ; 77: 260–271. doi:10.1016/j.yhbeh.2015.07.024.

Primate paternal care: interactions between biology and social experience

Anne E. Storey[a,*] and **Toni E. Ziegler**[b]

[a]Departments of Psychology and Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada A1B 3X9

[b]National Primate Research Center University of Wisconsin – Madison, Madison, Wisconsin, USA 53715

Abstract

We review recent research on the roles of hormones and social experiences on the development of paternal care in humans and non-human primates. Generally, lower concentrations of testosterone and higher concentrations of oxytocin are associated with greater paternal responsiveness. Hormonal changes prior to the birth appear to be important in preparation for fatherhood and changes after the birth are related to how much time fathers spend with offspring and whether they provide effective care. Prolactin may facilitate approach and the initiation of infant care, and in some biparental non-human primates, it affects body mass regulation. Glucocorticoids are involved in coordinating reproductive and parental behavior between mates. New research involving intranasal oxytocin and neuropeptide receptor polymorphisms may help us understand individual variation in paternal responsiveness. This area of research, integrating both biological factors and the role of early and adult experience, has the potential to suggest individually designed interventions that can strengthen relationships between fathers and their offspring.

One of Jay Rosenblatt's most important research contributions was determining how hormones influence the onset of maternal behavior and how experience with pups maintained it (Rosenblatt and Siegel, 1981). The interplay between biology and experience in mammalian fathers provides further insight into hormonal influences and the critical role of social experience for the onset as well as maintenance of paternal behavior. In this regard, the transition to paternal responsiveness more closely resembles the sensitization response that Jay Rosenblatt and colleagues had discovered in virgin rats, wherein extensive pup exposure preceded any hormonal change. Recent research in the hormonal basis of paternal behavior indicates that the hormonal state of one individual influences its own behavior and then can affect the behavior and hormonal state of the dyad partner (mate or young), as with Danny Lehrman's (1965) work on the ring dove.

Mammalian fathers show considerable individual and interspecific variation in the extent to which they exhibit paternal responsiveness and in many species, contact with the pregnant partner, as well as the young, are important in the transition. Here we review the function

*Correspondence author: Department of Psychology, Memorial University of Newfoundland, St. John's, NL, Canada, A1B 3X9; telephone: 709 864-7665; Fax: 709 864-2430. astorey@mun.ca.

and evolution of paternal behavior in primates, and then examine the interplay between social experience and each of the hormones implicated in parental behavior. Finally, we review recent findings about how hormones and social experiences affect and reflect the paternal brain. The review is organized with non-human primates first in each section, then humans. The two sections cannot always be directly compared since experiments performed on non-human primates can often not be done on humans and the recent fMRI studies have been mainly conducted in humans.

1. Evolution, distribution and function of paternal care in primates

1.1 Evolution, distribution and function of paternal care in non-human primates

Biparental care (care by both parents) has evolved repeatedly across vertebrate and invertebrate taxa (Dulac et al., 2014). While paternal care is quite rare in mammals, it is more common in primates than in other mammalian orders (Kleiman & Malcolm, 1981; Clutton-Brock, 1991; Opie et al., 2013). The sociality of primates may have led to an increase in co-operative care of infants (Hrdy, 2009) but there are other hypotheses concerning the repeated evolution of paternal care in primates. Lucas and Dunbar (2013) suggest that social monogamy evolves in mammals when females occupy small and discrete ranges such that males cannot monopolize more than one female. Infanticide risk may have led to close attendance by resident males which in turn increased social monogamy and bi-parental care (van Schaik & Kappeler, 1997; Dunbar, 1995; Palombit, 1999, Opie et al., 2013, Fernandez-Duque et al., 2009).

Primates species have flexible behavioral systems and with this comes high variability in social systems and in father-offspring parenting styles both between and within species. Biparental care allows the energetic demands to be shared between both parents, which can improve the number of surviving offspring a male produces (Saltzman and Ziegler, 2014). Paternal care of infants has been observed in many of the general classifications of non-human primates: strepsirrhines, platyrrhines, cercopithecoids and apes. Infant care by fathers and non-breeding males is also currently associated with a range of mating systems including monogamy, polyandry, and cooperative breeding. The ways in which a father interacts with his offspring are usually classified as direct (e.g., feeding and carrying) or indirect (e.g., protection) care and there is considerable variation in what behaviors fathers display towards offspring. Only a few species of lemurs (such as the red-bellied lemur, *Eulemur rubriventer*; Overdorff and Tecot, 2006) and the New World marmosets, tamarins, titi monkeys, and owl monkeys show direct care of their offspring (Fernandez-Duque et al., 2009). In contrast, wild male savanna baboons (*Papio cynocephalus*) are known to protect their probable offspring from attacks by peers but show no direct offspring care (Buchan et al., 2003; Charpentier et al., 2008). Male Barbary macaques (*Macaca sylvana*) will assist in teaching behavioral skills to their developing offspring after they are weaned (Burton, 1972).

Infant carrying is the best-documented form of paternal care in non-human primates. Infant carrying by males reduces female energy expenditure. In addition to this advantage for females, infant carrying can benefit males by decreasing inter-birth intervals. There are, however, species differences in when and how much primate fathers carry their young. Similar to marmosets and tamarins, red-bellied lemurs often have twin births and fathers that

carry as much as mothers (Overdorff and Tecot, 2006). Father titi monkeys, *Callicebus cupreus*, carry infants almost exclusively from birth and they are the primary attachment figure for the developing infant (Hoffman et al., 1995). In contrast, Goeldii fathers carry infants only after 3 weeks of age (see Schradin et al., 2003). Common marmoset fathers are the primary care giver but share the carrying with their mate (Schradin et al., 2003). In contrast, Hylobatids often display social monogamy and reduced sexual dimorphism, yet only in the siamangs (*Symphalangus syndactylus*) do fathers actually carry their young and then only starting in the second year of the infant's life (Chivers, 1974). One factor related to how much fathers carry offspring is whether females have early post-partum estrus. Fathers carry young more often in species where females can lactate and be pregnant simultaneously, and thus carrying by males results in a reduction in the mother's energy expenditure that benefits both parents.

Our information on the biological systems that facilitate paternal care behaviors is generally limited to a few species of monkeys, often using captive individuals. These species include i.e., titi monkeys (*Callicebus cupreus*), common marmoset (*Callithrix jacchus*), black tufted-ear marmoset (*Callithrix kuhlii*), geoffroyi marmoset (*Callithrix geoffroyi*), and the cotton-top tamarin (*Saguinus oedipus*). Data from these species indicate that fathers show similar physiological changes as their mates. Marmosets and tamarins are the most notable for their cooperative care of infants. This extra-maternal care allows females to offset the costs of high reproductive output by limiting maternal investment in each offspring (Garber and Leigh, 1997). Both common marmosets and the cotton-top tamarins have multiple infants per birth, with a post partum ovulation that occurs as early as 10 and 13 days respectively, following birth (marmosets: Lunn and McNeilly, 1982; tamarins: Ziegler et al., 1987a). Post-partum conception rates are high, occurring in more than 80% of females (Ziegler et al., 1987) and thus, most mothers are lactating and pregnant at the same time. This high reproductive rate is energetically costly for mothers and so infant care support is required from the entire family. The ability to simultaneously lactate and conceive, as is seen for the callitrichid monkeys, is in part due to the lower frequency of nursing bouts allowed by mothers (Ziegler et al., 1990).

1.2 Evolution, distribution and function of paternal care in humans

Modern fathers contribute greatly to the emotional, cognitive and social development of their children (reviewed in Allen & Daly, 2007), as well as to long-established roles of providing resources, protecting, and teaching their children. A high degree of father involvement is not just a recent Western phenomenon: direct infant care by fathers has been documented in 40% of world societies (Barry & Paxson, 1971), with greater direct paternal care being associated with strong emotional bonds between parents (Whiting & Whiting, 1975; Broude, 1983; Belsky et al., 1991).

Paternal care in humans evolved independently from similar transitions in other primates. Paternal care is absent in our nearest relatives, making it difficult to determine how or why it evolved and whether it preceded or followed increases in pair bond strength. Since our closest relatives are either promiscuous or polygynous, with males providing little parental care, it is difficult to infer whether paternal care co-evolved with pair bonding or whether it

preceded or followed increased formation of long-term pair bonds. Lukas and Clutton-Brock (2013) argue that pair bonding came first in mammals as a response to solitary females being so widely distributed that males could defend only one female at a time. This explanation is unlikely to extend to humans, as we are (almost?) the only mammalian species with a long history of both pair bonding and group living. Opie et al. (2013) argue that high levels of male infanticide led to pair bond formation and paternal care. They suggest that this factor was particularly important in species with long pre-weaning periods relative to pregnancy duration such that strange males could hasten ovulation by killing offspring sired by other males. Another model proposes that human paternal care arose as an alternative path to reproductive success for subordinate males in polygynous groups (Gavrilets, 2012). While dominant males could guard and mate with multiple females, subordinate males could potentially sire offspring by forming bonds, more or less exclusively, with females and providing paternal care. This paternal care could include provisioning, transport and protection from infanticidal males. An attractive feature of the Gavrilets (2012) model is that it addresses a possible source for the individual variation in paternal care we see in humans: some males provide extensive paternal care to the children of one woman while others pursue a more promiscuous mating strategy with less paternal investment (Marks and Palkovitz, 2004; Apicella and Marlowe, 2006). Cross-cultural analyses identify paternal care and reduction of male-male competition for mates as key factors in the evolution of human pair bonding (Marlowe, 2001; Quinlan and Quinlan, 2007).

Gangestad (2011) suggests that male provisioning from hunting can be viewed as mating effort, parental effort, or perhaps both. Provisioning is mating effort if females prefer to mate with successful hunters. Provisioning can also be viewed as parental effort if offspring that receive it have better survival prospects than those who do not (e.g., Alvergne et al., 2009). One important benefit of this paternal care is that inter-birth intervals are shorter in humans than in comparable-sized primates with only maternal care (Gangestad, 2011). This quicker return to fertility after birth may be due to hunting efforts that brought more high quality food to the family or, as Gettler (2010) suggests, it may in part be due to reduction of maternal energy expenditure in mobile groups if fathers carried offspring. Gettler (2010) suggests that we have overstated the sexual division of foraging labor in ancestral groups based on modern hunter gathering populations and he cites evidence that infant transport by fathers, as in some other primate species, was important for reducing maternal energy expenditure in mobile foraging groups.

One way we might determine whether human paternal care is adaptive is by examining the underlying hormonal mechanisms. Gangestad (2011) argues that the association of paternal care with decreased testosterone (as opposed to increased testosterone with mating effort) suggests that human paternal care is an adaptation. Such an argument could also be made for the more recent research on oxytocin and vasopressin.

2. Overview of the hormonal basis of primate paternal care

2a. Overview of hormonal basis of primate paternal care: Non-human primates

While male and female primates have gonadal differences derived from their genetic sex, there are a number of anatomical similarities that suggest males could respond to infants, both behaviorally and hormonally, as do females. For example, male and female primates show nipple and duct development with no gross structural pre-pubertal sex differences (Daly, 1979). Only with the onset of puberty do females show changes in mammary development due to ovarian and adrenal steroids. These changes are not seen in males, although in monomorphic species such as the marmosets and tamarins, both sexes lack external differences in mammary development. Interestingly, blocking fetal androgen action in genetic males, can lead to full lactation in adult male rats with orchidectomy and stimulation from pregnancy hormones (Neumann and von Berswordt-Wallrabe, 1966). Thus, males are very responsive to their hormonal milieu and this in turn influences their behavior and physiology.

Primates demonstrate a long interval between conception and the stage where males can care for the young. Close association with the pregnant female may enable males to process the signals that promote the biological changes of fatherhood. A number of studies on expectant tamarin and marmoset fathers have revealed extensive physiological changes to the males prior to the birth of their infants. Both expectant father common marmosets and cotton-top tamarins get heavier during their mate's pregnancy (Ziegler et al., 2006). Males gain weight by mid-gestation and by the last month prior to birth they may have up to an 8% increase in their body mass. Increased weight is a response to their mate's pregnancy and helps to prepare the father for the energetic demands of infant care. Males are therefore responsive to the reproductive state of their mates (Ziegler et al., 2006).

Marmoset and cotton-top tamarin males respond to their mate's pregnancy with hormonal and physical changes that are similar to those in pregnant females. Ziegler et al. (2004a) showed that cotton-top tamarin males have elevated concentrations of prolactin, cortisol, estradiol, estrone, testosterone and dihydrotestosterone (DHT) in their urine starting at mid gestation with the steroids and prolactin reaching their highest concentrations in the last month of the gestation. Similarly, elevated estradiol, prolactin and testosterone concentrations have also been demonstrated for common marmoset males, again with concentrations peaking in the last month of gestation (Zeigler et al., 2009). These studies illustrate that males are well attuned to their mate's changing reproductive condition.

2b. Overview of hormonal basis of primate paternal care: Humans

Storey et al. (2000) examined the role of testosterone, prolactin and cortisol in the transition to human fatherhood. No doubt, Storey was greatly influenced by her critical-period exposure to Jay Rosenblatt's research on rat maternal behavior and by Alison Fleming's extensions from maternal rats to human mothers. Storey et al. (2000) used a cabbage patch doll as a baby substitute for expectant fathers, had a cross-sectional design and did not examine oxytocin or vasopressin. More recently computerized dolls (RealCare Baby) have been used to systematically assess paternal care (van Anders et al., 2011). Longitudinal

studies have demonstrated hormonal changes in individual men when they become fathers (Gettler et al., 2011b). Further, hormonal changes are greatest in the men who provide the most paternal care (Alvergne et al., 2009; Gettler et al., 2011; Abraham et al., 2014). Neuropeptides, primarily oxytocin and vasopressin, are now measured in plasma, saliva and urine and these hormones have been linked to responsiveness to mates and young. Intranasal sprays of these neuropeptides provide an experimental means to assess hormone-behavior interactions in humans (e.g., Weisman et al., 2012). Intranasal oxytocin produced differences in men's stress responses depending on whether or not they had experienced early parental loss (Meinlschmidt and Heim, 2007). Recent studies show that variation in neuropeptide receptor alleles is reflected in variation in parental behavior (Feldman et al., 2012).

Table 1 contains a comparative summary table of the hormonal mechanisms of paternal behavior in primates as is currently known.

3. Testosterone

3a. Testosterone in non-human primate fathers

Male primates need to have flexible hormonal responses since behaviors requiring high testosterone, such as mate guarding or territorial defense behaviors, co-occur with low-testosterone paternal care (Ziegler et al., 2004b). This flexibility is most evident in species where infant care behaviors co-occur with postpartum ovulation. For example, cotton-top tamarin fathers experience an increase in androgens that coincides with their mate's postpartum ovulation. However, mating behavior does not alter the high rates of father–infant interactions. Male marmosets that are not living with young show a significant increase in testosterone concentrations when smelling a novel periovulatory scent while fathers with young show little response to these odors (Ziegler et al., 2005).

Common marmoset infants influence their father's hormones to promote a more maternal-like father. Testosterone concentrations are low while males are caring for their offspring (Nunes et al., 2000; Ziegler et al., 2004b). Additionally, testosterone concentrations in black tufted-ear marmosets are lower for males that have more paternal experience and carry young more frequently than for other males (Nunes et al., 2001). Marmoset infant odors may work as signals that promote recognition of offspring and as primer by affecting paternal hormones. Experienced marmoset fathers show a significant decrease in serum testosterone concentrations within 20 minutes of contact with an isolated scent from their own infant (Prudom et al., 2008). In contrast, parentally inexperienced males show no changes in testosterone concentrations in response to unfamiliar infant odors. Further studies indicated that fathers' decreased testosterone was a specific response to their own infant during the period of early infant dependency (Ziegler et al., 2011). Fathers also showed an increase in estrogen in response to odors from their own dependent infants (Ziegler et al., 2011) and, interestingly, estrogen has also been implicated in the transition to fatherhood in men (Berg & Wynne-Edwards, 2001).

3b. Testosterone in human fathers

Storey et al. (2000) found that testosterone was lower in new fathers than in men sampled just before their babies were born. Of all our results, this finding is associated with the most subsequent research. Generally in North American studies, testosterone concentrations are lower in pair-bonded men and fathers than in single, childless men (Gray and Campbell, 2009). No differences have been found in the testosterone concentrations of fathers and non-fathers in some of the non-North American studies (reviewed in Gray and Campbell, 2009). Testosterone concentrations were lower in fathers than non-fathers in the Hazda who are highly paternal but not different in the nearby Dagota who spent little time with young children (Muller et al., 2007), suggesting that the extent of paternal contact is important rather than just fatherhood status. Gettler et al. (2011) showed that men's testosterone concentrations decreased from when they were single to when they became married fathers in a longitudinal study on Filipino men, a society with high levels of paternal care. This decrease in testosterone was greater in men whose children were younger when they were sampled, in men who spent more time caring for their children (Gettler et al., 2011) and in men who slept near their infants (Gettler et al., 2012b). Similarly, Alvergne et al. (2009) found Senegalese fathers had lower testosterone concentrations than non-fathers, with lowest testosterone concentrations being associated with greater amounts of paternal care, judged by their spouses, in both monogamous and polygynous families.

New fathers had variable, but on average, increased testosterone concentrations after listening to taped infant cries and holding their newborn for 30 minutes (Storey et al., 2000) or after simply listening to infant cries (Fleming et al., 2002). These findings appear to contradict the general findings that lower testosterone concentrations are associated with greater paternal responsiveness. Van Anders et al. (2011) used a RealCare computer-controlled infant surrogate to test how care conditions affect testosterone responsiveness. They found that when men could provide effective paternal care (comfort the infant surrogate so that it would stop 'crying'), testosterone concentrations decreased. When men could not comfort the infant surrogates, (computer control bracelet was not provided) their testosterone concentrations did not change. Men's testosterone increased when they heard infant cries with no doll present (so they could not provide care). None of the men in the comfort group showed an increase in testosterone whereas at least half of the men in the other two groups showed such an increase. Similarly, Weisman et al. (2014) found that men's baseline testosterone concentrations were negatively correlated with the number of positive interactions with their infants (e.g., affectionate touch, gaze) and positively correlated with how much infants expressed negative emotions (duration of sad face or crying during the interaction). Taken together, this literature suggests that it is not just being a father that affects testosterone concentrations but rather the amount and effectiveness of the paternal care that men provide. Testosterone increases in these contexts may simply reflect the men's discomfort during fairly novel (e.g., increase was only seen at two-week tests, not later, Storey et al., 2000) or unpleasant interaction (e.g., men cannot respond to the cries, Van Anders et al., 2011). Alternatively, these increases may also be involved in helping men counter any external threats to their infants (i.e., infanticide; see Palombit, 2000).

4. Prolactin

Prolactin is known for its role in promoting maternal behaviors in mammals (Bridges et al., 1997) and in promoting parental care in males and females of biparental bird species (Buntin et al., 1991). In the rat, prolactin regulates the onset of maternal behavior but not the maintenance, which is controlled by pup exposure (Rosenblatt and Siegel, 1981). The role of prolactin in mammalian paternal behavior is more subtle and possibly more species-specific than for some other hormones. Prolactin has been suggested as being involved in the transition from a non-paternal to a paternal state in male mammals (e.g., Schradin et al., 2003; Ziegler et al., 2004), including humans (Storey et al., 2000). Males from a number of biparental mammalian species show elevated prolactin while they are actively participating in infant care. These species include the Mongolian gerbil, California mouse and Siberian dwarf hamsters (Brown et al., 1995; Gubernick and Nelson, 1989; Reburn and Wynne-Edwards, 1999). The naturally biparental Siberian dwarf hamster, Phodopus campbelli, shows higher mRNA for prolactin receptors in the choroid plexus of the brain than non-paternal males of Phodopus sungorus (Ma et al., 2005). Prolactin suppression, however, has variable effects in animal studies: infant care behavior was lower in some studies (mixed sex group, Roberts et al., 2001a) or for specific measures (Ziegler et al., 2009), but paternal care was not affected in others (Brooks et al., 2005; Almond et al., 2006). Differences in behavioral testing conditions, specifically testing in small cages, may explain why some studies find no deficits because the constant close proximity between fathers and young may over-ride the effects of hormonal suppression. Support for this possibility comes from a study of prolactin suppression in female voles: no effects on maternal behavior were seen for females tested in small cages. In contrast, when families were housed in larger enclosures, prolactin-suppressed females stayed away longer from their pups than controls, though once they returned to the nest, their bout times were equivalent to controls (Walsh et al., 2009). Similarly, Ziegler et al. (2009) found that the only behaviors affected by prolactin suppression in common marmosets were those involved in approach or response from a distance. These results suggest prolactin concentrations and suppression should be evaluated in more naturalistic conditions. In one study to do this, Carlson et al. (2006b) found that helper meerkats (*Suricata suricatta*) with higher prolactin levels were more likely to stay with pups rather than to go off to forage. We have provided details on these studies to set the context for the further discussion in primates.

4a. Prolactin in non-human primate fathers

Researchers have suggested that prolactin has both a preparatory role and short-term response role in primate paternal behavior. Results have differed as to when and how much prolactin changes, with some differences being related to whether males have previous paternal experience and whether they are living with young during the experiment. Experienced cotton-top tamarins show a prenatal increase in prolactin (Ziegler & Snowden, 2000; Ziegler et al., 2004), with no significant increase during the period of infant rearing (Zeigler et al., 2000). This prenatal increase was not seen, however, when the experienced males were not living with offspring (Almond et al., 2008). First-time marmoset fathers did not show an increase in prolactin until after the young were born (Schradin & Anzenberger, 2004). Prenatal prolactin concentrations were higher in experienced fathers than non-fathers

in two species where males begin carrying infants right after birth but in this study, there was no post-natal increase (Schradin et al., 2003). In contrast, male Goeldi's monkeys (*Callimico goeldii*) do not start carrying infants until a few weeks after birth and in this species fathers' prenatal prolactin levels were not higher than non-fathers but males show an increase between the birth and the time they start carrying (Schradin et al., 2003). Mota et al. (2006) also found that marmoset males showed an increase in prolactin from before to after the birth, but the increase was greater in older male offspring that assisted with infant carrying than in the fathers. Taken together, these studies suggest that prolactin increases at or before the time males start carrying infants and that this preparatory phase may be affected by previous experience or whether males are living in family units with young.

Marmosets sampled just after infant carrying had higher prolactin levels than males sampled when they are not carrying (Dixson & George, 1982; Mota et al., 2006), results similar to those in experienced human fathers (Fleming et al., 2002; Delahunty et al., 2007, discussed in more detail in the next section). Schradin & Anzenberger (2004) point out that an alternative explanation is that higher prolactin levels may have caused these males to initiate carrying bouts, since prolactin concentrations preceding the carrying bouts were unknown. Such a possibility is consistent with the meerkat study (Carlson et al., 2006) in which helpers with higher prolactin concentrations were more likely to stay with pups, compared to helpers with lower levels.

In an attempt to determine a causal relationship of prolactin to paternal care behaviors, Ziegler et al. (2009) lowered (cabergoline) and raised prolactin (using human recombinant prolactin) in common marmoset fathers 3 weeks prior to and for 3 weeks following the birth of infants. Each male went through each treatment. There was little effect on paternal behavior with elevated prolactin in the experienced fathers, except as noted above.

Prolactin's most significant effect on marmoset fathers was in its involvement in energetics. Rather than a direct effect on the expression of paternal care, prolactin influences a male's weight during the infant care period. Elevated prolactin postpartum, when males are actively caring for infants, may work to prevent excessive weight loss during their added energetic demands (Ziegler et al., 2009b). Males lose a significant amount of weight while they are caring for infants. Prolactin implants prevented males from losing weight during the first three weeks after infant birth while lowering prolactin with cabergoline increased the amount of weight males lost. It would be interesting to conduct such a study on a natural population as it is likely that males with significant weight loss would show a decrease in paternal care.

Paternal experience in marmosets and tamarins affects their hormonal and behavioral responses to their mate's reproductive condition and their infant's sensory signals. While all marmosets and tamarins gain experience with infants through caring for their younger siblings, as they are cooperative breeders, it is the experience of being a father that provides for the major physical, endocrine and behavioral changes that appear to be important in ensuring the successful development of the infant.

4b. Prolactin in human fathers

As in male tamarins and marmosets, human fathers also have been reported to exhibit increased prolactin concentrations before the birth (Storey et al., 2000). Fathers with higher prolactin concentrations were more responsive to infant cries (Fleming et al., 2002) and they spent more time engaged in coordinated play with their infants than other men (Gordon et al., 2010b). Prolactin concentrations are higher in fathers than non-fathers in a sample of highly paternal men in the Philippines (Gettler et al., 2012a), whereas Grey (2007) found no difference in prolactin concentrations between residential and non-residential Jamaican fathers.

Experienced fathers of newborns show a significantly greater increase in prolactin after hearing infant cries or holding their babies than first-time fathers (Fleming et al., 2002; Delahunty et al., 2007). In contrast, women showed a significant prolactin increase in response to baby cries and a birth video even before their first babies were born (Delahunty et al., 2007). Thus, there appears to be a sex difference such that, for males, learning and exposure to social cues may be more important in the development of prolactin responsiveness than for females.

Prolactin reactivity (short-term changes following a social interaction) in human fathers is also related to the interaction patterns in father-infant contact. Two studies found that prolactin concentrations significantly declined after fathers interacted for 30-min with their toddlers (Gettler et al., 2011a; Storey et al., 2011). Greater prolactin declines were associated with greater paternal responsiveness: prolactin declines were greater in men who engaged in more childcare and whose wives judged them to be better fathers (Gettler et al., 2011a) or had held their babies more during the hours prior to testing (Storey et al., 2011). As with the animal studies, these results suggest that prolactin is involved in the timing and possibly the motivation to initiate bouts of parental care, but it may be less involved in the actual bouts. Perhaps high prolactin is important in motivating the initiation of contact, after which concentrations decrease unless the individual is stressed/or uncomfortable in the interaction. Storey et al. (2011) found no difference in prolactin reactivity for fathers tested after all-day contact or no contact with their infants before testing. However, in this case, the amount of time away depended on the men’s work schedules not their own motivation to initiate contact with their children. It would be better to test men before they re-connect with their infants and examine whether there is relationship between pre-contact (anticipation?) prolactin concentrations and the timing, quality or quantity of subsequent father-infant interactions.

5. Glucocorticoids

An earlier general view of glucocorticoids is that increases are always associated with negative consequences in social and parental interactions. Recent models suggest that moderate glucocorticoid increases can be part of normal coping with environmental challenges, whereas larger sustained increases can be pathological and associated with negative reproductive outcomes (Wingfield & Kitaysky, 2002; Romero et al., 2009). In keeping with this more nuanced view, elevated glucorticoids are associated with greater maternal responsiveness in humans (Fleming et al., 1997) and higher rates of provisioning

and in a few bird studies (e.g., Doody et al., 2008). One of the complexities of glucorticoid-behavior research is illustrated by the contradictory findings on the same population of meerkats: natural elevations in cortisol were associated with higher pup-feeding rates (Carlson et al., 2006) whereas cortisol injections that resulted in much higher levels were associated with greater nest attendance in females but were unrelated to foraging (Santema et al., 2013). In keeping with the models mentioned above, glucocorticoids effects on parental behavior reported in meerkats may differ with concentrations (i.e., injected higher than natural). Concentrations may also vary with how quickly the increase occurs: the change in cortisol from an injection may be perceived as a sudden emergency (e.g., such as a predator arrival), different than the moderate increase that is associated with challenges such as gradually deteriorating foraging conditions. We will try to evaluate whether such a nuanced view is also appropriate for understanding the effects of glucocorticoids in primate fathers.

5a. Glucocorticoids in non-human primate fathers

Glucorticoids in male primates appear to function in two main ways related to reproduction: they may facilitate paternal behavior in new fathers (Nunes et al., 2001) and they may promote communication of hormonal states within mated pairs (Ziegler & Snowden, 2000; Ziegler et al., 2004). Nunes et al. (2001) found that male marmosets that frequently carried infants had lower cortisol levels than low-carrying males. This result suggests that carrying infants is not extremely stressful but suggests that other stressors may impact both glucocorticoid levels and carrying frequency. Fathers raising their first litters, had higher cortisol levels than fathers raising their second consecutive litters, even without differences in carrying behavior, suggesting, as we do later for human males, that glucocorticoids may help new fathers focus on the appropriate behavioral requirements of the new role.

Glucorcorticoid levels of male cotton-top tamarins increase at about the same time as female levels increase during pregnancy (Ziegler et al. 2004a) and during the postpartum ovulation (Ziegler et al., 2004a Ziegler et al., 2009a). Though the mechanism of transmission within pairs is unknown, it presumably involves changes in arousal leading to behavioral changes to which the mate responds. Male cortisol and corticosterone levels peaked between weeks 13–16 of the 26-week pregnancy, approximately 1–2 weeks after female levels increased (Ziegler et al., 2004). Corticosterone concentrations were higher than cortisol concentrations during the mid-gestation peak in expectant male cotton-top tamarins, results that contrast with the general view that cortisol is the more important glucocorticoid in primates (Ziegler at al., 2009a). The mid-pregnancy rise of glucocorticoids in females may stimulate a glucocorticoid response in male tamarins as in humans where cortisol concentrations of expectant human parents are correlated (Storey et al., 2000). Despite being less consistent in their glucorticoid increases, less experienced males interacted with their mates more than experienced males (Ziegler et al., 2004a). It may be that behavioral coordination is more important for the transition to fatherhood in less experienced pairs, whereas hormonal coordination becomes more important as parental experience increases (as in the human prolactin study mentioned previously, Delahunty et al., 2007).

Both male and female tamarins also experience an increase in glucocorticoids just before postpartum ovulation. At this time, male glucocorticoid levels are positively correlated with their rising testosterone levels but these hormonal changes are not associated with any decrease in paternal care. Ziegler et al. (2004a Ziegler et al. (2009a) suggest that the increase in glucocorticoid concentration is involved in coordinating the hormonal status of the two partners. This suggestion is supported by the transient nature of the peaks, with the females' levels preceding those of the partners. Other studies have also found hormonal synchrony between dyad partners, involving glucocorticoids (Storey et al., 2000; Buttner et al., 2014) and other hormones (Weinstein et al., 2012).

5b. Glucocorticoids in human fathers

Cortisol concentrations are highest just prior to birth in both mothers (Fleming et al., 1997, Storey et al., 2000) and fathers (Storey et al., 2000). Men's cortisol concentrations typically were lower after testing than before, but this decrease was significantly greater for men tested just before their babies were born. The cortisol concentrations of expectant fathers were correlated with the cortisol concentrations of their pregnant partners (Storey et al., 2000; Berg & Wynne Edwards, 2002; Edelstein et al., 2014), similar to results in tamarins (Ziegler et al., 2004a). Although higher cortisol is associated with greater maternal responsiveness (Fleming et al., 1997), early adversity has been linked to higher concentrations of cortisol (Gonzalez et al., 2009) and deficits in human maternal care (e.g., Mileva and Fleming, 2011). Similar complexities exist for men: fathers who expressed concern after hearing baby cries show less of a cortisol decrease than men who did not express concern and partners of men with higher cortisol concentrations reported that they did more domestic work after their babies were born (Storey et al., 2007). In contrast, fathers whose partners reported that they found parenting more difficult that they expected had higher cortisol concentrations than other fathers (Storey et al., 2007). Further, men who spent more time with their toddlers before testing had a greater decrease in cortisol over the test period than men who had spent less time (Storey et al., 2011). Elevated concentrations of cortisol are thus associated with both positive (increased sensitivity) and negative (stress) aspects of human parental care.

6. Oxytocin and vasopressin

6a. Oxytocin and vasopressin in non-human primate fathers

Most reports on oxytocin in non-human primates have focused on pair-bonding behaviors rather than on paternal care. However in one study, intranasal oxytocin increased the tolerance of marmoset fathers when transferring food to weanling infants (Saito and Nakamura, 2011). Most of the work with oxytocin and vasopressin on non-human primates concerned how these hormones affect receptors in particular brain regions (e.g., Kozorovitskiy et al., 2006; see below).

Common marmosets and several other species of New World primates, as well as the tree shrew (*Tupaia belangeri*) have a variant of the oxytocin molecule, $Pro^{8}OT$ that is unusual, as oxytocin is a conserved molecule with no variation in other nonhuman primates (Lee et al.,

2011; Wallis, 2012). However, several of the species with this variant are not bi-parental or monogamous, questioning whether this difference in structure influences its function.

6b. Oxytocin and vasopressin in human fathers

The most exciting recent developments in the biological basis of human paternal behavior involve oxytocin (see Feldman, this issue). Oxytocin concentrations are higher in fathers than non-fathers (Mascaro et al., 2014) and levels increase in both parents during the first 6 months of parenthood (Gordon et al., 2010a). Unlike some other hormones implicated in human paternal behavior, there are no sex differences in parental oxytocin concentrations in blood and saliva. Thus, in some cases values are not analysed separately for men and women (e.g., Feldman et al., 2010a, Apter-Levi et al., 2014). Sex differences emerge when specific behaviors are examined: after interacting with their 3–6 month-old babies for 15 minutes, more ‘affectionate–contact’ mothers and more ‘stimulatory-touching’ fathers showed a significantly greater increase in oxytocin concentrations than other parents (Feldman et al., 2010a). Infants of parents whose oxytocin concentrations increased the most were higher in affect synchrony than low-oxytocin, low affect-synchrony parents (Feldman et al., 2010b, Gordon et al., 2010b).

Two current developments in oxytocin research have generated a great deal of attention: the effects of intranasal oxytocin and the discoveries that polymorphism in oxytocin receptor nucleotides is associated with differences in parental behavior and social responsiveness. Several studies have now demonstrated that intranasal oxytocin increases paternal responsiveness (Naber et al., 2010; Weisman et al., 2012, 2014). Intranasal oxytocin increased father’s responsiveness in a 15-min play-bout relative to the same fathers given a placebo, in fathers of both typically developing children (Naber et al., 2010, 2013) and autistic children (Naber et al., 2013). Specifically, oxytocin enhanced the fathers’ ability to provide structure (supports exploration in a way that is responsive to the child’s activities) and reduced fathers’ hostility during the interaction. Intranasal oxytocin administered to fathers significantly increased infants’ oxytocin concentrations and made both dyad members more socially responsive (Weisman et al., 2012). This research is reminiscent of Lehrman’s (1965) analysis in ring doves that shows how the hormonal state of one individual affected its behavior and subsequently affected the behavior and hormonal state of the dyad partner.

Meinlschmist and Heim (2012) found that intranasal oxytocin caused a decrease in men’s cortisol concentrations, a finding that fits with the idea of cortisol increasing arousal or anxiety while oxytocin may decrease them. The decrease was significantly less in men with early parental separation than in men from intact families. These results suggest that there is an early developmental component to this interaction between hormones that affects the degree to which oxytocin effectively reduces later stress.

Much current research has focused on single nucleotide polymorphisms (SNPs), which reflect variation in alleles coding for oxytocin receptors. Fathers and mothers who are homozygous for a specific oxytocin receptor SNP (*OXTR* rs1042778 TT, G>T), as well as for a specific CD38 receptor SNP (*CD38* rs3796863 CC, A>C, for an enzyme involved in oxytocin release) had lower plasma concentrations of oxytocin and lower frequencies of

parental touch than other parents (Feldman et al., 2012). Other oxytocin receptor SNPs have also been implicated in parental responsiveness: Marsh et al., (2012) found that intranasal oxytocin increased the preferences of male and female adults for infant over adult photos, specifically for those individuals who were homozygous GG for the *OXTR* rs53576 (A>G) SNP. It may be that the study of parental behavior, like recent research on autism (e.g., Jacob et al., 2007), would benefit from more extensive genotyping and haplotype analysis, in combination with behavioral analysis to determine the specificity of receptor-behavior interactions.

It appears that vasopressin is involved in a wider range of male reproductive activities than is oxytocin. Vasopressin enhanced men's responses to sexual cues (Guastella et al., 2011) and made men more likely to judge a face as aggressive, (Thompson et al., 2006), perhaps relating to male-male competition. A particular variant in the vasopressin *AVPR1a* receptor allele was associated with higher relationship discord in men than other variants (Walum et al., 2008) and men with higher AVP concentrations were more likely to report relationship distress than men with lower concentrations (Taylor et al., 2010). In contrast, for women, oxytocin was more closely related to these factors than vasopressin: certain variants in oxytocin receptors genes (Walum et al., 2012) and high oxytocin concentrations were related to relationship difficulties (Taylor et al., 2010). Apter-Levi et al. (2014) showed in both men and women that vasopressin was more involved with joint stimulating play with infants while oxytocin was more related to affectionate contact. Further, Gray (2007) found that the fathers of younger children had higher vasopressin concentrations than fathers of older children. Weisman et al. (2012) notes that vasopressin concentrations increase after oxytocin administration so it may be hard to disentangle effects of the two hormones.

7. Paternal Brain

One focus in the animal research on paternal behavior is the role of the distribution of vasopressin receptors (*AVPR1a*) in the brain. While this role is well established in rodents (Parker & Lee, 2001; Bales et al., 2004), it appears that the *AVPR1a* is not homologous between rodents and great apes (Fink et al., 2006) and it is not known whether it is homologous across primates. The focus in the human literature has been on vasopressin, oxytocin and to a lesser extent, testosterone in relation to brain areas associated with emotion, reward and decision-making.

7a. Paternal brain of non-human primate fathers

First-time and experienced marmoset fathers have a higher density of dendritic spines on pyramidal vasopressin neurons in prefrontal cortex compared to non-fathers (Kozorovitskiy et al., 2006). These results provide evidence for structural reorganization in the prefrontral cortex and a parallel enhancement in the abundance of vasopressin V1a receptors that indicate plasticity in the brain with parenting experience.

Most of the other neuropeptide studies on biparental non-human primates have been mainly focused on pair bonding. Few studies have examined the brain for receptor mapping, gene expression and structural plasticity in relationship to paternal care. The distribution of vasopressin producing cells, their projections and AVP receptors and oxytocin binding sites

have been mapped in the common marmoset opening the door for understanding the role of neuropeptides in social affiliations (Wang et al., 1997; Schorscher-Petcu et al., 2009).

Marmosets show differences in hypothalamic and pituitary hormones with paternal experience (Woller et al., 2012). Parentally experienced male marmosets without resident dependent infants show significantly higher concentrations of prolactin in their hypothalamus and reduced concentrations of dopamine compared to non-fathers. Only the experienced fathers had elevated oxytocin concentrations. This study suggests that differences in secretion of prolactin and oxytocin may be related to paternal experience in male marmosets. Unlike the other studies revealing experiential changes, the changes here for the experienced males were not a direct priming effect from infant sensory stimuli since none of the males were caring for dependent infants. These results lead to speculation that male brains undergo long-term changes after parental experience, as occurs in females. In biparental species, neuroplasticity and altered brain hormones apparently occurs in both sexes.

7b. Paternal brain of human fathers

Mascaro et al. (2014) suggest several hypotheses about how hormonal changes might affect various neural systems to promote paternal responsiveness and behavior. First, hormonal changes may facilitate the development of paternal responsiveness by enhancing the emotional or reward brain circuitry and by increasing the salience of sensory cues from social companions. Second, hormones may decrease the novel or aversive properties of young and/or increase the motivation to approach and provide care. Finally, hormonal changes may be involved in differential brain activation that diverts males from the mate acquisition component of reproductive effort towards the provision of paternal care. We will evaluate these possibilities in light of a number of the recent brain imaging studies.

Fathers showed greater brain activation to videos of infants (averaged between their own and a matched unfamiliar infant) than to a doll in several cortical areas including the orbitofrontal cortex, the superior, middle and inferior frontal gyri as well as in the caudate nucleus (Kuo et al., 2012). The inferior frontal gyrus was also more active in fathers viewing a video of their own infant compared to the unfamiliar infant, as were the supramarginal and middle temporal gyri. Fathers with greater activation of the right orbitofrontal cortex in response to infants during the scan had lower scores on measures of parental sensitivity (how much the father lets the infant control the interaction) and reciprocity (mirrors infant's behavior) during father-infant interactions. Fathers with higher testosterone concentrations after the infant interaction showed a significantly higher activation in caudate to their own compared to the other infant. Though low levels of testosterone are generally more closely linked to paternal responsiveness, the authors suggest that hormones may enhance the rewarding properties of infant stimuli. It may also be the case that men with higher testosterone focus more attention on their own babies than on infants in general, compared to possibly more paternal men with lower testosterone.

Mascaro et al. (2014) compared fMRI scans of fathers and non-fathers in response to infant and sexual stimuli. Fathers showed greater activation than non-fathers in areas associated with processing emotion in faces (caudal middle frontal gyrus), reward processing (orbital

frontal cortex) and mentalizing (temporo parietal junction). Testosterone was lower and oxytocin concentrations were higher in fathers than non-fathers. Compared to fathers, non-fathers showed greater activation to sexual stimuli in areas associated with reward and motivation to approach (nucleus accumbens and dorsal caudate). Mascaro et al. (2013) further examined the genetic basis for the individual variation in responses to infant cries in terms of the number of CAG nucleotide repeats in the androgen receptor (fewer repeats associated with higher aggression). They found that activity in the anterior insula, an area involved in empathy, was positively related to the number of CAG repeats and negatively correlated with having a restricting negative interaction, suggesting that the most effective fathers had intermediate activity in the anterior insula. Taken together, these studies provide support for all three hypotheses in Mascaro et al. (2014): the paternal brain shows greater empathy, perceives infant stimuli as more rewarding than the non-paternal brain and the brain can undergo a shift from focusing on sexual stimuli to focusing on infant nurturance. Changes in testosterone concentrations and individual differences in androgen receptors are implicated in these changes.

Despite the lack of difference in plasma concentrations of oxytocin and vasopressin in mothers and fathers, there are differences in activated brain areas that may support the sex differences in parent-infant behavioral interactions. Atzil et al. (2012) compared fMRI activation in fathers and mothers in response to viewing videos of their own or another infant. Parents showed a high level of intra-couple synchrony in several brain areas involved in empathy and social cognition. In addition, both fathers and mothers had significant correlations between blood concentrations of neuropeptide hormones and some critical brain areas. Fathers showed a significant positive correlation between activation of the amygdala and vasopressin concentrations whereas mothers showed a similar relationship between amygdala activation and oxytocin concentrations. In general, mothers' oxytocin concentrations were more closely related to emotional areas (amygdala and nucleus accumbens) and fathers more related to socio-cognitive areas (superior-occipital and temporal gyri and the left medial prefrontal cortex). The authors suggest that these sex differences reflect the more ancient and pervasive emotional role of mothering compared to the more recently evolved and more facultative, learning-based components in human paternal care.

Seifritz et al. (2003) found sex and experience differences suggesting, as in non-human primates, that parental experience directly modifies brain structure. Specifically, women responded to both infant crying and laughter with a deactivation of the anterior cingulate cortex, whereas men did not. Parents of both sexes showed greater response in the amygdala to the infant crying than laughing, whereas non-parents responded more to laughter.

Abraham et al. (2014) found similar results to Atzil et al. (2012) for the heterosexual couples in their study but their inclusion of a group of homosexual fathers suggests less of a sex difference and more an effect of parenting effort or intensity. They chose heterosexual couples in which the mothers were the distinct primary caretakers (PC) partnered by secondary care (SC) fathers. In addition, Abraham et al. (2014) tested homosexual couples in which both men were primary care (PC) fathers. Within the homosexual group, there were no differences between the biological and adoptive fathers in behavior, oxytocin

concentrations or the extent of activations in any brain areas tested. The PC mothers and PC fathers showed equally high concentrations of behavioral synchrony with their infants and the extent of amygdala activation, with concentrations that were significantly higher than those of SC fathers. Overall for fathers, time spent in childcare was positively correlated with the extent of amygdala activation. In contrast to findings for the amygdala, activation of the superior temporal sulcus (STS), part of the social-cognitive network, was equally high in PC and SC fathers and both were significantly higher than PC mothers. Maternal oxytocin concentrations were correlated with activation in the ventral anterior cingulate cortex, a component of the emotional bonding system, whereas both groups of fathers showed oxytocin concentrations that only correlated with activity in the STS. These results suggest that at least part of what were assumed to be sex differences may actually be differences in the time and energy individuals devote to the parental role. Support for this view comes from the time allotment of same-sex and different-sex parents: parents in same-sex (men or women) couples and women in different-sex couples spent more time with their children than men in the different-sex couples (data from the American Time Use Survey, Prickett et al., 2015).

8. Integrating steroids and peptides

Many researchers in this field have either looked at testosterone or some combination of oxytocin and vasopressin. Van Anders et al. (2011) proposed the ‘Steroid/peptide Theory of Social Bonds’ as an integrative conceptual framework, suggesting that we must study these interactions if we are to fully understand the physiological basis of parental behavior. They note that increases in oxytocin are involved in both the sexual system (e.g., orgasm and partner bonding) and ‘nurturance’ (e.g., affectionate interactions with mates and offspring). In contrast, testosterone concentrations change in opposite directions in these two relationship contexts. One prediction that follows from this framework is that the social context should determine whether increased oxytocin should be associated with (cause or result from?) an increase or decrease in testosterone. For example, increased oxytocin in a parental context should be associated with a decrease in testosterone. This prediction was not supported in a recent study by Weisman et al. (2014) who found that intranasal oxytocin produced the greatest increases in testosterone in the men who showed higher levels of paternal behavior. These researchers found, however, that men with the lowest baseline testosterone concentrations were initially the most paternal and had the largest testosterone increase. If increased testosterone does play a role in protective paternal tendencies, it may be that the intranasal oxytocin enhanced that response more in the lower-testosterone, highly parental men, compared to other men.

9. Unanswered questions and future directions

How specific are oxytocin effects? Given the spate of research on how intranasal oxytocin augments many positive (and a few negative) social behaviors, Churchland and Winkielman (2012) question whether oxytocin effects on behavior are specific to functional categories, or are more general, reducing anxiety in a way that facilitates social interactions (e.g., increasing comfort with eye contact). It appears that oxytocin’s enhancement of paternal behavior and other social interactions as in autistic individuals may reflect a similar relaxing,

anxiety-reducing effect of the hormone. They suggest that we may see specific effects because of the testing situations we set up, and it would be useful to see whether there are individual patterns or similarities across behavioral categories.

How important is prolactin in the onset and maintenance of primate paternal care? There are clear effects of prolactin on energy balance in non-human primate fathers but we need more naturalistic studies to determine whether prolactin, controlled by dopamine, functions to regulate parental tendencies and motivation to approach and care for young. We do know that hormonal changes are associated with how much time fathers and offspring are together and whether the paternal care is effective. However, we still do not know the biological basis of individual differences in the tendency for males to initiate contact with offspring as a mechanism to initiate these changes.

Another major, largely unanswered, question revolves around interactions of oxytocin with other hormones, specifically testosterone and vasopressin. This interaction could occur anywhere between the receptor level and behavior, the latter occurring if multiple hormones change behavioral tendencies in incompatible ways. A fruitful line of future research would be to compare oxytocin and testosterone responses to mating and parental stimuli in the same individuals. Further, we need to know whether peripheral concentrations of hormones can tell us much about brain mechanisms or whether plasma and cerebral spinal fluid concentrations are not related.

How can we use this research to inform education and propose interventions that will improve paternal care? Carter (2003) suggests that we need to know whether humans are like the most paternal rodent species where brain mechanisms enabling paternal care are established in neonates (e.g., oxytocin and vasopressin receptors) rather than in a more facultative experience-based way in adulthood as in species with more flexibility in paternal responsiveness. It appears that humans have an extended early period where parental loss, neglect and abuse can change neural and hormonal responses, producing long-term deficits in adult parenting behaviors. We do not know if this damage can be reversed and if so whether there is a critical period for doing so. We also do not know whether there is a physiological basis for variation in resilience after early parental deficits since there are clear individual differences in the damage resulting from these early traumas. Perhaps as we get a clearer understanding of how receptor polymorphisms and intranasal hormone applications interact with early experience to affect behavioral variation, we can move forward with more individually based treatments. Finally, this research suggests that it is important to provide education that promotes the importance of father-child bonds (starting at prenatal classes?) coupled with employment policies that allow men the time necessary to become warm and nurturing fathers. Research on synchronous responses within parental couples also points to the important role of the parental pair bond, not only for logistical support, but also for enhancing physiological mechanisms within couples that promote effective parental care.

10. Conclusions

There appear to be several similarities in the hormonal mechanisms underlying paternal behavior in all primates studied to date, despite the differences in what studies can be done

in the different species (see Table 1). In most cases, lower testosterone and higher prolactin concentrations are associated with higher levels of paternal responsiveness. Moderate increases in glucocorticoids may help to synchronize hormonal changes in pair members of all species studied. There is more neuropeptide research on humans in connection with paternal behavior, but the association of these compounds, particularly vasopressin, with pair bonding in non-human primates suggests that similar mechanisms may be involved in paternal behavior there as well.

Jay Rosenblatt and colleagues studied the rapid hormonally induced onset of maternal behavior in the rat and the role of pup exposure in maintaining maternal responses (Rosenblatt & Siegel 1981). Further, he found that virgin female rats and both intact and castrated males would act parentally if they were exposed to pups for several days, a process called sensitization (Rosenblatt, 1967). Overall, it appears that the onset of primate paternal care more closely resembles the sensitization process than it does the rapid hormonally induced onset of maternal behavior in parturient females. Hormonal changes are involved in primate paternal behavior but they appear to follow, rather than precede, social interactions. As with mammalian maternal care, hormones seem to be less involved in the maintenance of paternal behavior, although retaining low levels of testosterone may help males focus on offspring care rather than on mate acquisition. Prolactin may still play a role even after parental behavior has been established, but it may be involved in changes of motivation to approach young, effects that may be more readily observed in naturalistic settings, rather than in the lab. Glucorticoids appear to be involved in behavioral changes that coordinate preparatory physiological and behavioral changes within pairs. There is now clear evidence in this literature that a change in the hormonal state of one individual (increased via intranasal oxytocin) can affect the behavior and hormonal state of the dyad partner (the infant, Weisman et al., 2012), as Danny Lehrman and colleagues found in ring dove pairs. Recent imaging studies continue to inform us about the neural substrates for hormonal action in brain areas associated with parental behavior.

Acknowledgments

Funding for this research was obtained from the Natural Sciences and Engineering Research Council of Canada (Grant A7475) and from the School of Graduate Studies, Memorial University (AES) and from NIH (grants MH35215, co-applicant C. T. Snowden, MH070423, MH56413 and HD057684, The Wisconsin National Primate Research Center NIH base grant, P51RR000167/P51OD011106, the Institute for Clinical and Translational Research, the Clinical and Translational Science Award (CTSA) program of the National Center for Advancing Translational Sciences (NCATS), grant UL1TR000427 (TEZ).

References

Abraham E, Hendler T, Shapira-Lichter I, Kanat-Maymon Y, Zagoory-Sharon O, Feldman R. Father's brain is sensitive to childcare experiences. PNAS. 2014; 111:9792–9797. [PubMed: 24912146]

Allen, S.; Daly, K. FIRA-CURA report. Centre for Families, Work & Well-Being University of Guelph; 2007. The effects of father involvement: an updated survey of the evidence.

Almond REA, Brown GR, Keverne EB. Suppression of prolactin does not reduce infant care by parentally experienced male common marmosets (*Callithrix jacchus*). Horm Behav. 2006; 49:673–680. [PubMed: 16480723]

Almond REA, Ziegler TE, Snowden CT. Changes in prolactin and glucocorticoid levels in cotton-top tamarin fathers during their mate's pregnancy: the effect of infants and paternal experience. Amer J Primatology. 2008; 70:560–565.

Alvergne A, Faurie C, Raymond M. Variation in testosterone levels and male reproductive effort: Insight from a polygynous human population. Horm Behav. 2009; 56:491–497. [PubMed: 19664637]

Apicella CL, Marlowe FW. Men's reproductive investment decisions. Human Nature. 2006; 18:22–34. [PubMed: 26181742]

Apter-Levi Y, Zagoory-Sharon O, Feldman R. Oxytocin and vasopressin support distinct configurations of social synchrony. Brain Res. 2014; 1580:124–132. [PubMed: 24184577]

Atzil S, Hendler T, Zagoory-Sharon O, Winetraub Y, Feldman R. Synchrony and specificity in the maternal and the paternal brain: Relations to oxytocin and vasopressin. J Amer Acad Child and Adolescent Psychiatry. 2012; 51:798–811.

Bakermans-Kranenburg MJ, van IJzendoorn MH. Oxytocin receptor (OXTR) and serotonin transporter (5-HTT) genes associated with observed parenting. SCAN. 2008; 3:128–134. [PubMed: 19015103]

Bales KL, Kim AJ, Lewis-Reese AD, Carter CS. Both oxytocin and vasopressin may influence alloparental behavior in male prairie voles. Horm Behav. 2004; 45:354–361. [PubMed: 15109910]

Berg SJ, Wynne-Edwards KE. Salivary hormone concentrations in Mothers and fathers becoming parents are not correlated. Horm Behav. 2002; 42:424–436. [PubMed: 12488109]

Bisceglia R, Jenkins JM, Wigg KG, O'Connor TG, Moran G, Barr CL. Arginine vasopressin 1a receptor gene and maternal behavior: Evidence of association and moderation. Genes, Brain and Behavior. 2012; 11:262–268.

Bridges RS, Ronsheim PM. Prolactin (PRL) regulation of maternal behavior in rats: bromocriptine treatment delays and PRL promotes the rapid onset of behavior. Endocrin. 1990; 126:837–848.

Barry H, Paxson LM. Infancy and early childhood: cross cultural codes 2. Ethnology. 1971; 10:466–508.

Brooks PL, Vella ET, Wynne-Edwards KE. Dopamine agonist treatment before and after the birth reduces prolactin concentration but does not impair paternal responsiveness in Djungarian hamsters, *Phodopus campbelli*. Horm Behav. 2005; 47:358–366. [PubMed: 15708766]

Broude GJ. Male-female relationships in cross-cultural perspective: A study of sex and intimacy. Behav Sci Res. 1983; 18:154–181.

Brown RE, Murdoch T, Murphy PR, Moger WH. Hormonal responses of male gerbils to stimuli from their mate and pups. Horm Behav. 1995; 29:474–491. [PubMed: 8748509]

Buchan JC, Alberts SC, Silk JB, Altmann J. True parental care in a multi-male primate society. Nature. 2003; 425:1799–18.

Buntin JD, Becker GM, Ruzycki E. Facilitation of parental behavior in ring doves by systemic or intracranial injections of prolactin. Horm Behav. 1991; 25:424–444. [PubMed: 1937430]

Burton, FD. The integration of biology and behavior in the socialization of *Macaca sylvan* of Gibraltar. In: Poirier, F., editor. Primate Socialization. Random House; New York: 1972. p. 29-62.

Carlson AA, Manser MB, Young AJ, Russell AF, Jordan NR, McNeilly AS, Clutton-Brock T. Cortisol levels are positively associated with pup-feeding rates in male meerkats. Proc R Soc B. 2006a; 273:571–577.

Carlson AA, Russell AF, Young AJ, Jordan NR, McNeilly AS, Parlow AF, Clutton-Brock T. Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers. Horm Behav. 2006b; 50:94–100. [PubMed: 16527276]

Carter CS. Developmental consequences of oxytocin. Physiol Behav. 2003; 79:383–397. [PubMed: 12954433]

Charpentier MJE, van Horn RC, Altmann J, Alberts SC. Paternal effects of offspring fitness in a multimale primate society. Proc R Soc London B Biol Sci. 2008; 105:1988–1992.

Chivers, DJ. The siamang in Malaya A field study of a primate in tropical rain forest. Basel, Switz: S. Karger AG; 1974. p. 335

Churchland P, Winkielman P. Modulating social behavior with oxytocin: How does it work? What does it mean? Horm Behav. 2012; 61:392–399. [PubMed: 22197271]

Clutton-Brock, TH. The evolution of parental care. Princeton: Princeton University Press; 1991.

Daly M. Why don't male mammals lactate? J Theor Biol. 1979; 78:325–345. [PubMed: 513786]

Delahunty KM, McKay DW, Noseworthy DE, Storey AE. Prolactin responses to infant cues in men and women: Effects of parental experience and recent infant contact. Horm Behav. 2007; 51:213–220. [PubMed: 17150219]

Dixson AF, George L. Prolactin and parental behaviour in a male new world primate. Nature. 1982; 299:551–553. [PubMed: 6811949]

Doody LM, Wilhelm SI, McKay DW, Walsh CJ, Storey AE. The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. Horm Behav. 2008; 53:140–148. [PubMed: 17991465]

Dulac C, O'Connell LA, Wu Z. Neural control of maternal and paternal behaviors. Science. 2014; 345:765–770. [PubMed: 25124430]

Dunbar RIM. The mating system of callitrichid primates: 1. Conditions for the coevolution of pair bonding and twinning. Anim Behav. 1995; 50:1057–1070.

Edelstein RS, Wardecker BM, Chopik WJ, Moors AC, Shipman EM. Prenatal hormones in first-time expectant parents: longitudinal changes and within-couple correlations. Amer J Human Biol. 2014

Feldman F, Gordon I, Schneiderman I, Weisman O, Zagoory-Sharon O. Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. Psychneuro. 2010a; 35:1133–1141.

Feldman R, Gordon I, Zagoory-Sharon O. The cross-generation transmission of oxytocin in humans. Horm Behav. 2010b; 58:669–676. [PubMed: 20558167]

Feldman R, Zagoory-Sharon O, Maoz R, Weisman O, Gordon I, Schneiderman I, Shalev I, Ebstein RP. Sensitive parenting is associated with plasma oxytocin and polymorphisms in the Oxytocin receptor (OXTR) and CD38 genes. Biol Psychiatry. 2012; 72:175–181. [PubMed: 22336563]

Fernandez-Duque E, Valeggia CR, Mendoza SP. The Biology of Paternal Care in Human and Nonhuman Primates. Annu Rev Anthropol. 2009; 38:115–30.

Fink S, Excoffier L, Heckel G, Orians GH. Mammalian monogamy is not controlled by a single gene. PNAS. 2006; 103:10956–10960. [PubMed: 16832060]

Fleming AS, Ruble D, Krieger H, Wong PY. Hormonal and experiential correlates of maternal responsiveness during pregnancy and the puerperium in human mothers. Horm Behav. 1997; 31:145–158. [PubMed: 9154435]

Fleming AS, Corter C, Stallings J, Steiner M. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. Horm Behav. 2002; 42:399–413. [PubMed: 12488107]

Fries ABW, Ziegler TE, Kurian JR, Jacoris S, Pollak SD. Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. PNAS. 2005; 102:17237–17240. [PubMed: 16303870]

Gangestad, SW. Human adaptations for mating: Frameworks for understanding patterns of family formation and fertility. In: Booth, A.; McHale, SM.; Landle, NS., editors. Biosocial Foundations of Family Processes: Chapter 9. Springer; NY: 2011.

Garber PA, Leigh SR. Ontogenetic variation in small-bodied new world primates: implications for patterns of reproduction and infant care. Folia Primatologica. 1997; 68:1–22.

Gavrilets S. Human origins and the transition from promiscuity to pair-bonding. PNAS. 2012; 109:9923–9928. [PubMed: 22645330]

Gettler LT. Direct male care and hominin evolution: Why male-child interaction is more than a nice social idea. Amer Anthro. 2010; 112:7–21.

Gettler LT, McDade TW, Agustin SS, Kuzawa CW. Short-term changes in fathers' hormones during father–child play: Impacts of paternal attitudes and experience. Horm Behav. 2011a; 60:599–606. [PubMed: 21889939]

Gettler LT, McDade TW, Feranil AB, Kuzawa CW. Longitudinal evidence that fatherhood decreases testosterone in human males. PNAS. 2011b; 108:16194–16199. [PubMed: 21911391]

Gettler LT, McDade TW, Feranil AB, Kuzawa CW. Prolactin, fatherhood, and reproductive behavior in human males. Amer J Physical Anthro. 2012a; 148:362–370.

Gettler LT, McKenna JJ, Agustin SS, Kuzawa CW. Does Co-sleeping Contribute to Lower Testosterone Levels in Fathers? Evidence from the Philippines Plos One. 2012b; 7:e41559. [PubMed: 22957016]

Goncharova ND, Lapin BA. Effects of aging on hypothalamic-pituitary-adrenal system function in non-human primates. Mech Ageing Devel. 2002; 123:1191–1201. [PubMed: 12044968]

Gonzalez A, Jenkins JM, Steiner M, Fleming AS. The relation between early life adversity, cortisol awakening response and diurnal salivary cortisol levels in postpartum women. Psychoneuroendo. 2009; 34:76–86.

Gordon I, Zagoory-Sharon O, Leckman JF, Feldman R. Oxytocin and the development of parenting in humans Biol. Psychiatry. 2010a; 68:377–3.

Gordon I, Zagoory-Sharon O, Leckman JF, Feldman R. Prolactin, oxytocin, and the development of paternal behavior across the first six months of fatherhood. Horm Behav. 2010b; 58:513–518. [PubMed: 20399783]

Gray, PB.; Campbell, BC. Human male testosterone, pair bonding and fatherhood. In: Ellison, PT.; Gray, PB., editors. Endocrinology of social relationships: Chapter?. Harvard University Press; Cambridge: 2009.

Gray PB, Parkin JC, Samms-Vaughan ME. Hormonal correlates of human paternal interactions: A hospital-based investigation in urban Jamaica. Horm Behav. 2007; 52:499–507. [PubMed: 17716675]

Guastella AJ, Kenyon AR, Unkelbach C, Alvares GA, Hickie IB. Arginine vasopressin selectively enhances recognition of sexual cues in male humans. Psychoneuroendo. 2011; 36:294–297.

Guberneck DJ, Nelson RJ. Prolactin and paternal behavior in the biparental California mouse, peromyscus californicus. Horm Behav. 1989; 23:203–210. [PubMed: 2744739]

Hrdy, SB. Mothers and others: The evolutionary origins of mutual understanding. Harvard University Press; Cambridge, Massachusetts: 2009.

Hoffman KA, Mendoza SP, Hennessy MB, Mason WA. Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. Dev Psychobiology. 1995; 28:399–407.

Jacob S, Brune CW, Carter CS, Leventhal BL, Lord C, Cook EH Jr. Association of the oxytocin receptor gene (OXTR) in Caucasian children and adolescents with autism. Neurosci Lett. 2007; 417:6–9. [PubMed: 17383819]

Kleiman DG, Malcolm JR. The evolution of male parental investment in mammals. Quarterly Review of Biology. 1981; 52:39–68. [PubMed: 857268]

Kozorovitskiy Y, Hughes M, Lee K, Gould E. Fatherhood affects dendritic spines and vasopressin V1a receptors in the primate prefrontal cortex. Nature Neuroscience. 2006; 9:1094–1095. [PubMed: 16921371]

Kuo PX, Carp J, Light CK, Grewen KM. Neural responses to infants linked with behavioral interactions and testosterone in fathers. Biol Psych. 2012; 91:302–306.

Lee AG, Cool DR, Grunwald WC Jr, Neal DE, Buckmaster CL, Chen MY, Hyde SA, Lyons DM, Parker KJ. A novel form of oxytocin in New world monkeys. Biol Lett. 2011; 7:584–587. [PubMed: 21411453]

Lehrman, DS. Interaction between internal and external environments in the regulation of the reproductive cycle of the ring dove. In: Beach, FA., editor. Sex and Behavior. Wiley; New York, USA: 1965. p. 355-380.

Lukas D, Clutton-Brock TH. The evolution of social monogamy in mammals. Science. 2013; 341:526–530. [PubMed: 23896459]

Lunn SF, McNeilly AS. Failure of lactation in have a consistent effect on interbirth interval in the common marmoset, *Callithrix jacchus jacchus*. Folia Primatologica. 1982; 37:99–105.

Ma E, Lau J, Grattan DR, Loveljoy DA, Wynne-Edwards KE. Male and female prolactin receptor mRNA expression in the brain of a biparental and a uniparental hamster, *Phodopus*, before and after the birth of a litter. J Neuroendocrinol. 2005; 17:81–90. [PubMed: 15796758]

Marks L, Palkovitz R. American fatherhood types: the good, the bad, and the uninterested. Fathering. 2004; 2:113–129.

Marlowe F. Paternal investment and the human mating system. Behav Proc. 2000; 51:45–61.

Marsh AA, Yu HH, Pine DS, Gorodetsky EK, Goldman D, Blair RJR. The influence of oxytocin administration on responses to infant faces and potential moderation by OXTR genotype. Psychopharmacology. 2012; 224:469–476. [PubMed: 22763666]

Mascaro JK, Hackett PD, Gouzoules H, Lori A, Rilling JK. Behavioral and genetic correlates of the neural response to infant crying among human fathers. SCAN. 2014; 9:1704–1712. [PubMed: 24336349]

Mascaro JS, Hackett PD, Rilling JK. Differential neural responses to child and sexual stimuli in human fathers and non-fathers and their hormonal correlates. Psychoneuroendo. 2014; 46:153–163.

Meinlschmidt G, Heim C. Sensitivity to intranasal oxytocin in adult men with early parental separation. Biol Psychiatry. 2007; 61:1109–1111. [PubMed: 17141739]

Mileva-Seitz, V.; Fleming, AS. How mothers are born: A psychobiological analysis of mothering. In: Booth, A.; McHale, SM.; Landale, NS., editors. Biosocial foundations of family processes. New York: Springer; 2011. p. 3-34.

Mota MT, Franci CR, Sousa MBC. Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). Horm Behav 2006. 2006; 49:293–302.

Mota MT, Sousa MBC. Prolactin levels of fathers and helps related to alloparental care in commonmarmosets, callithrix jacchus. Folia Primatol. 2000; 71:22–26. [PubMed: 10686484]

Muller MN, Marlowe FW, Bugumba R, Ellison PT. Testosterone and paternal care in east African foragers and pastoralists. Proc, R Soc B. 2009; 276:347–354.

Naber F, van IJzendoorn MH, Deschamps P, van Engeland H, Bakermans-Kranenburg MJ. Intranasal oxytocin increases fathers' observed responsiveness during play with their children: A double-blind within-subject experiment. Psychoneuroendo. 2010; 35:1583–1586.

Naber FBA, Poslawsky IE, van IJzendoorn MH, van Engeland H, Bakermans-Kranenburg MJ. Brief report: Oxytocin enhances paternal sensitivity to a child with autism: A double-blind within-subject experiment with intranasally administered oxytocin. J Autism Developmental Disorders. 2013; 43:224–229.

Neumann F, Elger W, von Berswordt-Wallrabe R. The structure of the mammary glands and lactogenesis in feminized male rates. J Endo. 1966; 36:353–356.

Nunes S, Fite JE, French JA. Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). Anim Behav. 2000; 60:857–865. [PubMed: 11124885]

Nunes S, Fite JE, Patera KJ, French JA. Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets (*Callithris kuhlii*). Horm Behav. 2001; 39:70–82. [PubMed: 11161885]

Opie C, Atkinson QD, Dunbar IR, Shultz S. Male infanticide leads to social monogamy in primates. PNAS. 2013; 110:13328–13332. [PubMed: 23898180]

Overdorff, DJ.; Tecot, SR. Social pair-bonding and resource defense in wild red-bellied lemurs (eulemur rubriventer). In: Gould, L.; Sauther, ML., editors. Lemurs: Ecology and Adaptation. Springer science; New York: 2006. p. 237-256.

Pal SB. The pattern of urinary excretion of corticosteroids in rhesus monkeys (macaca mulatta). Endokrinologie. 1979; 73:359–362. [PubMed: 115672]

Palombit RA. Infanticide and the Evolution of Pair Bonds in Nonhuman Primates. Evol Anthro. 1999:117–129.

Parker KJ, Lee TM. Central vasopressin administration regulates the onset of paternal behavior in *Microtus pennsylvanicus*. Horm Behav. 2001; 39:285–294. [PubMed: 11374914]

Prickett KC, Storey-Martin A, Crosnoe R. A research note on the time with children in different- and same-sex two-parent families. Demography. 52:905–918. In press. [PubMed: 25911578]

Prudom SL, Broz CA, Schultz-Darken N, Ferris CT, Snowdon C, Ziegler TE. Exposure to infant scent lowers serum testosterone in father common marmosets (*Callithrix jacchus*). Biol Lett. 2008; 4:603–605. [PubMed: 18755659]

Quinlan RJ, Quinlan MB. Evolutionary ecology of human pair-bonds. Cross-Cultural Research. 2007; 41:149–166.

Reburn CJ, Wynne-Edwards KE. Hormonal change in males of a naturally biparental and a uniparental mammal. Horm Behav. 1999; 35:163–175. [PubMed: 10202124]

Riem MME, Pieper S, Out D, Bakermans-Kranenburg MJ, van IJzendoorn MH. Oxytocin receptor gene and depressive symptoms associated with physiological reactivity to infant crying. SCAN. 2011; 6:294–300. [PubMed: 20400491]

Roberts RL, Lawler TL, Wegner FH, Norcross JL, Newman JD. Prolactin levels are increased after infant retrieval and carrying in parentally inexperienced common marmosets. Physiol Behav. 2001; 72:713–720. [PubMed: 11337003]

Roberts RL, Jenkins KT, Lawler T Jr, Wegner FH, Newman JD. Bromocriptine administration lowers serum prolactin and disrupts parental responsiveness in common marmosets (*Callithrix j. jacchus*). Horm Behav. 2001a; 39:106–112. [PubMed: 11243738]

Romero LM, Dickens MJ, Cyr NE. The reactive scope model — A new model integrating homeostasis, allostasis, and stress. Horm Behav. 2009; 55:375–389. [PubMed: 19470371]

Rosenblatt, JS.; Seigel, HI. Factors governing the onset and maintenance of maternal behavior among nonprimate mammals. In: Klopfer, PH.; Gubernick, DJ., editors. Parental Care in Mammals. Springer; US: 1981.

Saito A, Nakamura K. Oxytocin changes primate parental tolerance to offspring in food transfer. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2011; 197:329–337. [PubMed: 21225271]

Santema P, Teitel T, Bennett N, Clutton-Brock T. Effects of cortisol administration on cooperative behavior in meerkat helpers. Behav Ecol. 2013

Satlzman W, Ziegler TE. Functional significance of hormonal changes in mammalian fathers. J Neuroendo. 2014; 10:685–696.

Schorscher-Petcu A, Dupre A, Tribollet E. Distribution of vasopressin and oxytocin binding sites in the brain and upper spinal cord of the common marmoset. Neuroscience Letters. 2009; 461:217–222. [PubMed: 19539696]

Schradin C, Reeder DM, Mendoza SP, Anzenberger G. Prolactin and paternal care: comparison of three species of monogamous new world monkeys. J Comp Psychol. 2003; 117:317–324. [PubMed: 14498808]

Schradin C, Anzenberger G. Development of prolactin levels in marmoset males: from adult son to first-time father. Horm Behav. 2004; 46:670–677. [PubMed: 15555510]

Seifritz E, Esposito F, Neuhoff JG, Luthi A, Mustovic H, Dammann G, von Bardeleben U, Radue EW, Cirillo S, Tedeschi G, Di Salle F. Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. Biol Psychiatry. 2003; 54:1367–1375. [PubMed: 14675800]

Storey AE, Walsh CJ, Quinton RL, Wynne-Edwards KE. Hormonal correlates of paternal responsiveness in new and expectant fathers. Evol Hum Behav. 2000; 21:79–95. [PubMed: 10785345]

Storey, AE.; Delahunty, KM.; McKay, DW. Are elevated cortisol levels associated with reduced or enhanced parental responsiveness?. Poster presented at the Parental Brain Conference; Boston, MA. 2007.

Storey AE, Noseworthy DE, Delahunty KM, Halfyard SJ, McKay DW. The effects of social context on the hormonal and behavioural responsiveness of human fathers. Horm Behav. 2011; 60:353–361. [PubMed: 21767539]

Taylor SE, Saphire-Bernstein S, Seeman TE. Are plasma oxytocin in women and plasma vasopressin in men biomarkers of distressed pair-bond relationships? Psychological Science. 2010; 21:3–7. [PubMed: 20424014]

Thompson RR, George K, Walton JC, Orr SP, Benson J. Sex-specific influences of vasopressin on human social communication. PNAS. 2006; 103:7889–7894. [PubMed: 16682649]

Torii R, Moro M, Abbott DH, Nigi H. Urine collection in the common marmoset, *Callithrix jacchus*, and its applicability to endocrinological studies. Primates. 1998; 39:407–417.

Van Anders SM, Goldey KL, Kuo PX. The Steroid/Peptide theory of social bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. Psychoneuroendo. 2011; 36:1265–1275.

Van Anders SM, Tolman RM, Volling BL. Baby cries and nurturance affect testosterone in men. Horm Behav. 2012; 61:31–36. [PubMed: 22001872]

van Schaik CP, Kappeler PM. The infanticide risk and the evolution of male-female association in primates. Proc Biol Sci. 1997; 264:1687–1694. [PubMed: 9404030]

Wallis M. Molecular evolution of the neurohypophysial hormone precursors in mammals: comparative genomics reveals novel mammalian oxytocin and vasopressin analogues. Gen Comp Endo. 2012; 179:313–318.

Walsh C, Ralph T, Storey A. Enclosure size and hormonal state affect timing of nest return in female meadow voles (*Microtus pennsylvanicus*). J Comp Psychol. 2009; 123:115–124. [PubMed: 19450018]

Walum H, Westberg L, Henningsson S, Neiderhiser JM, Reiss D, Igl W, Ganiban JM, Spotts EL, Pedersen NL, Eriksson E, Lichtenstein P. Genetic variation in the vasopressin receptor 1a gene (*AVPR1A*) associates with pair-bonding behavior in humans. Proceedings of the National Academy of Sciences, USA. 2008; 105:14153–14156.

Walum H, Lichtenstein P, Neiderhiser JM, Reiss D, Ganiban JM, Spotts EL, Pedersen NL, Anckarsäter H, Larsson H, Westberg L. Variation in the oxytocin receptor gene is associated with pair-bonding and social behavior. Biol Psychiatry. 2012; 71:419–426. [PubMed: 22015110]

Wang Z, Toloczko D, Young LJ, Moody K, Newman JD, Insel TR. Vasopressin in the forebrain of common marmosets (*Callithrix jacchus*): studies with *in situ* hybridization, immunocytochemistry and receptor of autoradiography. Brain Research. 1997; 768:147–156. [PubMed: 9369311]

Weisman O, Zagoory-Sharon O, Feldman R. Oxytocin administration to parent enhances infant physiological and behavioral readiness for social engagement. Biol Psychiatry. 2012; 72:982–989. [PubMed: 22795645]

Weisman O, Zagoory-Sharon O, Feldman R. Oxytocin administration, salivary testosterone, and father-infant social behavior. Progress in Neuro-Psychopharmacology & Biological Psychiatry. 2014; 49:47–52. [PubMed: 24252717]

Wermter AK, Kamp-Becker I, Hesse P, Schulte-Körne G, Strauch K, Remschmidt H. Evidence for the involvement of genetic variation in the oxytocin receptor gene (OXTR) in the etiology of autistic disorders on high-functioning level. Am J Med Genet B Neuropsychiatr Genet. 2010; 153B:629–39. [PubMed: 19777562]

Whiting JW, Whiting BB. Aloofness and intimacy of husband and wives: a cross-cultural study. Ethos. 1975; 3:183–207.

Wingfield JC, Kitaysky AE. Endocrine responses to unpredictable environmental events: stress or anti-stress hormones? Integr Comp Biol. 2002; 42:600–609. [PubMed: 21708756]

Woller MJ, Sosa ME, Chiant U, Prudom SL, Kellety P, Moore JE, Ziegler TE. Differential hypothalamic secretion of neurocrines in male common marmosets: parental experience effects? J Neuroendo. 2011; 24:1–9.

Ziegler TE, Bridson WE, Snowdon CT, Eman S. Urinary gonadotrophin and estrogen excretion during the post-partum estrous, conception and pregnancy in the cotton-top tamarin. Amer J Primatology. 1987; 12:127–140.

Ziegler TE, Widowski TM, Larson ML, Snowdon CT. Nursing does affect the duration of the post-partum to ovulation interval in cotton-top tamarins (*Sagunius oedipus*). J Repro Fert. 1990; 90:563–570.

Ziegler TE, Snowdon CT. Preparental hormone levels and parenting experience in male cotton-top tamarins, *Sagunis oedipus*. Horm Behav. 2000; 38:159–167. [PubMed: 11038290]

Ziegler TE, Wegner FH, Carlson AA, Lazaro-Perea C, Snowdon CT. Prolactin levels during the periparturitional period in the biparental cotton-top tamarin (*Saguinus oedipus*): interactions with gender, androgen levels, and parenting. Horm Behav. 2000; 38:111–122. [PubMed: 10964525]

Ziegler TE, Jacoris S, Snowdon CT. Sexual communication between breeding male and female cotton-top tamarins (*Saguinus oedipus*) and its relationship to infant care. Amer J Primatology. 2004b; 64:57–70.

Ziegler TE, Washabaugh KF, Snowdon CT. Responsiveness of expectant male cotton-top tamarins, Saguinus oedipus, to mate's pregnancy. Horm Behav. 2004a; 45:84–92. [PubMed: 15019794]

Ziegler TE, Schultz-Darken NJ, Scott JJ, Snowdon CT, Ferris. Neuroendocrine response to female periovulatory odors depends upon social condition in male common marmosets, callithrix jacchus. Horm Behav. 2005; 47:56–64. [PubMed: 15579266]

Ziegler TE, Prudom SL, Schultz-Darken NJ, Kurian AV, Snowdon CT. Pregnancy weight gain: marmoset and tamarin dads show it too. Biol Lett. 2006; 2:181–183. [PubMed: 16810338]

Ziegler TE, Prudom SL, Zahed SR, Parlow AF, Wegner FH. Prolactin's mediative role in male parenting in parentally experienced marmosets (*Callithrix jacchus*). Horm Behav. 2009b; 56:436–443. [PubMed: 19664636]

Ziegler TE, Peterson LJ, Sosa ME, Barnard AM. Differential endocrine responses to infant odors in common marmoset (Callithrix jacchus) fathers. 2011

Table 1

Summary of relationships between hormone levels and paternal behavior in primates at different stages (e.g., fathers and non-fathers) and responses to infant cues

Hormone	Response type*	Non Human Primates	Humans
Testosterone	Stage	43% decease after birth, marmosets[1]; tamarins?	Lower in fathers than non-fathers in North American studies and/or cultures with high paternal care[4]; 26 – 37 % decrease after birth vs before [5, 6]
	Infant cues	52% lower in high-carrying marmosets, vs low carriers[2]; 46% lower after exposure to own vs novel infant odor[3]	10% decrease when men provided effective care, 20% increase if no care is possible[7]
Prolactin	Stage	50% prenatal increase in experienced tamarins, no change after birth[7]; 50% pre-natal increase, fathers > non-fathers, in early-carrying species[8]; 67% increase from before to after birth[9] or no change in marmosets[10]	30% higher just before birth, compared to earlier in pregnancy[4]; fathers higher than non-fathers[12] or no difference[13]
	Infant cues	> 100% increase, carrying vs non-carrying[11, 12]	10–30% increase in experienced fathers hearing cries and/or holding baby[14,15]
Cortisol	Stage	>100 % Prenatal, following female increases [16]	Prenatal increases, correlated with female levels[4,17,18]
	Infant cues	28% lower in high-carrying marmosets, vs low carriers[2];	–
Vasopressin (AVP)	Stage	30% more dendritic spines on AVP pyramidal neurons of prefrontal cortex of marmoset fathers than non-fathers[19]	Negative correlation between AVP and age of youngest child[13]
	Response	–	Positive correlation between AVP and amount of stimulatory contact parents had with babies [20]
Oxytocin (OT)	Stage	–	Fathers have higher OT levels than non-fathers[21]; Parental levels increase during first 6 months[22]
	Response	–	Intranasal OT increased interactions between fathers[23–4] or both parents and babies [25–6]

[1] Nunes et al., 2000;

[2] Nunes et al., 2001;

[3] Ziegler et al., 2011;

[4] Gray & Campbell, 2009;

[5] Storey et al., 2000;

[6] Gettler et al., 2011;

[7] Van Anders et al., 2011;

[8] Ziegler & Snowden;

[9] Schradin et al. 2003;

[10] Schradin & Anzenberger, 2004;

[11] Mota et al., 2006;

[12] Dixson & George, 1982;

[13] Gray et al., 2007;

[14] Fleming et al., 2002;

[15] Delehunty et al., 2007;

[16] Ziegler et al., 2004a;

[17] Berg & Wynne-Edwards;

[18] Edelstein et al., 2014;

[19] Kozorovitskiy et al., 2006;

[20] Apter-Levi et al., 2014;

[21] Mascaro et al., 2014;

[22] Gordon et al., 2010;

[23–4] Nabor et al., 2010; 2013;

[25–6] Weisman et al., 2012,;2014