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Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys

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ABSTRACT

The neurohormone oxytocin (OT) is positively involved in the regulation of parenting and social bonding in mammals, and may thus also be important for the mediation of alloparental care. In cooperatively breeding marmosets, infants are raised in teamwork by parents and adult and sub-adult non-reproductive helpers (usually older siblings). Despite high intrinsic motivation, which may be mediated by hormonal priming, not all individuals are always equally able to contribute to infant-care due to competition among care-takers. Among the various care-taking behaviors, proactive food sharing may reflect motivational levels best, since it can be performed ad libitum by several individuals even if competition among surplus care-takers constrains access to infants. Our aim was to study the link between urinary OT levels and care-taking behaviors in group-living marmosets, while taking affiliation with other adults and infant age into account. Over eight reproductive cycles, 26 individuals were monitored for urinary baseline OT, care-taking behaviors (baby-licking, -grooming, -carrying, and proactive food sharing), and adult-directed affiliation. Mean OT levels were generally highest in female breeders and OT increased significantly in all individuals after birth. During early infancy, high urinary OT levels were associated with increased infant-licking but low levels of adult-affiliation, and during late infancy, with increased proactive food sharing. Our results show that, in marmoset parents and alloparents, OT is positively involved in the regulation of care-taking, thereby reflecting the changing needs during infant development. This particularly included behaviors that are more likely to reflect intrinsic care motivation, suggesting a positive link between OT and motivational regulation of infant-care.

Introduction

Over the last decades, oxytocin (OT) has been shown to be versatilely involved in the regulation of mammalian social behaviors and bonding (Lim and Young, 2006), most importantly in maternal care and mother-infant bonds (Kendrick, 2000; Uvnäs-Moberg, 1996). Its ancient functions in female reproduction, related to cervix and uterus distension during labor (Blanks and Thornton, 2003; Kendrick and Keverne, 1989; Landgraf et al., 1983; Nissen et al., 1995), milk injection during lactation (Uvnäs-Moberg et al., 2001), and the regulation of maternal behavior (Feldman, 2007; Kendrick, 2000; Kendrick et al., 1987; Pedersen et al., 1994; Uvnäs-Moberg, 1996), probably formed the basis for derived OT functions in non-maternal social contexts (Broad et al., 2006; Kendrick, 2000; Lim and Young, 2006). However, less is known about the role of OT in alloparental care, i.e. care provided by non-mothers, including paternal care provided by fathers.

Among nonhuman primates, alloparental care is most frequent in the cooperatively breeding callitrichid monkeys (Digby et al., 2007). Whereas all group members cooperate in rearing offspring, reproduction is usually restricted to a dominant breeding pair (Digby et al., 2007; Garber, 1997; Goldizen, 2003), but mating systems and group composition show considerable flexibility, in particular in wild callitrichids (Garber et al., 2015; Goldizen, 1988; Solomon and French, 1997; Sussman and Garber, 1987). Reproductive success depends on the availability of alloparental care, which increases infant growth and survival, especially in common marmosets (Koenig, 1995; Rothe et al., 1993) but also in other callitrichid species (Sussman and Garber, 1987). After the first post-partum days, during which mothers typically are the primary care-takers in common marmosets (Koenig and Rothe, 1991; Mills et al., 2004), help is provided by fathers and other group members, who are mostly, but not exclusively, the adult and sub-adult offspring of the breeding pair, and who delay dispersal and help rearing their siblings (Digby et al., 2007; Garber, 1997; Goldizen, 1987; Yamamoto et al., 2014).

During early infancy, helping behavior mostly consists of carrying the offspring, which bears high energetic costs to carriers (Schradin and Anzenberger, 2001). Nevertheless, care-takers also compete over

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access to infants (Mills et al., 2004; Yamamoto and Box, 1997; Zahed et al., 2010), and particularly female helpers are not always tolerated by other group members to handle and carry infants as much as they attempt to (Albuquerque, 1999; Price, 1991). Hence, individual infant-carrying contributions may not necessarily correspond to intrinsic motivational levels, especially if more care-takers than infants are available. During later infancy until juvenile age, carrying continually decreases and is complemented by food provisioning to immatures. In contrast to infant-carrying, food provisioning can always be performed ad libitum and is usually not constrained by other group members. During peak provisioning periods, adults share up to 63% of provided food items with immatures, and 40% of these food transfers occur proactively (Martins et al., in preparation), i.e. are initiated by the adult who offers the food to the immature (Brown et al., 2004). Non-reproductive helpers show particularly high levels of proactive food sharing (48%) during that time, Alloparents thus seem to have high intrinsic care-taking motivation, and, in fact, helping in subordinates is not enforced by breeders through coercion or punishment (Snowdon and Cronin, 2007).

In marmoset mothers, labor and lactation as well as maternal infant-care after birth are accompanied by a number of hormonal changes: Towards labor, estradiol and progesterone levels decrease drastically (Chambers and Hearn, 1979) and are linked to post-partum sexual cycling independently of lactation (Kholkute, 1984), whereas prolactin levels increase and remain elevated during lactation (McNeilly et al., 1981). Reproduction-related OT patterns in callitrichid monkeys may be comparable to those of other primates, where plasma OT is elevated during late pregnancy and parturition (Hirst and Thorburn, 1996; Novy and Haluska, 1994), and during lactation in rhesus monkeys (*Macaca mulatto*, Amico et al., 1990) but not in Cynomolgus monkeys (*Macaca fascicularis*, Morris et al., 1980).

The hormones mentioned above are also involved in maternal care-taking behaviors and motivation: Sex steroids positively affect maternal responsiveness during late pregnancy in marmosets and tamarins (Pryce et al., 1993). Likewise, pre-partum estrogen levels are positively linked to subsequent maternal care-taking behavior in tamarins (Pryce et al., 1988), macaques (Bardi et al., 2003), and humans (Fleming et al., 1987; see also Maestripieri, 2001a, 2001b, and Saltzman and Maestripieri, 2011). Conflicting results were described for common marmosets (Pryce et al., 1995), black-tufted marmosets (Fite and French, 2000), gorillas (Bahr et al., 2001), and baboons (Bardi et al., 2004; see also Maestripieri, 2001a; Saltzman and Maestripieri, 2011). Primate maternal behavior can also be influenced by stress-related hormones and neuropeptides (Saltzman and Maestripieri, 2011), whereas there is no indication for a positive link of prolactin and maternal care based on the limited available evidence in marmosets (Saltzman and Abbott, 2005). OT seems to be fundamentally involved in motivational priming during mother-infant bonding in mammals (Carter, 1998; Maestripieri, 2001b) and it is positively involved in maternal behavior in rats (Fahrbach et al., 1984; Pedersen et al., 1994) and sheep (Kendrick et al., 1987), but such effects have not been studied in primates yet.

The neuroendocrine hypothesis suggests that hormonal priming may generally play a vital role in the mediation of infant-care motivation, which may provide an important complement to parenting experience, thus being particularly valuable for inexperienced mothers but also alloparental care-takers (Pryce, 1993). However, evidence for such effects in primates is still very limited and partly contradictory. Positive evidence related to non-maternal care exists for example for tamarin fathers, who show changes of testosterone, estradiol, and glucocorticoid levels in the pre-partum period as well as during infant-care, possibly preparing males for the impending birth and parenting role (Ziegler and Snowdon, 2000; Ziegler et al., 2004; Ziegler et al., 1996). Prolactin is also positively linked to infant-care in marmoset fathers and helpers (Dixson and George, 1982; Mota et al., 2006; Mota and Sousa, 2000; Roberts et al., 2001; Schradin and Anzenberger, 2004; Schradin et al., 2003), but these studies suggest that prolactin increases in response to infant-contact and -carrying rather than promoting such behaviors based on motivation-stimulating effects. Accordingly, experienced marmoset fathers could express normal paternal care even if prolactin was suppressed (Almond et al., 2006). In contrast, OT has been shown to stimulate alloparental infant-care motivation in different mammal species: In rodents, peripheral OT administration facilitated alloparental pup-retrieval, -licking, and -grooming in females (Bales et al., 2007), and OT-antagonist inhibited such behaviors in males (Bales et al., 2004). Peripheral OT administration also enhanced guarding, feeding, and association with pups in meerkats (Madden and Clutton-Brock, 2011), and intracerebroventricular OT administration facilitated paternal food sharing in marmosets (Saito and Nakamura, 2011). However, it remains to be established whether OT is also positively linked to alloparental behavior and motivation in non-reproductive primate helpers, and whether this link is reflected in endogenous OT responses, since the existing evidence mainly focusses on exogenous OT effects.

The aim of this study was to assess the role of OT in care-taking behavior in family groups of cooperatively breeding marmosets, with particular focus on the relationship between OT and care motivation in non-mothers. We longitudinally followed five family groups of common marmosets over a total of eight reproductive cycles. During each reproductive cycle, we collected baseline OT levels from morning void urine and data on care-taking behaviors (infant-carrying, −licking, −grooming, and proactive food sharing) and affiliative behaviors between adult group members (grooming and huddling), over a total period of 12 weeks (starting one week before birth).

First, we investigated whether urinary OT levels increased immediately after infant-birth in mothers and other adult care-takers, which would be consistent with the neuroendocrine priming hypothesis (Pryce, 1993). Based on OT functions in mammalian birth (Kendrick, 2000; Landgraf et al., 1983; Nissen et al., 1995) and lactation (Uvnäs-Moberg et al., 2001), we expected OT levels of breeding females to be elevated after birth and during lactation until infant-weaning. Higher OT levels in response to the presence of new-born offspring were also expected in marmoset fathers, based on findings of positive peripheral OT responses in human parents (Feldman et al., 2011; Gordon et al., 2010; Nissen et al., 1995). Since non-reproductive helpers in marmosets also show high levels of alloparental care (Digby et al., 2007; Goldizen, 1987), we predicted a positive OT response also in helper individuals of both sexes.

Second we analyzed to what extent urinary OT patterns reflect care-taking behaviors, while taking affiliation with other adults, infant age, and care-taking experience into account. We also compared the effects in early and late infancy, because frequencies and importance of the different infant-directed behaviors change over time. The facilitating effects of exogenous OT on paternal food transfer in marmosets (Saito and Nakamura, 2011) and alloparental behaviors in other mammals (Bales et al., 2007; Madden and Clutton-Brock, 2011) suggest that OT may be positively associated with intrinsic care-taking motivation. We therefore expected urinary OT levels to be positively linked in particular to those care-taking behaviors that can be freely expressed by all individuals motivated to do so. During early infancy, this arguably mainly includes infant-licking and -grooming, since the immobile infants cannot be carried simultaneously by all motivated care-takers, but infants can be licked and groomed also on the backs of other care-takers. Furthermore, compared to licking and grooming, carrying is a more passive behavior once the infant sits on the carrier and may thus be less related to OT. During late infancy, carrying and licking decrease continuously and food sharing becomes more important. In particular proactive food sharing (Brown et al., 2004), which is initiated by the food possessor rather than a begging immature, was expected to be positively linked to OT during this period because it is dependent on intrinsic proactive motivation (Jaeggi and Gurven, 2013) and can be performed ad libitum by all motivated care-takers.