

Suppression of prolactin does not reduce infant care by parentally experienced male common marmosets (*Callithrix jacchus*)

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Abstract

High levels of prolactin have been found to correlate with the expression of paternal care in a variety of taxa. However, in mammals, there is little experimental evidence that prolactin is causally involved in the stimulation or maintenance of paternal care. Here, we suppressed prolactin production in paternally experienced common marmoset fathers in their family groups during the first 2 weeks after their infants were born. Circulating prolactin levels were suppressed using cabergoline (Dostinex: Pfizer), a long acting dopamine (D₂) agonist with minimal behavioural side-effects. A within-subject design was used to compare behavioural and hormonal data on 5 paternally experienced fathers during two consecutive births. Cabergoline reduced prolactin to negligible levels in all fathers without effecting testosterone, DHT and cortisol and without adverse side-effects. However, lowering prolactin had no significant effect on the expression of majority of the behaviour patterns associated with paternal care. These included infant carrying, infant grooming and the frequency with which fathers retrieved and rejected infants. The only infant-related behaviour to be affected was the frequency with which fathers touched, licked and investigated infants. We noted a marginally significant increase in this behaviour during cabergoline treatment. Despite the lack of effect on paternal care, cabergoline did exert an effect on the affiliative/sexual behaviour of fathers as there was a significant increase in the grooming behaviour fathers directed at and received from their mates during drug treatment. This study showed that experienced male marmosets can express paternal behaviour in the absence of the high prolactin levels normally seen after infants are born.

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Introduction

Hormonal changes in fathers before and during infant care have been widely documented (reviewed in Wynne-Edwards, 2001; Ziegler, 2000). One of the most well studied of these hormones is prolactin, a protein hormone with more than 350 known biological effects (Freeman et al., 2000). The role of prolactin in the induction and maintenance of maternal care has been extensively studied (reviewed in Keverne, 1996; Numan, 1994). In female mammals, prolactin begins to increase towards the end of gestation when it is crucial for inducing milk

production, and, in combination with progesterone and estrogen, prolactin reduces the latency of onset of maternal behaviour (Bridges et al., 1990). Elevated prolactin levels have also been seen in fathers prior to and during infant care in a range of taxa, including birds (Buntin, 1996; Buntin et al., 1991), rodents (Brown et al., 1995; Gubernick and Nelson, 1989; Reburn and Wynne-Edwards, 1999) and New World primates (Mota and Sousa, 2000; Schradin et al., 2003; Ziegler et al., 1996). Human fathers are also reported to exhibit increases in prolactin levels before and immediately after their babies are born (Storey et al., 2000). Prolactin levels were seen to be highest in men showing greater responsiveness to infant cries and in men reporting more pregnancy (couvade) symptoms. In addition, human fathers with high prolactin levels are more positive in their response to infant cries than fathers with low prolactin levels (Fleming et al., 2002).

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The apparently widespread correlation between prolactin and paternal behaviour has led researchers to question whether prolactin plays a causal role in stimulating or maintaining infant care in males. One approach used to investigate the role of prolactin in maternal care has been to artificially manipulate levels in individuals while they are caring for infants and compare their behaviour with control subjects or with the same individual with normal levels of prolactin (see Bridges and Ronsheim, 1990). Similar experimental studies have indicated a causal relationship between elevated prolactin and male parental behaviour in a number of species of birds (reviewed by Buntin, 1996, Ziegler, 2000). For instance, raising and lowering prolactin in male ring doves (*Streptopelia risoria*) have demonstrated that prolactin plays a direct role in stimulating incubation behaviour, the formation of nutritional crop milk and the frequency of chick feeding behaviour (reviewed in Buntin, 1996). In comparison, relatively few experiments involving manipulation of prolactin levels have been carried out in male mammals. An early study on rats (*Rattus norvegicus*) reported that administration of prolactin promoted parental behaviour in males, as well as in females (Sakaguchi et al., 1996). However, as male rats do not usually exhibit parental behaviour, it is difficult to extend these results to natural paternal care. A recent study by Brooks et al. (2005) manipulated prolactin in a naturally paternal mammal, the Djungarian hamster (*Phodopus campbelli*). Prolactin secretion was suppressed in parentally inexperienced males both before and after the birth of their first litter of pups, and paternal responsiveness was measured in terms of pup retrieval. This study found no effect of prolactin suppression on the paternal responsiveness of first time fathers. These results provide strong evidence that elevated prolactin around the time of birth is not crucial for the expression of paternal care in first time fathers in this species.

Among primates, the callitrichids (marmosets and tamarins) are ideal species in which to investigate the role of prolactin in paternal care as fathers care extensively for their offspring. For instance, callitrichid fathers contribute as much as 80% of the time that infants are carried during the first 4 weeks of life (Yamamoto, 1993). Fathers also retrieve distressed infants, groom them and provision them with solid food (Bales et al., 2000; Brown et al., 2004; Tardif, 1994). High male prolactin levels have been reported prior to and during the period of infant care in a number of callitrichid species, including cotton-top tamarins (*Saguinus oedipus*: Ziegler et al., 1996), common marmosets (Dixon and George, 1982; Mota and Sousa, 2000) and Goeldi's monkeys (*Callimico goeldii*: Schradin et al., 2003). Callitrichid primates are also characterised by high levels of alloparenting behaviour, in which individuals other than the parents provide care for infants (Tardif, 1994). In common marmosets, male and female alloparents are also reported to exhibit raised prolactin levels when infants are present (Mota and Sousa, 2000) or immediately after carrying infants (Roberts et al., 2001b).

One previous study has investigated the effects of suppressing prolactin on infant care in a common marmosets. Roberts et al. (2001a) reported that suppression of prolactin levels in non-

breeding male and female common marmosets eliminated or reduced alloparental care. While this study had only a small sample of males ($N = 2$), the data suggested that prolactin may be linked to infant care by males in this species: one of the males failed to retrieve infants, and the other exhibited a reduction in infant carrying following suppression of prolactin. These data suggest that prolactin could be linked to how responsive males are to infants in this species. However, common marmoset pairs who lack parental or sibling rearing experience are significantly less likely to successfully raise and respond to infants than parentally experienced pairs (Snowdon, 1996; Tardif et al., 1984). It is therefore difficult to draw firm conclusions about the role prolactin plays in paternal care as the test was carried out on parentally inexperienced alloparents responding to unfamiliar infants.

The aim of our study was to investigate the effects of suppressing prolactin levels on the expression of male parenting behaviour in paternally experienced common marmosets (*Callithrix jacchus*). To address this question more directly, all fathers in our experiment were paternally experienced and caring for their own offspring at the time of testing. Prior experience of parenting may strongly influence the link between hormones and behaviour and hence the effects of experimental hormone manipulation. In female mammals, experience with raising infants has been found to effect profoundly the way in which hormones help to stimulate and maintain maternal care (Keverne, 1996; Levy et al., 1996), possibly due to a remodelling of neural structures that produces a greater sensitivity to hormones (Broad et al., 1999; Levy et al., 1996). As we are only just beginning to understand the role hormones play in stimulating and maintaining paternal care, the extent to which and the way in which paternal experience and hormones interact in fathers is not known. In male ring doves, a single injection of prolactin facilitated chick feeding behaviour when they were presented with a foster chick, but only if they had had previous breeding experience (Lott and Comerford, 1968). This suggests that experiential factors alter the way in which the bird responds to prolactin in the presence of stimuli that would normally elicit parental behaviour. No such work has been done in mammals. However, callitrichids show hormonal differences between experienced and inexperienced fathers which might be indicative of an interaction between these two variables. Studies of cotton-top tamarins have reported that experienced fathers have higher levels of prolactin post-partum than inexperienced fathers (Ziegler et al., 1996) and that the increase in prolactin preceding birth occurs earlier than in inexperienced fathers (Ziegler and Snowdon, 2000; Ziegler et al., 2004). Post-partum prolactin levels also correlate positively with the number of births experienced by male cotton-top tamarins (Ziegler et al., 1996), although this has yet to be shown in common marmosets (Schradin and Anzenberger, 2004). In humans, experienced fathers show greater percentage increase in prolactin in response to infant cries than do first time fathers (Fleming et al., 2002).

We predicted that, if the elevated level of prolactin following the birth of infants is crucial to stimulating paternal behaviour in common marmoset fathers, then lowering prolactin during this

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