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Review article

The marmoset as a model for the study of primate parental behavior

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ABSTRACT

Parental behavior is important for the development of mammalian offspring. Research on the mechanisms underlying parental behavior, however, has been largely restricted to rodent models. As a consequence, although research on parent–infant relationships has been conducted using macaque monkeys for more than half a century, little is known about the neural mechanisms and brain regions associated with such behaviors in primates. This article reviews parental behavior and its endocrinological mechanisms in marmosets and tamarins, both cooperative breeders in the callitrichid family, and compares these findings with studies of macaque monkeys. The paper examines the similarities and differences between marmosets and humans, and suggests the possibility that marmosets can be a model for future studies of the neural underpinnings and endocrinology underlying human parental behavior.

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1. Introduction

Mammalian offspring cannot survive without parental care, and the social environment between offspring and carers has major

effects on development (e.g., Repetti et al., 2002). Parental behavior includes both nurturing behaviors that increase offspring fitness such as nursing and grooming (Krasnegor and Bridges, 1990), and non-nurturing behaviors that do not increase offspring fitness, such as rejecting an infant who wants to suck a nipple. This article focuses mainly on nurturing behavior by parents and other carers.

The neural and genetic mechanisms of mammalian parental behavior have been studied mainly in rodents, and researchers have identified various hormonal, neuromolecular, and genetic determinants, relevant neuroanatomical regions, and epigenetic effects

Abbreviations: PCA, principle component analysis; CSF, cerebrospinal fluid.

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of parental behavior in these animals (Kuroda et al., 2011). Since parental behavior is important for all mammals, it is reasonable to postulate that the underlying mechanisms may be conserved. However, mammalian parental behavior varies between phylogenetic groups, and rodents and humans have a different evolutionary history, so it is not clear to what extent we may extrapolate knowledge acquired from rodent studies to human parental behavior. One way to bridge the gap is to study species that are phylogenetically more closely related to humans, such as non-human primates. There are several important differences between reproductive processes in rodents and primates. First, since female primates produce relatively large infants and provide a great deal of maternal investment (Martin and Maclarnon, 1985), primate mothers may have a greater opportunity to influence the development, and subsequent phenotype and fitness of their offspring (Maestripieri and Mateo, 2009). Second, whereas rodent parental care typically relies on olfactory cues for parent/offspring recognition (Tachikawa et al., 2013), primates, including humans, rely more on visual cues for the expression of parental behavior (Glocker et al., 2009; Sato et al., 2012). Third, primate parental behavior is more responsive to the social environment than that of rodents (Maestripieri and Mateo, 2009).

Since the landmark study of Harlow (1958), primate studies of parent-offspring relationships have been mainly conducted on macaque monkeys. These studies have examined offspring recognition (e.g., Maestripieri and Call, 1996), manipulation of the parental environment (e.g., Maestripieri, 2005), and hormonal effects (Saltzman and Maestripieri, 2011). However, the underlying brain mechanisms of parental behaviors in primates have not been sufficiently pursued. For example, researchers have not yet identified the brain regions most important to particular parental behaviors in primates. This article reviews studies of parental behavior and its endocrinological mechanisms in marmosets and tamarins, both cooperative breeding primates in the callitrichid family, and compares these findings to studies on macaque monkeys. The review suggests that marmosets may serve as a useful model for future studies of the mechanisms of human parental behavior.

2. Parental behavior in callitrichids compared to macaque monkeys

2.1. Differences in features of reproduction

One of the most important features of callitrichid reproduction is high fertility. Females reach sexual maturity at 12 months, and males at 17 months (Abbott and Hearn, 1978; Harvey et al., 1987). Typically, one dominant female–male mating pair in each group monopolizes reproduction in a group of 3–15 individuals (Ferrari and Ferrari, 1989; Saltzman, 2003). Breeding females produce twins or triplets with birth weights of approximately 30 g (Tardif et al., 1998) twice per year (Tardif et al., 2003). One to two weeks after parturition, females begin estrus and ovulate again (Dixson and Lunn, 1987; Kholkute, 1984). If impregnated, they gestate their fetuses while nursing and carrying their infants (Lunn and McNeilly, 1982; Ziegler et al., 1990). As a result, the mating pair may produce four or more offspring per year. This is a much higher rate of reproduction than macaque monkeys, who are not sexually mature until the age of 3.5 years and who have a gestation period of 160–180 days, producing one infant per parturition (Melnick and Pearl, 1987). For researchers, it is therefore relatively much easier to collect extensive data on parturition and the infant rearing in callitrichids.

Another important feature of reproduction in callitrichids is cooperative breeding, wherein individuals other than the genetic



Fig. 1. Infant carrying by an older sibling. One infant attaches to the front of the sibling, another one on the back.

parents contribute to rearing the offspring (Fig. 1; e.g., Ferrari, 1992; Mills et al., 2004; Washabaugh et al., 2002; Yamamoto and Box, 1997; Zahed et al., 2010). The evolution of this strategy is thought to be related to the cost of parenting. Since callitrichid neonates have relatively large body weights compared to their parents (Leutenegger, 1973) and are either twins or triplets, the energetic cost of carrying them is high (Achenbach and Snowdon, 2002; Sanchez et al., 1999). Carrying infants reduces the mobility of the carriers (Schradin and Anzenberger, 2001). Breeding males begin to provide support to females at around parturition. Fathers play the role of midwife at the birth (Wynne-Edwards and Reburn, 2000). It has been suggested that the behaviors observed in callitrichid fathers, such as carrying, protecting, grooming, feeding, playing with, and staying near infants, are similar to those of humans (Whiten, 1987). Humans have also been considered to be cooperative breeders (Hrdy, 2005), and so we may gain insights into this aspect of human parental behavior and its mechanisms by studying the parental behavior of callitrichids.

In contrast, macaque monkeys live in groups ranging from 10 to over 100 individuals (Rowe, 1996). Females distance themselves from the group before parturition and birth their infants by themselves (Bardi et al., 2003c). After parturition, mothers essentially raise infants alone. During the week following birth, macaque infants remain in direct contact with their mothers. Around the second week, they start to leave their mothers to investigate their environment. Mothers demonstrate restrictive behavioral responses, such as grasping infants' limbs and pulling them back. As a result, during the first month, infants have almost no contact with group members other than their mothers (Berman, 1980; Hinde and Spencer-Booth, 1967; Hiraiwa, 1981; Nakamichi, 1989; Simpson et al., 1986).

Among callitrichids, infants are not only carried by their mothers but also start to be carried by other members of the group early in their development. In the first week, their mothers and fathers carry them more than other group members, but by the second week, older siblings start to demonstrate frequent carrying behavior (Ingram, 1977; Mills et al., 2004). Sometimes, the animals that are carrying the infants reject them by biting or rubbing them, then leaving the infants alone for a few minutes. This can happen even when the infants are only one or two weeks old in captive populations (Saito and Nakamura, 2011b). These rejected infants then emit a distress call that usually stimulates the adult animals to retrieve them (Epple, 1968). Infants also may spontaneously transfer from one caretaker to another (Tardif et al., 2002). Therefore, infant callitrichids both passively and actively come into contact with group

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