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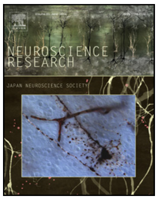

Marmosets as model species in neuroscience and evolutionary anthropology

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Marmosets are increasingly used as model species by both neuroscientists and evolutionary anthropologists, but with a different rationale for doing so. Whereas neuroscientists stress that marmosets share many cognitive traits with humans due to common descent, anthropologists stress those traits shared with marmosets – and callitrichid monkeys in general – due to convergent evolution, as a consequence of the cooperative breeding system that characterizes both humans and callitrichids. Similarities in socio-cognitive abilities due to convergence, rather than homology, raise the question whether these similarities also extend to the proximate regulatory mechanisms, which is particularly relevant for neuroscientific investigations. In this review, we first provide an overview of the convergent adaptations to cooperative breeding at the psychological and cognitive level in primates, which bear important implications for our understanding of human cognitive evolution. In the second part, we zoom in on two of these convergent adaptations, proactive prosociality and social learning, and compare their proximate regulation in marmosets and humans with regard to oxytocin and cognitive top down regulation. Our analysis suggests considerable similarity in these regulatory mechanisms presumably because the convergent traits emerged due to small motivational changes that define how pre-existing cognitive mechanisms are quantitatively combined. This finding reconciles the prima facie contradictory rationale for using marmosets as high priority model species in neuroscience and anthropology.

1. Introduction

Marmosets are increasingly used as model species in neuroscience research, and a rich set of basic research tools has been developed over the past decades (Kishi et al., 2014; Mansfield, 2003; Mitchell et al., 2014; Okano et al., 2012; Yamazaki and Watanabe, 2009). The use of primate models is advantageous because we are far more likely to deal with homology than when using rodent models, which is a crucial precondition for neuroscientific investigations that ultimately aim at an understanding of human cognitive processes. In contrast to other primate models, such as macaques, marmosets have several advantages. Their small body size of facilitates the handling and maintenance of these monkeys, and they easily breed in captivity and show high reproductive efficiency for a primate, by producing twins or even triplets every 5 months, and by becoming sexually mature at only 1.5 years. Thus, marmosets are ideal study subjects because they combine the convenience of rodent models with the close phylogenetic relationship of primate models.

At the same time, marmosets, and callitrichid monkeys in general, have moved into the focus of attention of evolutionary anthropologists who are interested in the evolution of human behavior and cognition. However, unlike neuroscientists, evolutionary anthropologists are interested in marmosets because they share traits with humans, but not with other primates, due to the convergent emergence of cooperative breeding. Cooperative breeding refers to reproductive systems in which individuals who are not the parents contribute to rearing the infants (Ligon and Burt, 2004; Wilson, 1975) and has independently evolved in callitrichid monkeys and humans. It can explain many of our derived life-history and demographic traits, as well as characteristic elements of our subsistence ecology (Hrdy, 2009; Kramer, 2010). The cooperative breeding model of human evolution also has a cognitive dimension because cooperative breeding is associated with a variety of psychological and cognitive consequences which have the potential to explain many of the discrepancies between human and great ape cognition (see below).

Similarities in socio-cognitive abilities between marmosets and humans due to convergence, rather than homology, raise the

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question whether these similarities also extend to the proximate regulatory mechanisms, which is particularly relevant for neuroscientific investigations. The aim of this review is to first provide an overview over the psychological and cognitive consequences of cooperative breeding in primates as well as their implications for human cognitive evolution. In the second part, we will zoom in on the domains of proactive prosociality and social learning in which common marmosets and other cooperatively breeding primates excel, and compare the proximate regulatory mechanisms that are involved in marmosets, humans, and other primates. Based on this review of available data we will propose that the unique profile of cognitive abilities in marmoset monkeys is best understood as selective up- and down regulation of cognitive mechanisms available to nonhuman primates in general, rather than as an addition of qualitatively new mechanisms.

2. Psychological and cognitive consequences of cooperative breeding in primates

Cooperative breeding in primates is associated with increased performance in many socio-cognitive tasks, but regular performance in non-social cognitive tasks (Burkart and van Schaik, 2010). However, it is unlikely that these cognitive consequences arose because sophisticated cognitive abilities were necessary in order to engage in high levels of allomaternal care, especially in light of the fact that callitrichids have brains that are small, even relative to their body size (Herculano-Houzel et al., 2007). Rather, the behavioral tasks related to cooperative breeding arguably require adaptations at the psychological and motivational level, which in turn facilitate performance in socio-cognitive tasks.

2.1. Tasks related to cooperative breeding in nonhuman primates

Callitrichid monkeys are subdivided in 20–30 marmoset and tamarin species, among them the common marmosets. All these species typically live in family groups composed of a breeding pair, adult helpers, and immatures. Most of the time, the helpers are adult offspring from the breeding pair; helpers stay in the group and help raising their siblings instead of becoming reproductively active themselves (Digby et al., 2007). Most importantly, the help by non-mothers is effective, since the number of group members, in particular males, is related to infant growth and survival in the wild (Garber, 1997) and even in captivity (Rothe et al., 1993). Although groups usually contain mostly kin, unrelated individuals may join the group and their behavior is often indistinguishable from that of related helpers (Burkart et al., 2007; Clutton-Brock, 2002; Faulkes et al., 2009).

Helpers and fathers contribute to child rearing by carrying the infants and later sharing food with them. During the first 5–6 weeks of their lives, callitrichid infants are carried 100% of the time. In bigger groups, the infants may spend most of their daytime on allomothers and go back to the mother only for breastfeeding, even though mothers may still be the primary care giver during night time (Fite et al., 2003, 2005). Individual contributions to carrying by alloparents vary considerably over time, perhaps representing some form of division of labor (Finkenwirth and Burkart, in preparation). Infants are always transferred directly from one caregiver to the next, rather than being deposited on a branch for the next carrier to pick it up, presumably in order to avoid that infants fall down and/or become subject to predation (a newborn callitrichid typically weighs only between 20 and 30 g).

Food sharing in callitrichids often follows the regular nonhuman primate pattern, with infants begging for food and adults tolerating them taking some of it. However, food-sharing patterns contrast from independently breeding primates in at least two ways. First, the frequency of food sharing is much higher. The first solid food that infants ingest is food shared by a caregiver, and weekly experimental food sharing trials during the main provisioning period (10–16 weeks of age) show that adults share 53% of all items they obtain with the offspring (breeders: 61%, helpers: 46%). Sharing is more pronounced with food items that are difficult (breeders: 74%, helpers: 53%) rather than easy to obtain (breeders: 54%, helpers: 42%, Martins and Burkart, 2013). Consistent with this result, immatures show a strong preference to accept novel food only if they acquire it via food sharing from a caregiver (Voelkl et al., 2006).

A second contrast is that in callitrichid monkeys, but not in other nonhuman primates, food sharing often also takes the qualitatively different form of proactive offering (Brown et al., 2004; Jaeggi et al., 2010a,b). In instances of proactive offering, the infant is not begging for food and may even be unaware that an adult found it. Rather, the adult takes the initiative for the food transfer. The adult, instead of eating the food himself, holds it in its outstretched hand, emits a specific food call and waits for the immature to come and take it.

Callitrichids not only cooperate in carrying infants and sharing food, but also share vigilance duties (Goldizen, 1987; Koenig, 1994), show more cooperative territory and resource defense than independently breeding primates (Willems et al., 2013) and engage in cooperative food harvesting (Garber, 1997). In sum, an adult member of a callitrichid group routinely carries out various cooperative tasks, and also needs to coordinate these activities with the other group members, which arguably requires several psychological and motivational predispositions to make such an interdependent system work smoothly.

This intense cooperation is at times punctuated by intense competition, in particular regarding breeding positions. Since females are utterly dependent on help to successfully raise their offspring, competition for breeding positions and thus allomaternal care is particularly strong in the female sex. Eventually, subordinate females try to breed themselves, which can lead to aggressive competition that may also include infanticide of infants born to subordinate females. Nonetheless, these same females act as regular helpers and contribute to cooperative tasks in the group at all other times (Digby et al., 2007).

2.2. Psychological and motivational correlates of cooperative breeding

What are the psychological and motivational prerequisites for carrying out and coordinating the cooperative activities observed in callitrichid monkeys? We believe there are at least three major prerequisites: social tolerance, proactive prosociality, and social monitoring.

First, the close proximity of individuals in many of these cooperative activities requires high levels of *social tolerance*. For instance, the necessary spatial and temporal behavioral coordination during infant transfer from one caregiver to the next leaves no room for tension between the caregivers because unsuccessful transfers have potentially lethal consequences for the infants. Since most of the time all animals in the group contribute to infant carrying, high social tolerance is necessary between all dyads in the group. Likewise, high levels of social tolerance are a precondition for food sharing interactions and cooperative food harvesting.

The existence of particularly high levels of social tolerance in cooperatively breeding primates has been suggested previously (e.g. Garber, 1997; Schaffner and Caine, 2000; Snowdon, 2001). The first direct quantitative comparative assessment, based on 24 groups of 15 different primate species with varying degrees of allomaternal care, shows that social tolerance is indeed associated with cooperative breeding (Burkart et al., 2014, Fig. 1a). In this comparative study, social tolerance was assessed in a simple access-to-food paradigm where captive social groups were sequentially provided

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