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Inequity aversion strategies between marmosets are influenced by partner familiarity and sex but not by oxytocin

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Cooperation among individuals depends, in large part, on a sense of fairness. Many cooperating nonhuman primates show inequity aversion (i.e. negative responses to unequal outcomes), and these responses towards inequity probably evolved as a means to preserve the advantages of cooperative relationships. However, marmosets (*Callithrix* spp.) tend to show little or no inequity aversion, despite the high occurrence of prosociality and cooperative breeding in callitrichid monkeys. Oxytocin (OXT) has been implicated in a wide variety of social processes, but little is known about whether OXT modulates inequity aversion towards others. We used a tray-pulling task to evaluate whether marmosets would donate superior rewards to their long-term pair mate or an opposite-sex stranger following OXT, OXT antagonist and saline treatments. We found that marmosets show inequity aversion, and that this inequity aversion is socially and sex specific. Male marmosets showed inequity aversion towards their pair mates but not towards strangers, and female marmosets did not show inequity aversion. OXT treatments did not significantly influence inequity aversion in marmosets. While OXT may modulate prosocial preferences, the motivations underlying cooperative relationships, such as inequity aversion, are multifaceted. More research is needed to evaluate the evolutionary origins, biological processes and social contexts that influence complex phenotypes like inequity aversion. Inequity aversion can differ within species in important and distinct ways, including between individuals who do and do not share a cooperative relationship. Overall, these findings support the view that inequity aversion is an important behavioural strategy for the maintenance of cooperative relationships.

A sense of fairness between individuals is an important feature for the preservation of long-lasting cooperative relationships in primates. Maintaining fairness in cooperative relationships requires the ability to recognize inequitable outcomes and the motivation to refuse them. There has been a long and rich interest in whether and to what extent primates understand differential reward outcomes. Nearly a century ago, it was first reported that young macaque monkeys trained to perform a response to receive a banana reward expressed 'disappointment', 'frustration' and refusal when the banana reward was substituted with a less preferred lettuce reward (Tinklepaugh, 1928). However, it was not until recently that these individual reward contrast effects were studied in a social context involving differential reward outcomes between partners (Brosnan & de Waal, 2003). Specifically, Brosnan and de Waal found that capuchin monkeys actively refused less preferred cucumber rewards after witnessing partners receive more preferred grape rewards. The decrease in the monkeys' response frequency and their refusal to accept less preferred rewards relative what they had observed others receiving is generally defined as inequity aversion (Fehr & Schmidt, 1999).

Inequity aversion is an important contextual feature that shapes cooperative behaviour in nonhuman primates. Nonhuman primates show an extraordinary range of social decision-making strategies across a wide collection of tasks aimed at measuring inequity aversion, including tray pulling, token exchanges, economic games or naturalistic behaviours (Brosnan & de Waal, 2014). Many of these social decision-making strategies reflect differences in cognitive and motivational capabilities, diversity in species-specific behaviours and disparities in nuanced methodologies

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across experiments. The expression of cooperative behaviour, and, specifically, the aversion to inequity is intimately linked to the evolution of an organism's social system. Inequity aversion likely evolved alongside cooperation as a means to optimize and maintain the best outcomes associated with cooperative relationships (Brosnan, 2011). Moreover, the presence of inequity aversion across many nonhuman primates, and the early emergence of inequity aversion and parochialism in human children (Fehr, Bernhard, & Rockenbach, 2008), suggest a shared evolutionary mechanism for facilitating cooperative behaviours, and there is converging evidence to support this view. Specifically, nonhuman primates that ordinarily cooperate in foraging or food-sharing situations (chimpanzees, capuchins, macaques) are often more sensitive to inequity (Brosnan, Schiff, & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Brosnan & de Waal, 2003; Fletcher, 2008; Hopper, Lambeth, Bernacky, & Brosnan, 2013; Massen, Van den Berg, Spruijt, & Sterck, 2012; Takimoto, Kuroshima, & Fujita, 2010) than nonhuman primates that do not regularly cooperate in foraging situations (squirrel monkeys and orangu-tans) (Bräuer, Call, & Tomasello, 2009; Talbot, Freeman, Williams, & Brosnan, 2011). However, not all studies show that chimpanzees and capuchins respond negatively to inequity (Bräuer et al., 2009; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009). Interestingly, callitrichids (marmosets and tamarins) and owl monkeys, species that exhibit biparental cooperation and form long-term pair bonds, are not as sensitive to inequity as one might expect given the prevalence of inequity aversion in species with cooperative relationships (Freeman et al., 2013; McAuliffe, Shelton, & Stone, 2014; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009). This lack of inequity aversion in callitrichids suggests there is either an inability to recognize and/or respond to resource inequities, or that maintaining biparental cooperation may confer a greater benefit to the family group (e.g. enhanced offspring survival) than losing a parental partner due to the avoidance of interactions that lead to minor inequities (Brosnan, 2011). Thus, investigating inequity aversion strategies in callitrichids serves as a critical test of whether inequity aversion is a requisite for the formation and maintenance of cooperative relationships.

The neurohypophysial hormone, oxytocin (OXT), has been implicated as a key neuroendocrine substrate of many social processes (Heinrichs, von Dawans, & Domes, 2009; Insel, 2010; Johnson & Young, 2015). Of particular interest, OXT is critical for mother–infant bonding and parental behaviour (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010; Feldman, Weller, Zagoory-Sharon, & Levine, 2007), it modulates pair bonding between opposite-sex partners (Cavanaugh, Mustoe, Taylor, & French, 2014; Smith, Agmo, Birnie, & French, 2010; Young & Wang, 2004) and influences prosocial decision making in primates (Brosnan, Talbot, et al., 2015; Chang, Barter, Ebitz, Watson, & Platt, 2012; Mustoe, Cavanaugh, Harnisch, Thompson, & French, 2015), and it has been emphasized as an important regulator of fairness, trust, cooperation and competition in humans (De Dreu, 2012; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Radke & de Bruijn, 2012; Zak, Stanton, & Ahmadi, 2007). While there is a general trend that OXT has mostly enhancing effects on sociality, there is increasing recognition and appreciation that the valence and magnitude of OXT effects are, in large part, context specific (van Anders, Goodson, & Kingsbury, 2013; Bartz, Zaki, Bolger, & Ochsner, 2011). It is also evident that these neuropeptide effects are highly diverse across species and social situations (Goodson, 2013). This multifaceted influence of OXT on social behaviour is especially apparent among social interactions that include social anxiety or social reward (Bethlehem, Baron-Cohen, van Honk, Auyeung, & Bos, 2014; Brosnan, Talbot, et al., 2015; Mustoe et al., 2015; Neumann & Slattery, 2015).

Marmoset monkeys (*Callithrix* spp.) offer important opportunities to explore the social and neuroendocrine factors that may regulate inequity aversion for a variety of reasons. First, marmosets are cooperative breeders, and in contrast to many other primates, they are highly prosocial and form long-term male–female cooperative relationships (Agmo, Smith, Birnie, & French, 2012; Burkart, Fehr, Efferson, & van Schaik, 2007; Evans, 1983; Schaffner, Shepherd, Santos, & French, 1995). Second, New World monkeys, including callitrichids, possess notably remarkable interspecific OXT and OXT receptor (OXTR) diversity relative to other mammals (Babb, Fernandez-Duque, & Schurr, 2015; Lee et al., 2011; Ren et al., 2015; Vargas-Pinilla et al., 2015; Wallis, 2012), and these varied OXT/OXTR systems potentially coevolved to modulate species-specific social behaviour such as social monogamy and paternal care (Ren et al., 2015; Vargas-Pinilla et al., 2015). Specifically, marmosets possess a modified OXT ligand with a leucine to proline (Pro^8-OXT) substitution at the eighth amino acid position, resulting in a significant change in the structure of the OXT ligand. These differences in OXT ligands allow for exploration between potential in vivo ligand specificity of OXT, which may contribute to a broader evolutionary understanding of the effects of neuropeptides on behaviour. Parental and social behaviour in marmosets is highly amenable to OXT treatment. For instance, treatment with Pro^8-OXT, but not with the consensus mammalian ligand (Leu^8-OXT), reduces both sociosexual behaviour and prosocial food sharing towards opposite-sex strangers (Cavanaugh et al., 2014; Mustoe et al., 2015). In addition, OXT enhances males' responsiveness to infant stimuli (Saito & Nakamura, 2011; Taylor & French, 2015) and mates' social attractiveness in long-term pairs (Cavanaugh, Huffman, Harnisch, & French, 2015), and basal OXT levels are synchronized with levels of affiliative behaviour (Finkenwirth, van Schaik, Ziegler, & Burkart, 2015). These findings highlight how OXT shapes the maintenance of cooperative social relationships (male–female pair bonds; parent–offspring bonds) in marmosets by reducing interest in opposite-sex strangers and enhancing interest towards infant stimuli, two characteristics that may preserve biparental cooperative relationships. However, the degree to which OXT regulates more complex sociocognitive decision-making processes, such as inequity aversion, has yet to be examined.

Research on inequity aversion has long favoured elucidating specific motivational contexts with a particular bias for studying individuals with established long-term cooperative relationships, including those between related or highly familiar social partners or between mates with or without offspring (Brosnan & de Waal, 2014). However, it is also important to consider the role of inequity aversion between strangers with no established social history as these emerging relationships may be regulated by fundamentally different social motivations. In this study, we were interested in evaluating the role of OXT in inequity aversion between both long-term mates and opposite-sex strangers. To achieve these objectives, we had three primary aims. First, we sought to determine whether marmosets would display inequity aversion or inequity tolerance in a food-sharing task using three separate inequity comparisons. Second, we examined whether inequity aversion and inequity tolerance vary depending on whether marmosets share a cooperative relationship (long-term pair mate) or no relationship (opposite-sex stranger). If inequity aversion is important for maintaining long-term cooperative social relationships in primates, then marmosets should display inequity aversion towards their long-term pair mate and display inequity tolerance towards opposite-sex strangers. Finally, we explored whether inequity aversion would be altered by OXT treatments. If inequity aversion is an important social feature of cooperative behaviour among marmosets, including pair bond maintenance and biparental cooperation, then we would expect OXT to enhance inequity aversion