



Original Article

Exploring the evolutionary foundations of empathy: consolation in monkeys

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ABSTRACT

Unsolicited third-party affiliation occurs when victims of aggression receive a spontaneous affiliative contact from a bystander. Consolation is a specific type of unsolicited third-party affiliation showing two key components: 1) it alleviates distress in the victims and 2) is preferentially directed towards friends. Consolation was thought to be present only in humans, chimpanzees, and bonobos linked to their higher cognitive and empathic abilities. Previous investigations in monkeys found unsolicited third-party affiliation in only two species with no evidence of consolation. In the research presented here we set out to test a number of hypotheses concerning third-party affiliation in *Macaca fuscata* and *M. tonkeana*, two species that differ remarkably for social style. *M. fuscata* is despotic, while *M. tonkeana* is one of the most tolerant species of macaques. We found no evidence of unsolicited third-party affiliation in *M. fuscata*, but it was present in *M. tonkeana*. In this species we found that unsolicited third-party affiliation reduced anxiety (measured by scratching) in the victims and was directed towards friends and especially towards females who experienced higher levels of anxiety compared to males. Third-party affiliation also occurred more frequently in the absence of reconciliation. All the key features used to recognize consolation in humans and great apes are present in *M. tonkeana* making it difficult not to conclude that consolation exists in this species. Since consolation is most often considered to be driven by empathy, our results suggest that Tonkean macaques are capable of empathetically reacting to the victim's state of anxiety. Our results support the *Social Constraints Hypothesis* showing that the degree of tolerance is a key factor in the expression of consolation. Investigating behavioral patterns driven by even the most basic forms of empathy requires the choice of an appropriate species and *Macaca tonkeana* is a good model to investigate the full phylogenetic range, evolutionary depth, and origin of empathy in primates.

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1. Introduction

For social species, including humans, aggression can have dramatic consequences not only for the individuals involved but also for the whole group (Aureli & de Waal, 2000; Esteban, Mayoral, & Ray, 2012). Conflict can generate further conflicts and/or can affect affiliative interactions in the group (Barash & Lipton, 2011; de Waal, 2000; Ellemers, 2012; Palagi & Cordoni, 2009; Watts, Colmenares, & Arnold, 2000).

Reconciliation, defined as an affiliative interaction between former opponents in the first minutes after a fight, is an effective conflict resolution mechanism (de Waal & Roosmalen, 1979). Reconciliation reduces the probability of further attacks, limits anxiety in the victim,

and restores the benefits associated with a good relationship (Aureli, Cords, & Van Schaik, 2002).

After a conflict, victims can also receive a friendly, spontaneous contact from a bystander not involved in the aggression, a phenomenon labeled “unsolicited bystander affiliation” or “unsolicited third-party affiliation” (Fraser, Koski, Wittig, & Aureli, 2009; Romero, Castellanos, & de Waal, 2010). This first spontaneous post-conflict affiliative contact from a third-party to the victim was called consolation and was reported for great apes and humans (chimpanzees: Fraser & Aureli, 2008; Koski & Sterck, 2007; Kutsukake & Castles, 2004; Palagi, Cordoni, & Borgognini Tarli, 2006; Romero & de Waal, 2010; Wittig & Boesch, 2003, 2010; gorillas, Cordoni & Palagi, 2007; bonobos, Clay & de Waal, 2013a,b; Palagi & Norscia, 2013; Palagi, Paoli, & Tarli, 2004; humans, Eisenberg, 1992; Fujisawa, Kutsukake, & Hasegawa, 2006). Consolation reduces the victim's anxiety, is provided by friends and is apparently based on empathy. Some researchers skeptical of the empathic basis of consolation still prefer to use the more neutral term, “unsolicited bystander affiliation” (Call, Aureli, & de Waal, 2002).

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Early studies using the same protocol applied to great apes failed to find evidence for consolation in four macaque species, *Macaca fascicularis*, *M. fuscata*, *M. sylvanus*, and *M. nemestrina*, (de Waal & Aureli, 1996). These data were reinforced when other investigators failed to reveal even unsolicited bystander affiliation in catarrhine monkeys (Schino, Geminiani, Rosati, & Aureli, 2004; Watts et al., 2000). Up to now unsolicited bystander affiliation was found in only two monkey species, but it lacked important attributes of consolation (Call et al., 2002; Schino & Marini, 2012). Call et al. (2002) suggested that consolation was absent in stump-tailed macaques because post-conflict third-party affiliation only limited further aggression by the victim. Schino and Marini (2012) concluded that there was no consolation in mandrills, because bystander affiliation did not reduce the victims' anxiety and was not received primarily from kin/friends.

Third-party affiliation towards victims was also observed in rooks (Seed, Clayton, & Emery, 2007), ravens (Fraser & Bugnyar, 2010), dogs (Cools, Van Hout, & Nelissen, 2008), and wolves (Palagi & Cordoni, 2009). Although these authors hypothesized that consolation might be present, it was never demonstrated. Up to now, consolation defined as third party affiliation biased towards friends and reducing anxiety was only demonstrated in chimpanzees, bonobos, and humans (Clay & de Waal, 2013a,b; Fraser, Stahl, & Aureli, 2008; Palagi & Norscia, 2013; Romero et al., 2010; Zahn-Waxler & Radke-Yarrow, 1990).

Consolation is considered an empathy-based phenomenon, but it does not necessarily require the most complex form of empathy (i.e. cognitive perspective taking, *sensu* de Waal, 2008). Empathy is a multilayered phenomenon, whose shared building blocks may provide a framework for more complex emotional and cognitive processes (Hecht, Patterson, & Barbey, 2012; Panksepp & Panksepp, 2013). Different levels of empathy are recognized according to neurobiological, psychological, and behavioral complexity (Hecht et al., 2012; Iacoboni, 2009). The ability to react to the feelings of others appears early in life (Clay & de Waal, 2013b; Hatfield, Cacioppo, & Rapson, 1994) and its neurobiological substrates were documented in human and non-human primates (Decety & Jackson, 2006; Rizzolatti, Sinigaglia, & Anderson, 2007). A subconscious, reflexive appreciation of others' emotional states does not necessarily imply the attribution of mental states (intentions). However, sensitivity to others' emotions is a building block of even the most complex forms of Theory of Mind (Seyfarth & Cheney, 2013). It may have evolved because natural selection has favored individuals that are motivated to "empathize" with others and take care of their social interactions (De Marco, Cozzolino, Dessi-Fulgheri, & Thierry, 2011; Seyfarth & Cheney, 2013). Both neurobiological and ethological findings (Mancini, Ferrari, & Palagi, 2013; Palagi, Leone, Mancini, & Ferrari, 2009; Paukner, Suomi, Visalberghi, & Ferrari, 2009) amply confirm that many non-human animals are able to emotionally connect to each other through mimicry and behavioral contagion, which represent the most basal building blocks of empathy (see the Russian Doll Model by Preston & de Waal, 2002). Only cross-species investigations, such as the research we present here, can shed light on how higher cognitive forms of empathy have evolved in humans.

We investigated this phenomenon by focusing on unsolicited third-party affiliation in *Macaca tonkeana* and *Macaca fuscata*. The 20 macaque species are organized in multi-male, multi-female social groups that vary on a gradient ranging from more intolerant (Grade 1) to more tolerant (Grade 4) social systems (Matsumura, 1999; Thierry, 2000). According to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996) these differences in social styles (de Waal & Luttrell, 1989), already present in infancy (Thierry, 1985a), influence a wide range of behaviors including aggression, affiliation, dominance, and nepotism (Aureli, Das, & Veenema, 1997; Balasubramaniam et al., 2012; Petit, Abegg, & Thierry, 1997; Thierry, 1985b, 1990). Despotic species like Japanese macaques (*Macaca fuscata*) have a strong, kin-centric power asymmetry between dominants and subordinates,

marked submission behaviors, unidirectional conflicts, and low levels of social tolerance (Aureli et al., 1997; Kutsukake & Castles, 2001). In contrast, more tolerant species, such as Tonkean macaques (*Macaca tonkeana*), have relationships, which are minimally influenced by rank and kinship. No formal indicators of subordination are present and the proportion of friendly interactions, measured by grooming rates, among non-kin is relatively high (Butovskaya, 2004; Butovskaya & Kozintsev, 1996). It was well known that conflict resolution mechanisms in Tonkean macaques differ from those of Japanese macaques (Schino et al., 2004). Reconciliation, quadratic affiliation, and peaceful interventions are more common in Tonkean macaques (Ciani, Dall'Olio, Stanyon, & Palagi, 2012; De Marco, Cozzolino, Dessi-Fulgheri, & Thierry, 2010; Demaria & Thierry, 2001; Petit & Thierry, 1994; Thierry, 1985a,b). For these reasons we thought that *M. tonkeana* might be a good model species to study the basis of unsolicited bystander affiliation in a monkey. According to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996), we expected to find unsolicited bystander affiliation in *Macaca tonkeana* and to confirm its absence in *Macaca fuscata* (Prediction 1).

We also wanted to test a number of hypotheses concerning third party affiliation. According to the *Substitute for Reconciliation Hypothesis*, third-party affiliation restores relationships between former opponents (Fraser & Aureli, 2008; Palagi et al., 2004; Schino & Marini, 2012). If, in *Macaca tonkeana*, the *Substitute for Reconciliation Hypothesis* (Fraser & Aureli, 2008; Palagi & Cordoni, 2009; Palagi et al., 2004; Romero & de Waal, 2010; Wittig & Boesch, 2003, 2010) explains the distribution of unsolicited bystander affiliation towards the victim, it is expected that this post-conflict mechanism would function as a substitute of reconciliation when post-conflict affiliation between the victim and the aggressor fails to occur (i.e. higher levels of unsolicited bystander affiliation in absence of reconciliation; Prediction 2).

The *Self-Protection Hypothesis* (direct benefits for the third-party) predicts that post-conflict third party affiliation reduces the redirection of aggression (Call et al., 2002; Koski & Sterck, 2009; Schino & Marini, 2012; Wittig & Boesch, 2010). In this view, redirection should be frequent and affiliation should be received primarily from individuals that are frequently the target of redirection. Apparently, Tonkean macaques show low levels of redirection (Thierry, 1985b) suggesting that the *Self-Protection Hypothesis* would not explain the potential presence of spontaneous bystander affiliation in this species. In order to test this conclusion we measured the frequency of redirected aggression. If third-party affiliation functions to protect the bystander from redirection, we should expect high levels of redirection (Prediction 3). We also would expect that bystanders affiliating with victims are individuals ranking below the victim and/or those individuals receiving the highest levels of redirection (Prediction 4).

The effect of third-party affiliation on reducing renewed aggression has been tested in several studies both to verify the *Tension Reduction* (Palagi et al., 2006) and *Self-Protection Hypotheses* (Schino & Marini, 2012; Wittig & Boesch, 2010). A benefit of third-party affiliation might be to lower the probability that the victim is subjected to further aggression (*Victim Protection Hypothesis*) (Palagi & Norscia, 2013). We tested the *Victim Protection Hypothesis* by checking if third-party affiliation protected the victim against further conflicts. If third-party affiliation protects the victim (*Victim Protection Hypothesis*), we expect it to significantly reduce the probability of renewed attacks on him/her (Prediction 5).

The presence of an agonistic event within a group can also increase anxiety and social tension in subjects not directly involved in the conflict (De Marco et al., 2010; de Waal, 2000). We tested the *Tension Reduction Hypothesis* by verifying whether it reduced the diffusion of aggression. If third-party affiliation reduces tension at the group level (*Tension Reduction Hypothesis*) and limits the risk of bystanders' involvement in subsequent conflicts, we expect it to significantly reduce the probability of aggression among all group members (Prediction 6), with an indirect benefit for the bystander. We

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