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Witnessing reconciliation reduces arousal of bystanders in a baboon group (*Papio hamadryas hamadryas*)

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Reconciliation is the occurrence of friendly behaviour between opponents shortly after an aggressive conflict. In primate groups, reconciliation reduces aggression and postconflict arousal. Aggression within a group can also increase arousal of bystanders (e.g. increase bystanders' rates of self-directed behaviour). Since reconciliation reduces aggression between opponents, we tested whether it also reduces self-directed behaviour in bystanders. Following aggression in a captive group of hamadryas baboons, one observer conducted a focal sample on one of the combatants to document reconciliation and a second observer simultaneously conducted a focal sample on a randomly selected bystander. Matched control observations were then collected on the same individuals in a nonaggressive context to obtain baseline levels of behaviour. The self-directed behaviour of bystanders was elevated after witnessing a fight compared to baseline levels. If combatants reconciled aggression, bystander rates of self-directed behaviour significantly decreased. If combatants did not reconcile aggression, bystander rates of self-directed behaviour remained at elevated levels, significantly higher than after reconciliation. If combatants affiliated with partners other than their original opponent, bystander rates of self-directed behaviour did not decrease. The rate of bystander self-directed behaviour after a combatant affiliated with its opponent was significantly lower than the rate after a combatant affiliated with other animals. Witnessing aggression increased arousal in bystanders, and reconciliation between the combatants was accompanied by reduced bystander arousal. The reduction was specific to contexts in which former opponents interacted. We suggest that bystanders recognized the functional significance of this conflict-resolution mechanism when it occurred in their group.

Sociality has evolved because individuals living in groups derive benefits such as increased foraging efficiency, cooperative protection against predators and increased defence against competitors (van Schaik & van Hooff 1983). Social living also has costs, however, as intragroup competition for resources inevitably produces aggressive conflicts (van Schaik 1989). To reduce the costs of such conflicts and maintain group cohesion, group-living animals have developed mechanisms to manage or resolve conflicts (Cords & Killen 1998). One such mechanism is reconciliation, in which animals involved in an aggressive conflict exchange affiliative contacts shortly after the fight (de Waal & van Roosmalen 1979). The mechanism is fairly widespread as reconciliation has been demonstrated in almost every primate species investigated (Aureli et al. 2002) as well as several group-living nonprimate species (domestic dogs, *Canis lupus familiaris*: Cools et al. 2008; wolves, *Canis lupus*: Cordoni & Palagi 2008; hyaenas, *Crocuta crocuta*: Wahaj et al. 2001; horses, *Equus caballus*: Cozzi et al. 2010; domestic goats, *Capra aegagrus*: Schino 1998; bottlenose dolphins, *Tursiops truncates*: Weaver 2003; ravens, *Corvus corax*: Fraser & Bugnyar 2011).

Research on the function of postconflict reunions between combatants has shown that the term 'reconciliation' is appropriate in that reconciliation restores disrupted relationships, decreases the likelihood of further aggression and reduces emotional arousal in the combatants (Aureli et al. 2002). Weaver & de Waal (2003) have emphasized the arousal reduction function of reconciliation and have proposed that reconciliation develops in young primates as an arousal control mechanism regulating emotional homeostasis after a conflict (see also Aureli & Smucny 2000). Rates of self-directed behaviour, such as scratching and self-touching, are reliable indices of arousal (Maestripieri et al. 1992) and are typically used to assess the arousal reducing function of reconciliation. For example, a combatant's rates of self-directed behaviour are

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elevated over baseline immediately after a fight (Schino et al. 1988; Aureli et al. 1989) and return to baseline levels following reconciliation (Castles & Whiten 1998). The return to baseline is specific to affiliative contact with the former opponent as contacts with third parties not involved in the conflict do not typically reduce rates of self-directed behaviour to baseline levels (Das et al. 1998; Romero et al. 2009).

In complex societies, triadic interactions sometimes occur in which other group members become involved in dyadic aggressive encounters and influence the outcome. Third parties are likely to join a fight and either aggressively aid the aggressor or defend the victim (Cheney & Seyfarth 1986, 1989; Aureli & van Schaik 1991; Aureli et al. 1992). Uninvolved third parties are also likely to affiliate with the aggressor or the victim in the aftermath of a fight (reviewed in: Das 2000; Watts et al. 2000). Furthermore, the third parties that affiliate are often the kin or other close associates of one of the combatants (Judge 1991; Das et al. 1997; Call et al. 2002; Fraser et al. 2008; Wittig & Boesch 2010). Affiliative interactions of third parties with former combatants have been interpreted as 'appeasement' of aggressors, 'consolation' to the victim, or 'substitute reconciliation' for one of the opponents (de Waal & van Roosmalen 1979; Palagi et al. 2006; Wittig et al. 2007; Fraser & Aureli 2008; Fraser et al. 2008; Romero & de Waal 2010, 2011; Wittig & Boesch 2010). Caution should be used when applying such terms, however, since they imply unknown underlying motivations of the animals and they involve largely untested functions. Recent work has tested the appropriateness of such terms and the potential causes and consequences of triadic postconflict interactions (Koski & Sterck 2007, 2009; Fraser et al. 2009; Romero et al. 2009; Romero & de Waal 2010; Wittig & Boesch 2010). For our purposes, we have operationally defined any postconflict affiliative contact between a third party and an aggressor or victim as 'third-party affiliation' without suggesting any underlying function.

On another level, dyadic aggression also influences the aggressive and affiliative behaviour among uninvolved bystanders (Cheney & Seyfarth 1989; Judge & Mullen 2005). For example, in captive hamadryas baboons, *Papio hamadryas hamadryas*, a bystander was more likely to affiliate with another bystander immediately after witnessing a fight (Judge & Mullen 2005). Furthermore, the self-directed responses of the bystanders increased after witnessing a fight and deceased after affiliating with another bystander. The bystanders also tended to seek out their preferred social partners for affiliation. The interaction appears to be a mechanism for decreasing the negative arousal induced by witnessing a fight within one's group. Such interactions have been termed 'quadratic' interactions because they involve four individuals, two of which were not involved in the original conflict (Judge & Mullen 2005). The results have been replicated in Tonkean macaques, *Macaca tonkeana*, in that uninvolved bystanders were more likely to affiliate with preferred partners following aggression and scratching tended to decrease following the affiliative episode (De Marco et al. 2010). In contrast, another replication using geladas, *Theropithecus gelada*, found no increase in affiliation or self-directed behaviour in bystanders following aggression (Leone et al. 2010). The authors proposed that the difference may have been related to the likelihood that a dyadic aggressive interaction might escalate to include a bystander. They suggested that the likelihood of further escalation may have been low in this tolerant species and witnessing a fight may not have increased bystander arousal, as measured by self-directed behaviour.

We hypothesized that if bystander arousal is influenced by expectancies for escalated or continued aggression within a group, bystander arousal should be affected by the presence or absence of reconciliation between two combatants. As mentioned, reconciliation reduces the likelihood of further aggression (Aureli et al. 2002). If a bystander recognizes the functional significance of reconciliation between two combatants, the interaction may signal a decreased likelihood of aggression and reduce a bystander's arousal. Therefore, we predicted that bystander rates of self-directed behaviour would increase after witnessing a fight and decrease if the combatants reconciled. If the combatants did not reconcile, we predicted that a bystander's self-directed behaviour would remain elevated. We also examined whether affiliation between a combatant and an uninvolved third party would influence the self-directed behaviour of a bystander. Although largely untested, some have suggested that third-party affiliative contacts with a combatant following a conflict may serve as a 'substitute' for reconciliation (Aureli & van Schaik 1991; Judge 1991; Wittig et al. 2007; Fraser & Aureli 2008; Wittig & Boesch 2010; Romero & de Waal 2011). If so, affiliative contacts between a combatant and any third party might reduce the likelihood of further aggression and be associated with reduced self-directed behaviour in bystanders. Conversely, a reduction in bystander self-directed behaviour might be specific to witnessing an act of reconciliation between former combatants, and affiliative interactions between a combatant and individuals other than the former opponent (i.e. third-party affiliation) would not lead to decreases in the self-directed behaviour of bystanders.

We used hamadryas baboons to test these predictions because virtually every pattern of postconflict interaction typically associated with reconciliation and third parties has been demonstrated in this species. Dyadic reconciliation has been found in hamadryas baboons, and combatants also interact with third parties significantly more following conflicts than during baseline periods (DeBolt 2003; Romero et al. 2009). Triadic postconflict interactions were bidirectional with both aggressors and victims initiating and receiving contacts from third parties. As mentioned above, the displacement activities of bystanders were elevated in the postconflict period in a hamadryas baboon group (Judge & Mullen 2005), indicating that bystanders were anxious after witnessing a conflict and are, therefore, poised to be influenced by a reconciliation between the combatants.

METHODS

Subjects and Housing

We conducted observations on a captive group of hamadryas baboons housed at Bucknell University in Lewisburg, Pennsylvania. The group contained 18 animals at the beginning of the study: one adult male, two subadult males, seven adult females, three juvenile males, four juvenile females and one male infant. Due to births, deaths and transfers to other facilities, the group contained 15 animals at the end of the study: one adult male, one subadult male, seven adult females, two juvenile males, two juvenile females and two male infants. All animals except the adult male were born into the group, which was originally established in 1968 from wild-caught animals. The adult male was introduced in 1996. The typical social structure of hamadryas baboons consists of several levels with the most basic level being a one-male unit consisting of an adult male, several females he recruits to form a harem, and their offspring (Abegglen 1984). Several one-male units, often with related males, are combined to form clans. Bands consist of several clans and bands may combine to form troops that often congregate at sleeping sites (Kummer 1968; Schreier & Swedell 2009). Within this four-tiered social structure, the group observed in this study would be considered a single one-male unit. We observed all individuals in the group as subjects except the infants because infants were rarely involved in conflicts. Furthermore, infants were not likely to have experienced the social cognitive development necessary to understand the social processes under investigation.