



Individual differences in chimpanzee reconciliation relate to social switching behaviour



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In recent years, the presence of stable individual variation in animal behaviour has been corroborated by studies across a wide variety of taxa and research disciplines. Reconciliation, or postconflict affiliation between former opponents, is a behavioural domain in which individual differences have not been systematically studied. Using a long-term data set comprising over 2000 conflict and postconflict observations in two groups of outdoor-housed chimpanzees, *Pan troglodytes*, we provide evidence for stable individual variation in reconciliation and test several hypotheses on how this postconflict mechanism relates to social switching behaviour. Results of generalized multilevel models revealed that individual differences remained a substantial source of variation in reconciliation after controlling for a number of situational variables (e.g. the nature of the relationship between opponents) shown by previous research to influence its occurrence. We further demonstrated a positive association between an individual's conciliatory tendency and three separate indices of social switching behaviour, proposing that individual differences in reconciliation may reflect a more fundamental motivation to switch between different social states. In addition to a discussion of potential motivational underpinnings, we provide an impetus for future work to consider how reconciliation relates to the broader constructs and themes identified within animal personality research. To the extent that individual differences in other aspects of conflict and postconflict repertoires exhibit temporal and cross-situational consistency, they too should inform our understanding of animal personalities. Delineating how these and other dimensions of sociality are in part driven by stable individual variation not only has implications for how social interactions themselves unfold, but ultimately for the fitness of the individuals therein.

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Stable individual differences in animal behaviour, often termed 'animal personalities', are the focus of a large and growing body of recent research (Bell, Hankison, & Laskowski, 2009; Dingemanse & Réale, 2005; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Such differences are manifest in evolutionarily meaningful patterns such as activity, mating, feeding, predation and sociality, ultimately translating into important fitness consequences for the individual (Sih, Bell, Johnson, & Ziemba, 2004). Conflict and postconflict repertoires are a social domain in which individual differences remain relatively unexplored. Reconciliation, first defined by de Waal and van Roosmalen (1979) as interopponent postconflict affiliation, represents an evolved strategy to preserve the benefits (and minimize the costs) of conflict-inherent group life. Initially

documented in chimpanzees, reconciliation has since been reported in over 30 primate species (reviewed in Aureli, Cords, & van Schaik, 2002) and an increasing number of nonprimates (reviewed in Schino, 2000), most recently in canids (Cools, Van Hout, & Nelissen, 2008; Cordoni & Palagi, 2008) and corvids (Fraser & Bugnyar, 2011). Two central assumptions of reconciliation are that it involves a switch between opposing motivational states (i.e. from hostility and fear to a positive inclination) and that this motivational shift serves to repair social relationships (de Waal, 2000). Accordingly, the valuable relationships hypothesis (VRH; de Waal & Aureli, 1997) predicts that reconciliation will be more frequent following conflicts between opponents who derive higher fitness benefits from their relationship (Kappeler & van Schaik, 1992), presuming conflicts actually disrupt such relationships (Aureli et al., 2002). The VRH been substantiated by both observational (reviewed in Watts, 2006) and experimental research (Cords & Thurnheer, 1993) across many nonhuman primate species, recently gaining further traction in the human literature (e.g.

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McCullough, Luna, Berry, Tabak, & Bono, 2010). But while its proponents have correctly pointed out that value in a given relationship is not always symmetric (i.e. equivalent for both partners; e.g. Cords & Aureli, 2000), the premise has not yet led to a systematic investigation of whether individuals are differently motivated to resolve conflict.

Recent work by Seyfarth, Silk, and Cheney (2012) demonstrates that other aspects of primate sociality are influenced by stable individual differences, in turn impacting an animal's fitness. In a principal component analysis of female baboon behaviour, researchers identified several personality styles to be associated with multiple measures of reproductive success. These individual dimensions influenced the strength and stability of social bonds (critical to fitness in this species: Silk et al., 2010), accounting for variance beyond that explained by kinship and dominance rank. Similarly, by studying how other social processes (for instance, reconciliation) are driven in part by stable individual variation, we stand to gain a more complete understanding of the adaptive consequences of behaviour. In addition to social personality traits (see also Koski, 2011), primate personality research has adopted diverse psychological approaches ranging from bold–shy continua (Wilson, Clark, Coleman, & Dearstyne, 1994) to five-factor models (reviewed in Freeman & Gosling, 2010) to the use of more recent motivational frameworks such as promotion and prevention orientations (Franks et al., 2013). The primary goal of the present study was to identify whether there are stable individual differences in reconciliation, controlling for other social variables known to influence its occurrence. If stable individual variation in reconciliation is indeed present, subsequent research might then consider including conciliatory tendency as a component of broader animal personality. That such variation has not been the subject of past research may be because reconciliation is often viewed as an interindividual, as opposed to intraindividual, phenomenon.

While social psychology has a longer tradition of recognizing that individual-level variables affect interrelational processes (Leary & Hoyle, 2009), even here relatively little specific consideration has been given to how individual differences shape reconciliation. The human literature typically emphasizes forgiveness, most commonly defined as the set of postconflict motivational changes whereby an individual becomes decreasingly motivated by negative inclinations and increasingly motivated by positive conciliation (McCullough, Worthington, & Rachal, 1997). Given how central an assumption this motivational shift between states is for reconciliation (de Waal, 2000), it could be that a more basic and general motivation for change underlies this behaviour. In particular, regulatory mode theory (RMT; Higgins, Kruglanski, & Pierro, 2003; Kruglanski et al., 2000) describes individual variation in locomotion motivation, a tendency for movement (and fast initiation of change) from state to state. As such, the secondary goal of the present study was to test whether RMT can help explain how individual variation in reconciliation may relate to more fundamental individual differences in motivation, namely the motivation to switch between different social states. It bears repeating that we refer to locomotion not as the biomechanics of animal movement, but as a motivational style, heretofore demonstrated in humans across a wide range of research domains (Higgins, 2012). Preliminary evidence reveals that people with strong locomotion motivation have higher and faster conciliatory tendencies following interpersonal conflicts (Webb, 2011). Indeed, recent work has extended psychological theories developed in relation to human personality to stable individual variation in animal behaviour (e.g. Uher, Asendorpf, & Call, 2008). Franks and colleagues (Franks, Higgins, & Champagne, 2012; Franks et al., 2013) have recently validated the use of similar motivational models (Higgins, 1997) in the study of personality differences across species.

We used a long-term data set of chimpanzee conflict and postconflict behaviour (1) to establish whether individual differences in reconciliation were present and, importantly, stable across time and situations (i.e. as a possible constituent of broader animal personality) and (2) to examine the relation between these differences and three behavioural measures of locomotion motivation (hereafter, social switching behaviour). Our first prediction was that stable individual variation in postconflict behaviour would be present when controlling for a number of other variables shown by previous studies to influence reconciliation (such as kinship, dominance and affiliation level). RMT provided a conceptual framework for our second prediction that individuals with higher conciliatory tendencies would exhibit more social switching behaviour. Overall, both the long-term nature and large sample size of the current data set make it a particularly good candidate for exploring these patterns and the stability of individual differences over time, especially given the high number of observations on spontaneously occurring behaviours. Although a number of past studies have reported different individual reconciliation rates (e.g. Preuschoft, Wang, Aureli, & de Waal, 2002), to our knowledge, ours is the first quantitative overview of that variation and an initial step in determining how it relates to a more basic tendency to switch between states.

METHODS

Subjects and Housing

Subjects were 31 adult and adolescent chimpanzees, socially housed at the Field Station of the Yerkes National Primate Research Center in Atlanta, Georgia, U.S.A. Two separate groups (FS1 and FS2) had access to indoor areas and large outdoor compounds (750 m² and 520 m², respectively) equipped with visual barriers, a variety of climbing structures and enrichment toys. Food and water were available ad libitum.

Group demographic compositions varied throughout the study period as a result of births, deaths and removals. At any given time, both groups comprised multiple adult males and at least twice as many adult females. Our analyses were limited to conflicts in which at least one of the opponents was 8+ years old, resulting in nine male subjects and 22 female subjects. Adults/adolescents had to be involved in more than 12 observed conflicts throughout the study period to be included as a subject. A more detailed description of the study subjects can be found in Romero and de Waal (2010, Table 2).

The Yerkes National Primate Research Center is accredited by the American Association for the Accreditation of Laboratory Animal Care. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University and were conducted in accordance with the ASAB/ABS's Guidelines for the treatment of animals in behavioural research and teaching.

Observations

The data analysed in the present study were collected between 1992 and 2000 for FS1 and between 1994 and 2000 for FS2. Throughout that time, controlled observation sessions were conducted approximately once per week in both study groups by the same trained research technician, Mike Seres (see de Waal, 1989 for details). During these 90 min sessions, all occurrences of agonistic interactions (defined by at least one of the following behaviours: tug, brusque rush, trample, bite, grunt-bark, shrill-bark, flight, crouch, shrink/flinch or bared-teeth scream; van Hooff, 1974; de Waal & van Hooff, 1981) were recorded, as well as affiliative interactions (kiss, embrace, groom, touch, finger/hand in mouth, play and mount).

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