

Responding to inequities: Gorillas try to maintain their competitive advantage during play fights

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ABSTRACT

Humans respond to unfair situations in various ways. Experimental research has revealed that also nonhuman species respond to unequal situations in form of inequity aversions, when they have the disadvantage. The current study focused on play fight behaviours in gorillas to explore for the first time if/how nonhuman species respond to inequities in natural social settings. Hitting causes a naturally occurring inequity among individuals and it was here specifically assessed how the hitting subjects and their partners engaged in the play chases that followed the hitting. The results of the present work showed that the hitting subjects significantly more often moved first to run away immediately after the hitting than their partners. These findings provide first evidence that nonhuman species respond to inequities by trying to maintain their competitive advantages. We conclude that nonhuman primates, like humans, may show different responses to inequities and that they may modify them depending on if they have the advantage or the disadvantage.

Keywords: inequity; fairness; competition; gorillas; play chase; social play

1. INTRODUCTION

Research on human responses to inequities has shown opportunistic attempts to keep competitive advantages (Arneson 1982; Fehr & Schmidt 1999) as well as violations of rational-choice decisions due to fairness-driven motives (Henrich *et al.* 2001; Fehr *et al.* 2008). While various nonhuman species seem to respond to unequal situations in form of inequity aversion (e.g., Brosnan & de Waal 2003; Brosnan *et al.* 2005; Range *et al.* 2009), these findings are based on experimental approaches, where special attention was paid to the subjects with the disadvantages. It remains thus to be empirically investigated how nonhuman species respond to inequities in natural social situations and how the individuals that have the advantages and disadvantages interact with each other. The current study explored for the first time if nonhuman species respond to naturally occurring inequities by focusing on play fight behaviours in gorillas.

According to competitive fitness models, some play fight behaviours such as hitting may provide one of the partners (the hitter) an advantage over the other (see Reynolds 1994). Play fights may thus represent an excellent social context to test responses to naturally occurring inequities. Similar to other types of play, they allow individuals to interact with their peers in rather unconstrained ways, although escalations into real fights may occasionally occur (Aldis 1975; Allen & Bekoff 2005). Real fights and fight-related behaviours, on the other hand, seem to be more strongly affected by the strengths and ranks of the competitors, e.g., a subordinate male is more likely to react aversively to someone of the same rank than to a dominant male.

Specifically, the present work assessed chases that followed inequities caused by hitting during play fights in gorillas. During chases of real fights, competitors

show two distinct behaviours where the fleeing individuals try to avoid getting caught or hurt by the chaser (see Aldis 1975). Play chases could, therefore, indicate two distinct responses to inequities in nonhuman species. In children, the game of tag also involves chasing followed by tagging/hitting, where the tagging child tries to run away from the other playmate (Aldis 1975; Reynolds 1994).

The approach of this study was to compare the chase-related behaviours of the hitting subjects (with the advantage) and their playmates (with the disadvantage). If the hitting subjects moved first to run away, this finding would provide first empirical evidence that nonhuman primates, like humans, may respond to inequities by trying to maintain their competitive advantage. On the other hand, if the hit subjects moved first to reciprocate the rough behaviour, such finding would provide empirical evidence of inequity aversion in nonhuman species in their natural social settings. Alternatively, with a finding inferring neither one of such behaviours among the playmates, there would be no evidence that hitting triggers responses to inequities in gorillas during play fights.

2. MATERIAL AND METHODS

a) Subjects, data collection, and coding

To examine the effect of hitting on chasing in gorilla play fights, the present work searched for chases in video clips on gorilla play that were previously recorded from six social groups by M. Davila Ross and L.-M. Gerhardt. Data on 21 subjects playing chase in 86 dyadic play bouts were obtained (for details on study subjects and groups, see Table S1). Dyadic play bouts began when two subjects showed a play action and ended when at least one of them showed no play action for 20 seconds or when a third individual interfered.

Play chases were defined by one subject fleeing and the other subject pursuing. Play chase bouts began with the first running movement of one of the subjects and ended once one subject stopped running. Their inter-chase intervals were <20 seconds. In addition to play chases, four mutually exclusive and exhaustive play actions were coded for each subject. Hitting represented all play fight behaviours of brief forceful physical contact, e.g., rough slapping and jumping on top of the playmate. Rough and tumble, in contrast, was defined by its longer-lasting forceful physical contact in play, e.g., wrestling and gnawing. The remaining play actions were soft grabbing (gently touching the playmate) and non-tactile play (e.g., contingently moving with the playmate).

For the play chases, the presence of the open-mouth faces (play faces) of each subject was coded starting five seconds prior to the chase and ending five seconds after the chase. Open-mouth faces may vary from baring no teeth to baring both tooth rows (Davila Ross *et al.* 2008). In addition, the subjects that moved first to run were identified.

One researcher coded all play actions and open-mouth faces. The inter-coder reliability was tested between this person and two other researchers. Agreements on coding were reached with Cohen's Kappa values of 80% for play actions and 92% for open-mouth faces (20 play bouts for each test). Three researchers identified which subjects moved first to run and only the bouts that were agreed upon by all (Kappa: 98%) were included to test for inequity responses. The video analysis was conducted using INTERACT 7.25 (Mangold, Arnstorf, Germany).

b) Data analysis

This study first scrutinized the overall chase-related behaviours of gorillas by analysing the subjects' play actions and use of open-mouth faces and then tested for

inequity responses by measuring the chase-related behaviours immediately following hitting of only one of the playmates (unequal hitting). Base rates of play actions were calculated based on one measurement per play bout. They were randomly selected ten seconds or more apart from the play chases. Statistical comparisons included Mann-Whitney U tests (corrected for ties) for the mean values of every subject and Fisher's exact tests for the number of subjects. All tests were two-tailed. For repeated analyses, Hommel-Hochberg corrections were applied.

3. RESULTS

a) Overall chase-related behaviours

Data on 21 subjects playing chase were obtained in 86 play bouts (86 play chase bouts). Of these subjects, 15 were chased by their playmates and 16 were chasing their playmates.

The play actions of the subjects that occurred immediately prior to the play chases were statistically compared to their base rates in Figure S1. No significant difference was found for hitting ($p > 0.050$; Mann-Whitney U). Play chases were predominantly preceded by non-tactile play (37% of the times). The chased and chasing subjects were also compared in their play actions immediately following play chases in Figure S2. The chased subjects significantly more often engaged in non-tactile play at the end of a chase than their playmates ($p = 0.012$), while the chasers then significantly more often hit the chased subjects ($p = 0.013$).

In addition, the chased and chasing subjects were compared in the use of their facial expressions in Table S2. The chased subjects produced significantly less open-mouth faces during the chase ($p = 0.007$).

The results also showed that, while running, the chased and chasing subjects

(N=8) reversed their chase roles during eight play chase bouts. Hitting occurred prior to each of these role reversals (see supplemental video).

b) Testing for inequity responses in chase-related behaviours

Data on unequal hitting prior to play chases were obtained in eleven play bouts. A total of eight subjects unequally hit their playmates and seven subjects were unequally hit.

Their chase-related behaviours were compared in Figures 1 and 2. Figure 1a shows that the hitting subjects made the first move to run in significantly more play chase bouts than their playmates ($p=0.026$, $Z=-2.31$; 87.5%+19.0% of play bouts; Mann-Whitney U). In addition, Figure 1b shows that the hitting subjects ran away in significantly more play chase bouts than their playmates ($p=0.004$, $Z=-2.90$; 85.4%+14.1%). Altogether, seven of eight hitting subjects moved first to run away and were then chased by the other playmates. For a representative scene of such ‘hit-and-run’ chase behaviours, see Figure 2.

When, instead of unequally hitting, the subjects were unequally soft grabbing (N=6), they did not move first to run but were still chased in all play bouts ($n=3$). Parenthetically, comparisons between the subjects that moved first to run and their playmates showed no significant differences in who ran away, i.e., was chased ($p=0.380$; $Z=-0.88$; 54.8%+45.2% of play bouts; Mann-Whitney U). These results indicate that there is no link between moving first/second and running away/after in gorilla play chase.

4. DISCUSSION

Taken together, the present work provides first empirical evidence that gorillas are sensitive to inequities during their naturally occurring social interactions (play fights).

The subjects, that hit their playmates unequally prior to a play chase, significantly more often moved first to run away than their playmates. The current study provides therefore first empirical evidence that nonhuman species may try to maintain their competitive advantages when responding to inequities. These findings suggest that humans are not unique in their ability to modify their responses to unequal situations depending on whether they have the advantage or the disadvantage (for inequity aversion, see Brosnan & de Waal 2003; Brosnan *et al.* 2005; Range *et al.* 2009).

Great apes, thus, may not only show self-regarding behaviours (chimpanzees: Silk *et al.* 2005; Jensen *et al.* 2006), but they also seem to behave competitively by obtaining an advantage over others and by then trying to maintain it (present study). Interestingly, the study subjects did not seem to run first when they only softly grabbed their playmates instead of hitting them. Although these results should be considered with caution as such soft grabbing was observed in only three play bouts, they provide first indication that great apes might perceive the roughness of their own behaviours toward others and the extent to which they violate a social situation and adjust their behaviours accordingly. These traits are considered pivotal for cooperation and safeguarding fitness (Fehr & Fischbacher 2004).

Data further revealed important differences in the behaviours of the chased and chasing subjects. The latter ones predominantly displayed open-mouth faces while running after their playmates and hit them more often at the end of the chase than vice versa. Such distinctive play roles might help individuals to acquire more refined communicative skills, integral for a wide range of social contexts (Power 2000). The capacity to take the perspective of others might be enhanced by such role play (Bateson 1956; Bekoff 2001), which forms an important prerequisite for empathy-related behaviours in humans (Eisenberg *et al.* 2006). Reversals of these distinctive

chase roles in the gorillas of this study occurred consistently after hitting, similar to the game of tag in children (Aldis 1975; Reynolds 1994).

It remains unknown to what extent unequal play itself gives animals a more competitive edge. Allen and Bekoff (2005) claimed that animals experiencing unequal situations in form of social play are better equipped to conform their actions to social imperatives in more serious situations, where inequities could lead to aggressive retaliation, e.g., when defending resources. Our finding that gorillas respond to inequities during play fights provides first empirical support that animals playfully explore the ramifications of inequities. Further research is needed to assess inequities during natural social interactions in nonhuman species, research that is likely to enhance our knowledge on the evolution of social competitiveness, fairness, and morality in humans.

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FIGURES

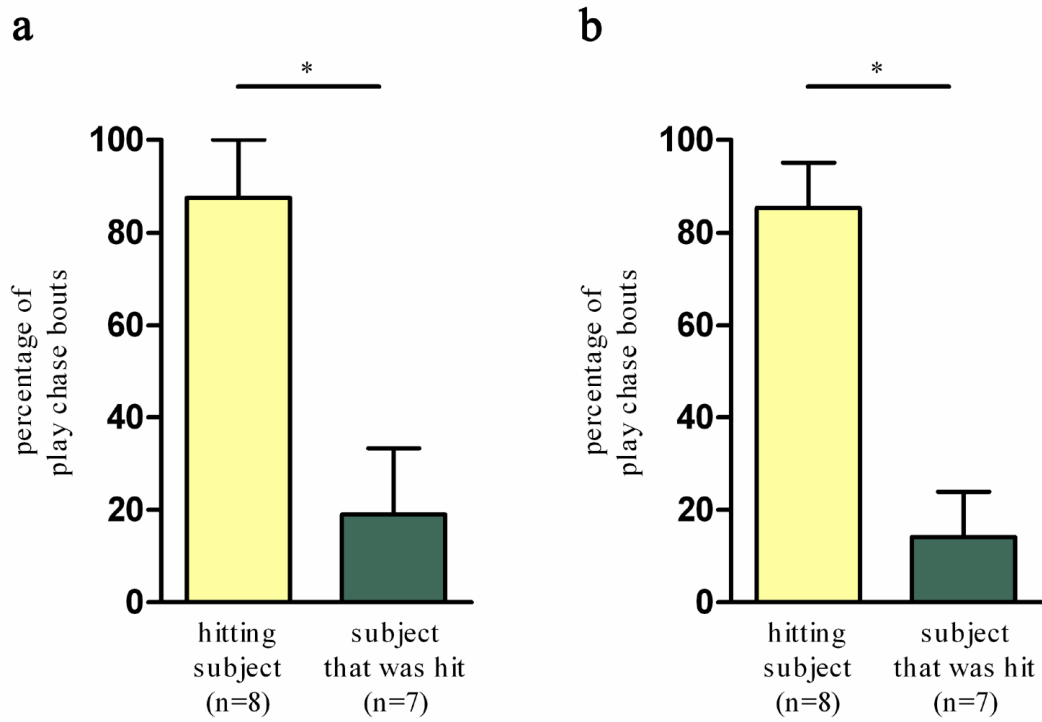


Figure 1. Mean number (+s.e.m.) of play chase bouts preceded by unequal hitting of every subject. Hitting subjects and their playmates were compared in (a) who made the first move to run and (b) who ran away, i.e., was chased.

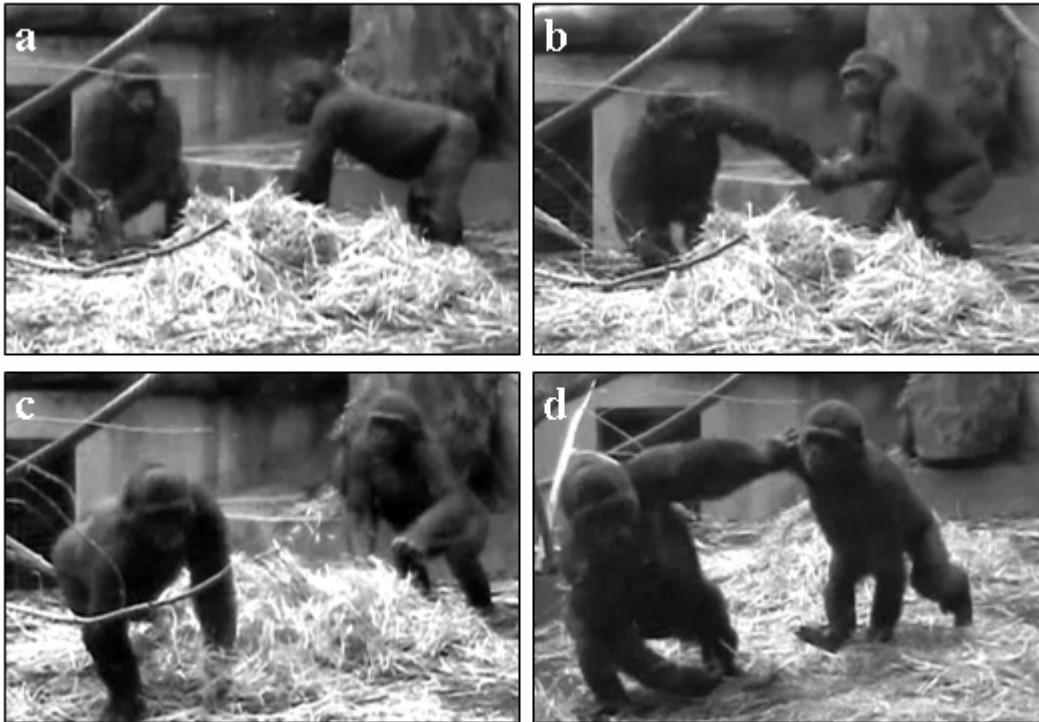


Figure 2. ‘Hit-and-run’ play chase in gorillas. The individual on the left (a-b) hits the individual on the right and (c-d) then runs away. The individual on the right (c-d) responds by chasing. Seven of eight subjects displayed this ‘hit-and-run’ behaviour.