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

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Humans respond to unfair situations in various ways. Experimental research has revealed that non-human species also respond to unequal situations in the form of inequity aversions when they have the disadvantage. The current study focused on play fights in gorillas to explore for the first time, to our knowledge, if/how non-human species respond to inequities in natural social settings. Hitting causes a naturally occurring inequity among individuals and here it was specifically assessed how the hitters and their partners engaged in play chases that followed the hitting. The results of this work showed that the hitters significantly more often moved first to run away immediately after the encounter than their partners. These findings provide evidence that non-human species respond to inequities by trying to maintain their competitive advantages. We conclude that non-human 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; social play

1. INTRODUCTION

Research on human responses to inequities has shown opportunistic attempts to keep competitive advantages (e.g. [1]) as well as violations of rational-choice decisions owing to fairness-driven motives (e.g. [2]). While various non-human species seem to respond to unequal situations with inequity aversion (e.g. [3–5]; cf. [6]), these findings are based on experimental approaches, where special attention was paid to the subjects with the disadvantages. It remains to be empirically investigated how non-human species respond to inequities in natural social settings and how the individuals that obtain advantages and disadvantages interact with each other in these situations. The current study explored for the first time, to our knowledge, if non-human species respond to naturally occurring inequities by focusing on play fights in gorillas.

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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 [7]. 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 [8,9]. 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. subordinate males are more likely to react aversively to males of the same rank than to dominant ones.

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 [8]. Play chases could, therefore, indicate two distinct responses to inequities in non-human 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 [7,8].

The approach of this study was to compare the chase-related behaviours of the hitters (with the advantage) and their playmates (with the disadvantage). If the hitters moved first to run away, this finding would provide, to our knowledge, first empirical evidence that non-human 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 non-human species in their natural social settings. Alternatively, with a finding inferring neither one of such behaviours, there would be no evidence that hitting triggers responses to inequities in gorillas during play fights.

2. MATERIAL AND METHODS

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 (Allwetterzoo Munster, Zoo Berlin, Zoo Hannover, Zoo Wilhelma with two groups, and Zoo Zurich) by M. Davila Ross and L.-M. Gerhardt. Data on 21 subjects playing chase in 86 dyadic play bouts were obtained (for further details on subjects, see electronic supplementary material, table S1). Dyadic play bouts began when two subjects showed a play action and ended when one playmate showed no play action for 20 s 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 less than 20 s. 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 was defined by long-lasting forceful physical contact during play, e.g. wrestling. 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 5 s prior to the chase and ending 5 s after the chase. Open-mouth faces may vary from baring no teeth to baring both tooth rows [10]. 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

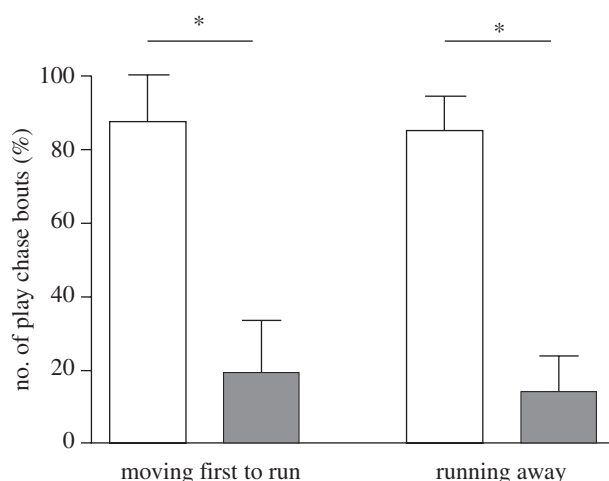


Figure 1. Mean number (+s.e.m.) of play chase bouts preceded by unequal hitting of every subject. Hitters and their playmates were compared in who made the first move to run and who ran away. White bars, hitter ($n=8$); grey bars, subject that was hit ($n=7$). The asterisks denote significant differences in values between hitters and their playmates.

Cohen's kappa values of 80 per cent for play actions and 92 per cent for open-mouth faces (20 play bouts per test). Three researchers identified which subjects moved first to run and only bouts agreed upon by all (kappa: 98%) were tested for inequity responses. The videos were analysed using INTERACT 7.25 (Mangold, Arnstorf, Germany).

This study first scrutinized the overall chase-related behaviours of gorillas by analysing the subjects' play actions and 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). All statistical 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 chase bouts. Of these subjects, 15 were chased by their playmates and 16 were chasers.

The play actions of the subjects that occurred immediately prior to the play chases were statistically compared with their base rates (electronic supplementary material, figure S1). No significant difference was found for hitting ($p > 0.050$; Mann–Whitney U -test). Play chases were predominantly preceded by non-tactile play. The chased and chasing subjects were also compared in their play actions immediately following play chases (electronic supplementary material, 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 ($p = 0.013$). Additional comparisons revealed that the chased subjects produced significantly less open-mouth faces during the chases than the chasers ($p = 0.007$; electronic supplementary material, table S2).

The results furthermore 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 (electronic supplementary material, video).

(b) Testing for inequity responses in chase-related behaviours

Data on unequal hitting prior to play chases were obtained in 11 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 1 shows that the hitters 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 -test). Figure 1 also shows that the hitters 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 hitters moved first to run away and were then chased by the other playmates. Figure 2 shows a representative scene of such 'hit-and-run' behaviours. 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 all 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 -test). 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 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. Therefore, the current study provides, to our knowledge, first empirical evidence that non-human species may try to maintain their competitive advantages when responding to inequities. These findings suggest that humans are not unique in being sensitive to inequities when they have the advantage and the disadvantage (inequity aversion in nonhuman species: [3–5]) and in their ability to modify their responses to these situations accordingly.

Great apes, thus, may not only show self-regarding behaviours (chimpanzees: [11,12]), but they also seem to behave competitively by obtaining an advantage over others and by then trying to maintain it (gorillas: 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 towards 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 [1].

Data further revealed important differences in the behaviours of the chased and chasing subjects. The



Figure 2. ‘Hit-and-run’ 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 behaviour (electronic supplementary material, video).

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 [13]. The capacity to take the perspective of others might be enhanced by such role play [14,15], which forms an important prerequisite for empathy-related behaviours in humans [16]. Reversals of these distinctive chase roles in the gorillas of this study occurred consistently after hitting, similar to the game of tag in children [7,8].

It remains unknown to what extent unequal play itself gives animals a more competitive edge. Allen & Bekoff [9] claimed that animals experiencing unequal situations in the 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 (for a comparative perspective on fairness and play, also see [17]). Our finding that gorillas respond to inequities during play fights provides, to our knowledge, first empirical support that animals playfully explore the ramifications of inequities. Further research is needed to assess inequities during natural social interactions in non-human species, research that is likely to enhance our knowledge on the evolution of social competitiveness, fairness and morality in humans.

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