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Personality influences responses to inequity and contrast in chimpanzees

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Several species besides humans respond negatively to inequity (i.e. receiving a less preferred outcome as compared to a social partner). Among primates, the taxon for which inequity responses have been most comprehensively studied, there are large individual differences in responses that have, thus far, not been well explained by demographic features such as sex, rank and age. Recent evidence shows that individuals' personalities are important in explaining differences in behavioural outcomes in other contexts. Thus, in the current study, we explored whether personality was associated with chimpanzees' responses to both inequity and contrast (i.e. receiving less than anticipated). Chimpanzees were paired with multiple members of their social groups. These pairs alternated trading a token to receive food rewards that either differed from what their partner received (inequity condition) or from what was initially offered (contrast condition) and we compared their responses to a control in which both subjects were offered and received the same reward for trading the token. We predicted that both personality and the quality and length of the pairs' relationship would influence subjects' reactions to unequal outcomes, as measured by their refusal to exchange tokens. The quality of subjects' relationships, based on a weighted average of grooming, contact and proximity, did not correlate with refusals to exchange, whereas pairs that had lived together longer were less likely to refuse in the contrast condition than were pairs that had lived together for less time. Considering personality, some of the dimensions influenced responses to both inequity and contrast similarly, but the more 'social' personality dimensions ('extraversion' and 'agreeableness') were more strongly correlated with sensitivity to inequity. These results highlight the importance of considering individual differences, including personality, when evaluating responses in cognitive and behavioural tests.

In numerous species, if an individual gets a reward that is less preferred than the reward given to a social partner, the individual will respond negatively by refusing to (1) continue participating in the interaction or (2) accept the offered reward. Such responses have been documented in humans (Yamagishi et al., 2009) and in a number of nonhuman primate species (Brosnan, 2013; Price & Brosnan, 2012), dogs (Horowitz, 2012; Range, Horn, Viranyi, & Huber, 2009, Range, Leitner, & Virányi, 2012) and corvids (Wascher & Bugnyar, 2013), and have been explored in fish (Raihani, McAuliffe, Brosnan, & Bshary, 2012; for a review of this literature, see *Social Justice Research*, *25*(2–3)). Intriguingly, however, responses to inequity are highly variable within species, as evidenced by the differences found in chimpanzees' responses both across studies (Bräuer, Call, & Tomasello, 2009; Hopper, Lambeth, Schapiro, & Brosnan, 2013) and within the same study (Brosnan, Schiff, & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Hopper, Lambeth, Schapiro, & Brosnan, 2014). For example, inequity responses in nonhuman primates are influenced by rank, with dominant individuals typically responding more strongly when they receive less than a social partner (Bräuer et al., 2009; Brosnan et al., 2010; Takimoto & Fujita, 2011). In addition,

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there is some evidence that responses to inequity are influenced by age (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013), sex (Brosnan et al., 2010; Hopper, Lambeth, et al., 2014; Hopper, Price, et al., 2014) and social group (Brosnan et al., 2005), but these patterns are not consistent across studies (Price & Brosnan, 2012), nor can they explain all variation.

What other factors could affect responses to inequity? In light of the fact that responses to inequity may represent consistent individual differences in behaviour (Hopper, Lambeth, et al., 2014; Hopper, Price, et al., 2014), one potential explanatory factor is personality, or 'those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving' (Gosling, 2001, page 46). However, to date, no previous work has examined the impact of an individual's personality on their response to inequity. This lack of previous work on personality's relationship to responses to inequity is somewhat surprising given that personality has proved to be important to understanding individual differences in behavioural responses in a number of species and circumstances (Carere & Maestripieri, 2013). In particular, studies of nonhuman primate species show that they have stable, consistent personalities (Massen, Antonides, Arnold, Bionda, & Koski, 2013; Morton et al., 2013; for a review in nonhuman primates see Freeman & Gosling, 2010), which also correlate with their responses in behavioural experiments (e.g. Hopper, Lambeth, et al., 2014; Hopper, Price, et al., 2014; Massen et al., 2013). The personality dimensions that have been identified to apply to nonhuman primates include some dimensions that are more social (e.g. 'dominance', 'extraversion') and others that are more experiential (e.g. 'openness', 'methodical'; Freeman, Brosnan, et al., 2013; Freeman, Sullivan, et al., 2013). Thus, different personality traits may influence how animals respond in different social and nonsocial contexts (Carter, Marshall, Heinsohn, & Cowlishaw, 2013; van Oers, Klunder, & Drent, 2005). Given this pattern, we hypothesize that personality will also influence animals' evaluations of food rewards in different contexts (i.e. social situations that create inequity compared to situations that contrast expected with received rewards).

In addition to correlating with cognitive and behavioural responses, animals' personalities also relate to their social interactions with their groupmates (Kurvers et al., 2010; Massen & Koski, 2014; Mehrabian, 1996). For example, studies investigating the relationship between chimpanzee personality ratings, collected from caregivers familiar with the individuals, and observed social behaviours, collected by a separate set of individuals at another time period, have shown that the factor of 'extraversion' correlates positively with affiliative behaviours and negatively with aggressive behaviours; similarly, the personality factor of 'dominance' correlates positively with agonistic behaviours and negatively with submissive behaviours (Freeman, Brosnan, et al., 2013; Freeman, Sullivan, et al., 2013; Murray, 1995; Pederson, King, & Landau, 2005; Vazire, Gosling, Dickey, & Schapiro, 2007). Furthermore, a recent study of 38 captive chimpanzees showed that subjects who spent more time sitting in contact with each other ('friends') were more similar in 'sociability' than were nonfriends (Massen & Koski, 2014). In addition, among nonkin friends, 'friendship' also correlated with 'boldness' and 'grooming equity'.

In humans, relationship quality influences decisions surrounding inequity, such that people in close relationships are less likely to respond negatively to inequity than are mere acquaintances (Clark & Grote, 2003). Work in nonhuman primates has resulted in conflicting evidence as to whether relationship quality influences responses. There is evidence that rank influences responses to inequity in primates (Bräuer et al., 2009; Brosnan et al., 2010; Takimoto & Fujita, 2011), but a study that explicitly tested relationship quality in longtailed macaques, *Macaca fascicularis*, found that relationship quality did not influence subjects' responses (Massen, van den Berg, Spruijt, & Sterck, 2012). Even in chimpanzees, one of the most-studied species in tests of inequity, evidence is mixed regarding the impact of relationship quality on responses to inequity. For example, adult chimpanzees who were housed in species-atypical arrangements (in pairs or in a recently formed social group), responded negatively to inequitable outcomes, while chimpanzees who had been housed in the same species-typical group for decades did not (Brosnan et al., 2005). This finding points to the potential importance of relationship quality in chimpanzee responses to inequity. However, a more recent study with chimpanzees, using the same methodology but conducted at a different facility, found that group membership did not make a difference, but sex and rank did (Brosnan et al., 2010). Untangling the degree to which these reported differences are due to the impact of relationship quality or duration versus differences in the subjects' personalities requires testing these two potential influences within the same study.

Empirical considerations of inequity focus on whether individuals respond negatively to an outcome that differs from the outcome experienced by another individual, where the task implicitly involves a social comparison. However, comparisons can also be made in the absence of a social context; for example, an individual can compare the achieved outcome with their expected outcome (based on experience). This comparison is often referred to as a 'contrast effect' (Reynolds, 1961) or 'frustration' (Roma, Silberberg, Ruggiero, & Suomi, 2006) and probably draws on the same cognitive mechanism as used in inequity decisions (Price & Brosnan, 2012). Essentially, inequity decisions compare the outcome with social referents whereas contrast decisions compare the outcome with nonsocial referents (such as past experience). Most studies of inequity consider both inequity and contrast, and these studies show that there is variability both within species (e.g. there are sex differences in contrast effects in squirrel monkeys (*Sairmiri* spp.); Talbot, Freeman, Williams, & Brosnan, 2011) and across species (e.g. while squirrel monkeys respond to contrast effects, marmosets, (*Callithrix spp.*) and owl monkeys (*Aotus spp.*) do not; Freeman, Sullivan, et al., 2013). What we do not know, however, is whether these effects are differentially influenced by social and demographic factors. For instance, features directly related to individuals' interactions with one another, such as rank and relationship quality, may influence decisions with an explicitly social referent (i.e. inequity) differently than those without such a referent (i.e. contrast effects).

Here, we explored the impact of personality and relationship quality on responses to inequity and contrast effects in chimpanzees. We selected chimpanzees because previous research has demonstrated a high degree of individual variability in their responses to tests of inequity and contrast effects (Bräuer et al., 2009; Brosnan et al., 2005, 2010; Hopper, Lambeth, et al., 2014; Hopper, Price, et al., 2014), indicating that some as-yet unidentified factor, or factors, may be influencing their responses. To do this, we tested chimpanzees in a commonly used inequity paradigm in which they traded a token with an experimenter to receive a food reward. Sometimes this food reward was a less preferred reward than the one given to their partner (inequity condition) and sometimes both the subject and partner were shown a preferred reward but given a less preferred one (contrast condition). The chimpanzees' responses in both were compared to a control condition in which the subjects were given the same, less preferred reward as their partner (equity condition). To explore how personality influenced chimpanzees' responses, we included measures of the chimpanzees' personalities as an explanatory variable, which were collected as part of a wider study by Freeman, Brosnan, et al. (2013). We additionally explored how