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Fairness in Non-human Primates?

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Abstract Humans have a sense of fairness, i.e. an interest in the ideal of equity. This sense allows them to compare their own efforts and subsequent outcomes with those of others, and thus to evaluate and react to inequity. The question is whether our closest living relatives, the non-human primates, show the behavioural characteristics that might qualify as necessary components to a sense of fairness, such as inequity aversion. In this article, we review the five different experimental approaches to studying behaviours related to fairness in non-human primates, including their underlying logic and main findings that represent the current state of research in this field. In the critical condition of all these studies, a subject and a conspecific partner have either to invest different efforts or receive different outcomes while observing each other. The main question is whether—and how—subjects react to unequal situations that humans would perceive as 'unfair'. Taken together, the results from all five approaches provide only weak evidence for a sense of fairness in non-human primates. Although apes and monkeys are attentive to what the partner is getting, they do not seem to be able or motivated to compare their own efforts and outcomes with those of others at a human level. Even though the debate is still on-going, we believe that a full sense of fairness is not essential for cooperation. Obviously, apes and monkeys are capable of solving problems cooperatively, without a strong, humanlike sense of fairness. They are mainly interested in maximizing their own benefit, regardless of what others may receive. It is thus possible that a sense of fairness only exists rudimentarily in non-human primates.

Keywords Animal cognition · Inequity aversion

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Introduction

What does it mean to be 'fair'? Imagine two people are asked to pull a cart. I pull it together with my partner Max. We share the work equally, which means we both pull the cart equally far, thereby investing the same amount of energy—that is the *effort*. When we are done, Max receives 8 euros and I receive 2 euros—the *outcome*. That is not fair! As a human, I do not only perceive that difference in outcome, but I also dislike it and judge it as unfair. This is true whether the judgment is made by me or by Max; with respect to fairness, we do not like receiving either more or less than our partners.

Humans have evolved special skills and motivation for collaborating with one another (Fehr & Fischbacher, 2003, 2004a; Fehr & Schmidt, 1999; Gintis, Bowles, Boyd, & Fehr, 2003; Melis & Semmann, 2010; Stevens & Hauser, 2004; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Our cooperation is more stable and therefore—in the long run—more successful if we share both *effort* and *outcome* equally because that is the best trade-off situation for both of us. However, individuals have to be confident that their partners are cooperative (Clutton-Brock & Parker, 1995; Fehr & Fischbacher, 2004a; Gächter, Herrmann, & Thoni, 2004; Tennie, Frith, & Frith, 2010). Therefore, it is hypothesized that humans have developed their sense of fairness, i.e. an interest in the ideal of equity. This skill allows us to compare our own efforts and subsequent outcomes with those of others—and thus to evaluate and react to inequity. It furthermore enables us to detect cheaters who invest less effort and/or gain bigger outcomes relative to others. Humans express a strong sense of fairness when they are personally affected (Fehr & Fischbacher, 2003, 2004a; Fehr, Fischbacher, & Gächter, 2002; Fehr & Rockenbach, 2004; Fehr & Schmidt, 1999; Gintis et al., 2003), and they even punish third parties for their unfair behaviour in situations where they do not personally suffer from inequity—even if such punishment is costly (Fehr & Fischbacher, 2004b; Fehr & Gächter, 2002; see also Raihani & McAuliffe, 2012, previous issue).

One of the most fascinating questions in contemporary comparative psychology is whether we share this distinctive characteristic with our closest living relatives, the non-human primates. As we know, chimpanzees cooperate with each other in various situations (Boesch, 1994; Langergraber, Mitani, & Vigilant, 2007; Melis, Hare, & Tomasello, 2003; Mitani, 2006). However, at first glance a sense of fairness does not seem essential for cooperation—at least as long as resources are abundant and my own fitness is not influenced by the inequity (e.g. I produce the same number of offspring and can provide the same parental care for them with a 2-euro compared to an 8-euro outcome). However, under natural conditions such a scenario is rare, if not highly improbable. Therefore, there is no doubt that cooperation becomes more successful and stable if individuals are able to compare their own efforts and outcomes with those of others and react accordingly (Brosnan & de Waal, 2003; Fehr & Fischbacher, 2003).

To shed light on the question of whether non-human primates show evidence for fairness, there are five different experimental approaches that dominate the field. In these approaches, researchers investigate different features that are essential

ingredients for a sense fairness, such as an aversion to inequity. In particular, 'disadvantageous inequity aversion' has been tested, i.e. how primates respond to inequitable outcomes against themselves.

In the following sections, we briefly illustrate the underlying logic of these approaches and present their main findings. One commonality of all the studies presented is that in the critical condition a subject and a conspecific partner will observe each other either invest different efforts or receive different outcomes. The central question is whether—and how—subjects react to unequal situations that humans would usually perceive as 'unfair'. So far, mainly great apes and capuchin monkeys have been tested (see also evidence in fish: Raihani & McAuliffe, 2012, previous issue, and dogs: Range, Leitner, & Viranyi, 2012, previous issue and Horowitz, 2012, prevous issue, and recently some other monkey species Price & Brosnan, 2012, previous issue). Besides being closely related to humans, these former species are known to cooperate and share food with each other (chimpanzees: Boesch, 1994; de Waal, 1992; capuchin monkeys: de Waal, 2000; Perry & Rose, 1994; Rose, 1997).

First Approach: Different Outcomes

The most basic approach to investigate fairness is to test 'disadvantageous inequity aversion' in an experimental setup in which the subject and the partner receive different kinds of food without any prior effort (great apes: Bräuer, Call, & Tomasello, 2006; capuchin monkeys: Dindo & de Waal, 2007; Dubreuil, Gentile, & Visalberghi, 2006; Fontenot, Watson, Roberts, & Miller, 2007; Roma, Silberberg, Ruggiero, & Suomi, 2006), as demonstrated in Fig. 1. According to our initial example, neither Max nor I is required to invest any effort; we do not have to pull the cart. However, we receive different outcomes—Max receives 8 euros, while I receive 2 euros.

Instead of different amounts, different *kinds* of food (low vs. high quality) were used to test monkeys and apes. This was due to anticipated problems in the experimental procedure. Partners might have taken longer to eat if they were given a larger amount of food. This might in turn have led to reactions on the part of the subject, which were not caused by inequity aversion but instead by impatience, as subjects had to wait longer for their food (although an effect of a delay was not found by Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). The precondition for participating in these studies was that subjects had to display a clear preference for one kind of food (the preferred food, hereafter PF) compared to another kind of food (the less-preferred food, hereafter LF). This preference was determined in a pre-test, in which subjects had to choose between two kinds of food.

The procedure was the following: The subject and the partner sat in adjacent rooms (or sometimes, next to each other) with full visual and auditory access to each other. The human experimenter (hereafter E) sat in front of them and handed over the food. A session started when E handed one food piece to the subject. If the subject did not take the food, E placed it inside the cage or within reach of the subject. E went on alternately feeding both subjects until each of them had received a certain number of food pieces (typically 25). E tried to make sure that both

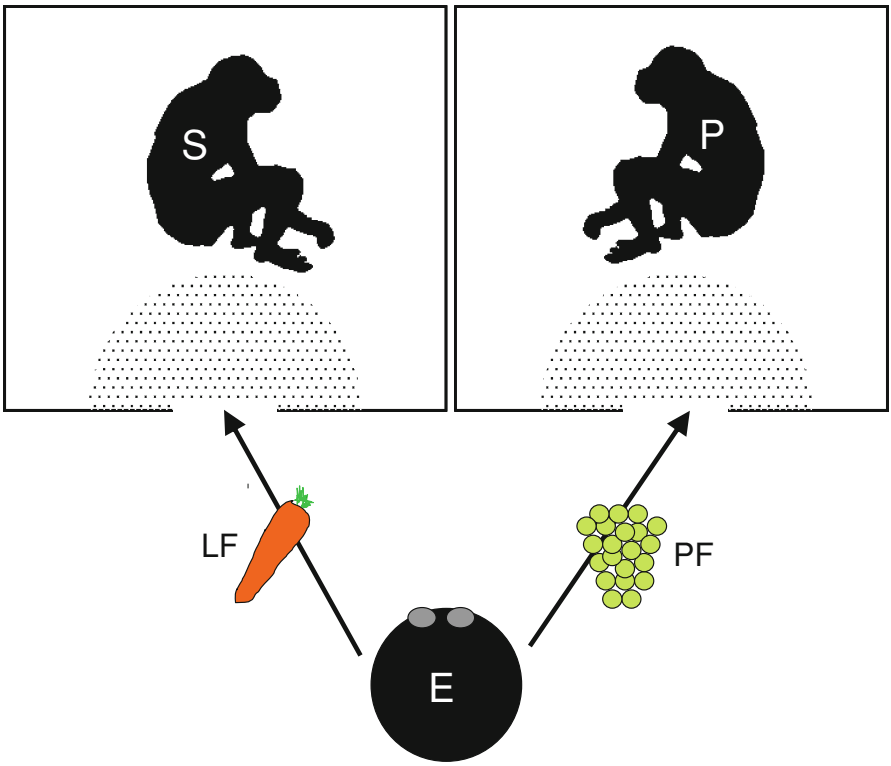

Fig. 1 Setup with different outcomes for subject (S) and partner (P) given by a human experimenter (E)

subjects were able to get the food and they behaved in the same way in all conditions. The subject was always given the low-value reward (LF; typically carrots or cucumber), while the outcome for the partner varied according to the condition. In the equity condition, the partner received the same kind of food. In the inequity condition, the partner received better food (PF; typically grapes). A score was given depending on whether the subject reacted differently in the two conditions. To this end, how often they ignored (i.e. they did not touch) the food pieces offered to them was counted. In addition, the total amount of time subjects spent away from the 'feeding area' in front of E—where they could acquire the food—was also recorded and coded.

The main finding of all studies was that neither apes nor capuchin monkeys reacted negatively when the reward was unequally distributed (Bräuer et al., 2006; Brosnan et al., 2010; Dindo & de Waal, 2007, Dubreuil et al., 2006; Fontenot et al., 2007; Roma et al., 2006). Subjects did not reject the LF if the partner received PF, nor did they show signs of increased frustration by leaving the feeding area in the inequity condition.

In the rare cases in which refusals occurred, it seemed that the subjects' frustration was not caused by inequity aversion. Dubreuil et al. (2006) demonstrated that capuchins rejected the LF because of the mere presence of the PF. In their

study, subjects received the LF while the PF was either not present, hidden in front of the subject, accumulated in an empty cage, or given to the partner. Refusals to initiate the trial and refusals to take and eat the LF were higher when the PF was present (either hidden or accumulated) in sight but out of subject's reach. The authors concluded that capuchins' refusals were due to mere frustration at seeing and not being able to obtain the PF in a purely non-social context. Similarly, Roma et al. (2006) showed that signs of frustration (such as rejection of the food) also occur because of the well-documented frustration effects that arise when subjects are initially given a high-quality reward and this is then followed by low-quality rewarding (Tinklepaugh, 1928, but see Bräuer & Call, 2011). In such cases, frustration and/or rejection is a consequence of subjects' individual experience of a quality change regardless of any social aspect.

As we have seen, no non-human primates tested thus far showed signs of frustration when a partner was given better food with no effort required to obtain it. Nevertheless, great apes (Bräuer et al., 2006), and capuchin monkeys (Dindo & de Waal, 2007; Dubreuil et al., 2006) seemed somewhat attentive to what the partner was receiving. Capuchins ate more of the LF when the partner was consuming the PF, indicating that their behaviour was indeed socially facilitated (Dindo & de Waal, 2007; Dubreuil et al., 2006; Galloway, Addessi, Fragaszy, & Visalberghi, 2005). Bräuer et al. (2006) found that great apes ignored fewer food pieces and waited longer in front of E when a conspecific received better food than the subjects themselves. Moreover, chimpanzees begged more vigorously when the conspecific received PF. Bräuer et al. (2006) concluded that instead of inequity aversion, simply seeing another individual receive high-quality food created the expectation of receiving the same food oneself. Apes perceived the situation as 'it is grape-feeding-time', and they expected to receive PF because this food was distributed, rather than because the partner got better food.

However, as Brosnan and de Waal (2006), Dindo and de Waal (2007) and Brosnan et al. (2010) have pointed out, effort might be a key aspect, which facilitates inequity aversion. According to their argument, it is important that the provision of food is contingent on task performance. Only if subjects invest energy are they able to compare or judge how they and their partner are rewarded for the same performance. The experimental approaches described below follow that logic.

Second Approach: Same Effort/Different Outcomes

Figure 2 shows the general setup in which subjects have to invest some form of effort to receive food (great apes: Bräuer, Call, & Tomasello, 2009; Brosnan, Schiff, & Waal, 2005; Brosnan et al., 2010; capuchin monkeys: Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007). With respect to our initial example, this means that Max and I pull the cart together and invest the same effort, but our outcomes differ (Max receives 8 euros and I receive 2 euros). The effort typically required of non-human subjects consists of handing over a token to the experimenter to receive a reward. These tokens are little objects such as doubloons, small granite rocks or plastic tubes. A number of studies have demonstrated that non-human primates demonstrate a flexible understanding of how to use tokens in exchange for

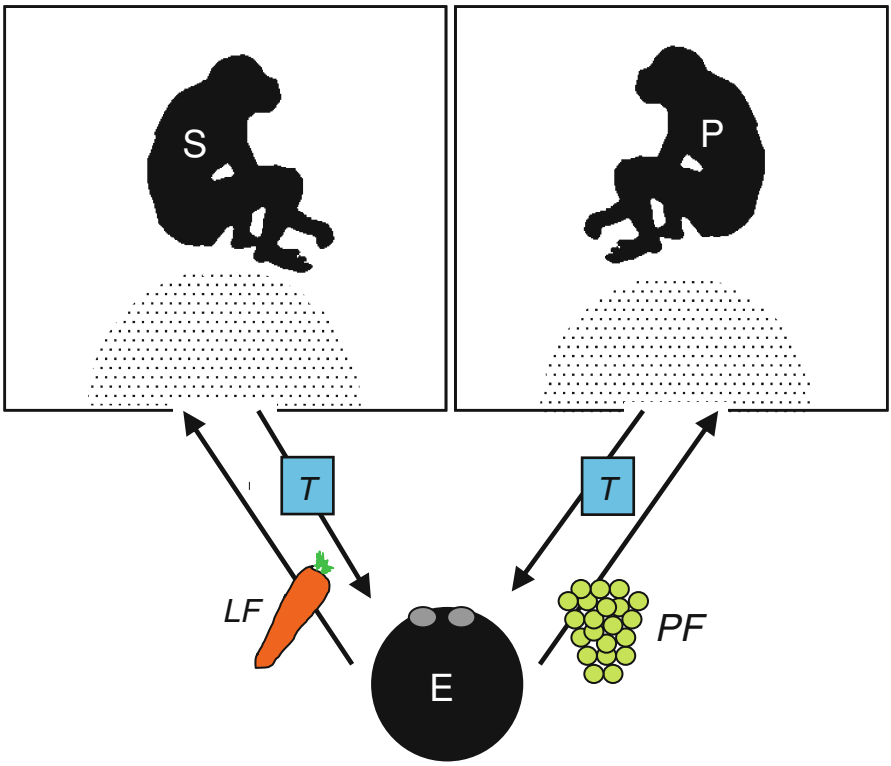

Fig. 2 Setup with same effort and different outcome for subject (S) and partner (P) given by a human experimenter (E)

food (Addessi, Mancini, Crescimbene, & Visalberghi 2011; Brosnan & de Waal, 2004a, 2004b, 2005; Chen, Lakshminarayanan, & Santos, 2006; Pelé, Dufour, Thierry, & Call, 2009; Westergaard, Liv, Rocca, Cleveland, & Suomi, 2004).

The basic procedure of this approach is similar to the first one. The human experimenter (E) sat in front of subject and partner. Subjects either shared a room (Brosnan et al., 2005, 2010) or were spatially separated, either side-by-side or across from one another, but potentially able to touch each other through the mesh (Bräuer et al., 2009; Brosnan & de Waal, 2003; van Wolkenten et al., 2007). In all studies, they could clearly see what E was doing and what the partner was getting. Instead of handing over the food, E handed over a token to the partner. After the partner had taken the token, E asked for its retrieval by opening her hand. When the partner returned the token, E gave a piece of food to her. Then E handed the token to the subject and proceeded in the same way as with the partner. E continued exchanging tokens and food with both animals until each of them had received, typically, 25 pieces of food. Again there were two main conditions: In the inequity condition, the subject received the LF in exchange for a token, whereas the partner was given the PF in exchange for a token. In the equity condition, both animals received the LF in exchange for a token. A score was given depending on whether subjects refused to

eat the food and/or to return the token as well as on latency, i.e. how long they spent away from the area in front of E.

This procedure was first used with capuchin monkeys. Brosnan & de Waal (2003) found that the monkeys refused to exchange LF when the partner had received better food for her token. However, these findings have been challenged on a number of empirical and methodological grounds. Most importantly, it seems problematic that in their equity condition the PF was not present and visible for the subjects. Thus, it is possible that the capuchin subjects had rejected the LF in the inequity condition only because of the mere frustrating presence of the PF (Dubreuil et al., 2006; Wynne, 2004). Van Wolkenten et al. (2007) therefore implemented an equity condition in which a bowl with the PF was always present—moreover, the PF was waved in front of the subject before each trial. Although it remains questionable whether this new equity and inequity conditions are then still comparable—as a different food than they received was never waved in front of the subject in the inequity condition—van Wolkenten et al. (2007) found that capuchin monkeys exchanged more tokens in the equity than in the inequity condition (one-tailed effect).

Brosnan et al. (2010) tested chimpanzees in a similar design. They also used two equity conditions. In one condition, the PF was waved in front of the subject before each trial (as in van Wolkenten et al., 2007) whereas in the other one the bowl with the PF was just present. The latter allows for the best comparison to the inequity condition. Brosnan et al. (2010) found that male but not female chimpanzees rejected exchanges for LF more often when the competitor received better food compared with situations in which better food was just visible. In a similar study, subjects from two groups refused to exchange in the unequal situation, whereas subjects from a third group basically never refused (Brosnan et al., 2005).

Bräuer et al. (2009) tested chimpanzees, bonobos and orang-utans by applying the equity condition in which the bowl with the PF was just present. In contrast to studies mentioned above, in this case, the subjects did not refuse the LF more when a competitor had received the PF. However, social factors such as group size, group coherence and group-specific traditions might influence chimpanzees' tolerance for inequity, as emphasized by Brosnan et al. (2005). It might be due to these factors that inequity aversion was only found in some but not in other chimpanzees groups. Support for this view comes from data of a different *Pan* species. Bräuer et al. (2009) found that subjects of the bonobo group refused their LF if the partner received PF for exchanging the token, but owing to the low number of subjects, it was difficult for us to draw a firm conclusion. Thus, it seems plausible that species and populations vary in their propensity for displaying aversion to inequity. Nevertheless, based on the current data, conclusions should be carefully drawn as there is only mixed evidence so far that apes and capuchin monkeys react to inequity when they and their partner exchange food for a token (Bräuer et al., 2009; Brosnan et al., 2005; van Wolkenten et al., 2007).

Third Approach: Different Efforts/Same Outcome

In this approach, subject and partner invest different amounts of effort and receive different outcomes. This might mean that I pull the cart alone and get paid while

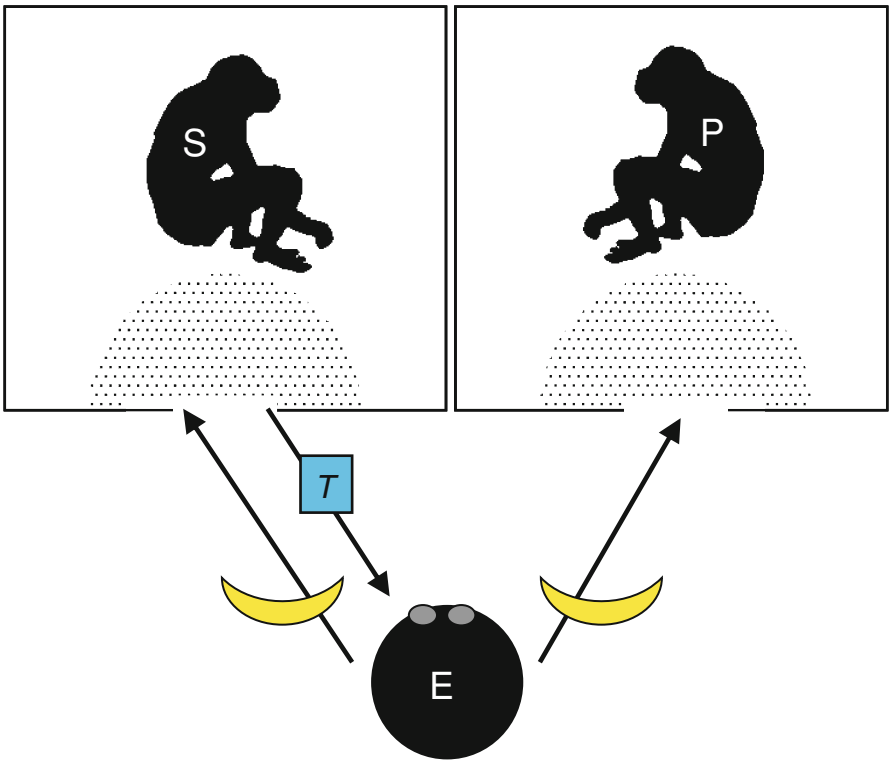

Fig. 3 Setup with different effort and same outcome for subject (S) and partner (P) given by a human experimenter (E)

Max receives money as well even though he did not invest any effort. Similarly, capuchin monkeys (Fontenot et al., 2007; van Wolkenten et al., 2007) and chimpanzees (Brosnan et al., 2010) had to exchange food for a token while the partner received food for free (see Fig. 3). Using various conditions they found no difference in the subjects' exchange behaviour when the partner was given food for free compared to the situation when the partner had to exchange a token as well (Brosnan et al., 2010; Fontenot et al., 2007; van Wolkenten et al., 2007). Again, it seems that neither capuchin monkeys nor chimpanzee subjects were able or willing to evaluate the effort–outcome ratio of another individual relative to their own.

However, there is one problem with all three of the approaches described above: It is somewhat unclear how subjects should react in unfair situations. What behaviour would, for example, clearly indicate inequity aversion? Henrich (2004) pointed out that refusals to exchange or accept food might not be a good measure, as they actually increase, given the inequity between subject and partner. In all studies described so far, subjects could not do anything to change the situation, and that is why they should have accepted everything regardless of whether or not the partner got better food. Henrich (2004) argues that even humans will not reject unless their behaviour could affect the partners' pay-off, although recent studies have

demonstrated that humans may indeed behave in this way (Yamagishi & Mifune 2009). Nonetheless, it is useful to test a setup in which individuals can actively prevent unequal situations and intervene when they are frustrated. It is possible that apes and monkeys seek to avoid inequity as soon as they are more than just passive observers and recipients.

Fourth Approach: Choice Between Same and Different Outcomes ('Dictator Game')

In this approach, subjects can choose between a selfish and a pro-social option, that is, one that benefits a partner. They have a choice between an equal outcome for both primates and an unequal outcome in their own favour or in favour of the partner (see Fig. 4). According to our example, I pull a light cart alone, investing a small amount of effort, and can decide about my own as well as my partner's outcome. I can either choose a selfish option, representing advantageous inequity, in which I alone receive 5 euros and Max receives nothing, or I can choose a pro-social option of equity, whereby Max and I both receive 5 euros (even though we invested slightly different amounts of energy beforehand). The third option is to create a pro-social case of disadvantageous inequity by deciding that I get 5 euros while Max

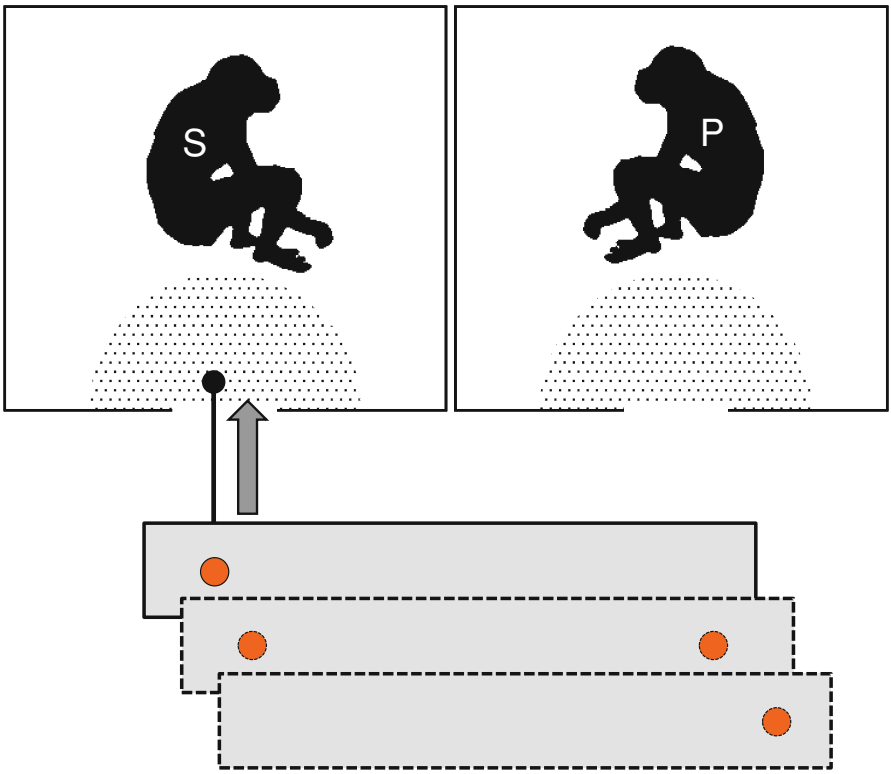

Fig. 4 Setup with a subject (S) choosing between same and different outcome and a passive partner (P)

receives 10 euros. It is important that there is *no* extra effort for me in decision-making when I make a pro-social decision as compared to the one that benefits me. In other words, I always get 5 euros, and my effort is always the same regardless of my partner's outcome (equal amount, less or more money).

Silk et al. (2005) tested chimpanzees in both a social and a non-social setting by giving them a choice between two trays with food. Subjects could choose between pulling a tray that contained one piece of food for themselves and one for a partner in an adjacent room (1/1) and one pro-containing only one piece of food, for themselves (1/0). None of the chimpanzees tested more often preferred the 1/1 option when a partner was present compared to the non-social condition in which the subject was alone, indicating that the presence of a partner did not change their choices. These findings are very robust and have been replicated with a number of different chimpanzee populations. In addition, different apparatuses have been used to guarantee that the chimpanzees tested understood the consequences of their choices, still without results indicating pro-social behaviour on the part of the chimpanzees (Jensen, Hare, Call, & Tomasello, 2006; Vonk et al., 2008; Yamamoto & Tanaka, 2010).

Horner, Carter, Suchak, and de Waal (2011) raised the same question but used a different set-up. They argued that in the Silk et al. (2005) paradigm subjects might be cognitively preoccupied by the mere presence of the two food amounts on the trays. To deal with this concern, they decided to use tokens instead of real food. Following the same logic as the above studies, their chimpanzees could choose between two differently coloured tokens: one 'selfish' token resulting in a reward for the actor only (1/0), and the other 'pro-social' token rewarding both the actor and a partner (1/1). Interestingly, the seven chimpanzees tested preferred the pro-social option only when a partner was present, but not when the partner was absent. Unfortunately, the non-social condition without a partner was conducted after the social condition, which might have facilitated potential order effects. That is, chimpanzees may have simply lost their preference for the 1/1 option over time. Further studies should shed light on this question by counterbalancing social and non-social control conditions in this promising paradigm.

The general picture for monkeys seems to be somewhat different, as there is evidence from different studies using different species that they prefer equity. When given the choice between a 1/1 and a 1/0 food tray, capuchin monkeys and long-tailed macaques (but not cotton-top tamarins; see Cronin, Schroeder, & Snowdon, 2010; Stevens, 2010) reliably preferred the equal option (Lakshminarayanan & Santos, 2008; Massen, van den Berg, Spruijt, & Sterck, 2010, see also Colman, Liebold, & Boren, 1969). Similarly, in a set-up with two kinds of tokens representing the same distributions (1/1 and 1/0), capuchin monkey subjects preferred the 1/1 option, although it should be mentioned that the crucial non-social control was missing in this study (de Waal, Leimgruber, & Greenberg, 2008).

In the above options, the partner could be rewarded with less than or the same as the subject, and still sometimes preferred equity. They may behave similarly when the choice is between *more* than or the same as themselves. Fletcher (2008) presented evidence that capuchin monkeys prefer equity as they avoid disadvantageous inequity. The monkeys could choose between two options, 1/1 and 1/3, and

preferred the equitable option over the altruistic option when their own costs/effort levels were the same (but see Lakshminarayanan & Santos, 2008).

The picture changes when subjects themselves do not receive any reward. In a study by Jensen et al. (2006), chimpanzees did not distinguish between a 0/0 option and a 0/1 option, in which only the conspecific partner got food (the subject got nothing in either case). They rarely pulled the tray, which was most likely due to a generally low motivation to invest any energy for a zero-outcome. Similar results were found with cotton-top tamarins (Stevens, 2010). In contrast common marmosets preferred the 0/1 outcome in the same situation, they provided the partner with food although they received no food for themselves, and thus, they showed other regarding preferences (Burkart, Fehr, Efferson, & van Schaik, 2007). That means, however, that—for different reasons—none of the tested primates species showed inequity aversion in that particular situation, i.e. reliably preferred the 0/0 option. Rather, they were indifferent between the options. In another study, Jensen, Call, and Tomasello (2007b) demonstrated once more that chimpanzees showed no sensitivity to an unequal distribution of outcomes. Here, subjects did not differentiate between a situation in which they simply lost their food and an unequal situation in which their food was given to a partner—although they showed a physical reaction (collapsing the table) when food was actively stolen by the partner.

In conclusion, although there is some evidence that some monkey species prefer outcomes which reward their partners over those that do not, chimpanzees do not seem to have a preference for an equal outcome in a tray-pulling paradigm. Nevertheless, chimpanzees do behave pro-socially in other situations. They open a door for an unrelated group member and help others to obtain a tool that they need, but cannot obtain alone (Melis, Hare, & Tomasello, 2008; Warneken, Hare, Melis, Hanus, & Tomasello, 2007). Melis et al. (2010) found that chimpanzees helped conspecifics to obtain food and non-food items, but only in the situation in which the donor could not get the food herself and when recipients clearly indicated their willingness to get the food or tried to get the attention of the donor. Thus, a key factor for eliciting helping behaviour is whether the recipient provides cues signalling the need for help (Melis et al., 2010, but see Horner et al., 2011). It remains striking that chimpanzees do not behave pro-socially in the tray-pulling task. Given that they help conspecifics in various other situations, and that both chimpanzees and monkeys appear to understand the task, it is somehow puzzling that they show no clear preference for equity when doing so would require no extra effort on their part.

Fifth Approach: Choice Between Same and Different Outcomes and Veto ('Ultimatum Game')

In the 'Ultimatum game', the subject can choose between an equal and an unequal option, but—in contrast to the 'Dictator game'—the partner can reject the whole deal and therefore jeopardize both outcomes (see Fig. 5). In other words, I can decide the outcome for Max and myself. However, Max then has a choice of whether to accept or reject my offer, with both of us missing out in the latter case.

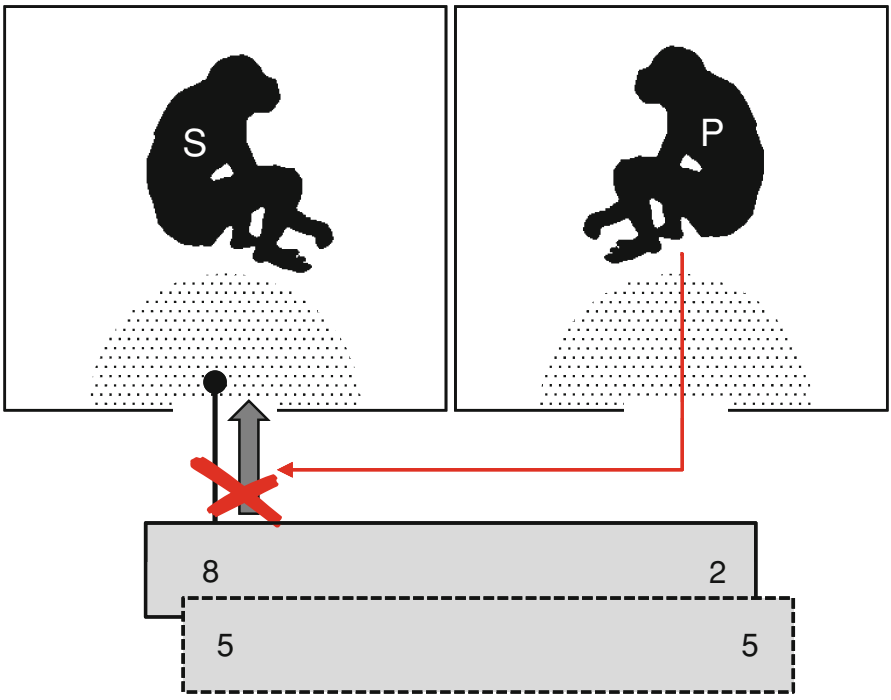

Fig. 5 Setup with a subject (S) choosing between same and different outcomes and an active partner (P) ('Ultimatum Game')

Humans in industrialized societies usually propose something close to equity: 5 euros for both of us—and Max will usually accept. If I make an unequal offer, for example, 8 euros for me and 2 for him, then Max will probably reject (Fehr & Fischbacher, 2004b; Henrich et al., 2006).

Jensen, Call, and Tomasello (2007a) tested chimpanzees in four versions of this game in which subjects always had the choice between two offers. One offer was always the unequal 8/2 option in which the subject received eight pieces of food whereas the partner would receive two pieces. The other options varied from 10/0 (unequal and most disadvantageous distribution for the partner), to 5/5 (equality), to 2/8 (unequal and most advantageous distribution for the partner). Not surprisingly, subjects preferentially chose the options in which they received the most food (8/2 or 10/0) and not the equal offer (5/5). The most significant finding, however, was that partners accepted every offer as long as they received some amount of food. This means that partners did not reject unequal offers even though the subject had the option of making an equal offer. They reliably rejected only zero offers (10/0). Obviously, they were only interested in their own outcome, no matter what the partner got, which led the authors to conclude that chimpanzees are rational maximizers and without any sensitivity to inequality.

Special Cases

Taken together, the results from all five experimental approaches described above provide only weak evidence for fairness in non-human primates. However, besides cultural variations (Henrich et al., 2010) there are also situations in which humans are not strictly averse to inequity. For example, as a human I would probably accept unequal outcomes in favour of Max if Max were my son. A decision in favour of one's own kin is a contribution to the survival of one's own genes (Hamilton, 1964; Trivers, 1971). In their study, de Waal et al. (2008) showed that capuchin monkeys preferred the 1/1 option compared to the 1/0 option overall, but that this preference was much stronger towards the subjects' own kin than towards strangers from another social group. Arguably, this could be seen as evidence for an equity preference, but also as evidence that pro-social tendencies increase with social closeness. However, various other studies have not supported the view that kinship influences subjects' reactions to inequity (Horner et al., 2011; Jensen et al., 2006, 2007a; Yamamoto & Tanaka, 2010).

There is another example in which humans would potentially accept unequal outcomes—if Max is my friend and we have a close relationship. Indeed, Brosnan et al. (2005) found evidence for inequity aversion in a short-term group but not in a long-term group of chimpanzees. Those authors suggest that in the long-term group, subjects showed no reaction to inequity because of their close relationship, which brought them to the conclusion that tolerance for inequity may increase with social closeness in chimpanzees (Brosnan et al., 2005). So far, other studies have not replicated the main finding that the kind of relationship influenced subjects' reactions to inequity (chimpanzees: Bräuer et al., 2006; Horner et al., 2011; cotton-top tamarins: Cronin et al., 2010).

Finally, there is a third scenario in which humans might accept inequity: If Max is my boss, I might accept that he gets more just because of his dominance. In great apes, Bräuer et al. (2006) found that subjects refused more pieces of food when they were dominant over their partner than when they were subordinate to them. Similar results were found by Brosnan et al. (2010). The interpretation is that dominant subjects are more frustrated about disadvantageous inequity, while subordinates might be more ready to accept inequity in a dyadic interaction. In contrast to the 'high' expectations of a dominant individual, the subordinate is more likely to accept any offer. This seems reasonable because in real-world competition the subordinate will most probably be deprived of monopolizable food by the dominant individual and should therefore be willing to accept whatever is left (Bräuer et al., 2006). The findings of Jensen et al. (2007b) point in a similar direction. According to their data, subjects were less likely to prevent a dominant partner from eating when this dominant individual had stolen the food from the subject before.

In a study with capuchin monkeys, the hierarchy status of the partner individual also had an influence on the behaviour of the subject (Takimoto, Kuroshima, & Fujita, 2010). Instead of the food amount, here they varied the *kind* of food subjects and partners could obtain. In one condition, subjects could choose between the option PF/PF and PF/very bad food. There was some evidence that subjects preferred the option with PF for the partner if the partner was subordinate to them,

but not if they were dominant to them. The authors concluded that subjects had a preference for equity or other-regarding preference, but only when paired with a subordinate. However, owing to the low number of capuchin subjects ($n = 4$), it is very difficult to draw any further conclusion here. Moreover, Massen et al. (2010 and 2011) tested long-tailed macaques and found that dominant individuals behave more pro-socially than subordinates. If subordinates have the choice, then they preferentially pull the tray for the most dominant partner (Massen, Luyten, Spruijt, & Sterck, 2011; Massen et al., 2010). It should also be mentioned that other studies did not find any influence of group hierarchy on subjects' reaction to inequity in chimpanzees (Horner et al., 2011) or in capuchin monkeys (Fontenot et al., 2007).

Discussion

Considered together, the results from different labs where different approaches and research paradigms were applied seem to only provide weak evidence for fairness in non-human primates. Neither apes nor capuchin monkeys reacted negatively when a reward was unequally distributed (without requiring effort to receive it) or when subjects had to invest effort to obtain food while another individual received it for free (Bräuer et al., 2006; Brosnan et al., 2010; Dindo & de Waal, 2007; Dubreuil et al., 2006; Fontenot et al., 2007; Roma et al., 2006; van Wolkenten et al., 2007). When both subject and partner had to invest effort to receive food, there was evidence for inequity aversion in some of the non-human primates tested, but not in every case (Brosnan et al., 2005, 2010; van Wolkenten et al., 2007; Massen study; but see Bräuer et al., 2006, 2009; Brosnan, Flemming, Talbot, Mayo, & Stoinski 2011; Talbot, Freeman, Williams, & Brosnan 2011). Strong variability between not only populations or species, but also methodical flaws may be responsible for the currently rather fuzzy empirical picture. In situations in which great apes could actively decide over the outcome for themselves and their partners by pulling a tray with food pieces, they did not show a clear preference for equity, but were instead typically indifferent between equity and outcomes favouring themselves. Apparently, the situation might be different in capuchin monkeys, who preferred equity as they provided the partner with food (de Waal et al., 2008; Lakshminarayanan & Santos, 2008), but never more food than they received themselves (Fletcher, 2008, but see Lakshminarayanan & Santos, 2008). Finally, data from Jensen et al. (2007a) showing that chimpanzees were rational maximizers in an ultimatum game—by accepting any non-zero offer—speak against the notion that they are averse to inequity.

This summary leaves us with the question of why we do not see a strong sense of fairness in non-human primates. There are four possible reasons for this, and they concern the cognitive abilities and the motivation of apes and monkeys. The first reason might be that non-human primates are simply not attentive to what others are receiving. This seems unlikely as subjects did behave differently depending on the partner's outcome in a number of the studies described (e.g. Bräuer et al., 2006; Brosnan et al., 2005; Burkart et al., 2007; Jensen et al., 2007b; Lakshminarayanan & Santos, 2008; Massen et al., 2010; van Wolkenten et al., 2007). Apes also

distinguished between a social situation in which the partner was present and received food and a non-social situation (Bräuer et al., 2006). Moreover, various studies of social facilitation have shown that there are certain situations in which non-human subjects do pay attention to what others are eating (Galloway et al., 2005; Visalberghi, Sabbatini, Stammati, & Addessi, 2003). Thus, it seems quite unlikely that subjects are simply not attentive to what others are receiving. The second reason might be the missing cognitive capability of directly comparing one's own *outcome* with those of others (Melis & Semmann, 2010; Stevens & Hauser, 2004)—something that humans almost automatically do in various contexts (Fehr & Fischbacher, 2003, 2004a; Fehr et al., 2002; Fehr & Rockenbach, 2004; Fehr & Schmidt, 1999; Gintis et al., 2003). The third possible reason why non-human primates showed a weak sense of fairness might be that they seem to lack the ability to compare their own *efforts* to those of others. These two aspects—*outcomes* and *efforts*—need to be considered in relation to each other to allow a sense of fairness. Only if I can successfully determine my own cost/benefit ratio in a given situation, I am able to perceive a certain scenario as fair or unfair. It is exactly this cognitive flexibility that allows human individuals to perceive the similarity (fair or unfair) of different situations even though the single parameters (total outcome and total effort) differ dramatically between one event and the other.

Finally, it is also possible that non-human primates are attentive to others and even able to compare *outcomes* and *efforts* to those of others, but that they simply do not care. In other words, they are simply lacking the motivation to evaluate and avoid inequity, which allows them to just focus on maximizing their own benefit. Both the cognitive and the motivational aspect are needed for a full-fledged notion of fairness as we find it throughout human cultures (Fehr & Fischbacher, 2003, 2004a; Henrich et al., 2006, 2010).

From the data available currently, we cannot tell whether the absence of many aspects of fairness is due to a cognitive or motivational lack in non-human primates. One question that arises is how crucial such a sense of fairness actually is for successful cooperation. In particular, the question is whether one needs a full sense of fairness—i.e. an interest in the ideal of equity—or whether some aspects of it, such as inequity aversion or the ability to compare outcomes are essential.

If we define cooperation in its widest sense, namely as behaviour that is beneficial to another individual or to both individuals involved in a task (Melis & Semmann, 2010), then a sense of fairness is not essential. Ants and amoeba probably do cooperate without comparing their own efforts and outcomes with those of others (Melis & Semmann, 2010). However, even if we talk about more complex collaborative problem solving, animals might be successful without the described aspects of fairness. Indeed, some observations certainly seem to point in that direction. We know from field studies that non-human primates cooperate when they breed, when they acquire food, compete for mates and when they protect conspecifics or defend territories (Boesch & Boesch-Achermann, 2000; Burkart, Hrdy, & Van Schaik, 2009; Geissmann & Orgeldinger, 2000; Mitani, 2006; see Melis & Semmann, 2010 for a review). According to Boesch and colleagues, chimpanzees in Tai National Park not only coordinate their actions during a hunt, but their different 'roles' are also rewarded differently. Active hunters get more

meat than non-hunters, and good hunters receive the most meat (Boesch & Boesch-Achermann, 2000; Boesch & Boesch, 1989). Others have challenged this fairness-based interpretation by emphasizing other factors (e.g. social rank) that sufficiently explain meat-sharing patterns in chimpanzee populations (Gilby, Eberly, & Wrangham, 2008; Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992; Stevens & Gilby, 2004).

A number of recent experimental studies have addressed the question of how primates cooperate and what they understand about their partners' roles and efforts in cooperative tasks. In most of these studies, pairs of subjects were confronted with a food retrieval task in which the food was placed on an out-of-reach platform. In order to get the food, subjects had to cooperate by simultaneously pulling a rope. Capuchin monkeys and cotton-top tamarins were able to solve the problem although it is still a matter of debate whether they fully understand the role of the partner (Cronin, Kurian, & Snowdon, 2005; Hattori, Kuroshima, & Fujita, 2005; Mendres & de Waal, 2000; Visalberghi, Quarantotti, & Tranchida, 2000; see also de Waal & Suchak, 2010). Brosnan, Freeman, & de Waal (2006) tested how capuchin monkeys responded to distributional inequity in such a food retrieval task. Subjects could freely choose whether to participate and—depending on the partner's behaviour—which reward they received for their participation. While the equity of the reward distribution did not affect success or pulling behaviour, cooperation was three times higher for pairs in which partners took turns receiving the better reward as compared to those in which one dominated the better reward.

The majority of the chimpanzees tested have been very successful in coordinating their pulling efforts. It also turned out that their ability (and/or willingness) to coordinate was strongly dependent on their relationship to the partner. Dyads that were observed sharing food outside the testing context cooperated much better than chimpanzees that were less tolerant of each other (Melis, Hare, & Tomasello, 2006b). Supporting evidence comes from experimental studies with bonobos, which are more successful than chimpanzees at solving such kinds of problems (Hare, Melis, Woods, Hastings, & Wrangham, 2007). Those authors have proposed that this is exactly because of bonobos' generally higher tolerance levels compared to chimpanzees (although see Jaeggi, Stevens, & van Schaik 2010). In this regard, it is interesting that in the recent study by Bräuer et al. (2009), bonobos were indeed the only ape species with a tendency to show aversion to inequity.

In addition to tolerance as a factor facilitating cooperation, there is also strong evidence that at least chimpanzees have some knowledge of the specific 'technical' contribution of the partner in a cooperative task (Hirata & Fuwa, 2007; Melis et al., 2006a, 2006b). They recruit a partner only when solving the problem requires collaboration, and when given a choice between different partners they prefer the most skilful collaborator (Melis, Hare, & Tomasello, 2006a).

In a recent study Melis, Hare, and Tomasello (2009) were able to show that chimpanzees also coordinated their actions when they had to negotiate which tray to pull—the one with the unequal or the equal amount of food (e.g. 10/1 and 5/5 respectively). This created a conflict of interests between partners because failure to work together resulted in a zero outcome for either partner. Remarkably, the

chimpanzee pairs cooperated successfully in 78–94 % of the trials. Dominant individuals preferred the unequal option to obtain the largest outcome. However, subordinates were also able to get their way—the equal option—in 22–56 % of trials. The authors discuss whether sensitivity to inequity had an impact on the behaviour of the chimpanzees tested. While dominants showed no preference for equity—as they always offered selfish splits—one could argue that subordinates showed signs of inequity aversion because they often refused unequal offers that were disadvantageous for them. Those subordinates were seemingly dissatisfied whenever they received less food than the dominant in exchange for equal effort after cooperation. However, it is also possible that the subordinates' refusals resulted from a pragmatic approach, i.e. that they were simply attempting to manipulate the dominants' behaviour to acquire a larger reward for themselves (i.e. the equal tray). Indeed, in a control condition in which the equal tray was not reachable and they could choose whether to pull or not, subordinates accepted the disadvantageous unequal split. If they were averse to inequity, then they should not have pulled in this condition.

The findings from these cooperation studies are thus in line with findings discussed above about fairness—at least for chimpanzees. Apparently, subjects behave as rational resource maximizers without any strong preference to equitable outcomes even in a cooperative context. It seems that our strong sense of fairness is indeed something uniquely human and exists only rudimentarily in non-human primates. While cooperation in animals might typically be maintained in a rather passive way, humans have evolved active enforcement mechanisms, such as reward, punishment and reputation building. That in return may have required humans to evolve unique cognitive mechanisms to keep track of individuals' contributions in collaborative activities and to control for cheaters (Melis & Semmann, 2010).

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