

## Capuchins (*Sapajus apella*) and their aversion to inequity

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Humans have a strong sense of fairness and are usually averse to unequal treatment for the same action. Ever since Brosnan and de Waal showed a similar effect in capuchin monkeys (*Sapajus apella*), various studies, using different experimental methods and study populations, have been conducted to investigate whether animals show inequity aversion like humans do. Since capuchin monkeys are still the best-studied animals in this area, our first aim was to synthesise the findings in this literature. We found that there is mixed evidence for inequity aversion in capuchin monkeys. Our second aim was to explore this variation by focusing on the following factors: the type of task used, the feeding regime outside the experiment and the monkeys' social environment. We found that responses to inequity systematically varied as a function of the task demands and the feeding regime, but not the social environment. Tasks, in particular pulling tasks, that required effort from the participants to get the food were more likely to detect evidence of inequity aversion. Moreover, monkeys that had access to food before or after testing, were more likely to show inequity aversion than those who were temporarily limited in their access to food. We hope this chapter raises awareness for the complexity of the concept and generates new testable hypotheses, which might advance our understanding of the theoretical foundations of inequity aversion.

**Keywords:** Capuchin monkeys, inequity, inequity aversion, fairness, food sharing

## Introduction

*You are not you when you are hungry – Snickers®*

Humans across cultures have a strong sense of fairness (Debove, Baumard, & André, 2017; Fehr & Schmidt, 1999). Fairness is usually studied in resource allocation tasks, in which individuals receive equal or unequal treatments for the same or different actions (e.g. Cowell, Sommerville, & Decety, 2019; Schmidt, Svetlova, Johe, & Tomasello, 2016). Humans are generally averse to unequal treatment for the same action or equal treatment of different actions, i.e. they protest, reject unfair offers and even punish those who act unfairly (Henrich et al., 2006; Oosterbeek, Sloof, & van de Kuilen, 2004). Interestingly, they respond to both disadvantageous, i.e. receiving less than others, and advantageous, i.e. receiving more than others, situations (Fehr, Bernhard, & Rockenbach, 2008). Thereby, we act unlike *Homo economicus*, who tries to maximize her own gains and who should accept unfair offers as long as the offers are greater than zero (Henrich et al., 2005). Instead however, we pay close attention to what others get in relation to what we get (see above). This behaviour is deeply rooted and develops early in middle childhood across different societies (Blake et al., 2015).

Despite its ubiquity, the evolution of inequity aversion is difficult to explain because it involves costly acts, e.g. punishment, and often leads to benefits being lost, even if they are smaller than that of others. Thus, this behaviour is not only costly, but also seems to provide no benefits to the actor and consequently should not evolve. Although inequity aversion serves no obvious immediate benefits, the behaviour might have evolved because of its delayed benefits. First, although individuals should accept any offer that is providing them with at least some benefits, selection acts on relative levels. This means that individuals compete with others and aim at receiving more benefits than others to outcompete them. Therefore, comparing outcomes and responding negatively to different outcomes is beneficial to maximise relative outcomes (Fehr & Schmidt, 1999). Second, most individuals can choose to interact with partners from a pool of several (Noë & Hammerstein, 1995). Responding negatively to unfair partners can thus be in the interest of the actor by either ensuring this partner will

behave fairly in future interactions or by withdrawing from interacting with this unfair partner in the future (André & Baumard, 2011). Third, such partner choice based on fairness has important consequences for the evolution of cooperation, which provides additional benefits (e.g. Melis & Semmann, 2010). This is because cooperation can be favoured and stabilised through fairness (Brosnan, 2011; Debove et al., 2017).

Given that inequity aversion has adaptive significance, is widespread in humans and emerges early in our ontogeny, it is surprising how little we know about its evolutionary origins. By studying inequity aversion in several species, we can make inferences, for instance, about when and under which conditions this behaviour might have evolved and whether the evolution has happened in steps (cf. Brosnan, 2013). One of the first studies on inequity aversion in animals investigated the behaviour of the brown or tufted capuchin monkey, *Sapajus [Cebus] apella* (Brosnan & de Waal, 2003), which is a highly social New World primate from South America (fig. 1). In this study, the monkeys could exchange a token for a food reward. However, while one monkey received a cucumber for the token, a neighbouring monkey received for the same action a much more valued reward, in this case a grape. Although the cucumber was better than nothing, the monkeys either refused to eat the cucumber or refused to hand back the token in approximately half of the trials. This effect was only shown in females and was even more pronounced, when the partner received the grape for free while the other monkey had to work for its cucumber piece.

Almost 20 years and dozens of publications later, capuchin monkeys have become one of the best-studied species in this area. (Note that this study has also stimulated research in several other species, which are reviewed by McGetrick & Range, 2018). However, the results in capuchins have not always been consistent, with a number of studies failing to replicate the original findings. Variation in results between studies is commonly attributed to methods, and additional studies have shown that some of this variation can indeed be attributed to methods. For instance, evidence of inequity aversion is dependent on the effort required from participants (Brosnan & de Waal, 2014). In effort-free tasks, responses to inequity do not occur despite unequal food distribution. In other cases, assigning variability

to methods is more problematic because some studies have been conducted in different labs using the same methods, but they have produced discrepant results.

The aim of this chapter is to synthesize the available evidence in an attempt to explain this variation by asking does the variation simply reflect noise or are differences related to the conditions under which monkeys are studied? Ultimately, by synthesising what has been learned from studying these monkeys, including the factors that affect their responses, we are hoping to draw the wider implications for the theoretical foundations of inequity aversion. The chapter is organized as follows. First, we provide an up-to-date overview of the literature with an emphasis on the different tasks that have been employed. Second, we investigate the variation in the outcome of such studies by comparing the feeding regime outside the experiment and the monkeys' social environment. If necessary, we complemented the information listed in each of the studies with contacting the main researchers who conducted the studies to share information on three areas: feeding regime, subject relationships, and social housing. We close by drawing some implications that we hope will contribute to advance our understanding of inequity aversion in animals.

### **Inequity aversion in capuchin monkeys: the state of the art**

Our survey of the literature returned 17 studies on inequity aversion in capuchin monkeys (see tab. 1). Fifteen of the studies correspond to one of the following three tasks: token exchange, bar/drawer pulling and free-food distribution. Next, we focus in more detail on each of the tasks by presenting their basic procedure and main results. Because some studies included multiple experiments and included more than one task, we will use the word 'dataset' to refer to a particular experiment or task within a published paper and will reserve the word "study" to refer to the published study itself.

### *Token exchange*

Researchers have used this task primarily to study inequity aversion and prosociality (cf. Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016), including the motivational basis for rejecting food items. The basic procedure consists of pairs of capuchins exchanging a token for food with an experimenter. Thus, this task requires some effort (give the token) to obtain the food item. While one of the capuchins obtains a high-quality food item for her effort (e.g., grape), her partner obtains a low-quality item (e.g., cucumber) for the same effort. Researchers measure the willingness to exchange the token and whether the low-quality food is eaten. Although the quality of the reward received by the subject is the most common manipulation, researchers have also varied inequality in other ways including effort (extra cost for the same reward) and the quantity (less food for equal effort). Most studies have used transferring high-quality food to an empty cage (no social comparison possible) as a control condition but some studies have included no token exchange (see free-food distribution section) and varied whether high-quality food is visible or not. Five data sets have yielded evidence of inequity aversion and five have not. Researchers have reported evidence for inequity aversion for quality and effort but not quantity. Moreover, some of the positive results concern only females, and most studies used only interactions with familiar partners.

### *Bar/drawer pulling*

This task has been primarily used to investigate inequity aversion and the factors that may modulate its appearance. Moreover, this task has been used to validate the finding of the token exchange task by adding a different paradigm that eliminates some of the limitations of the original task. The bar/drawer pulling task, just like the token exchange task, incorporates effort in the form of pulling a bar or drawer. Unlike the token-exchange task, the experimenter does not play an integral role in the task. She simply sets it up and conspecifics solely interact with each other. Pairs of capuchins sit side-by-side separated by a partition or face each other with the apparatus placed between them. Depending on the type of apparatus used, the subject can pull a bar or drawer to deliver food to herself and/or

the partner. It is important to note that studies using this design measure whether subjects make fair or unfair offers, while the token-exchange and free-food distribution tasks measure the response to fair or unfair offers. Typically, the subjects can choose between equality (e.g., one grape for each partner) and advantageous inequality (e.g., one grape for the subject and none for the partner). Some studies have also used disadvantageous inequality (e.g., no grape for the subject and one for the partner). Alternatively, researchers have manipulated effort instead of quality by keeping the quality between the two options equal but making one of them harder to pull. Four of the five datasets have produced evidence of inequity aversion in quantity or effort. Owing to the diverse food item combinations used, next we provide a more detailed presentation of the results.

Fletcher (2008) reported that capuchin operators preferred equity over disadvantageous inequity, which is consistent with token exchange studies in which subjects were typically the recipients. Takimoto, Kuroshima and Fujita (2010) also used this method but contrasted equity and advantageous inequity. They found that capuchins facing subordinate recipients preferred equity over advantageous inequity, further reinforcing the notion of a preference for equity. However, Takimoto and Fujita (2011) could not replicate this result except when both partners played a role in obtaining the food, but not when the operator alone provided the food. Takimoto and colleagues (2010) also found that when the subordinate recipient was behind an opaque occluder, subjects no longer preferred equity over advantageous inequity.

Monkeys facing a dominant individual responded somehow differently. They showed indifference between equity and advantageous inequity when the dominant was visible, which could be construed as a weak preference for advantageous inequity. However, they displayed an overt preference for advantageous inequity when the dominant recipient was behind the opaque occluder. Takimoto and Fujita (2011) did replicate their original result (indifference) in the case of a dominant recipient and just like it was the case for subordinate recipients, subjects shifted to a preference for the equitable option when both partners contributed to obtaining the food. Brosnan, Freeman and de Waal (2006) also used a bar-pulling cooperative task that required both monkeys to simultaneously pull a bar to bring

food within reach. In some cases, both monkeys received the same type of food but in other cases one of the monkeys got better food than the other. Brosnan and colleagues (2006) reported that capuchins solved the task regardless of the food that each of the partners obtained, seemingly indicating a lack of inequity aversion. However, partners who alternated more often which food they obtained in the unequal condition were more successful than those who did not.

Takimoto et al. (2010) also contrasted disadvantageous and advantageous inequity when facing a subordinate or a dominant recipient. Here the equity option was not available and they found that capuchins preferred disadvantageous inequity (they gave more to others than what they got themselves) but they showed indifference between the options, which in this case can be construed as a form of equity, when they faced the dominant recipient. In summary, most datasets, in some form or another, seem to indicate a preference for equity although the use of different choice options and the small sample size makes drawing robust conclusions extremely difficult.

#### *Free-food distribution*

Researchers have used this task primarily to investigate the effect of effort on inequity aversion responses and less prominently to assess the modulating effect of social factors such as tolerance and dominance as well as the contribution of frustration in determining responses. The basic arrangement for this task is the same of the token-exchange task except that the experimenter provides food to the subject and the partner without requiring the transfer of a token. Thus, unlike the previous two tasks, this task does not require any effort from any of the participants to obtain food.

Just like in the token-exchange task, subjects and partners in the experimental condition receive food items that differ in quality, or in the case of one study, quantity. Several studies did not include any control conditions other than an equality condition, partly because this task is often used as a control for the token exchange task. Those studies that included control conditions varied whether the partner was absent or present but unable to reach the food given to her. All five studies using this setup have

found no evidence of inequity aversion. This means that capuchins are indifferent to the gains of others when they have spent no effort in obtaining the food.

*Effect of different tasks on likelihood to find inequity aversion*

Table 2 summarizes the results of these tasks and also includes two studies using other paradigms that have provided no evidence of inequity aversion in capuchin monkeys. Two findings are particularly noticeable. First, the bar/drawer pulling task has produced mainly positive results, the free food distribution task uniformly negative results and the token exchange task has produced mixed results. Second, the three laboratories with the higher number of studies have produced opposing results. Researchers working with the capuchins from the 'Language Research Center at Georgia State University' and the 'Yerkes National Primate Research Center of the Emory University' have reported positive results in the token-exchange task. Researchers working with the 'Primate Center of the Institute of Cognitive Sciences and Technologies' capuchins have reported uniformly negative results in three of the tasks. The rest of the laboratories present a mixture of positive and negative results, which taken in isolation are hard to interpret due to the small sample size.

Different methods, different populations, and different laboratories have produced a mix of positive and negative results. This resulted in a lively and still ongoing debate about whether the studies test inequity aversion or whether confounding effects can explain the findings (e.g., Bräuer & Hanus, 2012; Henrich, 2004b; McAuliffe et al., 2015; Wynne, 2004). The initial findings were challenged on the grounds that they may indicate frustration at not getting a more valuable visible food rather than reflect any sort of social comparison (Dubreuil, Gentile, & Visalberghi, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006). However, inequity responses disappear when effort is eliminated in the effort-free food distribution task (e.g., Dindo & de Waal 2007; reviewed in Brosnan & de Waal 2014). This means that even though a discrepancy in food allocation, and hence frustration between partners is still present, capuchins do not reject food of lower quality than their partners. Other researchers questioned these findings by arguing that rejecting lower quality exacerbates the effect that caused the response



in the first place because the partner is unaffected by the subject rejecting food of a lower quality (Henrich, 2004b; McAuliffe et al., 2015). In fact, by rejecting low quality food the subject *increases* rather than *decreases* the inequity with her partner. While this is the case for token-exchange and free-distribution tasks, bar/drawer pulling tasks investigate whether subjects choose a fair or unfair distribution and hence avoid this issue.

Some of the failures to replicate have been attributed to the physical arrangement of the participants. In some studies partners sit side-by-side separated by some partition (e.g., mesh) while in other studies they face each other. De Waal (pers. comm., 15 April 2020) mentioned that the spatial disposition of the individuals might be important, with side-by-side arrangements more likely to yield evidence of inequity aversion. Indeed, most positive findings were obtained using side-by-side designs. However, three studies used an arrangement where partners faced each other in a drawer pulling task but they still found evidence of inequity aversion (cf. tab. 1). This suggests that the spatial disposition cannot explain all the variation in the data.

As effective as some of these counterarguments can be in explaining some of the negative results, some tasks do replicate the methods of the original studies, including effort present and the right spatial disposition and still find no evidence of inequity aversion in the token exchange or the bar/drawer pulling tasks (cf. tab. 1 & 2). At the same time, some of the proposed confounding effects have been addressed but could not fully explain why studies resulted in positive findings. So, the mixed evidence remains. Confronted with mixed results, readers have two basic options: dismiss a subset of them on methodological grounds or consider the possibility that both subsets may be valid as they reflect the natural variation in the prosocial behaviour of capuchin monkeys. Our intention in writing this chapter was not to add just another piece to the long list of articles pointing out the weaknesses in this literature (e.g., Bräuer, Call, & Tomasello, 2006). Our goal here was to explore the second option by taking a more holistic approach that we hope will bring some balance and clarity. To do so, we turn our attention to the between-study factors that might account for this currently unexplained variability.

## **Factors that could influence behaviours in unequal situations**

When we disregard datasets that involve effort-free situations ( $n=5$ , tab. 2; cf. Brosnan & de Waal 2014), nine datasets find evidence for inequity aversion, while six do not (see tab. 2). Interestingly, our review of the literature revealed some consistent results within laboratories (tab. 2). As we have outlined above, the studies differ in various aspects but investigate the same concept. Thus, the studies can be considered as conceptual replications (Nosek & Errington, 2020).

Mixed findings suggest that inequity aversion may not be a reliable finding. Still, it is surprising to find so many positive findings in this case. One explanation is that different conclusions might be explained by a confirmation bias, i.e. unconsciously biased experimental design, data collection, data analyses or publication (Ioannidis, Munafò, Fusar-Poli, Nosek, & David, 2014; Stevens, 2017). Another explanation might be that studies based on small sample sizes are more likely to result in wrong conclusions (Colquhoun, 2014) and are less likely to be replicable (Farrar & Ostojić, 2019). Given that the median sample size is only eight (tab. 1), this might be a source of concern. Furthermore, there is marked variation in the response between participants (Price & Brosnan, 2012). Hence the small sample size and noisy measurements make the finding vulnerable to different conclusions and hence reduced replicability.

However, more than half of the studies have resulted in positive findings, obtained in several laboratories, which make confirmatory biases and false positive explanations unlikely. Variation in results may represent systematic differences that can inform the theoretical foundation and generalisability of inequity aversion. Here, we argue that capuchin monkeys might show inequity aversion, but only under some conditions. Different research groups seem to find almost exclusively either positive or negative evidence, which might point towards conditional-dependent evidence (tab. 2). Methodological approaches of different research groups vary inevitably from each other, as the study subjects and keeping conditions differ greatly from each other. Although the differences seem minor, they might represent systematic differences that could affect findings, leading to this mixed picture. Here, we

argue that moving beyond the question ‘whether inequity aversion in capuchins exists or not’ to asking ‘under which conditions is it expressed’ is more informative. We hope that by identifying those sources of variation and their impacts on inequity responses, we might be able to advance the theory of inequity aversion.

To investigate such sources of variation, we proposed several factors and predicted their influence on inequity aversion responses in capuchin monkeys. We then discussed those factors with authors of the studies, listed in table 1, to complement our literature review. We asked them about the feeding and housing conditions of their monkeys and the relationship between the participants (box. 1). Almost all researchers shared such information with us, covering the main research facilities which included the Graduate School of Letters of Kyoto University [JP], Laboratory of Comparative Ethology of the National Institutes of Health Animal Center [USA], Language Research Center at Georgia State University [USA], Primate Center of the Institute of Cognitive Sciences and Technologies [IT] and Yerkes National Primate Research Center of the Emory University [USA]. Thus, our chapter covers information about 13 of the 17 published studies. We summarise the information in tab. 3. Below we discuss the factors that may influence inequity responses. We distinguish in our predictions whether the factors might decrease the motivation to engage with the task and whether the factors might bias the response of the monkeys for the low- or high-value food option.

### *1. Food before testing*

*Hypotheses:* Individuals tested before feeding, i.e. when they are a bit hungry, might be more likely to engage in the task and less likely to reject a low-value offer compared to those that were tested directly after feeding, i.e. they are less hungry. For instance, children tested in the morning without breakfast showed a decline in memory and attention (Wesnes, Pincock, Richardson, Helm, & Hails, 2003). Hence capuchin monkeys without their breakfast might also pay less attention to the task and are more likely to take any option. Hungrier individuals might also show the opposite response because they may perceive the high-value offer as so rewarding, that they are more likely to protest and reject the low-

value offer in order to try to get access to the better food. A similar effect was observed in Norway rats (*Rattus norvegicus*). When given the choice between three food options, here normal chow, Special K and chocolate-flavoured cereals, hungry rats preferred the chocolate cereals, whereas satiated rats showed no difference between the two cereals (Barbano & Cador, 2005). This result suggests that hungry rats show a stronger response for high-value food, which might be similar to the monkeys under such conditions.

*Results:* We found that monkeys that were either fed before the experiment, e.g. a little reward for entering the testing compartment, or still had food from a previous feeding available (e.g. *ad libitum* feeding) were more likely to show inequity (3 facilities). In contrast, monkeys that received their food after the test or had to wait in a transport box without food before the test were less likely show inequity aversion (3 facilities). Please note that there is one exception, i.e. a lab that only feeds their monkeys in the evening and tests them in the morning (#1 in tab. 3). The studies in this lab were consistently conducted as first studies in the morning and resulted in support for inequity aversion. Hunger has not received much attention in such tasks. A study on rats that were food restricted still found evidence for inequity aversion (Oberliessen et al., 2016). Similarly, the time of the last meal did not change inequity aversion in children (Bowie, 2013), nor the evaluation of unequal situations (Huppert, Shaw, & Decety, 2020). However, we are not aware of a study manipulating hunger levels to determine its effects on inequity aversion. For example, hunger might change impulsivity that can lead to the acceptance of any food rewards, even if this is a suboptimal choice (Laude, Pattison, & Zentall, 2012; Mayack & Naug, 2015).

## 2. Food after testing

*Hypotheses:* Individuals who have constant access to food, i.e. also after testing, might be more likely to engage with the task and accept any, i.e. also the low-value, offers simply because they might prefer working for food than just receiving food for free during feeding times (Inglis, Forkman, & Lazarus, 1997; but see Anselme, Dreher, & Güntürkün, 2018). In contrast, individuals who have access to food

after the testing could be more likely to reject low-value food than those who do not have such access because they can afford rejecting food options in light of the constant food availability. In other words, a cucumber might be of so low value that it might be better to wait until returned to the main cage to feed on monkey chow.

*Results:* All research facilities that reported *ad libitum* access to food or fed goodies to their subjects after testing, find consistent evidence for inequity aversion in capuchin monkeys (2 facilities). One facility (#4, tab.3) provides no *ad libitum* food to their monkeys but finds evidence for inequity aversion in capuchins. Here, the monkeys are fed four times a day in addition to receiving regular snacks, which is probably comparable to *ad libitum* feeding. The monkeys of lab #1 (tab. 3) were fed every evening and tests were done early in the morning. Although their access to food is more restricted, all studies of this lab resulted in evidence for inequity aversion. It is important to note, that these monkeys are used to several tests a day and the studies that we included here were consistently conducted the first in the morning. The monkeys probably learned that there will be other tests, involving food, right after this test. Furthermore, they commonly received the remainder of their daily ration when returned to their home cage. Hence these monkeys had the expectation of receiving additional food right after testing. Research facilities that feed their monkeys at specific times (usually once or twice a day) and where there is usually no left over available before or after the testing, find no evidence for inequity aversion (3 facilities).

Taken together these results seem to indicate that monkeys who had access to (potentially better) food after the test are more likely to reject low-quality food compared to monkeys whose access to food is more regimented. In a sense, one could argue that inequity aversion is a trait of monkeys who can “afford” it. Food availability can alter the perception of risk in this situation, which is known to change food-related decisions (Watson & Platt, 2008). Facilities that found no evidence for inequity aversion could repeat some of their tasks and vary whether monkeys receive plenty of food for some days in contrast to their normal feedings scheme. This would help to investigate the role of *ad libitum*

feeding experimentally. In addition, the risk-taking behaviour of monkeys from different facilities could be compared to study different risk perceptions of the monkeys depending on their feeding scheme.

### *3. Food quality of the rewards in comparison to daily food*

*Hypotheses:* If the food rewards in the test are perceived as more valuable compared to their normal diet, e.g. monkey chow, the individuals might be more likely to engage with the task and they might be more likely to accept also low-value offers. Dogs, for instance, prefer variation in their training rewards (Bremhorst, Bütler, Würbel, & Riemer, 2018) and hence monkeys could aim for a similar effect by accepting any offer to increase variation. Especially, if the low-value offer is comparable to the daily diet but not the high-value offer, individuals might be more likely to reject the low-value offer. Children, for instance, request and eat more high-value food, if this type of food was not in their normal diet for an extended period of time compared to when the same food was part of their diet (Fisher & Birch, 1999).

*Results:* Almost all the rewards used in the studies were part of the monkeys' diet in some form. They were either used in training or preference phases, regularly used in other experiments or part of their normal daily diet. We found some variation regarding which reward was part of their diet, i.e. both rewards or only the low-/high-value reward. Of those facilities that commonly report positive evidence, all used rewards that are part of the monkeys' diet. More specifically, three based their experiments on rewards that were part of their diet, while one facility used rewards dependent on the roles of the participants that were either both or only one part of their diet. Although it seems that using rewards that are part of the diet increases the likelihood of finding inequity aversion, this finding stands in contrast to our predictions and should be investigated further before drawing any conclusions. Further, we only had information from two facilities that consistently find no evidence. Both facilities reported that only one reward was part of the monkeys' diet. However, this was in one situation the high and in the other the low-value reward. Hence, we conclude that familiarity with the rewards is

unlikely to explain the variation in the findings. Still, future studies should record this detail to investigate whether the relative value of rewards influences the likelihood of finding a certain outcome in these studies.

#### *4. Familiarity and tolerance between participants*

*Hypotheses:* The more individuals are familiar and tolerant towards each other, the less likely they might protest and reject the low-value option compared to when they are tested with a stranger because they do not begrudge their familiar partner the food. While this effect was shown in a study on chimpanzees, *Pan troglodytes* (Brosnan, Schiff, & de Waal, 2005), it was not found in long-tailed macaques, *Macaca fascicularis* (Massen, van den Berg, Spruijt, & Sterck, 2012) and in another study on chimpanzees (Brosnan et al., 2015).

*Results:* All researchers reported that the subjects were familiar and highly tolerant with each other. Therefore, this cannot explain the variation in the available data. One study, set out to investigate inequity aversion in dependence of relationship quality, found that the effect was more pronounced between familiar partners (de Waal, Leimgruber, & Greenberg, 2008). Future studies could also compare inequity responses between strongly and less strongly bonded individuals to assess the impact of relationships.

#### *5. Social housing*

*Hypotheses:* Individual- or pair-housed individuals might lack the same opportunities that group-housed individuals encounter to practise fairness. Hence, such monkeys might be less likely to reject low-value offers because they might not have faced such situations often enough to respond adequately. In contrast, individual or pair-housed individuals might be more likely to reject low-value offers because the consequences of their behaviour are minimal since punishment can only be exhibited by maximally one partner instead of a whole group. This effect was suggested for chimpanzees housed in pairs or in a group (Brosnan et al., 2005).

*Results:* Four facilities reported that they house their monkeys in small groups, i.e. below five individuals. Two of them report consistently no evidence for inequity aversion. It should be noted, however, that the other two facilities kept their monkeys in pairs or trios and still found evidence for inequity aversion (#3 & #5 in tab. 3). This shows that social housing is unlikely to impact the likelihood of finding inequity aversion in these monkeys.

### 6. Group stability

*Hypotheses:* The longer individuals have lived together, the more likely they have formed stable social bonds and dominance hierarchies. Based on increased predictability of their partner's behaviour, the individuals might be more likely to engage in the task, shown in chimpanzees (Brosnan et al., 2015), and less likely to reject the low-value offer, also demonstrated in chimpanzees (Brosnan et al., 2005). Alternatively, one could predict that the longer individuals have lived together, the more they pay attention to fairness because they repeatedly experience fair or unfair situations together. Hence, they might be more likely to reject low-value offers in the presence of such a partner. Although plausible, this effect was not shown in chimpanzees that show inequity aversion independent of how stable their group was (Brosnan et al., 2015).

*Results:* All research facilities reported that they worked with stable groups, which precludes us from drawing any conclusions on whether it might influence responses to unequal situations. This demonstrates that group stability cannot explain the variation in the published studies. This factor is difficult to assess in future studies because it is questionable to interrupt the group stability for research purposes. Social structures change if some individuals are temporarily removed or die (Byrne, Abbott, & Suomi, 1996), which can be used for future studies. Naturally, however, stable and unstable groups differ in many aspects and unstable groups are rare, complicating the interpretation of a finding.

### 7. Dominance

*Hypotheses:* Subordinates might be more likely to accept a low-value food offer in the presence of a more dominant individual than *vice versa*. This effect was found, for instance, in chimpanzees



((Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010), but see (Brosnan et al., 2005)) and rats (Oberliessen et al., 2016). This effect is likely to be different in dominant partners that might be less likely to accept low-value offers. Nevertheless, a study investigating inequity aversion in apes found no evidence that inequity aversion was exhibited more strongly in dominants (Bräuer et al., 2006). In addition in long-tailed macaques, dominant and subordinate individuals did not differ in their response (Massen et al., 2012).

*Results:* Female and male capuchin monkeys form dominance hierarchies (e.g. Janson 1985). Accordingly, all researchers reported that there were some dominance differences between the participants. However, in retrospect it is difficult to assess how strong these differences were. Dominance can change the behaviour of these monkeys in such tasks (see above). However, to what extent is currently unclear. Hence, future studies could assess the dominance rank of individuals and incorporate this in their findings.

## **Conclusions**

In this chapter, we reviewed the evidence for inequity aversion in capuchin monkeys. Ever since the first report in 2003, several studies have followed, conducted in nine different laboratories with several monkey populations and using various methods. While nine datasets resulted in evidence for inequity aversion, six did not support this finding and five provided results that are difficult to interpret. This variation cannot solely be explained by different task designs. While free-food distribution tasks do not provide any evidence for inequity aversion in capuchin monkeys, the token-exchange and bar/drawer-pulling task result in overall positive, but also mixed evidence. An interesting pattern is, however, that different laboratories seem to provide consistently either positive or negative findings. By investigating methodological details, we aimed at exploring this variation. We found that social factors, e.g. familiarity or dominance between participants and social housing, explained no variation in the data. In contrast, feeding schemes explained some of the variation.

There was a good match between studies that resulted in positive evidence and participants having access to food after the test. Related to this, monkeys that had access to food shortly before testing, because they were either fed or had food from the last feeding still around, were also more likely to show inequity aversion compared to those that waited in a box without food or their breakfast was delayed because of the testing. Monkeys provided with plenty of food might perceive the situation as less risky or might respond less impulsive compared to monkeys provided with more temporally scattered food. These results suggest that capuchin monkeys differ in their response to unequal situations based on their feeding regimes.

Although we did not find evidence for the other proposed factors, additional factors might be interesting to explore in future studies, which might increase the variation further, but are difficult to assess retrospectively. For example, the energetic state or weight of the participants might be interesting. Individuals that are in greater need of food because they are in a poorer or more energy-demanding (e.g., pregnant) conditions might be more likely to accept any food offer and are thus less likely to show inequity aversion. In addition, personality differences, e.g. in extroversion and agreeableness, has been shown to affect inequity aversion in chimpanzees (Brosnan et al., 2015) and might also affect responses in capuchins. Personality is heritable (Penke, Denissen, & Miller, 2007) and often colonies are based on a few maternal lines. Hence, capuchin populations might also differ in their personalities, leading to variation in the findings.

We would like to end with a word of caution. We acknowledge that our findings are based on only five research facilities and thus represent a small sample size, even though they represent almost all studies on this species. Broadening this approach to other species might give insights into the generalisability of our finding. Currently, we cannot establish a causal relationship between the different feeding schemes and responses to inequality. Instead, we hope that our findings will stimulate future research, using carefully controlled experimental methods to test the here generated hypotheses. Eventually, this will help us to refine the theory of inequity aversion and clarify under which conditions individuals show this behaviour that is so common among humans of all cultures.

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**Box. 1** Additional methodological details

- Did the monkeys have *ad libitum* food or were there short times when there was no food available for them? yes/no
- Were the food rewards, used for the experiment, part of their normal diet? yes/no
  - If yes, which one? high-quality/ low-quality/ both
- Were the monkeys fed before the experiments? yes/no/some
- Were the monkeys tested with familiar in-group members? yes/no
  - If yes, would you say most of them were bonded? yes/no
  - If yes, were there dominance differences between test individuals? yes/no
- Were the monkeys housed in a social group with more than one social partner? yes/no
  - If yes, with more than five partners? yes/no
  - Are the monkeys housed in mixed-sex groups? yes/no
- Was the group established at least one year prior to the experiment? yes/no
- Was the dominance hierarchy stable when the experiment(s) was (were) conducted?  
yes/no
- If there are any studies that did not follow these general practices, we would greatly appreciate if you could point them out to us.





Figure 1 Capuchin monkeys

Inti (male) eating two spring onions while being observed by three females. The monkeys live in the RZSS Edinburgh Zoo's Living Links Research Center. Picture taken and kindly provided by Kate Grounds.

Table 1: Overview of studies investigating inequity aversion in capuchin monkeys

Evidence	Inequality	Benefit		Control	Task	Parti- cipants	Training	N	Sex	Age	Reference	Study motivation
		-/+	+/-									
Yes (in ♀)	Quality	x		No exchange, empty cage	Token exchange	Side-by-side, separated	Familiar with task	10	5♂, 5♀	Adult & subadult	(Brosnan & de Waal, 2003)	Inequity aversion
Yes	Quality	x	x	NA	Bar pulling	Side-by-side, separated	Familiar with task	10	2♂, 8♀	Adult & subadult	(Brosnan et al., 2006)	Equity for cooperation
No	Quality	x		Partner cannot reach food	Effort-free food distribution	Side-by-side, separated	No training	12	12♀	4-30	(Dindo & de Waal, 2007)	Equity and effort
Yes	Quality, effort	x		High value reward visible or invisible	Token exchange	Side-by-side, separated	Familiar with task or trained for 6 months	13	4♂, 9f	>4	(van Wolkenten, Brosnan, & de Waal, 2007)	Greed, frustration alternative
Yes (when familiar)	Quality		x	Covered experimenter's face	Token exchange	Side-by-side, separated	Familiar with task	8	8♀	Adult & subadult	(de Waal et al., 2008)	Equity in different relationships
Yes (in quality condition)	Quality, quantity	x		High value reward visible or invisible	Token exchange	Side-by-side, separated or together	Familiar with task	6	5♂, 1♀	7-22	(Talbot et al., 2018)	Violation expectation, separation
								7	7♂	5-10		
Yes	Quantity	x		Empty cage	Pull drawer	Opposite, separated	Familiar with task	8	8♂	13-21	(Fletcher, 2008)	Expectancy violation
Yes	Quantity	x	x	Empty cage, blocked visual contact	Pull drawer	Opposite, separated	10 sessions per 10 trials	6	3♂, 3♀	6-13	(Takimoto et al., 2010)	Control partner's reward distribution
Yes	Effort	x	x	Empty cage	Pull drawer	Opposite, separated	12-18 sessions per 12 trials	6	3♂, 3♀	8-15	(Takimoto & Fujita, 2011)	Effect of dominance

No	Quantity	x		NA	Effort-free food distribution	Side-by-side, together	No training	7	4♂, 3♀	Adult & subadult	(Amici, Call, & Aureli, 2012)	Social tolerance and dominance
No	Quantity	x	x	Empty cage	Token exchange, bar pulling	Side-by-side, separated	Training varied between tasks and subjects	10	?	?	(Amici, Visalberghi, & Call, 2014)	Species comparison
No	Quality	x		Empty cage	Effort-free food distribution	Side-by-side, separated	No training	6	2♂, 4♀	4-18	(Dubreuil et al., 2006)	Equity and effort
No	Quality	x		NA	Token exchange	Side-by-side, separated	?	11	11♀	6-26	(Silberberg, Crescimbeni, Addessi, Anderson, & Visalberghi, 2009)	Frustration alternative
No	Quality	x		NA	Effort-free food distribution	Side-by-side, separated	No training	8	8♀	Adult (mean: 9.75)	(Roma et al., 2006)	Frustration alternative
No	Quality	x	x	Partner cannot reach food	Rotating tray	Opposite, separated	3 phases; 13-20 sessions per 16 trials	8	2♂, 6♀	4-17	(McAuliffe et al., 2015)	Costly task
No	Quality	x	x	Empty cage	Token exchange	Side-by-side, separated	3 training and 5 preference phases; 20 trials each	4	1♂, 3♀	adult	(Sheskin, Ashayeri, Skerry, & Santos, 2014)	No-cost task
No	Quality, effort	x		Empty cage	Token-exchange, food distribution	Opposite, separated	Familiar with task	5	5♀	3.5-21	(Fontenot, Watson, Roberts, & Miller, 2007)	Equity and effort

We describe for each study whether it resulted in evidence for inequity aversion and whether the study used advantageous (+/-) or disadvantageous (-/+) situations for the actor. We also distinguish in which commodity the situations were unequal, i.e. quality (high vs. low quality rewards), quantity (more or less of the same reward) and effort (same or different action for the same rewards). Further, we describe the task and control situations and whether the participants were tested facing each other or sitting side-by-side and whether they were separated from each other or together in the testing room. Finally, we specify how many subjects were tested, their age and sex.

Table 2. Overview of different task designs to study inequity aversion in capuchin monkeys

Laboratory	Tasks				TOTAL
	Token exchange	Bar/Drawer pulling	Free-food distribution	Other	
Yerkes/LRC	++++	+	-		+++++ / --
Rome	--	-	--		----
Kyoto		++			++
NIH	+		-		+ / -
Yale	-			-	--
New Iberia	-		-		--
UGA		+			+
<b>TOTAL</b>	+++++ / ----	++++ / -	/ ----	/ -	+9 / -12

Table 3: The impact of food, partners and housing on inequity aversion

<b>Laboratory</b>		<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5*</b>	<b>6</b>	<b>7</b>	<b>8*</b>	<b>9*</b>
<b>Evidence for inequity aversion</b>		yes	yes	yes	yes	yes	no	no	no	no
<b>Food</b>	<b>Fed / or food available before testing</b>	no	yes	yes	yes	?	no	no	no	?
	<b>Ad libitum feeding</b>	no	yes	yes	no	?	no	no	no	?
	<b>Rewards part of diet</b>	yes	yes	yes (quality) and no (quantity)	yes	?	yes	yes	?	?
	<b>Which reward</b>	one or both	both	both	both	?	low	high	?	?
<b>Partner</b>	<b>Partner familiar/tolerant</b>	yes	yes	yes	yes	yes	yes	yes	?	yes
	<b>Partner bonded</b>	yes	yes	yes	yes	?	yes	yes	?	?
	<b>Dominance difference</b>	yes	yes	yes	yes	?	yes	yes	yes	?
<b>Housing</b>	<b>Housed with more than one partner</b>	yes	yes	some	yes	no	yes	yes	no	yes
	<b>Housed with more than five partners</b>	yes	yes	no	yes	no	no	yes	no	yes
	<b>Mixed-sex housing groups</b>	yes	yes	no	yes	?	yes	yes	yes	yes
	<b>Stable housing group</b>	yes	yes	yes	yes	?	yes	yes	NA	?
	<b>Stable dominance hierarchy</b>	yes	yes	yes	yes	?	yes	yes	NA	?

We complemented our literature review with information about the feeding schemes, relationship of participants with each other and housing conditions of the capuchin monkeys. The labs were assigned numbers to provide anonymised data. For labs marked with an asterisk, we had either no contact details or we had not received a reply to our e-mail. Two labs (#3 and #7) were part of the same facility, but the colonies were kept very differently, which is why we split up the labs. We tried to fill in the information for those studies based on the information given in the articles. Question marks indicate missing information.