Choices behind the veil of ignorance in Formosan macaques

Authors: Yi-Ta Lu[1†], Wei-hsiang Hwang[2†], Yi-Tsung Hsieh[1], Tsung-Yu Ho[1], Jian-Da Zhu[1], Chun-I Yeh[2], Chen-Ying Huang[1]

Affiliations:

[1]Department of Economics, National Taiwan University, Taipei, Taiwan.

[2]Department of Psychology, National Taiwan University, Taipei, Taiwan.

*Correspondence to: chenying@ntu.edu.tw or ciyeh@ntu.edu.tw.

† These authors contributed equally to this work.

Abstract: An ongoing debate regarding the evolution of morality is whether other species show precursory moral behavior. The veil of ignorance (VOI) paradigm is often used to elicit human moral judgment but has never been tested in other primates. We study the division of resources behind the VOI in Formosan macaques. Monkeys choose the equal division more often than what pure selfishness would imply, suggesting a degree of impartiality. To better understand this impartiality, we measure a monkey's reactions to two directions of inequity: one regarding inequity to its advantage and the other to its disadvantage. We find that disadvantageous inequity aversion correlates with the degree of impartiality behind the VOI. Therefore, seemingly impartial behavior could result from a primitive negative reaction to being disadvantaged. This suggests a mechanism to explain a tendency toward impartiality.

Significance Statement: Morality plays an important role in helping people cooperate. To understand the evolutionary basis of morality, we study whether other species show morally relevant behaviors. We run an experiment on monkeys to measure their division of resources. When their own advantage cannot be guaranteed, a stronger aversion to being disadvantaged could make an unequal division unattractive, resulting in an equal division. Therefore, a seemingly moral choice, such as the equal division of resources, could result from an aversion to being disadvantaged. Because an equal division should help cooperation, this suggests an evolutionary account of morality based on cooperation.

One Sentence Summary: Monkeys appear to act impartially behind the VOI, and their degree of impartiality correlates with the strength of disadvantageous inequity aversion.

Introduction

According to Darwin (1), morality rests on the need to cooperate. Morality regulates the interactions among individuals and enables smooth cooperation. Smooth cooperation in turn benefits individuals. Moral behaviors are hence selected. This evolutionary account raises the interesting question whether morality is uniquely human, as other species also cooperate. Nonhuman primates are particularly worthy of such investigation due to their evolutionary proximity to humans and sociality.

Previous research in nonhuman primates focuses on how a decision-maker (DM) reacts when it is aware how much it is receiving compared to a conspecific (2-13). If a DM is other-regarding, perhaps including reacting negatively to inequity, its reaction may lead to a more equitable outcome, which then makes future cooperation more likely. Hence, inequity aversion can regulate cooperation among individuals and is therefore morally relevant. One influential experiment shows that monkeys reject a lesser reward upon observing that a conspecific receives a better one (5). This suggests a specific direction for inequity aversion, called disadvantageous inequity aversion, as the DM receives less than the conspecific. The continuing research debates lively, with some researchers supporting the existence of inequity aversion (5, 8, 13-17) while others do not (7, 9, 10, 12, 18). The literature on this subject is extensive, including the study of several species (2, 4). Moreover, the ways how ecological factors such as kinship (19), social ties (20), and rank (13, 21) influence inequity aversion are examined. Overall, nonhuman primates are inequity averse to various degrees, but no definite conclusion has been reached regarding this subject as a whole.

We seek to assess the mixed results in the literature by studying a new morally relevant behavior. The use of a new behavioral assay can extend existing knowledge in two ways. First, it can tell us more about the specific moral behavior the new assay is designed to measure. Second, it can help us reexamine previously studied behaviors (here, inequity aversion) from a new perspective.

The new behavior we study is choices behind the veil of ignorance (VOI), as proposed by Harsanyi (22, 23) and Rawls (24). The VOI is a canonical paradigm used to bring about impartial judgments. The key of this paradigm is to elicit judgment in an impersonal way such that as the DM divides resources, it is ignorant about how much it personally will receive. For a DM dividing resources with a conspecific, behind the VOI, it only knows that the division applies to them. If the resources are divided unequally, one will be advantaged and the other disadvantaged. However, in this case, the DM cannot know who in particular will be advantaged, so it has no means of dividing resources in a way that directly favors itself. Its choices are therefore impersonal. Such impersonal choices, made from behind the VOI, are often shorthanded as VOI choices. They reflect the DM's judgment on what constitutes an impartial division.

In light of the VOI concept, previous nonhuman experiments have been conducted in front of the VOI, so to speak, as the DM knows how much it will receive as it is making the decision. The inequity measured by these experiments is either advantageous, as when the DM receives more

than a conspecific does or disadvantageous, when the DM receives less. By contrast, our main experiment is behind the VOI: we elicit impartial judgments. Naturally, impartiality and inequity are different, but we hypothesize that they might be connected. The ignorance that exists behind the VOI implies the DM can only know that the division applies to a conspecific and itself. When the resources are divided unequally, one of the two will be advantaged, and the other will be disadvantaged. If the DM is eventually advantaged, then ex post there is advantageous inequity. On the other hand, if the DM is eventually disadvantaged, disadvantageous inequity arises. This logic suggests that an unequal VOI division could have two possible consequences, depending on whether the DM is eventually advantaged or disadvantaged. Therefore, the VOI choices could be linked to these two directions of inequity. Whether both directions are important for determining VOI choices is an empirical question that our experiment will address.

We study a suite of choices from both behind and in front of the VOI, in Formosan macaques (*Macaca cyclopis*). We hope to contribute to the literature in three ways. By studying choices made from behind the VOI, we may obtain evidence indicating whether monkeys exhibit impartial behavior. By studying choices in front of the VOI, we can infer whether monkeys are inequity concerned, following previous work. By comparing choices made from behind and in front of the VOI, we can draw conclusions on how they are linked. This linkage leads us to speculate a possible underlying factor for it, which may further explain the mixed results found in the literature.

Results

The backbone of our experiment was a mini-dictator game between a DM monkey and a passive recipient monkey (RM). The DM faced two preset choices, where one was equal and the other was unequal. It made a choice of distribution of resources for itself and the RM. The RM had no choice. We described the apparatus, the pretests and the details of the experiment in **Materials and Methods**. As a quick summary, in the pretests, we made sure of two things. First, because the way in which the rewards were distributed between the DM and RM was key to this research, we tested whether the DM would take the distribution of rewards into account. Second, we made sure that the DM understood the spinning technique we introduced to implement the VOI condition. We also addressed a prepotent bias observed in primates (9).

We presented results in four steps. In the first step, we compared how often an equal division was chosen behind the VOI with a benchmark when the DM was alone, to infer whether the DM showed signs of impartiality. In the second step, we measured the advantageous and disadvantageous inequity concerns of the DM. In the third step, we linked VOI choices to these inequity concerns. This addressed how VOI choices might be determined and how influential the inequity concerns were. In the fourth step, we speculated on a possible underlying factor for the linkage we observed. We summarized our test results in Table S1 so that they could be quickly looked up when necessary.

Step 1: VOI

In the VOI condition, the DM chose between an equal division and an unequal division. We used grapes as the reward. The DM and RM each received 2 reward units in the equal division. This was represented by (2, 2). The unequal division had 3 reward units for the advantaged and 1 unit for the disadvantaged. We represented this by (3, 1). We counterbalanced the choice display whenever possible.

In the VOI condition, when making a choice, the DM should be ignorant of how much it would receive. Hence, after the DM made a choice, we spun the selected division. Half of the time, it was spun one loop. The other half of the time, it was spun one and a half loops (Fig. 1A, Movie S1). In Fig. 1A, we illustrated the case where the DM chose the unequal division. After this choice, if the selected division was spun one loop, the DM received 1 unit and the RM 3 units. This would make DM disadvantaged and the RM advantaged. If the selected division was spun one and a half loops, the reverse would occur. The DM received 3 units and was advantaged. In case the equal division was chosen, spinning had no effect, but we still spun for consistency. By spinning the selected division, monkeys could see that a division applied to them but the DM could be advantaged or disadvantaged. This visually implemented the impersonalization of the VOI and was meant to make it easy to understand (Movie S1). Each DM-RM pair received 32 trials carried out over 4 days.

We ran the VOI condition on 19 pairs of monkeys. This exhausted all possible DM-RM pairs in the lab. On average, DMs chose the equal division (2, 2) 33.56% of the time (standard deviation = 7.41%). Choice frequencies ranged from 21.43% to 46.88% (Fig. 1B). To understand whether this choice frequency was high or low, we compared the VOI condition with a control condition. The control condition was exactly the same as the VOI condition, with the single exception that no RM was present (Fig. 1C, Movie S2). As before, a division of (2, 2) gave the DM 2 units no matter how it was spun. Hence, it was a safe choice. A division of (3, 1), on the other hand, gave the DM 3 units half of the time. However, there was no RM for the other 1 unit, the remainder of the division. The other half of the time, the DM received 1 unit. Hence, (3, 1) was a risky choice. The control condition measured risk preferences and was hence called the Risk condition. Each DM received 32 control trials carried out over 4 days.

Because morality guided behavior to facilitate cooperation with others, the pursuit of self-interest should not be regarded as an indication of morality. In the Risk condition, self-interest was the only possible goal. Hence, if we found no difference between the VOI and Risk conditions, we would conclude that there was no evidence of impartiality. On the other hand, if we found a difference, there were two possibilities. The equal division could be chosen more often in the VOI condition. This case indicated impartiality. On the contrary, if the equal division was chosen less often in the VOI condition, this would suggest the opposite of impartiality.

Impartiality

DMs chose the equal division 22.54% of the time (standard deviation = 5.36%) in the Risk condition. Recall that they chose the equal division 33.56% of the time in the VOI condition. Hence, monkeys chose the equal division more often when an RM was present than when the RM was not

present. This was not just true on average. To see that, we measured the degree of impartiality for each DM-RM pair. We took the frequency the equal division was chosen and subtracted the corresponding frequency when the DM was alone in the Risk condition. This frequency difference was taken to reflect impartiality of a DM in the presence of an RM. In each case, impartiality was positive, as in all 19 pairs, DMs chose the equal division more often in the VOI than in the Risk conditions (Fig. 1B).

To test whether this degree of impartiality was positive, we ran a two-level random intercept regression. Because any two pairs with the same DM were correlated, the DM was modeled as a random effect to account for it. This was often used for repeated measurements of individuals (25). We explained the details in **Supplementary Materials**.

The intercept, estimating the average frequency difference between the VOI and Risk conditions across DMs, was positive and significant (intercept = 0.11, z score = 7.12, $p < 0.001$, all tests were two-tailed, n = 19 unless otherwise specified). DMs chose the equal division 11% more in the VOI than in the Risk condition, a significant difference. This was a strong indication that the monkeys were influenced by the presence of an RM to choose impartially from behind the VOI.

Step 2: In front of the VOI

To place impartiality behind the VOI in context, we compared decisions from behind the VOI to those from in front of the VOI. This was done to establish whether it was the resulting inequity that made the unequal division unattractive. From behind the VOI, the choice of an unequal division lead to the DM experiencing advantageous inequity or disadvantageous inequity. On the other hand, if the equal division was chosen, there would be no inequity. It was possible that inequity made the unequal division unattractive and hence the equal division was chosen. With no theory to constrain which direction of inequity would matter for the VOI choices, we studied both types of inequity. If inequity was the reason for impartiality behind the VOI, we would expect to find a link between inequity and VOI choices. This would allow us to speculate on the factor that could explain this linkage.

We ran what we called the Social condition to measure inequity. The setup was similar to that of the VOI, but we did not spin the choice after the DM's decision was made. Hence, the DM knew how much it would receive and was in front of the VOI.

Advantageous inequity

The Social condition had two sub-conditions: advantageous (Ad) and disadvantageous (Dis). In the Ad sub-condition, the DM chose between an equal allocation and an advantageous allocation. The equal allocation, represented by (3, 3), gave the DM and RM 3 units each. The advantageous allocation, represented by (3, 1), gave the DM 3 units and the RM 1 unit. The DM thus had an advantage (Fig. 2A). Because the DM received 3 units in both allocations, self-interest had no role. If the DM was averse to being advantaged over the RM, it would choose (3, 3) (26).

We used the term "division" for the VOI condition but the term "allocation" for the Social condition to differentiate. For example, the unequal division (3, 1) behind the VOI would be spun, hence the DM did not know how much it would receive. On the other hand, the advantageous allocation (3, 1) in the Ad sub-condition would not be spun, hence the DM received 3.

The two allocations, (3, 1) and (3, 3), were chosen for the following reason. We wanted to understand why the equal division was chosen more often behind the VOI, that was, why the unequal division was chosen less often. When the unequal division was selected and spun so that the DM was advantaged, the outcome was the DM received 3 and the RM received 1. We therefore made the advantageous allocation the same as this outcome. Hence, the advantageous allocation was (3, 1). To ensure that the DM received the same in both allocations, such that self-interest had no role, the DM had to receive 3 units in the equal allocation. Finally, equity implied the RM should also receive 3. The equal allocation was therefore set to (3, 3).

Disadvantageous inequity

In the Dis sub-condition, the DM chose between an equal allocation (1, 1) and a disadvantageous one (1, 3). The DM received 1 unit in both allocations and only decided whether the RM received 1 or 3 units (Fig. 2B). This sub-condition measured disadvantageous inequity to indicate how averse the DM was to falling behind the RM (26). The two allocations (1, 1) and (1, 3) were designed with an analogous logic.

We also ran two control conditions, AdC and DisC. The capital letter C stood for control. AdC was the control experiment for the Ad sub-condition and was exactly the same as Ad, but with no RM present. In the case, the DM received 3 units no matter which choice it made (Fig. 2C). Likewise, DisC was exactly the same as Dis, except with no RM present. The DM therefore received 1 unit in each case, regardless of its choice (Fig. 2D).

These controls measured the idiosyncratic choices of each DM when alone and faced with two allocations. Because the DM received the same in both allocations, we predicted that the choice frequency would not differ from 50%. This was verified, as described in the **Materials and Methods**. Each DM-RM pair in the Social condition or each DM in the Control condition was tested via 16 trials carried out over 2 days.

Monkeys were averse to getting ahead

We summarized the two directions of inequity concerns first though they were not our main research interest. For advantageous inequity, on average, DMs chose the equal allocation (3, 3) 55.59% of the time in the Ad condition (standard deviation = 9.29%) and 45.31% of the time in the AdC condition (standard deviation = 3.13%). In other words, DMs chose the equal allocation about 11% more often when an RM was present.

To test whether the difference was significant, we calculated the strength of the advantageous inequity concerns. For each pair, we took the frequency with which the equal allocation was chosen in the Ad condition and subtracted the corresponding frequency by the DM in the AdC condition. This frequency difference marked the strength of advantageous inequity concerns. A positive strength meant that the DM chose the equal allocation more often when the RM was present. This showed an aversion to getting ahead. A negative strength meant that the DM liked to get ahead.

We found that DMs in most pairs (15 out of 19) exhibited a positive strength (Fig. 3A). In a two-level random intercept model, the intercept, estimating the average strength, was positive and significantly different from zero (intercept = 0.11, z score = 5.18, $p < 0.001$). Hence, monkeys chose the equal allocation more often when an RM was present. This indicated an aversion to getting ahead.

Aversion to falling behind varied by individual

For disadvantageous inequity, on average, DMs chose the equal allocation (1, 1) 48.68% of the time in the Dis condition (standard deviation = 10.74%) and 53.13% of the time in the DisC condition (standard deviation = 16.54%).

We similarly calculated the strength of disadvantageous inequity concerns. Positive strength meant that the DM chose the equal allocation more often when an RM was present, indicating an aversion to falling behind. Negative strength indicated a preference for falling behind. We found mixed evidence. On the one hand, the DMs in 5 pairs exhibited positive strength, but on the other hand, DMs in 11 pairs exhibited negative strength (Fig. 3B).

At face value, no consistent tendency was evident when an RM was present. This was also reflected by the intercept in a two-level random intercept model. The strength was not significantly different from zero (intercept = -0.04, z score = -0.49, $p = 0.627$). However, an interesting pattern was seen in Fig. 3B, namely that choices within each DM seemed to be similar, whereas choices across DMs were different (see bars within each DM and bars across DMs). This suggested that the inconsistency was due to individual differences. Moreover, the strength seemed to increase from left (the lightest DM) to right (the heaviest DM), so we therefore looked into individual differences.

Heavier monkeys were more averse to falling behind

If individuals differed in their responses when being disadvantaged, this could explain why we observed inconsistent disadvantageous inequity concerns. Because heavier animals might seldom get less food than others, we tested whether body weight explained disadvantageous inequity concerns. Indeed, we found that heavier monkeys showed a stronger aversion to falling behind (Fig. 3C).

We regressed the strength of disadvantageous inequity on the body weight of the DM in a two-level linear mixed model. The mixed model was similar to the random intercept model, except that body weight was added as a regressor. The regression coefficient associated with the body weight was 0.05 (z score = 4.76, $p < 0.001$), significantly different from zero. This meant that a DM that was 1 kg heavier tended to choose the equal allocation (1, 1) 5% more often. The weight difference between the heaviest and the lightest DMs in our experiment was about 8 kg. This would translate to an increased 40% rate of choices of the equal allocation for the heaviest DM than the lightest one. Hence, individually varying disadvantageous inequity aversion might have been due to differences in the DM's body weight.

This finding that body weight could account for disadvantageous inequity concerns among DMs did not apply to advantageous inequity. A similar regression for advantageous inequity had a slope of -0.01, which was not significantly different from zero (z score = -1.19, $p = 0.235$). Thus, lighter monkeys did not appear particularly averse to getting ahead (Fig. 3D). The aversion was consistent and did not vary among animals.

Step 3: Linking choices in front of the VOI with those behind the VOI

After summarizing the two directions of inequity concerns, we returned to our main research interest. We found strong evidence in favor of impartiality, as the monkeys chose the equal division more often behind the VOI. We also found a consistent advantageous inequity aversion and individually varying disadvantageous inequity aversion. We now turned to the empirical question of whether inequity aversion was the reason that we observed impartiality behind the VOI.

Disadvantageous inequity aversion correlated with impartiality

We addressed this empirical question by testing whether there was a correlation between inequity and VOI choices. We found a positive correlation between the strength of disadvantageous inequity concerns and the degree of impartiality behind the VOI. In other words, if a DM in a pair was more averse to falling behind, it also chose the equal division more often behind the VOI (Fig. 4A). By contrast, there was no correlation between the strength of advantageous inequity concerns and VOI choices (Fig. 4B).

Formally, we regressed the degree of impartiality on the strength of disadvantageous inequity concerns. In a two-level linear mixed model, the regression coefficient was 0.15, significantly different from zero (z score = 2.72, $p = 0.006$). This indicated that if a DM in a pair exhibited a 1% greater strength of disadvantageous inequity concerns, it chose the equal division 0.15% more often behind the VOI. Continuing our numerical comparison using the heaviest and lightest DMs, a 40% greater strength of disadvantageous inequity concerns predicted a 6% greater chance of equal division behind the VOI. A similar regression on advantageous inequity was not significant. The coefficient was -0.11 (z score = -0.99, $p = 0.324$).

Together, these pointed to the importance of disadvantageous inequity, a particular direction of inequity in front of the VOI, in explaining why monkeys appeared impartial behind the VOI. When the aversion to falling behind was stronger, we observed an increased tendency to be impartial behind the VOI. This could arise because when the DM was behind the VOI, it could not guarantee its own advantage. If the aversion to being disadvantaged was stronger, the DM might divide the resources more equally ex ante to prevent itself from being disadvantaged ex post. Hence it appeared impartial.

Furthermore, we could see that in Fig. 4A, the choices of each DM (as represented by DM-specific symbols) were close together. This suggested that the correlation between disadvantageous inequity and impartiality could be driven by individual differences. We examined this possibility in the next step.

Step 4: A possible underlying factor for the linkage

We observed a link between disadvantageous inequity concerns and impartiality in step 3. Because there was a correlation between body weight and disadvantageous inequity concerns as shown in step 2, one might wonder whether body weight was the reason for the link in step 3. To address this, we ran two exploratory analyses in **Supplementary Materials**. Results were consistent with this post-hoc hypothesis. We showed that the body-weight predicted part of disadvantageous inequity concerns correlated with the degree of impartiality behind the VOI. However, after removing this body-weight predicted part, the residual disadvantageous inequity concerns no longer correlated with the degree of impartiality. These results suggested that it was not disadvantageous inequity concerns per se that mattered. Instead, the key was the disadvantageous inequity concerns predicted by body weight. Hence, body weight could be the driving factor for the link between disadvantageous inequity concerns and impartiality.

Discussion

We study Formosan macaques' choices behind the VOI. We find that the monkeys choose the equal division of resources more often behind the VOI than in the Risk condition. This suggests impartiality. To understand impartiality better, we also study choices in front of the VOI, where we observe consistent advantageous inequity aversion and individually varying disadvantageous inequity aversion. The latter has an important role because the degree of impartiality is linked to this individually varying inequity aversion. Moreover, the body weight of each individual correlates with disadvantageous inequity and is likely the reason that we see a link between impartiality and inequity. The most parsimonious explanation of the linkage is as follows. Heavier monkeys are more averse to disadvantageous inequity. Because there is no way to guarantee how much a DM will receive behind the VOI, a stronger aversion to being disadvantaged makes it choose the equal division more often. This suggests that impartiality may be based on a primitive negative reaction to being disadvantaged. Thus, metaphysical reasoning may not be a necessary condition for precursory morality, including the impartial behavior studied here, in other species.

Because we compare the presence of an RM with its absence, an alternative explanation of our results is that the DMs are motivated by the presence of an RM, consistent with the social facilitation effect. However, this alternative explanation does not predict a specific directional effect. That is, it is not clear whether a more motivated DM would choose the equal division more often or less often behind the VOI. Hence, this is unlikely to explain our results. To further address this alternative explanation directly, we test whether the DMs are indeed differentially motivated, depending on whether an RM is present in **Supplementary Materials**. We examine two behaviors, namely bar pull failures and food refusals, which are often used to measure motivation. Monkeys rarely fail to pull a bar or reject food. The frequencies in the presence or the absence of an RM are not different. Hence the direct measurement of motivation does not support the social facilitation explanation. Perhaps this is because grapes, the rewards provided in this experiment, are highly valuable. In the literature, a "distraction control" is sometimes used, in which an RM is present but is denied access to rewards. The purpose is to control for the social facilitation effect. Because we do not find evidence for the social facilitation effect, our use of the absence of an RM as the control is justified.

Chimpanzees exhibit a prepotent bias, according to which they tend to choose the option that has have a greater amount of rewards (9). This bias may be thought to have influenced our results. Because both the equal division (2, 2) and the unequal division (3, 1) total 4, this bias has no role in the Risk or VOI conditions. In front of the VOI, we have clear evidence against such a bias. In the AdC condition, the option with a greater reward (3, 3) is chosen only 45.31% of the time. In the DisC condition, the option with a greater reward (1, 3) is chosen 46.87% of the time. Therefore, this bias cannot explain our results.

Similar to a report in capuchin monkeys (8), our monkeys are not that averse to falling behind, but some are averse to getting ahead. The range of cooperation behavior observed in Formosan macaques may provide a hint of this. Formosan macaques emit food calls to share information on the presence of food (27). They are also observed to co-feed as a group on a food patch and agonistic events do not increase with the number of individuals feeding on that patch (28). They allomother unrelated infants as frequently as kin-related infants (29). These cooperative behaviors, together with the evidence that larger groups have an advantage in inter-group competition (30), suggest that their capacity to cooperate may have been selected for due to the need to communally defend against other groups. Within a cohesive social structure (31), individuals are likely to be less competitive. This may make them react less strongly to disadvantageous inequity and in a similar vein, avoid seeking to get ahead.

We show that body weight correlates with disadvantageous inequity aversion and speculate that this is the reason that we see a link between impartiality and inequity. Because body weight is the best predictor of social rank (32-34), and rank often correlates with behaviors (15, 16), one may wonder whether results would be similar if we replace weight with rank. In **Supplementary Materials**, we assign an ordinal rank to our monkeys and analyze its effect. Step 2 holds up if we replace weight with rank: the assigned ordinal rank still correlates with the disadvantageous inequity aversion. That is, higher-ranked monkeys are more averse to being disadvantaged. However, we do not find full support for the conclusion that rank is the reason for the link between

impartiality and inequity. The difference in the results for weight and rank could be due to either or both of two reasons. First, weight is a trait marker, but rank is a state marker. A trait marker captures physiological differences, such as aggressive responses, more directly, whereas a state marker better reflects the influence of social structure. If the underlying mechanism is physiological, the trait maker may have better explanatory power. For example, weight but not rank correlates with the level of testosterone in Cynomolgus monkeys (35). Second, the assigned ordinal rank may be an imprecise measure of rank. Our data cannot provide further evidence. Therefore, the speculation that body weight could be the reason for the link between impartiality and inequity should be treated with caution. Clarification of the role of body weight would still require future research.

An alternative interpretation for the fact that some monkeys choose the equal allocation (3, 3) in the Ad condition and the disadvantageous allocation (1, 3) in the Dis condition is prosociality. In such a case, the DM prefers the RM and itself to receive a larger total. This interpretation seems as adequate as the inequity interpretation when we consider the Ad or Dis condition alone. However, when we link these choices in front of the VOI conditions to the behind the VOI choices, the interpretation based on prosocial motives seems unlikely. Both the equal division (2, 2) and the unequal division (3,1) give the DM and RM 4 in total, so a prosocial DM would not find the equal division more prosocial than the unequal division. Therefore, it cannot explain why the equal division is chosen more often. We thus interpret the link as a more inequity-averse DM showing a higher degree of impartiality behind the VOI. This is a benefit of studying a suite of choices. Doing so allows access to a range of behaviors that are more informative than a single choice behavior. Thus, certain interpretations become unlikely when we study multiple choice behaviors and seek to explain them altogether.

Studying a suite of choice behaviors may also shed new light on the debate whether inequity aversion exists in nonhuman primates. The existence of a behavior means animals show this behavior consistently. In our case, disadvantageous inequity aversion varies across individuals, so we do not find evidence for this direction of inequity aversion. However, by studying the VOI choices at the same time, we find a correlation between the VOI choices and disadvantageous inequity aversion. This suggests a role for disadvantageous inequity aversion that can only be appreciated when the VOI choices are also examined. In other words, an inconsistent behavior may still be important. Individual differences may average out so that the mean across individuals is close to zero and is therefore concluded as inconsistent. However, using a new behavioral assay, if a correlation is found between these individual differences (in our case, the strength of disadvantageous inequity aversion) and the behaviors in the new assay (the degree of impartiality), the early inconsistency in the results may be important. By focusing only on consistency, we may miss the importance of meaningful inconsistent behaviors.

In **Supplementary Materials**, we rule out the possibility that the DM and RM reciprocate each other, on top of the extra care we take to avoid this possibility when we run the experiment. Because we run conditions with no RM before their corresponding conditions with an RM, the order effect could be a potential confound. We describe the details in **Materials and Methods** and explain why it may not be serious. We further address the essence of the order effect, the time

effect, in **Supplementary Materials**. We should note, however, that the order effect cannot be ruled out.

Our results have implications for cooperation (36). Because there is always a chance of being disadvantaged behind the VOI, if the aversion to falling behind is strong, a DM may divide the resources more equally to prevent that from happening. Seemingly impartial divisions are made when a DM is behind the VOI and therefore unable to guarantee its own advantage. This, in turn, may support cooperation in the case of a risk. In a natural setting, such as in collaborative foraging, no one can know beforehand who will eventually be advantaged. However, animals may learn to divide opportunity equally in advance. In turn, this makes continuing cooperation likely. This resembles what is captured by the concept of the VOI. Moral behavior in humans is certainly much more elaborate and complex (37-39). In other species, pervasive aversion to falling behind may first evolve due to pressure to survive. However, this could also promote an equal division, making risky cooperation possible (36). We speculate that this channel helps develop precursory forms of morality, echoing the Darwinian notion that morality is based on cooperation (1).

Fig. 1

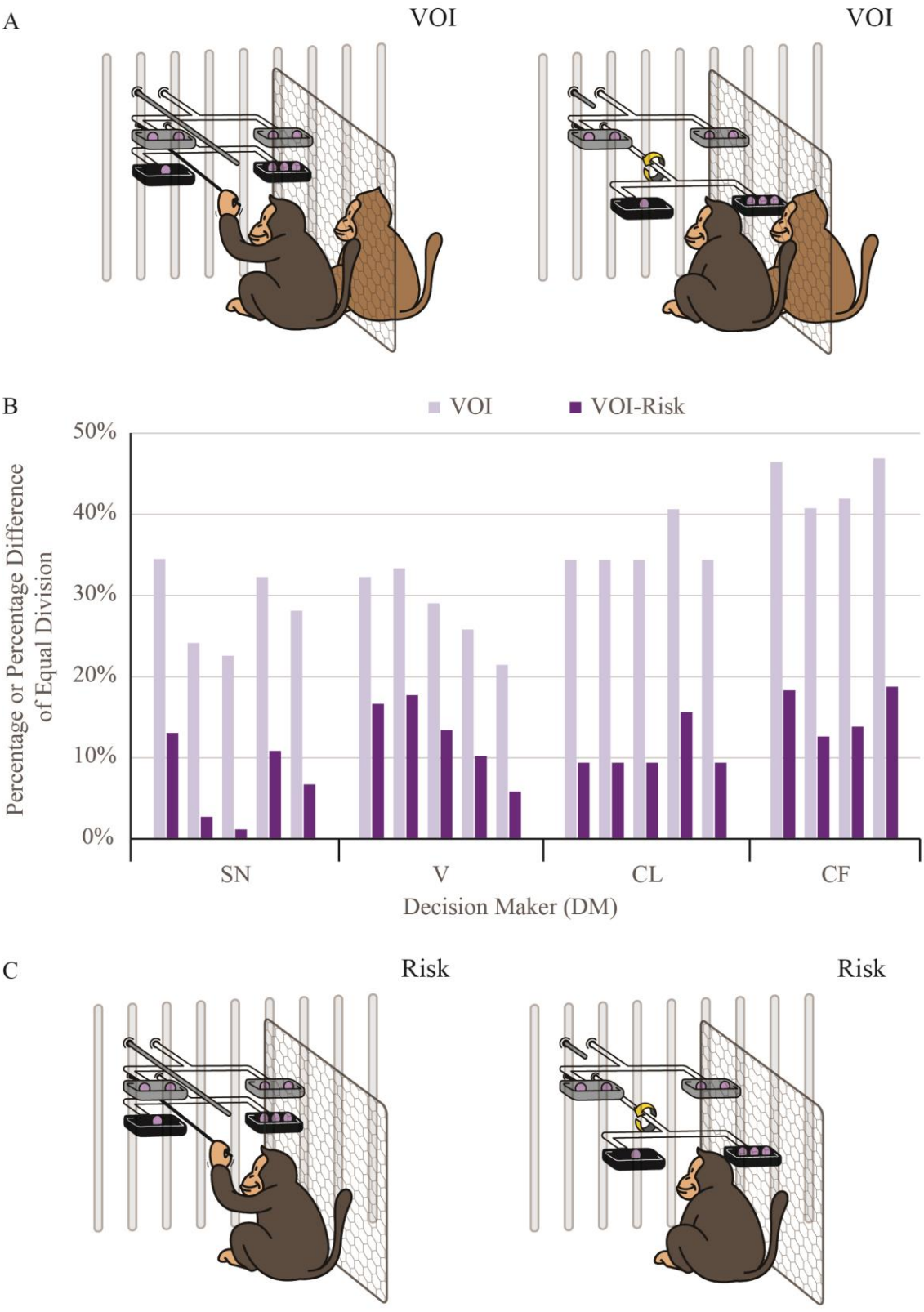

A
VOI
VOI
B
VOI
VOI-Risk
50%
40%
30%
20%
10%
0%
Percentage or Percentage Difference of Equal Division
SN
V
CL
CF
Decision Maker (DM)
C
Risk
Risk

Fig. 1. VOI and Risk.

A. Illustration of the VOI condition.
The apparatus had upper and lower trays. Each tray contained two food dishes, appearing on the left and the right. We placed in one tray an equally divided reward (2, 2) and in the other, an unequally divided one (3, 1). The DM chose between the two divisions. After the choice, half of the time the selected division was spun one loop so the left dish remained on the left. The other half of the time it was spun one and a half loops so the right dish came to rest on the left. The DM therefore did not know which dish it would have access to when making a choice. In this illustration, the DM (the dark brown monkey on the left) selected the unequal division, where it would receive 1 or 3 reward units equally likely. If the DM received 1, the RM (the light brown monkey on the right) received 3 and vice versa. We illustrated the case where the bottom tray was baited with the unequal division and 3 were in the right dish. However, we counterbalanced the choice displays.

B. Pair-by-pair breakdowns of the VOI choices and the VOI vs. Risk choices.
This figure showed the choice percentage for the equal division in VOI (in light purple) and this percentage difference between the VOI and Risk choices (in purple). We grouped pairs of the same DM together and assigned each DM's name (SN, V, CL, and CF). To facilitate understanding, we ordered the DMs by their body weight, so that body weight of the DM increased from left to right. Among the four DMs, monkey SN was lightest, followed by monkey V, monkey CL, and monkey CF. All of the purple bars were positive, indicating that the equal division was chosen more often behind the VOI than in the Risk condition for all pairs.

C. Illustration of the Risk condition.
The Risk condition was exactly the same as the VOI condition, except without an RM.

Fig. 2

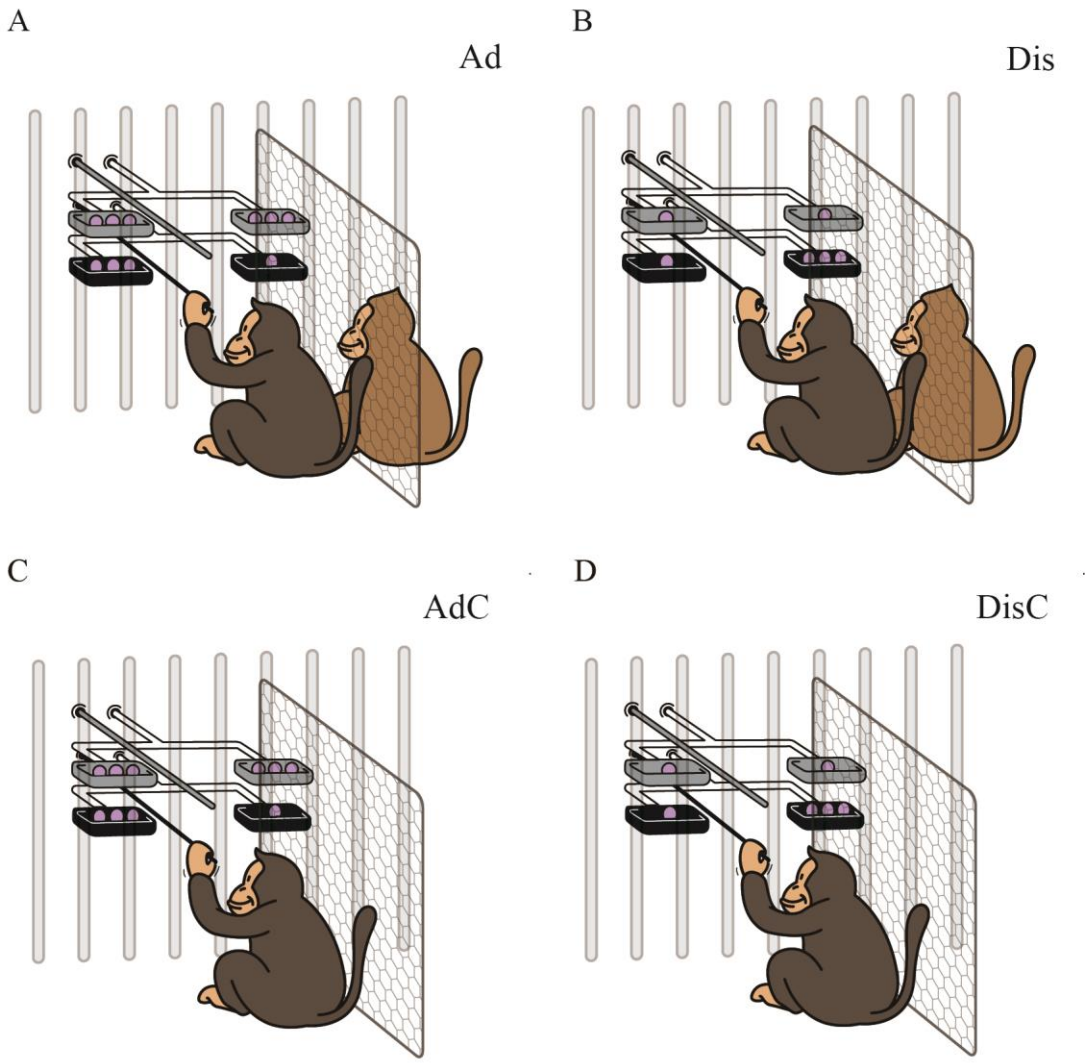


Fig. 2. Ad, Dis, AdC, and DisC.

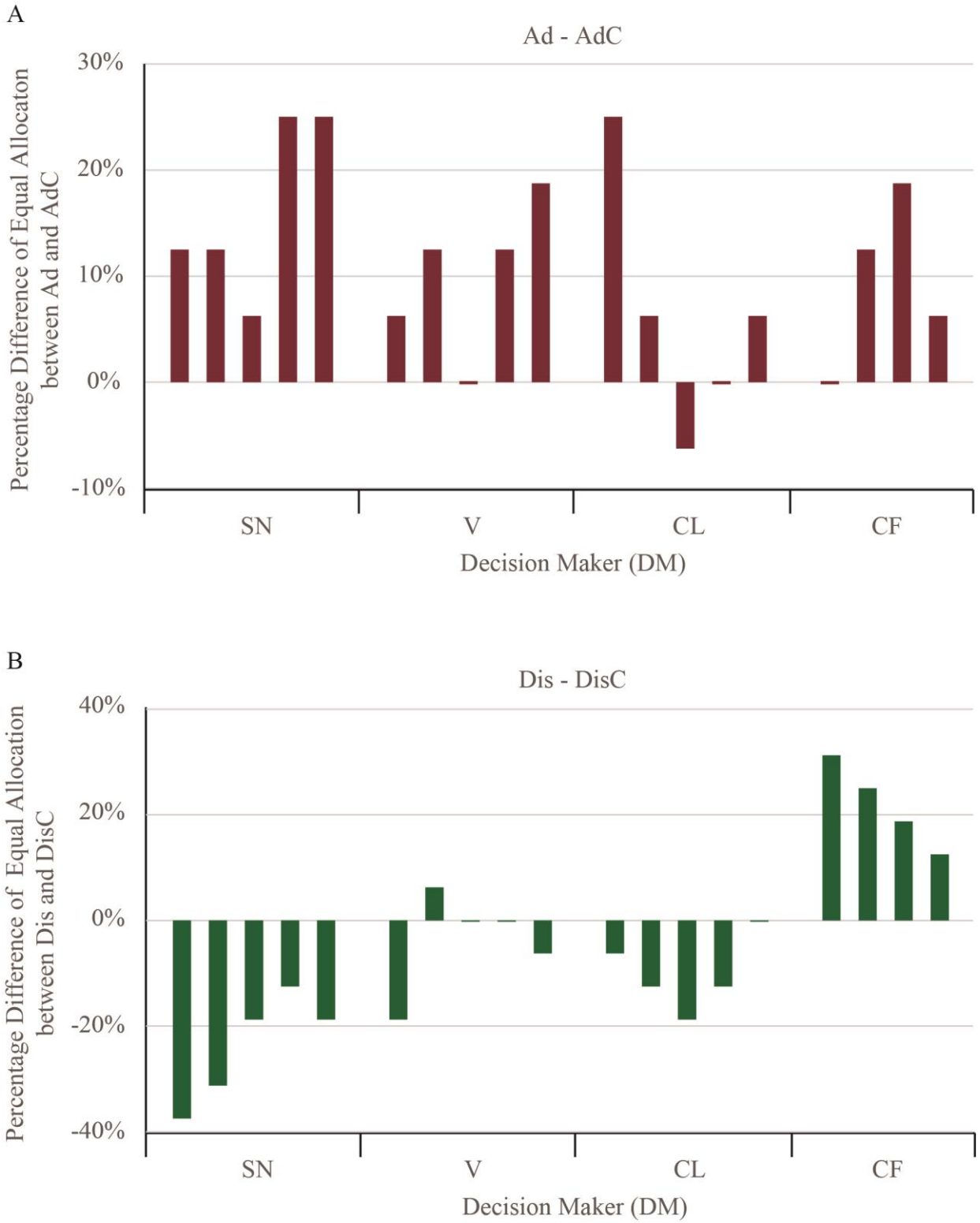
A. Illustration of the Ad condition.
The DM chose between the equal allocation (3, 3) and the advantageous allocation (3, 1). Unlike the case of the VOI condition, the selected allocation was not spun. Hence, the DM received 3 units, no matter which option it chose. This measured advantageous other-regarding concerns.

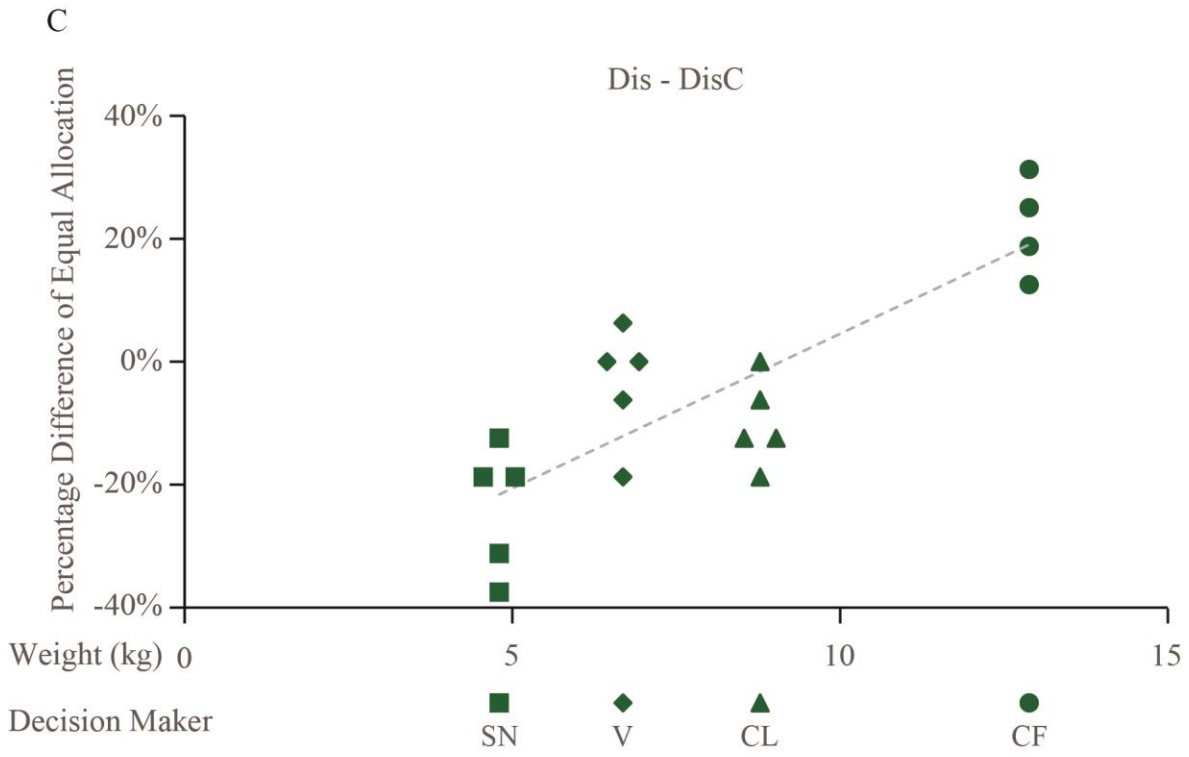
B. Illustration of the Dis condition.
The DM chose between the equal allocation (1, 1) and the disadvantageous allocation (1, 3). The selected allocation was not spun and the DM received 1 in all cases. This measured disadvantageous other-regarding concerns.

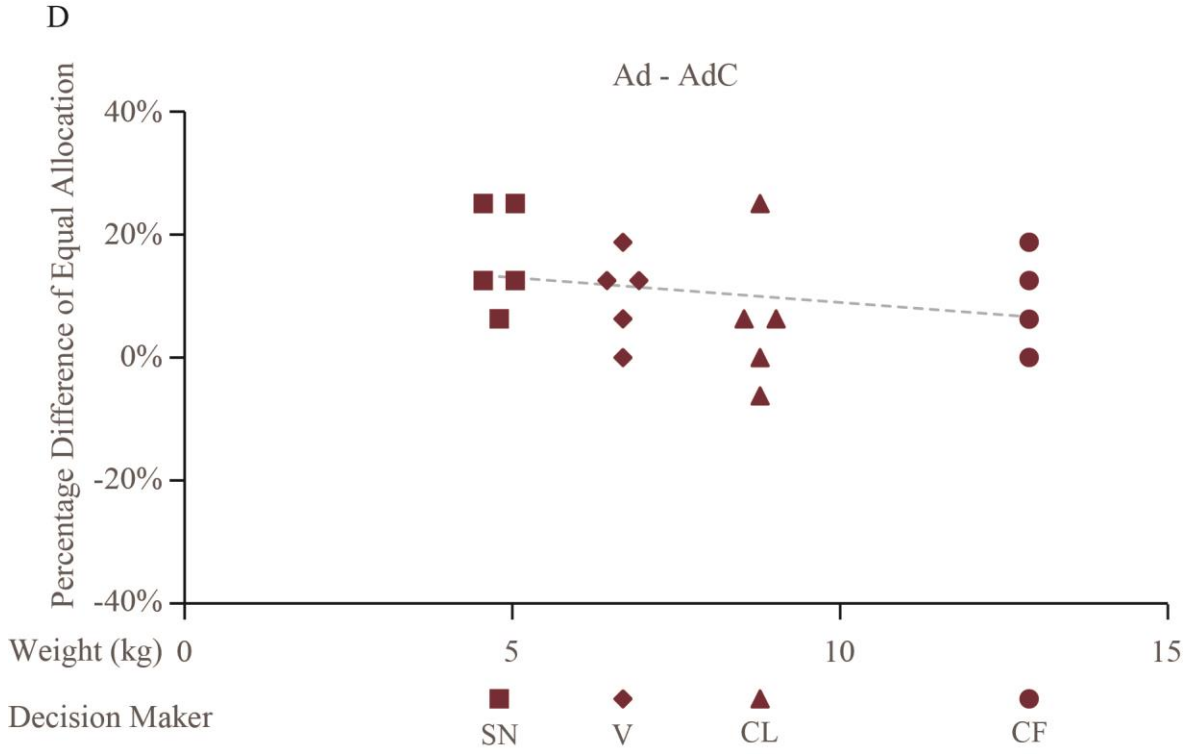
C. Illustration of the AdC condition.
It was the control experiment of Ad. It was exactly the same as Ad, except there was no RM.

D. Illustration of the DisC condition.
It was the control experiment of Dis and was exactly the same as Dis, except there was no RM.

Fig. 3


A
Ad - AdC
Percentage Difference of Equal Allocaton between Ad and AdC
30%
20%
10%
0%
-10%
SN
V
CL
CF
Decision Maker (DM)
B
Dis - DisC
Percentage Difference of Equal Allocation between Dis and DisC
40%
20%
0%
-20%
-40%
SN
V
CL
CF
Decision Maker (DM)


C
Dis - DisC
Percentage Difference of Equal Allocation
40%
20%
0%
-20%
-40%
Weight (kg) 0
5
10
15
Decision Maker
SN
V
CL
CF


D
Ad - AdC
Percentage Difference of Equal Allocation
40%
20%
0%
-20%
-40%
Weight (kg) 0
5
10
15
Decision Maker
SN
V
CL
CF

1
2

Fig. 3. Advantageous and disadvantageous other-regarding concerns.

A. Pair-by-pair breakdown of the Ad vs. AdC choices.
The figure showed the choice percentage difference of the equal allocation between Ad and AdC. Each bar reflected the strength of advantageous other-regarding concerns. In most pairs, we found a positive strength, consistent with the aversion to getting ahead. To facilitate the comparison, results for advantageous other-regarding concerns were all shown in dark red.

B. Pair-by-pair breakdown of the Dis vs. DisC choices.
This figure showed that both positive strengths (consistent with the aversion to falling behind) and negative strengths (consistent with loving to fall behind) were found. The DMs were ordered so that the body weight increased from left to right. The tendency for bars to become more positive from left (the lightest DM) to right (the heaviest DM) suggested that body weight might explain individual differences. Results on disadvantageous other-regarding concerns were all shown in dark green.

C. Body weight vs. disadvantageous other-regarding concerns.
There was a positive correlation between the body weight of the DM and the strength of disadvantageous other-regarding concerns. Heavier monkeys showed greater strength, consistent with a stronger aversion to falling behind. Distinct symbols were used for each DM to help visualize the choices of each DM. Some data points were jittered horizontally to make them all visible.

D. Body weight vs. advantageous other-regarding concerns.
There was no correlation between the body weight of the DM and the strength of advantageous other-regarding concerns. Some data points were jittered horizontally to make them all visible.

Fig. 4

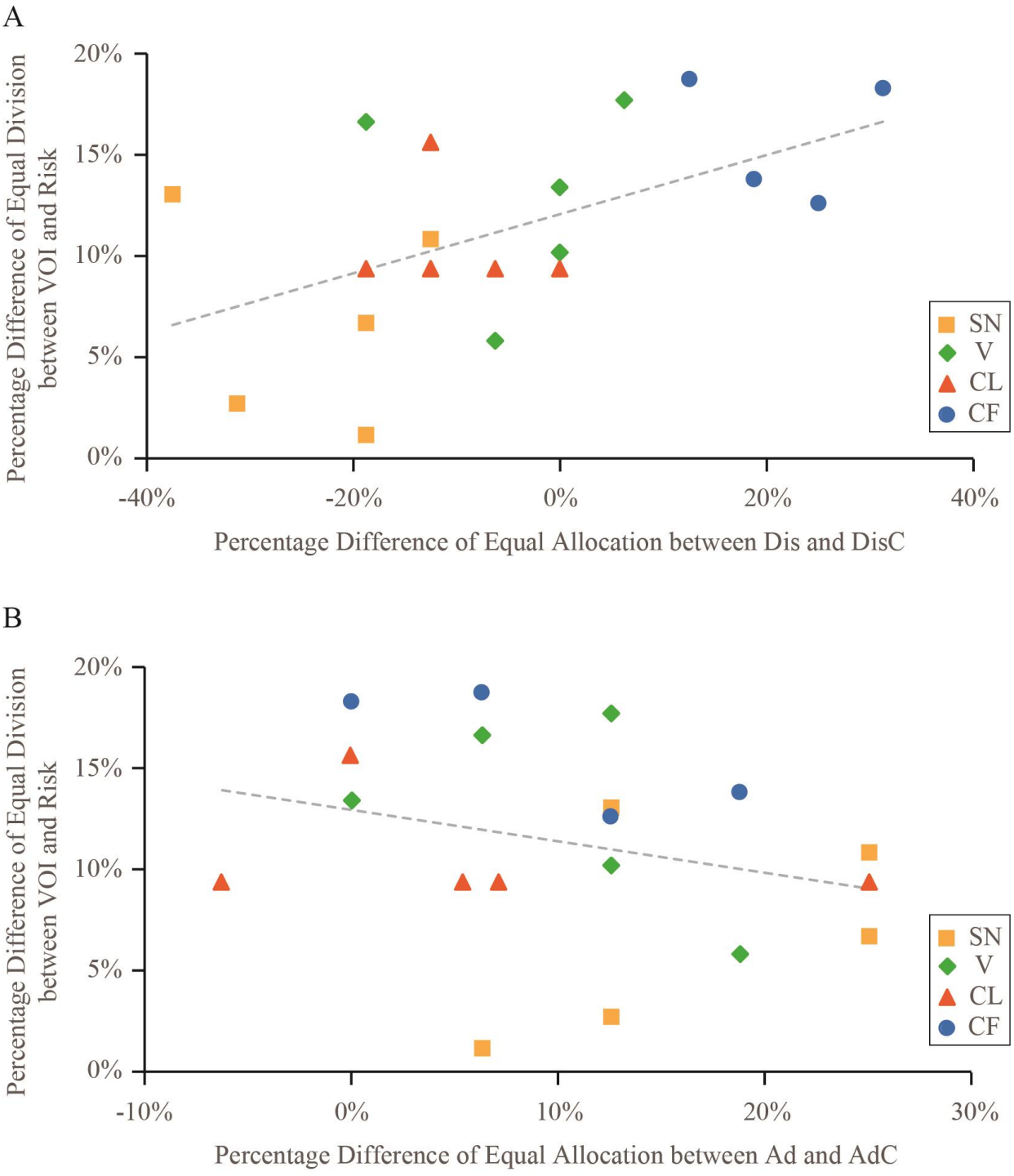

A
20%
15%
10%
5%
0%
Percentage Difference of Equal Division between VOI and Risk
-40%
-20%
0%
20%
40%
Percentage Difference of Equal Allocation between Dis and DisC
SN
V
CL
CF
B
20%
15%
10%
5%
0%
Percentage Difference of Equal Division between VOI and Risk
-10%
0%
10%
20%
30%
Percentage Difference of Equal Allocation between Ad and AdC
SN
V
CL
CF

Fig. 4. Inequity and impartiality.

A. Disadvantageous other-regarding concerns vs. impartiality.
There was a positive correlation between the strength of disadvantageous other-regarding concerns and the strength of impartiality. Distinct colored symbols were used for each DM to help visualize the choices of each DM. A DM showing a stronger aversion to being disadvantaged was more impartial. The choices of each DM were close together, suggesting that the correlation might be driven by individual differences. The inset showed the colored symbols for each DM monkey.

B. Advantageous other-regarding concerns vs. impartiality.
There was no correlation between the strength of advantageous other-regarding concerns and the strength of impartiality. Some data points were jittered horizontally to allow each point to be visible.

Supplementary Materials

This PDF file includes:

Materials and Methods
Table S1
Supplementary Text
Captions for Movies S1 and S2

Other Supplementary Materials for this manuscript include the following:

Movies S1 and S2

Materials and Methods

Apparatus

Six monkeys were each familiarized with the experimental apparatus. The apparatus had two sliding trays, upper and lower. Each tray was connected to a pull bar. The upper bar was connected to the upper tray, and the lower bar was connected to the lower tray. The monkeys made choices by pulling one of the two bars. Once a bar was pulled, the other bar was locked and could no longer be pulled. Each tray had two food dishes, one to the left and one to the right.

The monkeys were in a quadrant cage during the experiment. We used two compartments, one to the left and one to the right. The DM was always in the left compartment for each decision. Before making the choice, the two dishes on each tray faced the DM. Once a choice was made, the selected tray was slid forward at an angle so that the left dish was only accessible from the left compartment, and the right dish was only accessible from the right compartment.

In different experimental conditions, a passive RM may or may not be present in the right compartment, and the chosen tray may or may not be spun. The door between the left and right compartments was always closed unless otherwise noted.

Pretests

Four pretests were run with each DM alone before the main experiment. Because our major interest was in the distribution of rewards between the DM and RM, we made sure that the DM was able to attend to the dishes on its side and to the side of the RM. We designed pretests 1-3 for this purpose. Step by step, pretest 1 was performed to ensure that the DM was attending to the dish on its own side. Pretest 2 was done to make sure that it attended to the dishes on RM's side Pretest 3 was conducted to ensure that the monkey attended to both sides. To implement the VOI condition, we introduced spinning after pretest 3. Pretest 4 was intended to make sure that the monkey understood that the selected choice would be spun.

Pretest passing standard

Each pretest had 5 blocks. There were 12 trials in each block. A DM had to select the choice with the higher (expected) amount of rewards in at least 8 trials to pass a block. It had to pass at least 3 blocks to pass a pretest. The probability of a randomly behaving DM passing a pretest was 5%.

Our passing standard was different from the usual standard in the literature, in which a stricter standard was imposed to pass each block (such as 5 passes out of 6 trials or 10 passes out of 12 trials in a block). However, in the usual standard, the number of blocks allowed was not capped in advance. Because the number of blocks was not capped, the probability of passing a pretest using the usual standard was not known in advance. We chose our standard because we hoped to control the probability of passing a pretest in advance. In fact, when passing a block, 73% of the time monkeys chose the higher reward option more than 8 out of 12 times, the cutoff criterion that we used. When passing a pretest, 75% of the time, monkeys took less than 5 blocks, the maximum number of blocks that we allowed. These were taken as indications that the monkeys understood the experimental procedure.

Notation for the baited content

In the pretests and the main experiment, the reward unit was one-eighth of a grape. This was done to prevent the monkeys from losing motivation due to consuming too many grapes in a given experimental day. Moreover, they were hungry during the experiment, as a half-portion of the meal was given only after the experiment was complete. For ease of exposition, if a tray was baited with x units in one dish and y units in the other, this was notated by (x, y). In other words, we only referred to the baited content of a choice. When the position also mattered, i.e., whether x was in the left or the right dishes, we stated that in words.

Pretest 1: (3, 0) vs. (2, 0)

In this pretest, one of the two left dishes was baited with 3 units and the other with 2. We counterbalanced whether the upper or the lower tray was baited with (3, 0). Choice displays were always counterbalanced whenever possible. Hence, this was not be explicitly referred to again later on. A monkey was tested whether it would choose (3, 0). This was to show that the DM could reliably pay attention to the dishes on its side.

Pretest 2: (0, 3) vs. (0, 2)

In this pretest, one of the two right dishes was baited with 3 units and the other with 2. The door between the two compartments was open so that, after making a choice in the left compartment, a monkey could go to the right compartment to obtain the rewards. A monkey was tested whether it would choose (0, 3). This aimed to show that the DM could reliably pay attention to the dishes on the side of the RM.

Pretest 3: (1, 2) vs. (1, 1)

In this pretest, the two left dishes were both baited with 1 unit. One of the two right dishes was baited with 2 units and the other with 1. The door between the two compartments was open so that, after making a choice in the left compartment, a monkey could also go to the right compartment to obtain the rewards. A monkey was tested whether it would choose (1, 2). This was to ensure that the monkeys did not pass pretest 2 because of the omission of food on its side and that the DM was able to pay attention to the dishes on both sides.

Spinning

We spun the selected tray after pretest 3 to prepare the monkeys for the VOI/Risk condition. The spinning was carried out as follows. Half of the time, the selected tray was spun one loop so that the left dish remained on the left. The other half of the time, it was spun one and a half loops so the right dish came to rest on the left. If an (x, y) tray was selected, because the DM was in the left compartment and could only access what was spun to the left, it amounted to receiving x half of the time and receiving y half of the time.

The monkeys went through many trials after pretest 3 to familiarize them with the spinning. After the familiarization trials, we proceeded to pretest 4. Because the familiarization trials were crucial in ensuring the monkeys understood the spinning, we described them in detail. The content of these familiarization trials varied. One key principle was that the monkeys had never pre-experienced pretest 4 or any VOI/Risk situation in which the spinning was carried out. The other principle was the familiarization trials went from easy to difficult to help monkeys learn gradually.

Because the DM could only access what was on the left, when the selected tray was not spun, only the left dish mattered. But when it was spun, the initial baiting position became irrelevant, as the right dish could also come to rest on the left. Hence, the familiarization trials were designed to ensure that the monkeys could understand that the initial baiting position was irrelevant due to spinning. We designed three types of trials to familiarize monkeys with this.

With spinning, because both the left and right dishes could come to rest on the left, a DM should take both into account. Suppose the optimal choice in a spinning case was called tray A. In the first type of trials, only one tray was baited with rewards. Hence even if a monkey focused on the left, by coincidence it chose tray A because only A had rewards. In the second type, we baited the two left dishes with the same amount of reward. Hence, if a monkey focused on the left, it would be indifferent and chose A half of the time. In the third type, we baited tray A with a smaller reward on the left. Hence, a monkey focusing on the left would not choose A. Because a monkey focusing on the left would choose A less and less likely from the first type of trials to the third type of trials, the first type was easier than the second, which was in turn easier than the third. Therefore, generally, the first type proceeded before the second, which proceeded before the third. Depending on how well the monkey learned, within a given type, we progressed to make the trials gradually more difficult.

The first type was denoted by (L, R), (0, 0). Tray A was baited with L on the left and R on the right, but the other tray was baited with nothing. This type was easy, as tray A was the obvious choice. Indeed, the monkeys chose tray A 90.18% of the time. The purpose of this type was to allow the monkeys to experience the consequence of spinning when they were not yet familiar with it.

The second type was denoted by (L, R*), (L, R). Both trays were baited with rewards L on the left. On the right, one tray was baited with R* and the other with R where R*>R. Hence tray A was (L, R*). This type was less easy because taking only what was on the left into account, the two trays were equally good. However, if the monkeys understood the selected tray would be spun, they would consider A to be better. During the first 30 trials, the DM's choice of A ranged from 17 to 19 times. This was not significantly different from 50% for every DM (the smallest p-value among all DMs was 0.2000). This showed that initially the monkeys were unaffected by what was baited on the right despite having experienced spinning from trials of the first type.

In the third type, one tray had a larger reward on the left. However, this tray in fact was dominated by the other tray when one understood that spinning made the initial baiting position irrelevant. This type was denoted by (L*, R), (L, R*), where one tray had L* on the left, R on the right; the other tray had L on the left, R* on the right. We made L*>L. Hence, by focusing on the left, (L*, R) seemed to be the better choice. However, we made R* large and R small, such that R*>L* and L>R. Hence, if one ignored the initial baiting position, the (L, R*) tray actually dominated the (L*, R) tray. This type really required the monkeys to understand that spinning made the initial baiting positions irrelevant. Had they kept focusing on the left, they would miss the possible large reward R* and would likely received the small reward R. As expected, this type of trial was not easy for the monkeys. However, they did learn over time. Because we made trials progressively more difficult depending on how well the monkeys learned, we compared the first 30 trials to the last 30 trials of the same difficulty. Overall, during the first 30 trials, the monkeys chose the dominating

tray only 53.0% of the time. The frequency increased by 20.2% to 73.2% of the time in the last 30 trials. This increment was significant (z score = 4.19, p = 0.000). After these familiarization trials, we proceeded to pretest 4.

Pretest 4 (2, 4) vs. (3, 1)

This pretest aimed to show that monkeys understood spinning. One tray was baited with 2 units in the left dish and 4 in the right dish. The other tray was baited with 3 in the left dish and 1 in the right dish. If a monkey did not understand spinning and focused on the two left dishes, then a rational response was to choose (3, 1), because 3 was better than 2. On the other hand, if it understood spinning made the initial baiting position irrelevant and both could be spun to the left, then since the bigger reward of the (2, 4) tray was greater than that of the (3, 1) tray (i.e., 4 > 3) and the smaller reward of the (2, 4) tray was also greater than that of the (3, 1) tray (i.e., 2 > 1), it should choose (2, 4). This pretest, like the third type, tested the essence of spinning. However, the monkeys had never experienced this pretest before. It was new to them.

Explanations on why monkeys did not pass pretest 4 because they preferred a greater sum of rewards

Chimpanzees were found to exhibit a prepotent bias that they were biased toward the option with a greater sum of rewards (9). Because the (2, 4) tray had a greater sum than the (3, 1) tray, a DM might have passed pretest 4 due to this bias instead of having understood spinning.

This possibility was unlikely in our data for the following reasons.

First, if a DM preferred the tray with a greater sum, at the early stage of type 2 familiarization trials, no matter whether a DM had understood spinning or not, it should choose the (L, R*) tray more often than the (L, R) tray. This was because if a DM did not understand spinning, this preference for a greater sum should lead to the choice of (L, R*). On the other hand, if a DM understood spinning, it had an additional reason to choose (L, R*), as spinning made R* accessible half of the time. But as stated above, this was not the case. None of the DM's choice of the (L, R*) tray was significantly different from 50% during the first 30 trials. This showed that monkeys at this stage were not yet affected by the dishes on the right side.

Second, choices in the AdC and DisC conditions did not support that monkeys preferred the tray with a greater sum either. In the AdC condition, a DM chose between (3, 3) and (3, 1). If it preferred the tray with a greater sum, it would choose (3, 3). However, (3, 3) was chosen only 45.31% of the time. In the DisC condition, a DM chose between (1, 1) and (1, 3). This prepotent bias predicted the choice of (1, 3). However, it was chosen 46.87% of the time. None of the DM's choice was significantly different from 50%, consistent with the conclusion that the monkeys were not affected by the inaccessible right dishes. This was shown in the bottom panel of Table S1.

Type 2 trials were done before pretest 4. The AdC and DisC conditions were part of the main experiment and therefore were run after pretest 4. Hence, we did not find evidence that monkeys preferred the tray with a greater sum either before or after pretest 4. This bias was unlikely a concern in our data.

There were 6 monkeys in the lab. We did not make any selection, so all of them went through the same procedures. Two monkeys did not pass the pretests and could only act as RM. We had at most (6 - 2) * (6 - 1) = 20 DM-RM pairs. However, two monkeys attempted to fight through the dividing mesh when they were paired, so we were unable to pair them in the experiment. One of them failed the pretests, leaving 20 – 1 = 19 DM-RM pairs. We exhausted all 19 possible pairs.

The main experiment

The main experiment had four conditions: Risk, VOI, Control and Social. In a human experiment (40), by carrying out the experiment in different orders, no order effect was found: whether the VOI condition was run first or second did not matter. Based on this, we ran the conditions with no RM before the conditions with an RM. The Risk condition was run first, then the VOI condition, followed by the Control condition and finally the Social condition. The order of the AdC and DisC conditions was counterbalanced across subjects. Similarly, the order of the Ad and Dis conditions was counterbalanced across subjects.

Order effect

Because we did not counterbalance the order of conditions, in principle, the order effect could be a confounding factor. However, our data provided some evidence that it was likely not a serious concern.

(1) Choices were consistent with a clear preference or self-interest

First, one possible reason that order might have had an effect was due to learning. If monkeys learned over time, there might be the concern that choices in the conditions with no RM were random because they were run earlier, and learning might not have been adequately completed. However, in the Risk condition, DMs clearly showed a preference for risk instead of choosing randomly. Each individual's choice frequency ranged from 15.63% to 28.13%, all consistent with risk loving. We used the binomial test to examine whether the choice frequency of each monkey equaled 50%. All DMs' choice frequency was significantly different from 50%. In the AdC and DisC conditions, because the DM received the same amount in both allocations, the choice frequency should not have differed from 50%. This was indeed the case. None of the DM's choice was significantly different from 50%. These tests were in the bottom panel in Table S1. In all three conditions with no RM, every DM's choices were consistent with a clear preference or self-interest. Hence, their choices were not likely to be the result of not having learned well.

(2) The essence of the order effect: Time effect

Second, we examined the order effect, taking the risk and VOI conditions as an example. If there were an order effect, whether the Risk condition was run before or after the VOI condition would be important. This could happen when a condition run earlier in time differed from the same condition run later in time. Although our data could not directly address the order effect, we could address the essence of it, namely, the time effect, indicating whether we observed choice in the same condition changed as time went. We did not find any such evidence. This was shown in section (6) Time Effect in **Supplementary Materials**.

These two pieces of evidence indicated that the order effect was likely not serious.

Details to avoid reciprocation

Each condition was divided into blocks of 8 trials. For instance, there were 32 trials for each DM-RM pair in the VOI condition. Because we only ran one block on any given day, this meant that each DM-RM pair met over four days. To minimize the possibility of reciprocation, we ran the experiment with the following three restrictions. First, there were at least three days before any two monkeys met again. Second, a monkey could only act as a DM once a day. In that situation, it could at best act as an RM once later on the same day. Third, if a monkey first acted as an RM on one day, it could not act as a DM on the same day. At most, it could act as an RM twice in one day.

Ethics statement

The monkeys resided in quadrant home cages similar to the experimental cage. Two monkeys were housed in each cage but were always separated by a dividing mesh and could not interact with each other directly. The experiment was approved by the Council of Agriculture, Executive Yuan, Taiwan, and the Institutional Animal Care and Use Committee of National Yang-Ming University under permit numbers 1010601 and 1050303. All experimental procedures were performed in accordance with the guidelines of the U.S. Department of Agriculture.

Videotaping

The experiment was videotaped from two angles: one in the direction of the food trays, recording the available choices, and the other in the direction of the monkeys, recording the DM's choices. One experimenter coded the DM's choices. A blind observer coded a random selection of 20.11% of trials by watching the videotapes. Cohen's kappa was 1, implying complete agreement.

Acknowledgments

This work was supported by the Ministry of Science and Technology of Taiwan (grant no. 103-2410-H-002 -008 -MY3). We acknowledge the generous support of the animal research center at National Yang-Ming University, Taipei, Taiwan in providing the monkey subjects, animal care, and lab facility. We thank the keepers at the animal center of National Yang-Ming University, especially Fang-Chen Lin. The experimental apparatus was developed with the help of Ching-Chang Liao at the mechanical factory of National Taiwan University. We thank Jen-Te Wang and Zong-Yang Ho for their assistance in parts of the experiment. We thank Sarah Brosnan, Ming Hsu, Chou Po Hung, Jun-Yi Leu, Kelly Olds, Tomas Sjostrom and Shih-Wei Wu for their help and insightful comments. We thank Minna J. Hsu and Hsiu-Hui Su for providing information on the ecology of Formosan macaques. We are grateful to National Pingtung University of Science and Technology and Taipei zoo for helping retiring the monkeys after the experiment.

Table S1 Summary for the Test Results

Test conditions		**Results**
Impartiality		
Null hypothesis: VOI = Risk	Options: (2, 2) vs. (3, 1)	Percentage of choosing the equal division: VOI: 33.56%, Risk: 22.54%, **p < 0.001** Monkeys are impartial (Fig. 1B).
Other-regarding concerns		
Null hypothesis: Ad = AdC Dis = DisC	Options: (3, 3) vs. (3, 1) (1, 1) vs. (1, 3)	Percentage of choosing the equal allocation: Ad: 55.59%, AdC: 45.31%, **p < 0.001** Dis: 48.68%, DisC: 53.13%, p = 0.627 Monkeys show advantageous other-regarding concerns, consistent with the aversion to getting ahead (Fig. 3A, B).
Other-regarding concerns and body weight		
Correlation between weight and Ad-AdC Dis-DisC		Regression coefficient before weight for Ad-AdC: -0.01, p = 0.235 Dis-DisC: 0.05, **p < 0.001** Heavier monkeys show stronger disadvantageous other-regarding concerns, consistent with the stronger aversion to falling behind (Fig. 3C, D).
Impartiality and inequity		
Correlation between the degree of impartiality (VOI-Risk) and Ad-AdC Dis-DisC		Regressing the degree of impartiality on Ad-AdC: -0.11, p = 0.324 Dis-DisC: 0.15, **p = 0.006** Stronger aversion to falling behind correlates with a higher degree of impartiality (Fig. 4A, B).
Examining conditions with no RM using the binomial test		
Null hypothesis: Risk = 50% AdC = 50% DisC = 50%	Options: (2, 2) vs. (3, 1) (3, 3) vs. (3, 1) (1, 1) vs. (1, 3)	Risk loving for all DMs (**p < 0.02** for all DMs) Close to 50% for all DMs (p > 0.8 for all DMs) Close to 50% for all DMs (p > 0.08 for all DMs)

The main results are highlighted in red.

Supplementary Text

We explained the concept of the two-level regressions and reported several supporting results.

(1) Two-level regressions

We used the VOI vs. Risk result to illustrate the two-level regressions that we ran. For each pair in the VOI condition, we took the frequency the equal division was chosen and subtracted the corresponding frequency when the DM was alone in the Risk condition. This difference reflected the strength of impartiality: a higher difference meant that the DM chose the equal division more often in the VOI condition. The dependent variable was this strength of impartiality. Because we had 19 pairs, there were 19 data points. The two-level random intercept model had the first level being the pair and the second level being the DM. If we denoted the dependent variable by VOI-Risk because we calculated the difference, "two-level" implied a need for two subscripts, one for the pair (the first level) and the other for the DM (the second level). Each data point was presented as $\text{VOI-Risk}_{\text{pair i, DM j}}$, indicating the strength exhibited in pair i by DM j.

The two levels could be spelled out as follows:

(E1) $\text{VOI-Risk}_{\text{pair i, DM j}} = \beta_{\text{DM j}} + \varepsilon_{\text{pair i, DM j}}$
(E2) $\beta_{\text{DM j}} = \gamma + \mu_{\text{DM j}}$

(E1) meant the strength was determined by who the DM was (the $\beta_{\text{DM j}}$ term) and an error term (the $\varepsilon_{\text{pair i, DM j}}$ term). (E2) further specified that the $\beta_{\text{DM j}}$ term had a mean across all DMs (the γ term) and a DM-specific random error (the $\mu_{\text{DM j}}$ term).

If we substituted (E2) into (E1), we got
(E3) $\text{VOI-Risk}_{\text{pair i, DM j}} = \gamma + \mu_{\text{DM j}} + \varepsilon_{\text{pair i, DM j}}$

From (E3), it could be seen that we used 19 data points to estimate the mean across 4 DMs. Even where 19 data points (one data point for one pair) were present, γ was the average of 4 DMs. In the error structure, each DM had an individual specific random effect $\mu_{\text{DM j}}$, and there was also a randomness of each data point $\varepsilon_{\text{pair i, DM j}}$. This meant any two pairs with the same DM j had a shared random term $\mu_{\text{DM j}}$, so they could be correlated. In other words, the DM was modeled as a random effect to account for the correlation within each DM. Hence, we did not treat the 19 points as independent. When we reported that we found a significant difference between VOI and Risk, we were testing whether the overall intercept γ was significant.

If we instead averaged data points of each DM first and ran regressions using the 4 averaged data points (corresponding to 4 DMs), our results did not change qualitatively. We preferred the two-level regressions because we used as much information as possible.

(2) Motivation or arousal

One potential explanation of our findings was that DMs were more motivated/aroused with the presence of an RM than without it. We looked into two behaviors, namely, bar pulls and food

refusals, which were often used to measure motivation/arousal. If monkeys were more motivated, they would pull bars more often and refuse food less often. In our experiment, probably because grapes were highly valuable rewards, the frequency of failing to pull a bar or food refusal was very low. We did not find that DMs were more motivated/aroused when an RM was present.

In the Risk condition, the DMs failed to pull a bar only 3.1% of the time. In the VOI condition, the percentage was only 4.4%. The difference was not significant (p = 0.6263) in a two-level random intercept regression. As for food refusals, the DMs never refused foods in the Risk condition and only did so 0.33% of the time in the VOI condition. These two frequencies were not statistically significantly different either (p = 0.3042).

In other conditions (Ad, AdC, Dis, and DisC), DMs never failed to pull a bar or refuse foods. There was thus no need to perform continuing statistical tests. Overall, there was no evidence that DMs were more motivated/aroused when an RM was present.

(3) Modulation by body weight

We observed a link between disadvantageous inequity concerns and impartiality in step 3. Because there was a correlation between body weight and disadvantageous inequity concerns as shown in step 2, we wondered whether body weight was the reason that we saw the link in step 3. To show the importance of the body weight for modulating the correlation between disadvantageous inequity concerns and choices behind the VOI, we proceeded with two sets of regressions. In the first set, we showed that the body weight predicted part of the disadvantageous inequity concerns accounted for the impartiality behind the VOI. In the second set, we showed that after removing this body weight predicted part, the residual disadvantageous inequity concerns no longer accounted for the impartiality behind the VOI.

With the first set, we proceeded in two steps. We used a two-level linear mixed model in each step. In the first step, we regressed the strength of disadvantageous inequity concerns (the proportional difference that the equal allocation was chosen between Dis and DisC, denoted as Dis-DisC) on the body weight of the DM to obtain the fitted strength of the disadvantageous inequity concerns (denoted as $\widehat{Dis - DisC}$). This was the predicted strength, as predicted by the body weight. Then, in the second step, we regressed the proportional difference that the equal division was chosen between VOI and Risk (denoted as VOI-Risk) on this predicted strength. The coefficient of the predicted strength was 0.18 (z score = 2.89, p = 0.004) and was statistically significant.

Illustratively, we ran
Dis-DisC on body weight to get $\widehat{Dis - DisC}$.
Then, we ran
VOI-Risk on $\widehat{Dis - DisC}$.
(p = 0.004)
This result indicated that the choice difference between VOI and Risk could be explained by the body weight predicted strength of disadvantageous inequity concerns.

In the second set, we also proceeded in two steps. In the first step, we regressed the strength of disadvantageous inequity concerns on the body weight to obtain the residual (denoted as (Dis-

DisC)-($\widehat{Dis - DisC}$). Then, in the second step, we regressed the proportional difference that the equal division was chosen between VOI and Risk on the body weight and the residual. The coefficient of the body weight was 0.01 (z score = 2.89, p = 0.004), and it was statistically significant. The coefficient of the residual was 0.01 (z score = 0.10, p = 0.924), but it was not significant.

Illustratively, we ran
Dis-DisC on the body weight to get the residual (Dis-DisC)-($\widehat{Dis - DisC}$).
Then, we ran
VOI-Risk on the body weight and the residual (Dis-DisC)-($\widehat{Dis - DisC}$).
(p = 0.004) (p = 0.924)
This result indicated that the choice difference between VOI and risk could not be explained by the residual disadvantageous inequity concerns if we removed what was predicted by the body weight.

These two results together suggested the importance of the body weight. The body-weight predicted strength of disadvantageous inequity concerns accounted for the difference between VOI and Risk. However, the body-weight **un**predicted disadvantageous inequity concerns did not account for the choice difference between VOI and Risk. Hence, the body weight was a key factor in modulating the correlation between the disadvantageous inequity concerns and the impartiality behind the VOI.

(4) Correlation between the body weight and the ordinal rank

Our monkeys were never in a shared space. Hence, we were unable to observe who took food first and who escaped from whom in the shared space to determine their ranks. However, we did observe some behavior, such as the following: when we fed them, whether feeding a particular animal before another would arouse the latter and whether moving the cage an animal was in during housekeeping would elicit some display of the other. There was a consensus among the animal keepers and experimenters on the ranks. If we assigned ordinal ranks to our six monkeys arguably arbitrarily according to this consensus, such that the highest-ranked animal got 6 and the lowest-ranked animal got 1, the Pearson correlation coefficient between the body weight and the assigned ordinal rank among the DMs was 0.915, which was high.

The assigned ordinal rank was subjective, and the body weight measure was objective. Hence, we reported the body weight result in the main text. We also tested whether the results on the body weight still held if we replaced the body weight with the assigned ordinal rank. Recall that the regression of the strength of disadvantageous inequity concerns on the body weight of the DM had a positive slope of 0.05 (z score = 4.76, p < 0.001). When we replaced the body weight by the ordinal rank, the slope was again positive at 0.07 (z score = 2.25, p = 0.025) and still significant. In other words, if a DM was assigned an ordinal rank that was higher by a value of 1, it chose the equal allocation (1, 1) that was 7% more. That is, monkeys with higher assigned ranks were more averse to falling behind.

In a similar vein, recall that the regression of the strength of advantageous inequity concerns on the body weight of the DM had a slope of -0.01 (z score = -1.19, p = 0.235) and was not significant.

If we replaced the body weight with the ordinal rank, the slope was again negative at -0.01 (z score = -0.69, p = 0.488) and still not significant. Thus, we did not find that monkeys with higher assigned ranks were more or less averse to getting ahead.

In summary, although we did not have a direct measure of ranks, the assigned ranks exhibited similar effects to the body weight for the results in step 2.

Regarding the two results in step 4, even though the estimated coefficients did not change much, reflecting the high correlation between weight and rank, significance did change for one result.

The first set of regressions addressed whether the predicted strength of disadvantageous inequity concerns explained the degree of impartiality. The coefficient of the predicted strength, now predicted by rank, was 0.15 (z score = 1.40, p = 0.163), and was not significant. Recall that the similar coefficient for weight was 0.18 (z score = 2.89, p = 0.004) and therefore was significant. Hence, the rank predicted result differed from the weight predicted result.

The second set of regressions addressed whether the unpredicted strength no longer explained the degree of impartiality. Here, it was still the case that the unpredicted strength (now by rank) did not explain the degree of impartiality. The coefficient of the residual was -0.02 (z score = -0.17, p = 0.863) and thus was not significant. Recall that the similar coefficient (by weight) was 0.01 (z score = 0.10, p = 0.924) and nonsignificant. Hence, the lack of significance did not change. After removing the rank predicted part, the residual disadvantageous inequity concerns no longer accounted for the impartiality behind the VOI.

(5) Possibility of reciprocation

Some primate experiments took advantage of a large number of subjects so that each DM-RM pair met only once (6). We were unable to do that because we had few monkeys in the lab. Moreover, it required a substantial amount of time to familiarize the monkeys with the apparatus and the design. Hence, each pair met multiple times. In addition to the care we took to avoid the possibility of reciprocation (as described in **Materials and Methods** on the three restrictions when we paired monkeys), below we examined our data to see whether there was evidence of any such influence.

Reciprocation could have occurred in the VOI and Social conditions. If a pair reciprocated each other in the VOI condition, this might be seen if, when the DM chose the equal division frequently, the RM reciprocated by also choosing the equal division frequently when the roles were reversed the next time they met. We thus regressed the proportion a previous RM chose the equal division the next time a pair met on the proportion a DM chose the equal division this time. If reciprocation existed, the coefficient was expected to be significantly positive. The regression coefficient was 0.10 (z score = 0.70, p = 0.484, n = 42), and it was not significant in a two-level linear mixed model. Hence, there was no evidence that monkeys reciprocated in the VOI condition.

In the Social condition, because the DM received the same reward in both allocations, we defined the allocations that gave the RM more as favoring the RM. This translated to the (3, 3) allocation in the Ad condition and the (1, 3) allocation in the Dis condition. If a pair reciprocated each other in the Social condition, we could see this when if the DM favored the RM frequently, the RM

reciprocated by also favoring the DM frequently when their roles were reversed. We thus regressed the proportion of the RM's choices that favored the DM the next time the pair met on the proportion of the DM's choices that favored the RM this time. If reciprocation existed, the coefficient was expected to be significantly positive. The regression coefficient was 0.01 (z score = 0.06, p = 0.954, n = 42), which was not significant in a two-level linear mixed model. Hence, there was no evidence that monkeys reciprocated in the Social condition.

(6) Time effect

We addressed the possibility of time effect in two ways. First, we tested whether choices in any condition changed as time went by. Second, we tested whether choice differences between a condition and its control (VOI vs. Risk, Ad vs. AdC, Dis vs. DisC) were stable. In other words, we tested whether our results were stable.

For the first part, we looked into whether choices differed across blocks. We pooled the data in the Risk and VOI conditions to run a repeated measures ANOVA with condition (Risk or VOI), block, interaction, and DM as factors. The dependent variable was the choice frequency of the equal division. The main effect of the block was not significant (p = 0.3244), and neither was the interaction (p = 0.2326). Hence, choices did not differ across blocks. The block effect did not differ between the Risk and VOI conditions either. Of note, the main effect of the condition (Risk vs. VOI) was significant, consistent with the result we reported in the main text that the equal division was chosen more often in the VOI condition than in the Risk condition.

ANOVA: Condition (VOI or Risk), Block, Interaction

Source	Partial SS	df	MS	F	p-value Regular	p-value Box
Condition	0.2000	1	0.2000	8.37	0.0049	
Block	0.0843	3	0.0281	1.18	0.3244	0.2879
Interaction	0.1045	3	0.0348	1.46	0.2326	0.2380
DM	0.3049	3	0.1016	4.25	0.0077	
Residual	1.9366	81	0.0239			
Total	2.5884	91	0.0284			

Applying the same ANOVA to the data in the AdC and Ad conditions, we did not observe a block effect (p = 0.0923) or an interaction between block and condition (p = 0.8801).

ANOVA: Condition (Ad or AdC), Block, Interaction

Source	Partial SS	Df	MS	F	p-value Regular	p-value Box
Condition	0.0725	1	0.0725	3.09	0.0866	
Block	0.0698	1	0.0698	2.98	0.0923	
Interaction	0.0005	1	0.0005	0.02	0.8801	
Subject	0.0626	3	0.0209	0.89	0.4547	
Residual	0.9145	39	0.0234			
Total	1.1834	45	0.0263			

Similarly, applying the same ANOVA to the data in the DisC and Dis conditions, we did not observe a block effect (p = 1.000) or an interaction between block and condition (p = 1.000).

ANOVA: Condition (Dis or DisC), Block, Interaction

Source	Partial SS	Df	MS	F	p-value Regular	p-value Box
Condition	0.0115	1	0.0115	0.71	0.4058	
Block	0.0000	1	0.0000	0.00	1.0000	
Interaction	0.0000	1	0.0000	0.00	1.0000	
Subject	0.1653	3	0.0551	3.40	0.0272	
Residual	0.6338	39	0.0162			
Total	0.8111	45	0.0180			

For the second part, we examined whether our major results held if we split all conditions into two halves. For instance, the VOI condition was split into VOI 1, the first half; and VOI 2, the second half. If time were the reason why the equal division was chosen more often behind the VOI than in the Risk condition, because we ran the Risk condition before the VOI condition, Risk 1 and VOI 2 were most separated in time and hence differences in choices between them could be expected to be large. On the other hand, Risk 2 and VOI 1 were least separated in time. The difference between them, by the same reasoning could be expected to be small. We intended to see whether the VOI vs. Risk difference was primarily driven by time, so that VOI 2 vs. Risk 1 would be significantly different but VOI 1 vs. Risk 2 would not.

We found that the equal division was chosen significantly more often in two combinations (including VOI 1 vs. Risk 2, least separated in time; and VOI 2 vs. Risk 2, which had an intermediate separation of time). In the remaining two combinations (VOI 1 vs. Risk 1, with an intermediate separation of time; VOI 2 vs. Risk 1, most separated in time), the equal division was still chosen more often in VOI. The p-values were 0.051, 0.057 respectively, right on the margin of significance. Hence, the increased choice of the equal division in VOI was quite stable. It was not driven by a particular combination that was most separated in time, namely VOI 2 vs. Risk 1. This supported that the elapsed time between VOI and Risk did not influence the results. We cautioned that the use of only a quarter of our data in each combination would make estimations noisier and less likely to be significant.

We next examined disadvantageous inequity concerns. Before, we showed that the strength was not significantly different from zero; now, it was still so in all four combinations (the smallest p-value among the four combinations was 0.542). Before, body weight could significantly account for the strength positively; now this was still the case in all four combinations (the largest p-value among the four combinations was 0.026). Hence, the results of disadvantageous inequity concerns were stable.

Regarding advantageous inequity concerns, before, we observed a significant tendency to dislike getting ahead, but body weight could not account for it. Here, we needed to qualify our earlier results. Though body weight still could not account for it (the smallest p-value among the four combinations was 0.455) and the tendency was still to dislike getting ahead, we did not find

significance in all combinations. We found one strong significance (p-value smaller than 0.001) and three insignificances (p = 0.067 in one combination and p-value greater than 0.1 in two remaining combinations). Though the average tendency was significantly positive, this did not apply to all combinations. Again, the use of a smaller amount of data made estimations noisier and less likely to be significant.

Overall, the impartiality behind the VOI and disadvantageous inequity concerns were robust even when data were split into halves and all possible combinations were considered. The advantageous inequity concerns were not significant in all combinations and needed to be qualified. Because our main contribution regarded VOI choices and the connection between VOI choices and disadvantageous inequity aversion, the conclusion of our results held up when the time effect was considered.

Captions for Movies

Movie S1

VOI: The top panel of the movie shows a view toward the monkeys, and the bottom panel shows a view toward the food trays. When facing the monkeys, the DM (Little Babe) is on the right and the RM (Coffee) on the left. The upper tray is baited with (3, 1) where 3 is in the left dish and the lower with (2, 2). The DM pulls the upper bar. The upper tray is then spun one and a half loops.

Movie S2

Risk: The upper tray is baited with (2, 2) and the lower with (1, 3) where 1 is in the left dish. The DM (Venus) pulls the lower bar. The lower tray is then spun one and a half loops.

References

1. Darwin C. The descent of man, and selection in relation to sex. Princeton, N.J.: Princeton University Press; 1981.
2. Brosnan SF, de Waal FB. Evolution of responses to (un)fairness. Science. 2014;346(6207):1251776.
3. Tomasello M, Vaish A. Origins of human cooperation and morality. Annu Rev Psychol. 2013;64:231-55.
4. Brosnan SF. Justice- and fairness-related behaviors in nonhuman primates. Proc Natl Acad Sci U S A. 2013;110 Suppl 2:10416-23.
5. Brosnan SF, De Waal FB. Monkeys reject unequal pay. Nature. 2003;425(6955):297-9.
6. Jensen K, Call J, Tomasello M. Chimpanzees are rational maximizers in an ultimatum game. Science. 2007;318(5847):107-9.
7. Brauer J, Call J, Tomasello M. Are apes inequity averse? New data on the token-exchange paradigm. Am J Primatol. 2009;71(2):175-81.
8. Lakshminarayanan VR, Santos LR. Capuchin monkeys are sensitive to others' welfare. Curr Biol. 2008;18(21):R999-1000.
9. Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, et al. Chimpanzees are indifferent to the welfare of unrelated group members. Nature. 2005;437(7063):1357-9.
10. Jensen K, Hare B, Call J, Tomasello M. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc Biol Sci. 2006;273(1589):1013-21.

11. Burkart JM, Fehr E, Efferson C, van Schaik CP. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. Proc Natl Acad Sci U S A. 2007;104(50):19762-6.
12. Sheskin M, Ashayeri K, Skerry A, Santos LR. Capuchin monkeys (Cebus apella) fail to show inequality aversion in a no-cost situation. Evol Hum Behav. 2014;35(2):80-8.
13. Takimoto A, Kuroshima H, Fujita K. Capuchin monkeys (Cebus apella) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. Anim Cogn. 2010;13(2):249-61.
14. Massen JJM, Van den Berg LM, Spruijt BM, Sterck EHM. Inequity aversion in relation to effort and relationship quality in long-tailed Macaques (Macaca fascicularis). American Journal of Primatology. 2012;74(2):145-56.
15. Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Schapiro SJ. Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes. Anim Behav. 2010;79(6):1229-37.
16. Melis AP, Hare B, Tomasello M. Chimpanzees coordinate in a negotiation game. Evol Hum Behav. 2009;30(6):381-92.
17. Hopper LM, Lambeth SP, Schapiro SJ, Bernacky BJ, Brosnan SF. The Ontogeny of Social Comparisons in Rhesus Macaques (Macaca mulatta). Journal of Primatology. 2013;2(1).
18. McAuliffe K, Chang LW, Leimgruber KL, Spaulding R, Blake PR, Santos LR. Capuchin monkeys, Cebus apella, show no evidence for inequity aversion in a costly choice task. Anim Behav. 2015;103:65-74.
19. Yamamoto S, Tanaka M. The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. Animal Behaviour. 2010;79(3):595-602.
20. Brosnan SF, Schiff HC, de Waal FB. Tolerance for inequity may increase with social closeness in chimpanzees. Proc Biol Sci. 2005;272(1560):253-8.
21. Massen JJM, Luyten IJAF, Spruijt BM, Sterck EHM. Benefiting friends or dominants: prosocial choices mainly depend on rank position in long-tailed macaques (Macaca fascicularis). Primates. 2011;52(3):237-47.
22. Harsanyi JC. Cardinal Utility in Welfare Economics and in the Theory of Risk-taking. J Polit Econ. 1953;61(5):434-5.
23. Harsanyi JC. Bayesian Decision-Theory and Utilitarian Ethics. Am Econ Rev. 1978;68(2):223-8.
24. Rawls J. A theory of justice. Cambridge, Mass.: Belknap Press of Harvard University Press; 1971.
25. Quene H, van den Bergh H. On multi-level modeling of data from repeated measures designs: a tutorial. Speech Commun. 2004;43(1-2):103-21.
26. Fehr E, Schmidt KM. A theory of fairness, competition, and cooperation. Q J Econ. 1999;114(3):817-68.
27. Hsu MJ, Chen LM, Agoramoorthy G. The vocal repertoire of Formosan macaques, Macaca cyclopis: Acoustic structure and behavioral context. Zool Stud. 2005;44(2):275-94.
28. Hsu MJ, Kao CC, Agoramoorthy G. Interactions between visitors and Formosan macaques (Macaca cyclopis) at Shou-Shan Nature Park, Taiwan. Am J Primatol. 2009;71(3):214-22.
29. Hsu MJ, Lin SI, Lin JF, Lin TJ, Agoramoorthy G. Non-Maternal Infant Handling in Wild Formosan Macaques of Mount Longevity, Taiwan. Folia Primatol (Basel). 2015;86(6):491-505.

30. Hsu MJ, Lin JF, Agoramoorthy G. Effects of group size on birth rate, infant mortality and social interactions in Formosan macaques at Mt Longevity, Taiwan. Ethol Ecol Evol. 2006;18(1):3-17.
31. Thierry B, Mewa S, Kaumanns W. Macaque societies: a model for the study of social organization. Cambridge; New York, NY: Cambridge University Press; 2004. xv, 418 p. p.
32. Morgan D, Grant KA, Prioleau OA, Nader SH, Kaplan JR, Nader MA. Predictors of social status in cynomolgus monkeys (Macaca fascicularis) after group formation. American Journal of Primatology. 2000;52(3):115-31.
33. Tokuda K, Jensen GD. Determinants of dominance hierarchy in a captive group of pigtailed monkeys (Macaca nemestrina). Primates. 1969;10:227–36.
34. Bernstein IS, Mason WA. Group formation by rhesus monkeys. Anim Behav. 1962;11(1):28-31.
35. Morgan D, Grant KA, Prioleau OA, Nader SH, Kaplan JR, Nader MA. Predictors of social status in cynomolgus monkeys (Macaca fascicularis) after group formation. Am J Primatol. 2000;52(3):115-31.
36. Queller DC, Strassmann JE. The veil of ignorance can favour biological cooperation. Biol Lett. 2013;9(6):20130365.
37. Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E. Two Key Steps in the Evolution of Human Cooperation: The Interdependence Hypothesis. Curr Anthropol. 2012;53(6):673-92.
38. Melis AP. The evolutionary roots of human collaboration: coordination and sharing of resources. Ann N Y Acad Sci. 2013;1299:68-76.
39. Blake PR, McAuliffe K, Corbit J, Callaghan TC, Barry O, Bowie A, et al. The ontogeny of fairness in seven societies. Nature. 2015;528(7581):258-61.
40. Schildberg-Horisch H. Is the veil of ignorance only a concept about risk? An experiment. J Public Econ. 2010;94(11-12):1062-6.