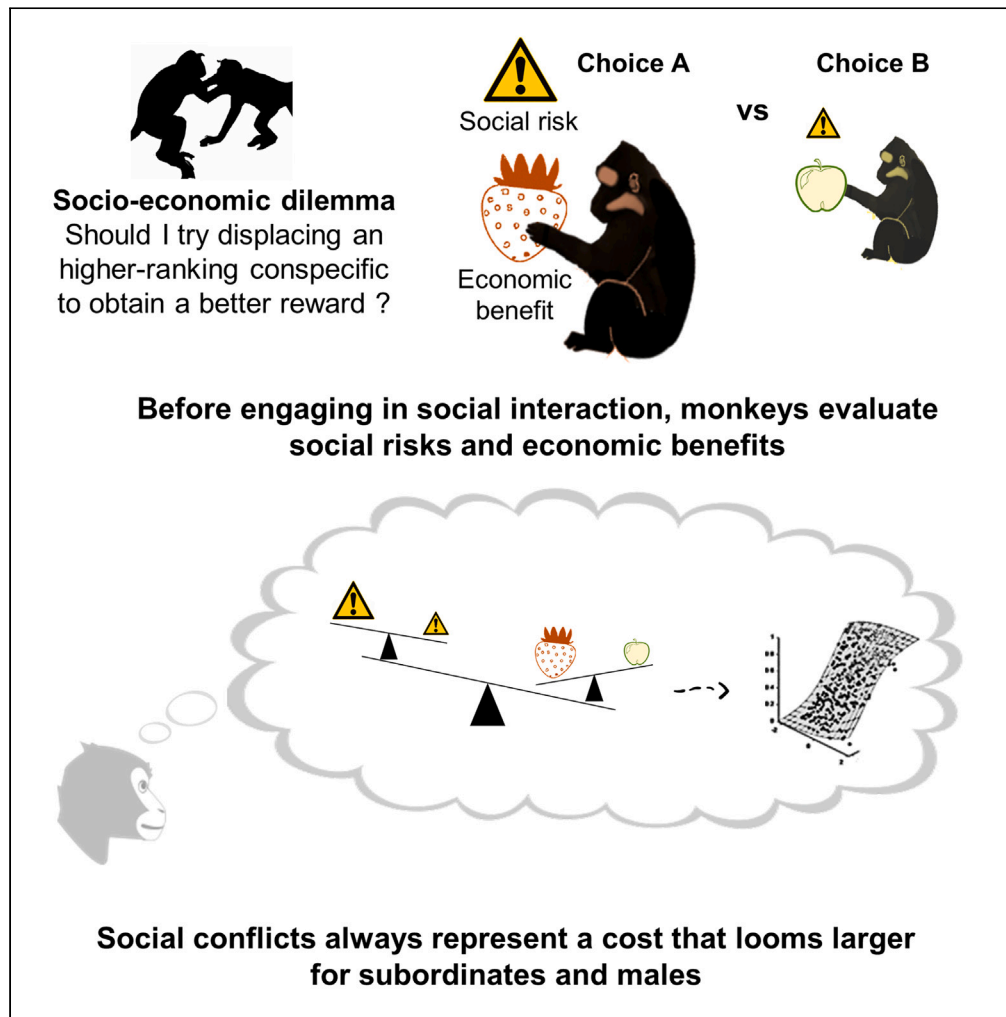


Article

Is this worth the trouble? Strategic conflict management in Tonkean macaques



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Highlights

This study provides an original methodology in conflict management research

Macaques integrate both economic and social components in conflicts' decision-making

Social rank conditions the weights of the social and economic components in decision

Social conflicts always represent a cost that looms larger for subordinates and males

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Article

Is this worth the trouble? Strategic conflict management in Tonkean macaques

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SUMMARY

Conflict management entails preventing and repairing damages resulting from social conflicts. While previous research has emphasized post-conflict actions like reconciliation, the understanding of how primates weigh the costs and benefits of conflict remains limited. Uncovering this hidden but fundamental aspect of conflict management requires addressing actively avoided social conflicts. In a study involving semi-free ranging Tonkean macaques, individuals were presented with social dilemmas: displacing a peer to access a preferred juice reward or opting for a peer-free but less preferred one to avoid conflict. The results showed that subjects attributed a cost to the social conflict and did not demonstrate a systematic drive to dominate. Decision modeling revealed integration of peer hierarchy and reward subjective value, with subjects' own social rank impacting the balance between these social and economic dimensions. Overall, this research highlights how primates strategically address group cohesion and peacekeeping, sometimes at the expense of personal preferences.

INTRODUCTION

Given the existence of a certain degree of interpersonal dependency in a world of limited and shared resources, social conflicts are inevitable. Social conflicts start with an incompatibility among the actions, goals, or interests of at least two agents and end through combat, compliance, or lack of opposition of either one or both agents.^{1,2} Frequent and serious intraspecific conflicts are detrimental to group living animals.^{3–5} A critical question is thus when to fight and the answer theoretically depends on both costs incurred by aggression and benefits gained from aggression. Many factors influence the costs and benefits of aggression, including the value of a contested resource, an individual's relative fighting ability, but also the relatedness between competitors.^{6,7} Conflicts indeed involve not only the risk of injury, but also endangers valuable social relationships resulting from numerous interactions that may represent a form of long-term social investment.^{8–13} In theory, evolution should have favored not only "limited war" conflicts type within species³ but also strategies to avoid, mitigate, or resolve social conflict between individuals that are mutually dependent. However, conflict remains a recurrent feature of social groups, present at every stage of life and conflict management represents a daily challenge in many animals' species.^{14–17} In primates, socio-cognitive abilities may further help dealing with conflicts in order to maintain spatial cohesion among members while maximizing individual payoff. Aggression is a salient event which is part of a broader range of phenomena related to conflict management,^{1,18} including peacekeeping behaviors.^{19–22} To date, most studies about conflict management have focused on post-conflict behaviors such as reconciliation or third-party intervention.^{1,2,10,11} However, these complex behaviors can be considered as the tip of the iceberg of daily conflict management. Primates' conflict management is believed to rely on decision-making process that involves cost-benefit analysis carried out by each competitor, but such claim has never been formally proven.^{2,23} We further ignore (i) to what extent non-human primates evaluate and thus anticipate the cost associated with a social conflict, (ii) how it can be balanced by its potential payoff, and (iii) whether these two dimensions are integrated into a single decisional framework. Such knowledge is lacking because past studies were not able to consider situations where social conflicts were avoided by the monkeys and did not quantify the valuation processes involved in conflict management.²⁴ By tackling this underexplored topic, this study aims at revealing hidden but fundamental mechanisms by which monkeys manage conflictual social situations. We designed an innovative paradigm that allowed us to investigate primates' decision-making upstream of potential conflict, instead of the more classical downstream approach, focusing on conflict resolution. Semi-free ranging Tonkean macaques (*Macaca tonkeana*) could be rewarded with juice (upon providing correct response to a behavioral task) by using machines for automated learning and testing (MALT) that are in open access in the animals' wooded park.²⁵ However, as an individual decide to go to a MALT, the device can be already used by a conspecific and taking control over it implies a genuine risk of a social conflict.²⁶ We analyzed months of MALT usage and extracted different social situations where the monkeys had to decide whether they should displace a peer to use a given MALT. Importantly, each of the four MALT were similar except that it was filled with a juice of specific and unique flavor. We measured individuals' subjective preferences by considering the subject's decisions when all MALT were

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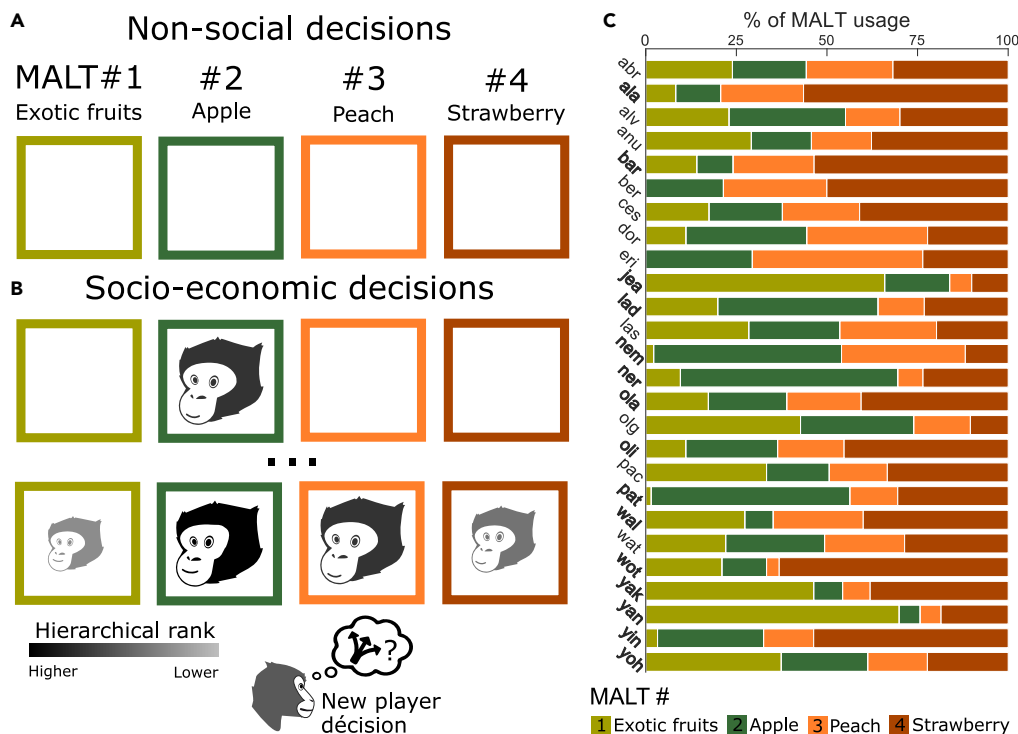


Figure 1. Description of the experimental paradigm

(A) Each machine for automated learning and testing (MALT) was filled with a juice reward of different and unique flavor. Semi-free ranging Tonkean macaques may face social dilemmas such as displacing a peer to reach their preferred juice reward or avoiding conflict by choosing a less preferred available reward. Non-social decision. We extracted $N = 8\,096$ situations where all MALT were unoccupied for more than 30 s before the beginning of the new player session. These data were used to compute individual preferences for juice flavors. Each individual displayed personal preferences to work on a specific MALT that is arguable driven by preference in reward flavor.

(B) Socio-economic decision. We considered a total of $N = 51\,954$ social dilemmas where a new player had to decide in which MALT he/she will work on. The hierarchical rank of others monkeys (depicted here from black to light gray for higher to lower ranking, respectively) were considered to model the new player social dimension of these decisions. The individual juice preference, measured in non-social context, was considered to model new player economic dimension of these decisions.

(C) Individual juice preferences in a non-social context. Note that most subjects had their own preferences for juice reward and no consistent preference can be found at the group level. Individuals that displayed significant preference for a reward flavor are written in bold (chi-squared test $p < 0.05$).

available (non-social context). When at least one MALT was already occupied by a peer (social context), the macaque can either choose to displace one of the current users or choose another MALT filled with a different, sometimes less preferred, juice flavor. In order to model the new player decision, we also considered the hierarchical rank of all the monkeys that were using the apparatus during these dilemmas. Therefore, we could quantify social and economic dimensions in this decisional framework. Using this unique paradigm, our aim was to shed light on the underlying cognitive processes allowing macaques to strategically handle and value conflict of interest.

RESULTS

Do macaque monkeys assign a cost to social conflict?

The decision we considered in this study consists in choosing in which MALT a new monkey player was going to work on. In order to characterize individuals' preference for juice flavor, we extracted situations where all MALT were unoccupied for more than 30 s before the beginning of the new player session (8 096 non-social decisions, Figure 1A). In order to test the integration of juice preferences with new player willingness to displace, or not, a peer that was working in a MALT, we considered situations where at least one MALT was occupied by another monkey (51 954 socio-economic decisions, Figure 1B). At the group level, no flavor of juice was preferred by every subject, each subject had their own subjective preferences for juice flavor (Figure 1C, 15 out of 26 subjects had a significant preference for at least one flavor, chi-squared test $p < 0.05$). For the next analysis, we only considered situations where the preferred MALT of each monkey was occupied by a peer while all other MALT were free (1 870 socio-economic decisions, Figure 2). We find that new players were less likely to access their preferred MALT if occupied by a peer, even by a lower ranking one (Figure 2A, Wilcoxon signed-rank test, $p = 0.019$). This effect was more significant when the MALT was occupied by a higher ranking peer (Figure 2A, Wilcoxon signed-rank test, $p < 0.001$; lower/higher ranking comparison: Wilcoxon rank-sum test, $p < 0.001$). At individual level, we did not find evidence that a new player was attracted by social conflict

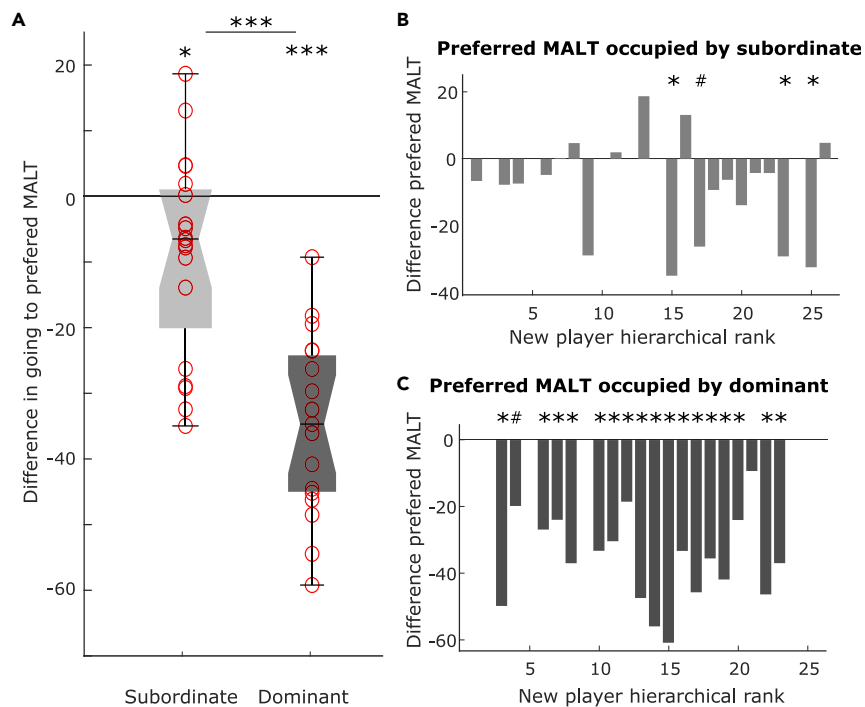


Figure 2. Effect of others' presence on preferred MALT selection

(A) Negative, positive, value means that the preferred MALT was respectively less, more, selected when other was in the player preferred MALT (y axis: Difference in going to preferred MALT). The presence of a subordinate (light gray, N subject = 20/26, N total decisions in social context = 788, Wilcoxon signed-rank test, $p = 0.019$) significantly decreases the new player's willingness to work on his/her preferred MALT. The effect is stronger if the preferred MALT was occupied by a dominant individual (dark gray, N subject = 19/26, N total decisions in social context = 1082, Wilcoxon signed-rank test, $p < 0.001$, Wilcoxon rank-sum test, $p < 0.001$).

(B and C) Analysis at the individual level. Difference in selecting more (positive values) or less (negative values) their preferred MALT for each subject (1–26 in x axis) when occupied by a subordinate (B, light gray) or a dominant (C, dark gray). In all panels, subjects with less than 10 decisions in social context were excluded from this analysis. In addition, the most dominant or the most subordinate individuals of the group cannot be logically included in the analysis considering individuals that were dominant or subordinate toward the player, respectively. In both panels, *, #, Fisher's exact test, uncorrected for multiple testing, $p < 0.05$ and $p < 0.1$, respectively.

with a lower ranking (Figure 2B, Fisher's exact test $p < 0.05$) or higher ranking individual (Figure 2C, Fisher's exact test $p < 0.05$). For the following analyses, we considered every situation where at least one MALT was occupied by a peer (social context, Figure 1B). Our model aimed at explaining the decision of the monkey to select a specific MALT considering the relative rank of the peer(s) that occupied each of the MALT. We thus modeled individual decisions when at least one MALT was used by a conspecific and the subject had to choose between the four MALT. We considered that if a monkey had chosen to use a MALT, this meant that it had a higher subjective value than the three other MALT. This can be modeled as the result of three distinct decisions between the chosen MALT (MALT X) and each of the three remaining unchosen ones (MALT Y, see methods). For each individual, we tested more precisely the influence of the hierarchical rank on the monkey decision by modeling these decisions using a binomial generalized linear model (GLM) (51 954 socio-economic decisions, Figure 3). When considering all subjects, we found that in 147 out 156 pairs of MALT (94%, 26 subjects with 6 pairs of MALT each, equal 156 pairs of MALT), the decision to work on a specific MALT was significantly influenced by the difference in hierarchical rank between the individual being in the chosen and the one being in the other MALT (mean population GLM, $\beta_{\text{rank}} = 1.19 \pm 0.03$, $p < 0.001$, $F = 1304$, $p < 0.001$, Figure 3A). Subjects that displayed juice preference had lower choice accuracy in their social decisions (Figures S1 and 4B).

Can reward value counterbalance the cost of social conflict?

Visual analysis of sigmoid representing social decisions in different pairs of MALT suggests that another factor than subjects' hierarchical ranks was influencing monkey's decisions (chosen examples in Figure 3B and all subjects in Figure S2). In this model, the location of the sigmoid on the x axis was assessed through its indifference points (circle point with a cross in Figures 3B and S2, representing the point of the sigmoid where the probability of choice is at 50/50, see methods). Here, the position of the indifference point can be interpreted as a basal difference in the subjective value of one MALT compared to another. We noted the existence of a variability in the position of the indifference point for each pair of MALT and for each individual. This variability may be explained by the influence of individual's juice flavor preferences in their social decisions. We tested this relation by regressing the position of the indifference point with the difference in preference of each pair of

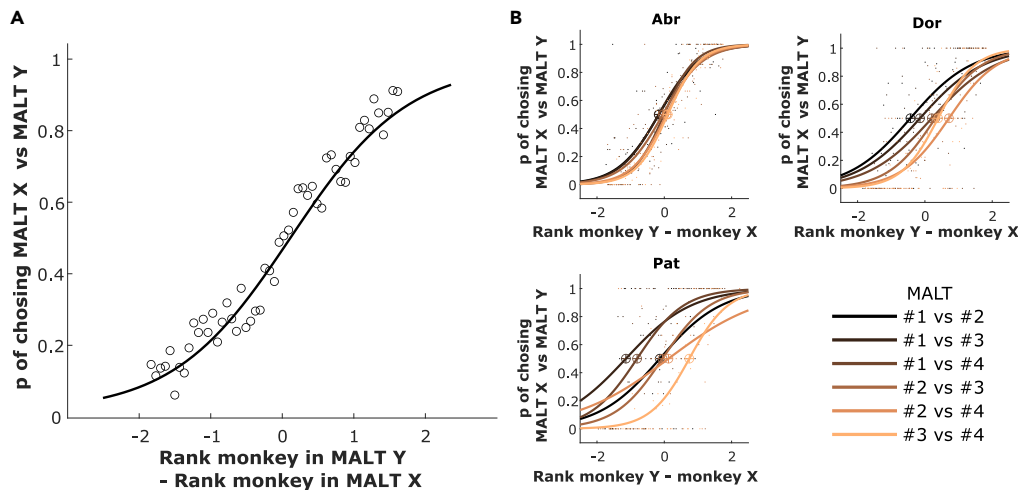


Figure 3. Influence of others' hierarchical rank on MALT selection

(A) We extracted 51 954 situations where at least one MALT was occupied by another monkey, at least 30 s before the beginning of the new player session. We considered the ordinal hierarchical rank difference between the monkey in the MALT chosen by the new player (MALT X) and the unchosen ones (MALT Y). Note that an unoccupied MALT was considered of the lowest ordinal rank plus 1. We used these differences to predict the decision of the new player to choose a specific MALT using a GLM with a logit link function ($\beta_{rank} = 1.19 \pm 0.03$, $p < 0.001$).

(B) We considered the decisions of each individual (e.g., *Abr*, *Dor*, *Pat*) and all the pairs of MALT on a two-by-two basis. Circle point with a cross represents the indifference point of each sigmoid (see methods). Note the existence of an individual variability in the position of the indifference point between pairs of MALT. In all panels, rank differences were normalized using Z score. All individuals' decisions for all pairs of MALT are shown in [Figure S1](#).

MALT when selected in a non-social context ([Figure 4A](#)). We also considered the steepness of each sigmoid in order to assess the precision of individuals' decisions ([Figure 4B](#)). We found that the position of indifference points correlates to individual's preference for juice flavor ([Figure 4A](#), Pearson correlation, $R = -0.62$, $p < 0.001$). The steepness of each sigmoid depicted partially in [Figure 3B](#) and exhaustively in [Figure S2](#) ([Figure 4B](#), Pearson correlation, $R = -0.03$, $p = 0.69$) did not correlate with individual's preference for juice flavor. These results suggest that a social dimension (peers rank) and an economic dimension (juice preference) were integrated in the decision of a new player to work on a given MALT. Interestingly, subjects that did not display a significant juice preference in non-social context ([Figure 1C](#)) had steeper sigmoid when deciding in a social context ([Figure 4B](#), Wilcoxon rank-sum test, $p < 0.001$; [Figure S1](#)). In order to estimate relative effect sizes, we included these two dimensions into a single logistic GLM to study the influence of an individual's rank on these socio-economic decisions. In a social context, when deciding which MALT a given monkey was going to use, we found that peers rank ($\beta_{rank} = 1.32 \pm 0.01$, $p < 0.001$) and juice preference ($\beta_{jpref} = 0.74 \pm 0.01$, $p < 0.001$, $F = 7081$, $p < 0.001$, [Figure 5A](#); [Tables S2](#) and [S3](#)).

Is there an effect of the subject's sex and hierarchical rank on its conflict management strategy?

When considering the socio-economic decisions of each player, we found that hierarchical rank significantly influences the value of β_{rank} and β_{jpref} decisions with β_{rank} being positively correlated ([Figure 5B](#), Spearman correlation, $N = 26$, $R = 0.78$, $p < 0.001$) and β_{jpref} negatively correlated ([Figure 5C](#), Spearman correlation, $N = 26$, $R = -0.71$, $p < 0.001$) to the subject's own hierarchical rank. This implies that when facing a conflict of interest, the decisions of lower ranking monkeys are mainly influenced by the rank of the competitor while the decisions of higher ranking monkeys are mostly driven by their own economic preferences. A stepwise analysis that considered subjects' age and sex confirmed that hierarchical rank was the best predictor of individuals' decisions in this context of conflict of interest (See [Tables S1–S3](#)). However, this analysis revealed that the association between β_{rank} and the monkeys own rank was more pronounced in male than in female subjects ([Figure 5C](#), Spearman correlation, males $N = 15$, $R = 0.85$, $p < 0.001$; females, $N = 11$, $R = 0.63$, $p = 0.044$; [Tables S1](#) and [S2](#)). Another main factor that should influence individual conflict management strategy is their level of social tolerance;²⁷ therefore, the residuals of the regression depicted in [Figure 5C](#) may be considered as an exploratory metric of social tolerance ([Figure S3](#)).

DISCUSSION

Macaque monkeys do not see social conflicts as intrinsically rewarding

Studying conflict management in large groups of monkeys showing complex social organization and structure allows the identification and quantifications of individual factors influencing primates' decisions in a context of upcoming conflict of interest. A hypothesis, first formulated by Maslow²⁸ in 1935, considered that animals may seek conflict over social status, which would correspond to a sort of dominance drive, an opportunity to dominate others, a will to power.^{29,30} In other words, a given individual may find an intrinsic motivation in social conflict with a lower ranking peer as it will assert its social status, which may even be considered as a form of social reward.³⁰ Our data do not support this

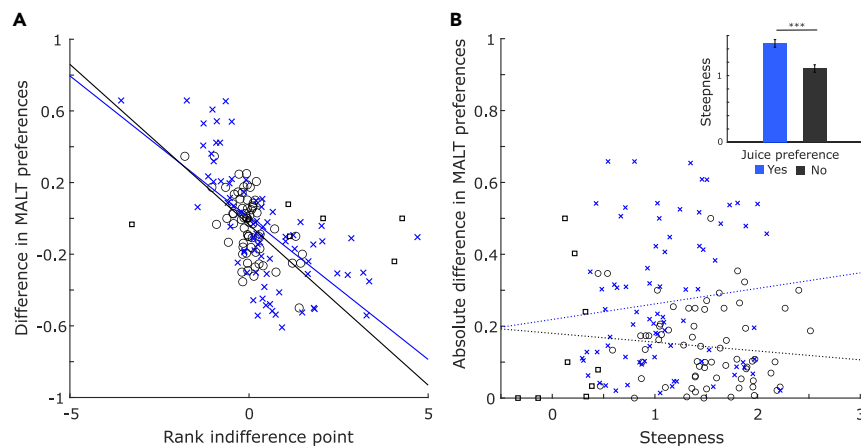


Figure 4. Juice preference measured in non-social context influences social decision

(A) Monkeys that displayed a significant juice preference in a non-social context are depicted in blue; monkeys that did not display juice preference are displayed in black. Rank indifference point is significantly correlated with the preference for MALT when chosen in a non-social context (Pearson correlation, blue crosses, $N = 68$, $R = -0.55$, $p < 0.001$; black circles, $N = 79$, $R = -0.55$, $p < 0.001$). Correlations between the displacement of indifference points and the difference in juice preference yield to a significant correlation demonstrating that both subjective preferences and others' social status were taken into account during these decisions. As these decisions require a balance between social and non-social dimensions, it can be considered as a socio-economic decision.

(B) The steepness of the sigmoid depicted in Figure 2 is not correlated with the absolute preference for MALT when chosen in a non-social context (Pearson correlation, blue crosses, $N = 68$, $R = -0.11$, $p = 0.38$; black circles, $N = 79$, $R = -0.11$, $p = 0.32$). The insert in the right corner of the panel represents the mean steepness between monkeys that displayed (blue) or not (black) a significant juice preference in a non-social context (Wilcoxon rank-sum test, $p < 0.001$). In both panels, squares represent estimates of the GLM that were not significant at individual level (GLM, $p < 0.05$, $N = 9$), these points were not used for the linear fits depicted in both panels, this does not influence statistical significance of any of these analyses. Error bars represent SEM.

hypothesis; in fact, we found that Tonkean macaques generally avoid social conflicts and can even forgo preferred reward to prevent them, albeit the opponent is of lower rank. Tonkean macaque is a notoriously tolerant species of macaque;³¹ it is worth noting that by using a similar protocol in more despotic species of non-human primates (such as *Macaca mulatta*), further research may find such dominance drive. Nonetheless, our results support the view that non-human primates consider social conflicts as a costly interaction that comprise the physical risk of combat and the damage to social relationships.

Cost and benefits of conflicts are integrated in monkeys' social decisions

Using an innovative and ecologically relevant protocol, our study demonstrates that macaque monkeys behave "as if" they integrate social and non-social variables to best manage conflicts of interest. One can argue that an efficient way to manage conflict is to avoid them as much as possible and adopt strategies, upstream of conflict, that prevent fighting from occurring. Previous video analysis of conflicts in the context of individuals accessing the MALT²⁶ revealed a very low occurrence of physical aggression (<1%), arguing for such efficient management of potentially conflictual situations, at least in this tolerant macaque species.³¹ In addition, previous behavioral observations suggest non-human primates adapt their affiliative behaviors in prediction or in response to competitive context of interactions to avoid conflicts or their escalations into damaging fights.^{32–37} Overall, we demonstrate that, based on their social knowledge, macaques estimate the cost associated with a social conflict and integrate social and non-social features in their decisional framework. Subjects who did not express a significant preference for juice in a non-social context were probably less likely to integrate these two characteristics into their decision-making framework. This suggests that, in the absence of the need to take juice preference into account, social decisions were more accurate (Figure 4C), arguing for genuine interactions between the social and economic dimensions of these decisions. Using images of conspecifics, past study has already suggested that social and non-social dimensions can be integrated during decision-making (e.g., pay per view³⁸). Our study adopts an ecological paradigm in a high number of subjects living in semi-free ranging naturalistic settings, which allow us to further demonstrate that the integration of social and non-social dimensions depends on individuals' sex and own hierarchical rank. Indeed, we found that the relative weight of the social and non-social dimension of this decisional framework covaries with individuals' hierarchical ranks. In addition, according to the steepness of the decision curves,³⁹ modeling of individuals' decisions suggests that monkeys view social dilemmas related to hierarchical rank in a probabilistic way and not in an all-or-nothing manner (as decisions curves can be better described as sigmoid than as step functions, e.g., Figures 3B and S1). Our results provide new insights into how macaques strategically manage conflictual situations and promote group cohesion. We further confirmed that in a context of potentially conflictual interactions, primates rely on their social knowledge.^{40–44} Other social dimensions such as kinship or affiliation were not included in our analysis as the interpretation of potential findings would be more ambiguous. Subjects that may seek or avoid conflict with, for instance, a MALT occupied by kin, a friend, or a potential sexual partner can be understood either as (i) a motivation for social contact, (ii) the avoidance of conflict with potential ally/mate, or (iii) a preference for conflict that should be of lower intensity. But the quality of the fit in the models (e.g., Figure 3A) shown in this paper suggests that there is

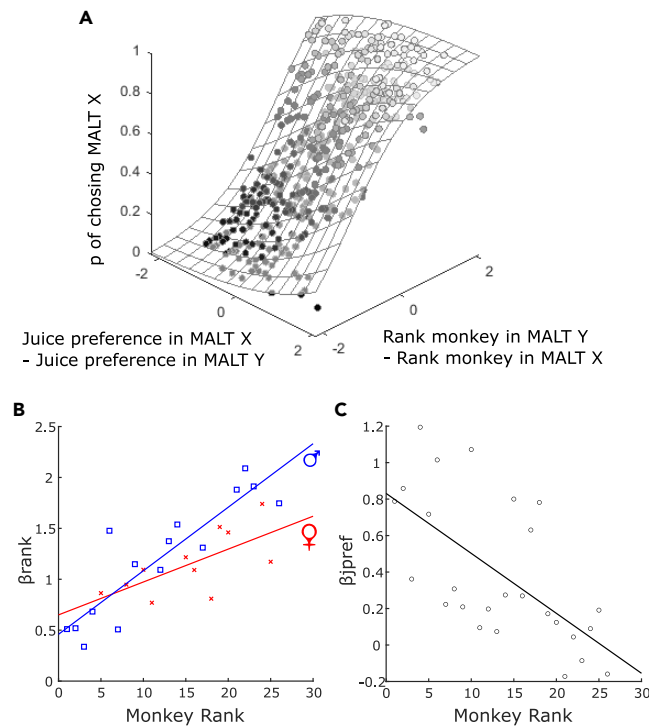


Figure 5. Effect of the new player's own hierarchical rank on its socio-economic decisions

(A) Graphical representation of socio-economic decisions in Tonkean macaque. To model socio-economic decisions, we used a GLM with a logit link function. Each dot represents mean decisions to work on MALT X (chosen) vs. MALT Y (unchosen) considering others' rank and player's juice preference for MALT X and Y (dark gray mostly choosing MALT Y, light gray mostly choosing MALT X). Peers' hierarchical rank and juice preference of the new player were significant predictors of monkey's decision $\beta_{rank} = 1.32 \pm 0.01$, $p < 0.001$ and $\beta_{pref} = 0.74 \pm 0.01$, $p < 0.001$. The differences in rank and juice preference were normalized using Z score. (B) The estimates of peers' hierarchical rank (β_{rank}) positively correlate with the new player's own hierarchical rank (Spearman correlation, $N = 26$, $R = 0.78$, $p < 0.001$). Stepwise analysis revealed that this association was significantly stronger for male (blue squares) than female (red crosses) subjects (Spearman correlation, males $N = 15$, $R = 0.85$, $p < 0.001$; females, $N = 11$, $R = 0.63$, $p = 0.044$). (C) The estimates of the new player juice preference (β_{pref}) negatively correlate with the new player's own social rank (Spearman correlation, $N = 26$, $R = -0.71$, $p < 0.001$).

little variability left to explain when solely considering hierarchical ranks. Overall, this is consistent with the idea that the dominance hierarchy plays a central role in the perceived cost of social conflict. Moreover, we found that the sex and own hierarchical rank of the decision-maker influence its socio-economic decisions. High-ranking individuals prioritize their own juices, ignoring other ranks, while low-ranking individuals primarily consider other ranks in their decisions. In the socio-ecology of macaque monkeys, males must earn their hierarchical rank while females inherit their mother's social rank;⁴⁵ therefore, dominance hierarchy should be more carefully considered in males' than females' daily social decisions. Our results support this hypothesis as we found that the effect of hierarchical rank on socio-economic decisions was stronger in males than females. We further demonstrate that age did not influence the relative weight of social and economic dimensions of these decisions. However, the modest quality of the fits when considering individual variability in the integration of cost and benefit of social conflicts (results depicted in Figures 5B and 5C) suggests that there should be more at play to understand individual socio-economic decisions. For instance, considering animals' personality may help to better explain the remaining variability⁴⁶ and can lead to an operational measure of social tolerance²⁷ (see Figure S3). In any case, these interesting issues represent current perspectives of this innovative line of research.

Toward socio-cognitive and neural basis of primates' conflict management

Specific cognitive processes (such as behavioral inhibition^{47,48}) should be crucial to adapt social responses to the many different contexts of interaction that primates have to face daily. Compared to dominants, we found that subordinates have to inhibit their own economic preferences more strongly in order to avoid social conflicts, suggesting that socio-economic decisions should be more cognitively challenging for lower ranking individuals. In our paradigm, the economic reward was sips of juice but our findings can be extended to other experimental or ecological context where the rewards are other type (such as during access to food⁴⁹ or foraging⁴⁴) or even a social reward (such as mating, affiliative interactions, or infant handling⁵⁰⁻⁵⁵). One may consider other dimensions that would influence the perceived cost of social conflict such as the likelihood of future retaliation (counter-aggression, defection, etc.). Tit-for-tat strategies may be a way for subordinates to impose a cost on the aggression of the dominant.^{56,57} Monkeys may also see social conflict as a disruption to others (such as preventing others from getting juice rewards in our case). Such high-order prosocial consideration would arguably rely on empathy and perspective taking abilities

and may be influenced by kinship and previous existing social links between individuals.^{42,58–62} Further research may investigate the weight of these different dimensions into the computation of the subjective cost of primates' social conflicts. It has been suggested that dominance status does not only rely on physical but also cognitive abilities of non-human primates.⁶³ The socio-cognitive skills revealed through our research are likely to play a significant role in allowing an individual to successfully navigate its social environment. The identification of the underlying neural substrates of socio-economic decisions may represent another valuable perspective of our findings. Several brain areas (such as orbitofrontal cortex, anterior cingulate cortex, amygdala, and basal ganglia) were shown to be implicated in the integration of social and non-social variables to guide decisions and are thus good candidates to support socio-economic decision-making.^{64–69} Implementing our behavioral paradigm to study the activity of these brain areas during ecologically meaningful social dilemmas remains a methodological challenge in monkeys that has been already explored using wireless recording in rodents.⁷⁰ Overall, our study suggests that conflict management, upstream of conflicts, involves complex socio-cognitive abilities that may be a hallmark of primates' cognition as humans and monkeys can avoid costly social conflicts in order to foster beneficial long-term relationships, sometimes at the expense of their immediate utility maximization.

Limitations of the study

Subjects in our study belong to a notably tolerant macaque species, and it would be of interest to apply a similar protocol to more despotic non-human primate species, like rhesus monkeys (*Macaca mulatta*). Our research did not encompass additional social factors, such as kinship or social affiliations, and we also did not take into account the personality of the animals.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.108176>.

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AUTHOR CONTRIBUTIONS

Conceptualization, H.M. and S.B.; methodology, H.M. and S.B.; data curation and formal analysis, S.B.; investigation and resources, H.M.; writing, H.M. and S.B.; visualization, S.B.; funding acquisition, H.M. and S.B.

DECLARATION OF INTERESTS

The authors declare no competing interests here.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Original code and data	Github - Zenodo	https://doi.org/10.5281/zenodo.8358951
Software and algorithms		
Matlab	R2022a, the Mathworks	https://fr.mathworks.com/
R	R Core Team	http://www.R-project.org/
Other		
MALT - RFID dual-antenna	Custom made	Pebayle et al., 2016 ⁷¹ ; SATT-B-5 FR

RESOURCE AVAILABILITY

Lead contact

Authors are willing to share all materials, datasets, and protocols used in the manuscript. Sébastien Ballesta (ballesta@unistra.fr) is the lead contact of this study.

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data reported in this paper will be shared by the [lead contact](#) upon reasonable request.
- All original code has been deposited at <https://github.com/sballesta/SocioEcoDecision/> and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon reasonable request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Animals

Data were collected in one social group of Tonkean macaques (*Macaca tonkeana*), all captive-born and housed at the Primate Center of the University of Strasbourg, France. Animals lived in semi-free ranging conditions in a wooded park of 3788m² with permanent access to an indoor-outdoor shelter (2.5 × 7.5m - 2 × 4m). The group included 28 individuals, data from 26 individuals (15 males) were considered. Subjects were aged of 10.7 ± 5.9 years. One individual was too young to use MALT and another never used these devices. Subjects were exposed during 252 ± 106 days to the MALT before the beginning of the data collection. One subject ('eri'), was exposed to the MALT for the first time during the data collection period (on the 12/02/2018), which still represents 245 days of exposure to the MALT before the end of the data collection period (on the 15/10/2018). Monkeys were fed with commercial primate pellets twice a day inside the indoor shelter and received fresh fruit and vegetables once a week. Water was provided *ad libitum* in the indoor shelter.

Ethics

Observations were conducted non-invasively and approved by the ethical committee of the Primate Center of the University of Strasbourg which is authorised to house non-human primates (registration n°B6732636). The research further complied with the EU Directive 2010/63/EU for animal experiments.

METHOD DETAILS

MALT (Machine for Automated Learning and Testing)

Automated data were collected using four MALT, which the monkeys could access directly from their living environment in order to willingly perform several cognitive tasks.^{25,26,72} The MALT were designed and developed at the Primate Center of the University of Strasbourg with their development being inspired by Fagot and Paleressompoulle's Automated Learning Device for Monkey.⁷³ A wooden shelter

housing four MALT devices was built along the park of Tonkean macaques in 2015. The four devices are spaced 65,5 cm from each other and placed 85 cm above the floor. Animals have free access to these devices, through meshing tunnels (h70 x L51 x L115 cm) linking their outdoor enclosure to the wooden shelter, from the 15th of February 2016. Each MALT was accessible freely 24/7, except for two-hour cleaning and refill sessions, at least twice a week. The four MALT were placed in the same room, but were visually separated from each other by opaque Trespa® boards. Monkeys were rewarded at the device for a correct answer by receiving a sip of liquid reward (two seconds of juice reward delivered by a peristaltic pump, corresponding to 1 mL ± 5% of diluted syrup, 1/10). Four different flavours of syrups (same sucrose concentration) were available during data collection (exotic fruits, apple, peach and strawberry). MALT allows automatic identification of each subject due to a RFID dual-detection system.⁷¹ For that purpose, subjects were all equipped with two RFID microchips (UNO MICRO ID / 12, ISO Transponder 2.12 * 12mm), injected into each forearm during the annual veterinary health check under appropriate anaesthesia. When the RFID chip of an animal is detected by the MALT, it resumes his/her personal experimental sessions, which remains open for 30 seconds after the last screen touch or RFID detection. If another animal tries to engage with the cognitive tasks while another individual's session is active, a displacement event (mentioning a 'winner' that managed to displace the 'loser') is recorded in our database. This method is currently unable to record situations in which the new player failed at displacing the other monkey. Social hierarchy of the group (see Figure S4) can be computed indifferently using these displacement events or more classical observation of spontaneous social conflicts.^{26,74}

QUANTIFICATION AND STATISTICAL ANALYSIS

Our dataset includes 26 MALT players, 260 days (between 23/03/2017 to 15/10/2018) where all of the four MALT were used for more than 30 minutes on a given day. We extracted 8 096 situations where all MALT were unoccupied for more than 30 seconds before the beginning of the new player session. These data were used to compute individual preferences for juice flavours. We considered in our model the mean subjective preferences for juice reward during the whole duration of data collection and thus approximate that these preferences were stable in time. We considered 51 954 social dilemmas where a new player had to decide in which MALT he/she will play while at least one of the MALT was already occupied by a peer. We also considered for specific analysis in Figure 2 a filtered dataset where only the preferred MALT was occupied by a peer before the new player decision, this corresponds to 1870 social dilemmas. To assess statistical significance in this analysis, we used Wilcoxon paired (signed-rank test) and unpaired test (rank sum test) when appropriate. Fisher's exact test, a statistical significance test used in the analysis of contingency tables, was used to assess the effect of the presence of another monkey (vs nobody) in the preferred MALT of the new player.

Dominance hierarchy was assessed using Elo-rating⁷⁵ and the package 'EloRating' in R,⁷⁶ ordinal ranks were used during data analysis and we approximated that hierarchical rank by using the mean elo-rating score over the experimental period. Elo-rating was used with a starting score of 1000, and the k factor (i.e., the maximal amount of 'points' an individual can get from an interaction, function: *optimizek*, package: *EloRating*) was optimised. Results of the Elo-rating analysis can be seen in Figure S4. The data used to compute the hierarchy is based on the displacements recorded at the MALT. It has been recently demonstrated that the use of these information provide a reliable assessment of dominance hierarchy, similar to the one obtains using more classical manual observations of behaviours.^{26,74}

Analyses were performed using custom scripts written in Matlab (R2022a, the Mathworks). GLM and stepwise analysis were performed using the function *fitglm* and *stepwiseglm*, respectively. Confidence interval of estimates were standard errors. MALT X, Y correspond to the chosen and unchosen MALT respectively. We considered decisions amongst the 4 MALT as pairs of decisions between the chosen (X) and the remaining three unchosen MALT (Y). With a total of 26 subjects and 6 pairs of MALT, we can consider a total of 156 pairs of MALT. We used classical logit link function defined as:

$$\text{Choice MALT X vs Y} = 1/(1 + \exp(-x)) \quad (\text{Equation 1})$$

In the model depicted in Figures 3 and S1, x was equal to:

$$x = \beta_0 + \beta \text{rank} (\text{Rank monkey MALT Y} - \text{Rank monkey MALT X}) \quad (\text{Equation 2})$$

From the fitted parameters,³⁹ we derived measures for the indifference point ($\exp(-\beta_0/\beta \text{rank})$) and the sigmoid steepness (βrank), used in the analysis depicted in Figure 4.

In the model depicted in Figure 5, x was equal to:

$$x = \beta_0 + \beta \text{rank} (\text{Rank monkey MALT Y} - \text{Rank monkey MALT X}) + \beta_j \text{pref} (\text{Juice preference MALT X} - \text{Juice preference MALT Y}) \quad (\text{Equation 3})$$

During data analysis, we approximated that the hierarchical rank of an unoccupied MALT was equal to the lowest ordinal hierarchical rank of the group plus 1 (here 26 + 1 = 27). Circumventing this approximation by only considering the situations where all the four MALT were occupied before the new player decision is not changing the main findings of this study. In order to find socio-demographic predictors of βrank and $\beta_j \text{pref}$, a stepwise analysis was performed, the initial models considered the subjects' age, sex, hierarchical rank, and strength of preference for juice measured in non-social context (p_{juice} , Figure 1C). p_{juice} was estimated as follow:

$$p_{juice} = \frac{1}{n} \sum_{i=1}^{n=4} |juice\ preference_i - 1 / n| \quad (\text{Equation 4})$$

Backward and forward model selection was allowed; the model starts without interactions. Model selection results are shown in [Tables S1–S3](#).