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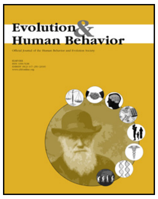

How do we decide when (not) to free-ride? Risk tolerance predicts behavioral plasticity in cooperation

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ABSTRACT

In collaborations, group productivity typically increases with more cooperators, but is also often subject to diminishing returns. This pattern provides a different view about cooperation from traditional social dilemmas: defection is not necessarily the dominant strategy. Rather, a frequency-dependent “anti-conformist” strategy (cooperate if many others defect, and vice versa) is often individually rational. This study addresses human cooperation under such marginally diminishing group productivity, focusing on the plasticity of cooperative choices. We conducted a two-part “team foraging” experiment, in which the most- or least-cooperative members in the first part were re-grouped separately for the second part. We observed that cooperating and defecting “types” emerged within a group over time but did not completely persist across groups, with some of the most cooperative members switching to become the least cooperative (and vice versa). Risk attitude was a key factor in this switching behavior: greater risk-takers showed greater behavioral plasticity. These results imply that human cooperation may be more context-dependent and behaviorally plastic than previously thought.

1. Introduction

Large-scale cooperation is a defining yet theoretically challenging characteristic of human societies (Bowles & Gintis, 2011). In psychology and behavioral economics, group cooperation has often been studied using the social dilemma framework (Dawes, 1980; Laury & Holt, 2008; Ledyard, 1995). However, when viewed through the lens of group production, most natural group tasks are not necessarily social dilemmas (Foster, 2004; Kameda, Tsukasaki, Hastie, & Berg, 2011).

When a group of individuals collaborates to produce some good, productivity usually increases monotonically with the number of cooperators, but this relationship often falls short of linearity. The biological literature provides a useful starting point for understanding why such nonlinear relationships are common. For example, the sentinel behavior of mammals and birds is a collective endeavor with marginally diminishing returns (Bednekoff, 1997; Trivers, 1971). In human terms, if a group of people are camping, there is a much larger benefit from the first camper keeping watch for bears than from the fifth, whose contribution adds little to the group's safety. More formally, let us denote the average probability of a single sentinel detecting an approaching predator as p. Assuming that there is no process loss (Steiner, 1972), the probability that a group with n individuals being on watch detects the danger successfully is then approximated by $1\text{-}(1\text{-}p)^n$ (Laughlin, 1980; Lorge & Solomon, 1955). This means that the group success in vigilance increases monotonically but diminishes at the margin, with an increase in the number of sentinels, n, in the group.

Social foraging, another key survival task, often shares this structure. When a flock of birds is searching for food, discovery of a rich food patch by a single bird results in other birds joining to forage in the same patch (Giraldeau & Caraco, 2000). The group success in locating a rich food patch is thus approximated by the identical function, $1\text{-}(1\text{-}p)^n$, where p denotes the average probability of a single bird encountering a rich patch and n refers to the flock size (Barnard & Sibly, 1981; see Foster, 2004 for other examples in the animal kingdom; see Kameda et al., 2011 for a review of human cases).

The difference between such situations and typical social dilemmas (in which free-riding always dominates or outperforms cooperation, e.g., linear public goods: Laury & Holt, 2008; Ledyard, 1995) is the productivity pattern shown in Fig. 1a. The incremental group return from each contribution diminishes with more cooperators. Depending on the cost of cooperation, this can lead to individual payoff functions as illustrated in Fig. 1b: if there are many other cooperators in the group, one is better off defecting; if there are no (or only a few) other cooperators, one is better off cooperating. In contrast to social dilemmas, the payoffs to individuals are frequency-dependent, so neither pure strategy (cooperation or defection) is dominant.

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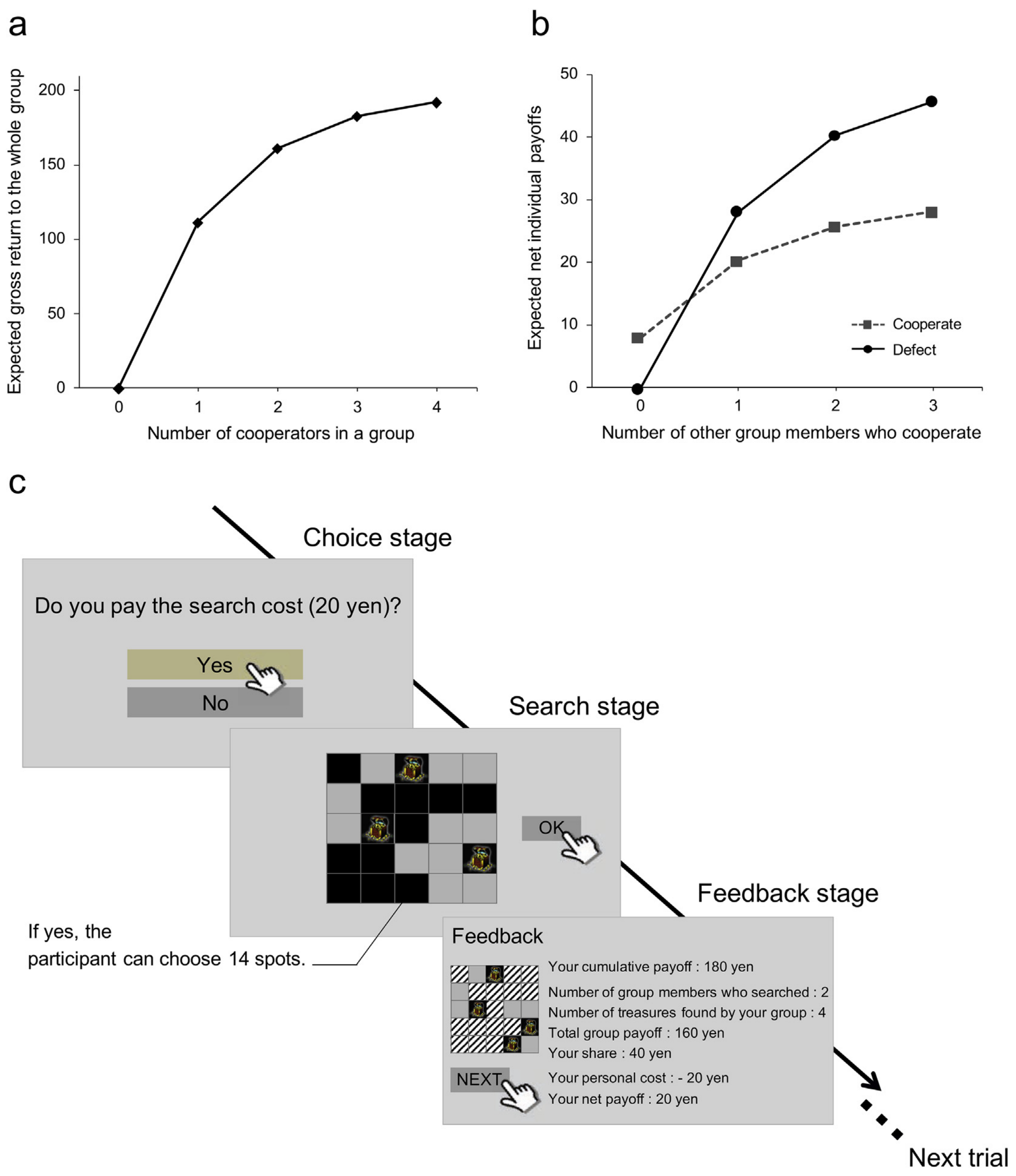

Do you pay the search cost (20 yen)?

If yes, the participant can choose 14 spots.

Your cumulative payoff : 180 yen
Number of group members who searched : 2
Number of treasures found by your group : 4
Total group payoff : 160 yen
Your share : 40 yen
Your personal cost : - 20 yen
Your net payoff : 20 yen

Fig. 1. Experimental setup. (a) The marginally diminishing group-return curve of the "treasure-hunt" task. When four participants engage in the task without mutually coordinating their search activity, mean group productivity (the total number of treasures found) increases monotonically with more cooperators (those who incur the personal search cost) but shows diminished marginal returns. (b) Mean individual net payoffs for choosing to cooperate or to defect. If there are no other cooperators, one is individually better off cooperating even after subtracting the cooperation (search) cost. But if there is at least one other cooperator in the group, one is better off defecting. Strategy payoffs are frequency-dependent, and no pure dominant strategy exists. (c) Time sequence in the treasure-hunt task.

The evolutionarily stable state of such social dynamics (aka. The producer-scrounger game: Giraldeau & Caraco, 2000; Giraldeau, Heeb, & Kosfeld, 2017) is a monomorphic population in which every individual adopts an identical mixed strategy (i.e. cooperating randomly with a uniform non-zero probability determined by the game payoff; Motro, 1991), or a polymorphic state where fixed proportions of individuals choose either cooperation or defection consistently (Dall, Houston, & McNamara, 2004). Although exact conditions for which of these states emerges remain to be established, factors such as the possibility of communication or signaling have been suggested to favor a stable behavioral polymorphism (Dall et al., 2004; Johnstone, 2001; Motro, 1991).

In previous behavioral-game research with humans, consistent individual differences in cooperation propensity have been repeatedly demonstrated in various laboratory settings such as public goods (e.g., Fehr & Fischbacher, 2004; Fischbacher, Gächter, & Fehr, 2001; Kurzban & Houser, 2001), dictator, and trust games (e.g., Yamagishi et al., 2013). Furthermore, a growing body of evidence (Pletzer et al., 2018; Yamagishi et al., 2013) suggests that some of these individual differences in cooperation may be predicted by enduring personality traits such as social value orientation (SVO: Van Lange, 1999), emotional abilities (Kaltwasser, Hildebrandt, Wilhelm, & Sommer, 2017) and self control (Kocher, Martinsson, Myrseth, & Wollbrant, 2017). However, the extent to which such personality traits can explain the coexistence of cooperators and defectors in human groups remains unclear.

This study explores the emergence and persistence of individual differences in human cooperation for group production. Here we present a two-stage experiment implementing a group situation characterized by marginally diminishing returns. Participants worked on a "team foraging" task in two consecutive parts. Based on previous research on the producer-scrounger game with human participants (Kameda et al., 2011; Kameda & Nakanishi, 2002, 2003; Toyokawa, Kim, & Kameda, 2014), we expected that substantive individual differences in cooperation rates would emerge over time within each group, deviating systematically from the uniform mixed strategy. Using participants' cooperation levels in Part 1, we then sorted them into new groups in Part 2, with the most- and least-cooperative individuals assembled separately. If individuals' cooperation propensities are stable, the gap in productivity between the two newly-sorted extreme groups should remain unchanged, or may even increase in Part 2. However, if cooperation is flexible according to group composition, defectors or cooperators will emerge in the most or the least cooperative group respectively, narrowing the initial productivity gap at the group level.

The sorting protocol above thus allows us to examine to what extent individual differences in cooperation, which are expected to emerge within a group, may persist across different groups. A similar experimental protocol was applied to birds (nutmeg mannikins) that engage in social foraging. In a laboratory setting, Morand-Ferron, Wu, and Giraldeau (2011) first observed how often each bird exploited (i.e., scrounged from) the findings of other flock members (rather than exploring for new food patches itself), and then sorted them into new groups according to this scrounging propensity. The overall scrounging-frequency in the "scrounger flock" was no higher than in flocks made up of intermediate- or low-frequency scroungers, suggesting that individual differences in social foraging among birds are group-dependent. Here, we modify this experimental protocol to study human cooperation. Our team-foraging task with marginally diminishing returns (Foster, 2004; Kameda et al., 2011) provides an ecologically representative platform to examine a role of frequency-dependent behavioral adjustment in the emergence of individual differences in human cooperation.

2. Material and methods

2.1. Participants

One hundred and sixty undergraduates (121 male, 39 female; mean age = 19.3 ± 1.2 years) were randomly selected from a subject pool at Hokkaido University (Sapporo, Japan) to participate in the experiment. This sample size was based on a previous study of the producer-scrounger game (Kameda et al., 2011; Kameda & Nakanishi, 2002, 2003). The study was approved by the Institutional Review Board of the Center for Experimental Research in Social Sciences at Hokkaido University, and written informed consent was obtained from each participant before the experiment. Participants were compensated for their participation based on their performance in the experiment (mean = 1168.6 ± 225.6 yen; 1 USD = 100 yen).

2.2. Procedure

In each experimental session, sixteen participants were called to the laboratory. Each participant was seated in a cubicle with a computer terminal. All instructions were simultaneously read aloud (via a headset worn by each participant) and displayed on the screen of each computer. No direct communication was allowed between participants, who remained completely anonymous to each other throughout the experiment, and were paid individually after the experiment. The entire session lasted 90 min. The experimental program was developed using z-Tree (Fischbacher, 2007).

2.3. Experimental task

The sixteen participants in each session were randomly assigned to four 4-person groups. The four participants in each group worked together on a "treasure hunt" task in which they searched collaboratively for five treasures hidden in a 5 × 5 grid (Fig. 1c middle). Each treasure, whose location was randomly shuffled in each trial, was worth 40 Japanese yen shared among all 4 group members (i.e., 10 yen each).

In each trial, participants first decided individually whether or not to pay the personal search cost of 20 yen, without any communication ("choice stage" in Fig. 1c). Each participant who paid the search cost was able to check 14 (of 25) spots individually without coordinating where to search with other members ("search stage"). Those who had decided not to pay waited for the searchers to finish their searches. Treasures found by any searchers in the group were shared evenly among all four members, irrespective of search cost payment, creating a producer-scrounger game (Giraldeau et al., 2017; Giraldeau & Caraco, 2000) among team members (Fig. 1b). At the end of each trial ("feedback stage"), each participant received feedback about their individual net payoff (10 yen × total number of treasures found − 20 yen if participant paid the search cost) and the number of members who had searched (cooperated) in the trial. This experimental setup yielded a nonlinear joint payoff in which the mean group productivity (the expected gross return) increased with the number of cooperators (searchers) but diminished at the margin (Fig. 1a). Participants were given the opportunity to work on five practice trials without payment, and then proceeded to the main session.

2.4. Main session

There were two parts. After the practice session, participants were instructed that they would be randomly re-grouped with three other participants as a new team. Part 1 consisted of each group working on the treasure-hunt task for 15 trials (though this number was not specified to participants), according to the same protocol as in the practice session. For Part 2, we ranked the members in each of the four groups according to their overall cooperation (search) rates in Part 1, and composed new 4-person groups by assembling the 1st-, 2nd-, 3rd-, and 4th-ranked members separately for Part 2. Participants were only instructed that they were re-grouped with three new members different from Part 1, but were not informed of the details of the composition. Participants then worked on the treasure-hunt task for 30 trials (once again unspecified to participants) in the new groups according to the same protocol from Part 1.

After Part 2, participants answered a post-session questionnaire including several personality scales that seemed relevant to cooperation in the producer-scrounger game. These were: (a) social value orientation (SVO) – measuring social preference for allocating rewards between oneself and another person (Van Lange, 1999); (b) sensation seeking – measuring preferred level of stimulation (Zuckerman, Kolin, Price, & Zoob, 1964); (c) risk preferences (Holt & Laury, 2002); (d) resource-allocation preferences as a third party (Kameda, Takezawa, Ohtsubo, & Hastie, 2010), and (e) perception of interdependence (Jin & Shinotsuka, 1996).

After completing the post-session questionnaire, each participant was paid according to individual performance in the experiment, thanked, and dismissed.

3. Results

3.1. Mean cooperation frequencies over time

Fig. 2 displays mean cooperation frequencies in Part 1. The mean number of cooperators in each 4-person group (collapsed across the 15 trials) was 1.73, which was significantly higher than the theoretical equilibrium frequency of one cooperator per group (see Fig. 1b), $t(39) = 8.97$, $p < .001$, 95% CI = [1.57, 1.90], $M = 1.73$, $SD = 0.52$. Notice that, in our treasure-hunt task, members' contributions determined group productivity stochastically — the number of treasures found could be different even if the same number of members cooperated in a group. Participants thus may have behaved cautiously to avoid the worst possibility of no cooperation (Fig. 1a). In line with this

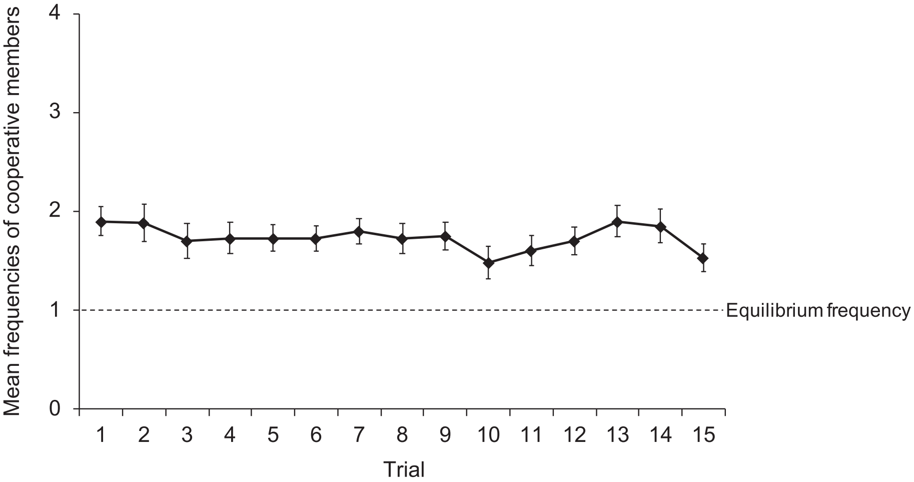

Fig. 2. Mean cooperation frequencies in Part 1. The horizontal line represents the theoretical equilibrium frequency of one cooperator per group. Error bars show standard errors of the mean.

interpretation, participants' risk attitudes determined from the post-session survey were generally biased toward risk aversion ($M = 4.68$, $SD = 1.91$, $t(148) = -8.45$, $p < .001$, 95% CI = $[-1.63, -1.01]$) from the risk-neutral point (= 6) of the scale (Holt & Laury, 2002).

More importantly, the mean cooperation frequencies did not deteriorate over time, $F(14, 546) = 0.88$, $p = .580$, $\eta_p^2 = 0.02$. This stationary pattern is markedly different from typical social-dilemma experiment results where cooperators decrease in number over iterated trials within a group (Fischbacher & Gächter, 2010; Horita, Takezawa, Inukai, Kita, & Masuda, 2017; Keser & Van Winden, 2000), but is consistent with the frequency-dependent dynamics (cooperate if many others defect, and vice versa) of the producer-scrounger game (Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002, 2003).

3.2. Emergence of "types" among participants

One stable state of the producer-scrounger dynamics is a monomorphic population in which all participants adopt the same mixed strategy: cooperating randomly with exactly the same probability determined by the game payoff. As shown in Fig. 1b, the individual payoff curves for cooperation (searching) and for defection in the treasure-hunt task intersect when the number of other cooperators is between 0 and 1, which implies that one is better off cooperating if there are no other cooperators, and better off defecting if there is at least one other cooperator in the group. Thus, an individually rational strategy for all participants in this experiment is cooperating randomly with probability 0.25 (=1/4).

The bar graphs in Fig. 3 show observed frequencies of participants' cooperative choices (search cost payments) in Part 1. The number of cooperative choices ranges from 0 (100% free riding) to 15 (100% cooperation) out of 15 trials. The dotted line shows the theoretical binomial distribution assuming that all participants adopt the individually rational probabilistic strategy (cooperating randomly with probability 0.25). As seen in Fig. 3, participants' behaviors were markedly different from the probabilistic strategy. The observed distribution is not unimodal with one peak at 25% as predicted from the model, but has three peaks at 0%, 50%, and 100%. A Kolmogorov-Smirnov two-sample test indicates that the observed distribution differed significantly from the game-theoretical distribution ($D = 0.469$, $p < .001$). Thus, consistent with previous results (e.g., Kameda et al., 2011; Kameda & Nakanishi, 2002, 2003), a group task with marginally diminishing returns also yielded substantial diversity in propensity for cooperation ("types") as in other behavioral games (e.g., Fischbacher et al., 2001; Yamagishi et al., 2013).

3.3. Did behavioral "types" persist across different social settings?

Fig. 4a compares group-level cooperation rates in Part 1 and Part 2. For Part 2, we simply averaged the cooperation rates of the four participants in each group over the 30 trials. For Part 1 (in which these participants had belonged to different groups), we averaged their corresponding cooperation rates as if they had belonged to the same group.

A 4 (Rank: 1st, 2nd, 3rd, or 4th) × 2 (Part: Part 1 or Part 2) repeated measures analysis of variance (ANOVA) of the group-level cooperation rates revealed no main effect of Part ($F(1, 36) = 0.00$, $p > .99$, $\eta_p^2 = 0.00$), again confirming that the average cooperation rates did not deteriorate over time in the producer-scrounger game (Fig. 2). The main effect of rank was significant ($F(3, 36) = 101.06$, $p < .001$, $\eta_p^2 = 0.89$). As seen in Fig. 4a, all ranks remained the same in both parts: rank 1 (the most cooperative group) in Part 1 was also rank 1 in Part 2, and the same held for ranks 2 through 4. This indicates that there were consistent individual differences in overall cooperation levels across the two parts.

However, the ANOVA also revealed a significant Rank × Part interaction effect, $F(3, 36) = 14.00$, $p < .001$, $\eta_p^2 = 0.54$. A paired-sample t-test with Bonferroni correction confirmed that cooperation rates of the 1st-ranked (most cooperative) groups declined significantly from Part 1 ($M = 0.74$, $SD = 0.06$) to Part 2 ($M = 0.65$, $SD = 0.11$), $t(9) = 3.68$, $p = .020$, 95% CI = $[0.04, 0.16]$, while those of the 4th-ranked (least cooperative) groups increased significantly from Part 1 ($M = 0.15$, $SD = 0.07$) to Part 2 ($M = 0.28$, $SD = 0.08$), $t(9) = -4.22$, $p = .008$, 95% CI = $[-0.20, -0.06]$.

It could be argued that these changes were simply due to a statistical regression to the mean. To address this possibility, we divided the 30 trials of Part 2 into halves of 15 trials each. Fig. 4b displays changes in the distributions of cooperative choices in each rank across the three phases: Part 1, and the first and the second halves of Part 2. As shown in this figure, 100%-free-riders (individuals that cooperated in 0 trials out of 15) emerged in the 1st-ranked (most cooperative) groups, while 100% cooperators emerged in the 3rd- and 4th-ranked groups. Contrary to an explanation based on regression to the mean, the distributions of cooperation became more U-shaped over time (with another peak around 50% cooperation in the 2nd- and 3rd-ranked groups in particular).

Taken together, these patterns suggest that, besides the persistent individual-level diversity in overall cooperation levels, participants' cooperative behaviors can also display plasticity in response to group composition. Contrary to the game-theoretical prediction of a uniform probabilistic strategy, participants displayed substantial individual differences in cooperation propensity, at least while they remained

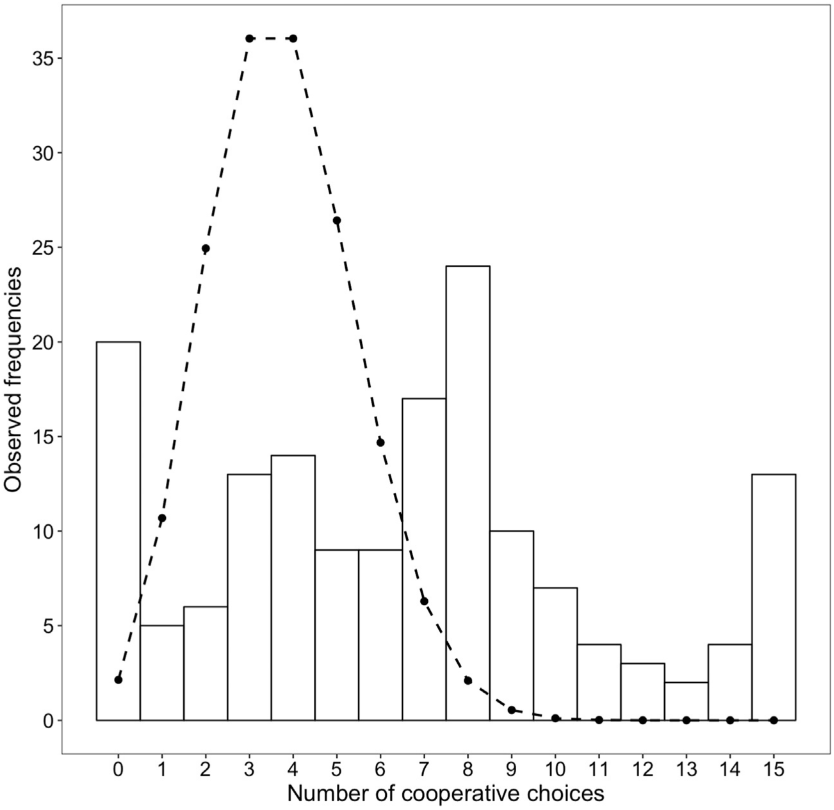

Fig. 3. The theoretical distribution of cooperative choices as predicted by the individually rational strategy (dotted line) and the observed distribution (white bars) in Part 1. The game-theoretical individually rational strategy is cooperating with the probability of 0.25. The x-axis refers to the number of cooperative (search) choices, which could range from 0 (100% free riding) to 15 (100% cooperation).

within the same group (Fig. 3). However, these “types” were not completely stable, but were able to change, even to the opposite types, when they found themselves in new situations (Fig. 4). This suggests that group composition (i.e., whom one is grouped with) can play a critical role in determining one's cooperation level, according to the producer-scrounger dynamics (Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002, 2003).

3.4. Did psychological scales predict participants' cooperation levels in the group task?

In the post-session questionnaire, participants answered several personality scales that seemed relevant to cooperation in the producer-scrounger game: SVO, sensation seeking, risk preferences, resource-allocation preferences as a third party, and perception of interdependence. Table 1 displays summary results of participants' responses to these scales as a function of their cooperation ranks in Part 1 (see the note accompanying Table 1 for explanations of each scale and its response categories).

In contrast to recent findings that individual differences in cooperation may be related to enduring personality traits (Kaltwasser et al., 2017; Kocher et al., 2017; Pletzer et al., 2018; Yamagishi et al., 2013), we found no statistical difference among the four cooperation ranks on any of the psychological scales examined. The male-female proportions were not different among the four ranks either.

However, participants' risk attitudes did affect how they adjusted their behaviors in response to the new social environments in Part 2 after group re-composition. Fig. 5 displays participants' cooperation rates during Part 2 as a function of their initial cooperation-ranks (1st and 2nd combined vs. 3rd and 4th combined) and their risk attitudes. Not surprisingly, cooperation rates were higher in Part 2 among the 1st and 2nd groups than the 3rd and 4th groups ($\beta = 0.33$, $t(145) = 4.28$, $p < .001$, 95% CI = [0.23, 0.73]). However, this main effect was qualified by a Rank × Risk-attitude interaction effect, $\beta = 0.19$, $t(145) = 2.42$, $p = .017$, 95% CI = [0.01, 0.11], as represented by the two regression lines. In Part 2, the more risk-seeking participants (toward the right on the horizontal axis) behaved less cooperatively in the more cooperative groups (1st- and 2nd-ranked), but more cooperatively in the less cooperative groups (3rd- and 4th-ranked). That is, participants with more risk-seeking attitudes tended to adjust their cooperation levels in the individually rational manner in response to the new group composition, lowering their cooperation rates in the overly-cooperative upper-ranked groups while raising their cooperation rates in the insufficiently-cooperative lower-ranked groups. In contrast, participants with more risk-averse attitudes (toward the left on the horizontal axis) tended to maintain their initial cooperation levels from Part 1 in Part 2. Note that risk attitudes affected how participants adjusted their cooperation levels to new social environments, but not their initial cooperation levels per se (see Table 1). No other psychological scale yielded a similar pattern.

4. Discussion

Research on behavioral games, including social dilemmas, has revealed that people exhibit substantial individual differences in their propensity to cooperate (e.g., Fehr & Fischbacher, 2004; Fischbacher et al., 2001; Kurzban & Houser, 2001; Pletzer et al., 2018; Yamagishi et al., 2013). We started with the observation that most natural group tasks are not necessarily social dilemmas (Foster, 2004; Kameda et al., 2011). Many collective tasks (e.g., risk monitoring and foraging) in nature have marginally diminishing productivity, such that the individually adaptive strategy is not necessarily a defection but often a mixed strategy in which one cooperates probabilistically according to the negatively frequency-dependent payoff structure (Motro, 1991). This study addressed whether cooperative diversity among individuals would still emerge in an ecologically representative collective-foraging situation (Giraldeau & Caraco, 2000), and if so, how robustly individual diversity would persist across different group compositions.

We found that the behavioral results were markedly different from the typical social dilemma experiments. In social dilemma experiments,

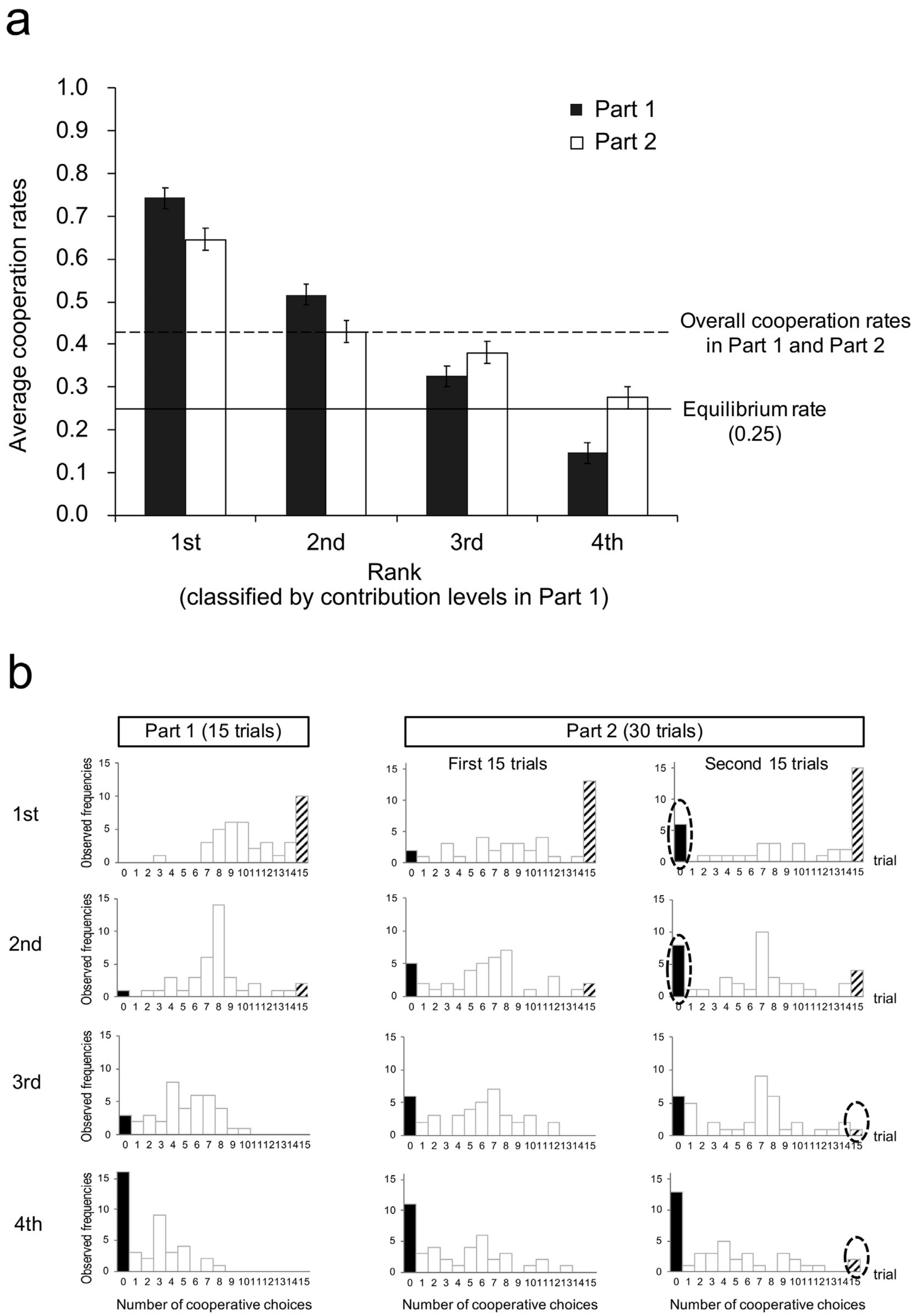

Fig. 4. Changes in cooperation rates between Part 1 and Part 2. (a) Comparison of the group-level average cooperation rates between Part 1 (black bars) and Part 2 (white bars). The horizontal solid line represents the theoretical (individually rational) cooperation rate of 0.25. The horizontal dotted line represents the overall cooperation rates collapsed across the ranks in Part 1 and Part 2 (both $M = 0.43$, which were significantly higher than the theoretical rate, $t(39) = 4.90$ in Part 1 and $t(39) = 7.28$ in Part 2, both $p < .001$). (b) Changes in the distributions of cooperative choices in each rank (the 1st-, 2nd-, 3rd-, and 4th-ranked groups) across Part 1 and the first and the second halves of Part 2.

cooperation rates usually decline over iterated trials within the same group (e.g., Horita et al., 2017), but such a pattern was not observed in this group task with marginally diminishing productivity (i.e., producer-scrounger game: Giraldeau et al., 2017; Kameda et al., 2011).

The observed stable cooperation pattern within a group (Fig. 2) is generally in line with the negative frequency-dependent dynamics (Fig. 1b) of the producer-scrounger game. At the same time, the behavioral results also showed several systematic deviations from the

Table 1

Cooperation ranks in Part 1 by psychological scale responses and sex.

Psychological scales	Cooperation rank				Statistical values
	1st	2nd	3rd	4th	
Social Value Orientation[a] (Van Lange, 1999)					
Percentage of Pro-social Respondents	21.3% (n = 32)	18.0% (n = 27)	16.7% (n = 25)	16.7% (n = 25)	$\chi^2(3, N = 150) = 1.64, p > .6$, Cramer's $V = 0.105$
Percentage of Pro-self Respondents	5.3% (n = 8)	7.3% (n = 11)	8.0% (n = 12)	6.7% (n = 10)	
Sensation Seeking Scale[b] (Zuckerman et al., 1964)					
Thrill and Adventure Seeking (TAS)	5.18 (0.43)	6.16 (0.44)	5.68 (0.43)	5.25 (0.44)	$F(3, 148) = 1.08, p > .3, \eta_p^2 = 0.022$
Experience Seeking (ES)	4.78 (0.35)	4.87 (0.35)	4.66 (0.35)	5.00 (0.36)	$F(3, 148) = 0.17, p > .9, \eta_p^2 = 0.003$
Disinhibition (DIS)	6.08 (0.28)	5.81 (0.28)	6.61 (0.28)	6.06 (0.28)	$F(3, 148) = 1.47, p = .225, \eta_p^2 = 0.030$
Boredom Susceptibility (BS)	2.55 (0.26)	3.38 (0.27)	2.55 (0.27)	2.94 (0.27)	$F(3, 148) = 2.17, p = .094, \eta_p^2 = 0.043$
Overall	18.61 (0.89)	20.22 (0.90)	19.50 (0.89)	19.25 (0.91)	$F(3, 148) = 0.55, p > .6, \eta_p^2 = 0.011$
Risk Attitude[c] (Holt & Laury, 2002)	4.60 (0.33)	4.64 (0.31)	4.65 (0.32)	4.82 (0.31)	$F(3, 148) = 0.09, p > .9, \eta_p^2 = 0.002$
Preferences for Distribution Rules[d] (Kameda et al., 2010)					
Percentage of Egalitarian Rule Endorser	16.3% (n = 17)	13.5% (n = 14)	12.5% (n = 13)	9.6% (n = 10)	$\chi^2(3, N = 104) = 1.32, p > .7$, Cramer's $V = 0.112$
Percentage of Merit (Proportionality) Rule Endorser	10.6% (n = 11)	13.5% (n = 14)	12.5% (n = 13)	11.5% (n = 12)	
Perception of Interdependency[e] (Jin & Shinotsuka, 1996)	21.5 (0.73)	21.62 (0.74)	21.38 (0.73)	20.66 (0.75)	$F(3, 156) = 0.34, p > .7, \eta_p^2 = 0.007$
Sex Ratio					
Percentage of Females	5.6% (n = 9)	7.5% (n = 12)	6.9% (n = 11)	4.4% (n = 7)	$\chi^2(3, N = 160) = 2.00, p > .5$, Cramer's $V = 0.112$
Percentage of Males	19.4% (n = 31)	17.5% (n = 28)	18.1% (n = 29)	20.6% (n = 33)	

Note: Unless specified otherwise, numbers in parentheses refer to standard error.

[a] Measure of preference for allocating rewards between oneself and another person. Social value orientation is operationally defined as a combination of weights attached to the welfare of an interaction partner relative to oneself in resource allocation (Van Lange, 1999). Participants categorized as "pro-socials" assigned positive weights to both their welfare and their partner's welfare, while "pro-selves" assigned positive weights to their own welfare but no or negative weights to their partner's welfare.

[b] Measure of preferred level of stimulation (Zuckerman et al., 1964), composed of four subscales (thrill and adventure seeking, experience seeking, disinhibition, and boredom susceptibility).

[c] Standard measure of risk attitudes in behavioral economics (Holt & Laury, 2002), where participants responded to ten paired lottery-choice decisions differing in risk levels. In the analysis, we reversed the original scale so the higher score indicating the more risk-seeking attitude; the score for risk-neutral attitude was 6.

[d] Measure of preferences for various resource-allocation schemes as a third party for those who differ in contribution levels (Kameda et al., 2010). Participants were classified as either endorsers of the egalitarian rule or the merit (proportionality) rule.

[e] Measure of subjective importance of direct and indirect reciprocity. Participants were asked to evaluate four questions regarding social interdependency on 7-point scales (Jin & Shinotsuka, 1996).

game-theoretical predictions.

First, cooperation rates ($M = 0.43$) were higher than the theoretical rate (0.25). Such inflated cooperation rates may reflect participants' risk-averse choices in response to the stochastic nature of our treasure-hunt task (Fig. 1c). Second, rather than the unimodal pattern predicted by the uniform probabilistic mixed-strategy, the distribution of cooperative choices revealed three peaks, at 0%, 50%, and 100% cooperation (Fig. 3). The emergence of such individual "types" (e.g., full defector, full cooperator: see also Kameda & Nakanishi, 2002, 2003; Kameda et al., 2011; Toyokawa et al., 2014) accords with results from the other behavioral games including social dilemmas (e.g., Fehr & Fischbacher, 2004; Fischbacher et al., 2001; Kurzban & Houser, 2001; Pletzer et al., 2018; Yamagishi et al., 2013).

However, more importantly to our argument, these "types" did not necessarily persist across different group settings. When placed in overly uncooperative (cooperative) groups, 100% cooperators (free-riders) emerged (Fig. 4b). These patterns imply that individual cooperation is stable within a group but adaptable across different settings, in accordance with the producer-scrounger dynamics ("cooperate if many others free-ride, but defect if many others cooperate": Giraldeau & Caraco, 2000; Giraldeau et al., 2017). Interestingly, as stated in the introduction, similar behavioral plasticity (especially from free-riding to cooperation) has recently been reported in non-human species including birds (Morand-Ferron et al., 2011) and ants (Hasegawa, Ishii, Tada, Kobayashi, & Yoshimura, 2016). While such behavioral plasticity among animals sometimes takes place over a long period of time (e.g., developmental time: Aplin & Morand-Ferron, 2017), we observed that participants adjusted cooperation levels rather quickly (within less than an hour) in our experiment. This indicates that human cooperation in group production is not necessarily fixed as "cooperative personality" but can be behaviorally plastic in response to local ecology and social interaction.

We also observed that the more risk-seeking participants revealed greater behavioral plasticity (adjusting cooperation levels in the individually rational manner to new social environments), whereas the more risk-averse participants tended to maintain their old behaviors. Several recent studies suggest that exploratory behaviors by humans as well as animals in unfamiliar environments are closely linked to risk-related traits like boldness and aggressiveness (Toyokawa, Saito, & Kameda, 2017; Wolf, van Doorn, Leimar, & Weissing, 2007). For example, differences in risk sensitivity may explain differentiated foraging behaviors in birds (Kawamori & Matsushima, 2012 for diet-menu differentiation between species; Wright & Radford, 2010 for foraging-niche partitioning within species). For humans, emerging neural

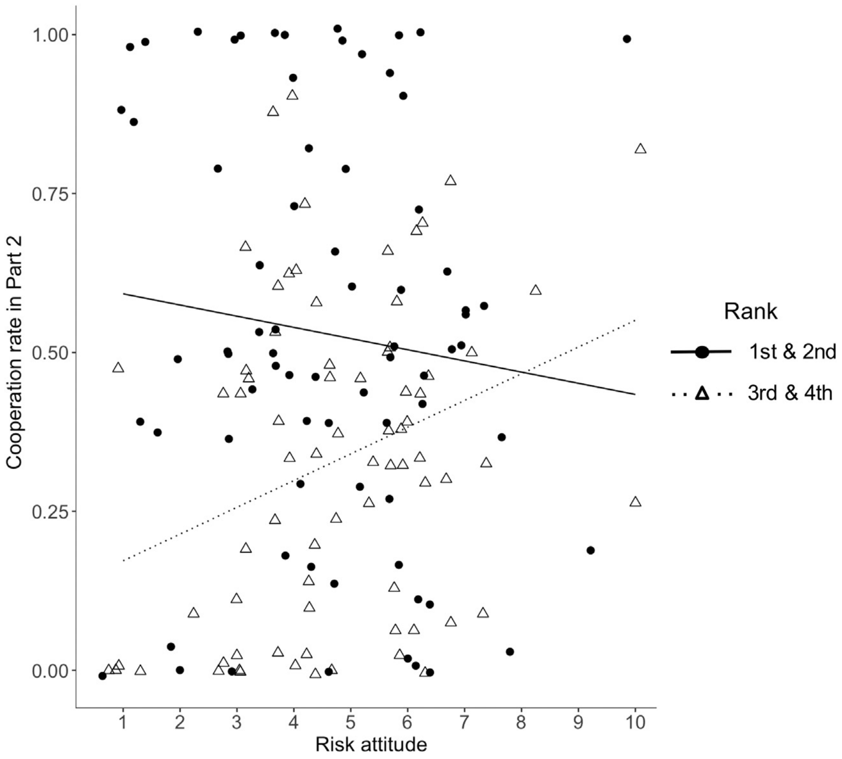

Fig. 5. Participants' cooperation rates in Part 2 as a function of cooperation ranks (1st and 2nd combined vs. 3rd and 4th combined) in Part 1 and risk attitudes. Risk-attitude scores ranged from 1 (most risk averse) to 10 (most risk seeking).

evidence suggests that individual risk attitudes may be a core dimension underlying various social and economic decisions (Kameda et al., 2016; Mobbs, Trimmer, Blumstein, & Dayan, 2018; Shenhav & Greene, 2010).

Previous research also indicates that learning ability may sustain flexible behavioral tactics depending on local ecology and social interaction (e.g., Dubois, Morand-Ferron, & Giraldeau, 2010; Ezaki, Horita, Takezawa, & Masuda, 2016; Katsnelson, Motro, Feldman, & Lotem, 2012). In an evolutionary game analysis of producer-scrounger behavior, Dubois et al. (2010) showed that learning agents that adjust behaviors in response to local conditions can invade a population of non-learning agents that play producer or scrounger with fixed probability. Interestingly, however, the analysis also showed that those flexible learners cannot dominate the population entirely, often yielding a mixed population where flexible learners and inflexible non-learners coexist. The theoretical analysis of Dubois et al. (2010) seems to concur with our observation that risk-seeking "switchers" and risk-averse "keepers" coexist. Along with an ability to learn, risk-seeking may permit finer tracking of changes in the reward structure of adaptive environments, enabling some individuals to employ more flexible behavioral tactics. Taken together, risk-tolerance and learning ability may be keys to flexible behavioral adjustment in both humans and animals, along with other personality traits such as exploration, boldness, and aggressiveness (Dall et al., 2004; Gosling, 2001).

Lastly, it seems important to consider why social value orientation (SVO: Van Lange, 1999) does not predict participants' cooperation in the producer-scrounger game, while it does predict individual cooperation in traditional social dilemmas (e.g., Yamagishi et al., 2013). Rand, Greene, and Nowak (2012) argued that dual (i.e., automatic/intuitive vs. controlled/deliberative) processes underlie human cooperation and that cooperative choices are often initiated by participants who intuitively employ "social heuristics" that are adaptive in everyday life (see also Rand et al., 2014). An fMRI experiment by Fermin et al. (2016) provides some support for this claim, showing that the volume of amygdala (a brain region associated with automatic emotive processes: Adolphs, 2009) was larger in prosocials and positively correlated with cooperation, while the volume of dorsolateral prefrontal cortex (a region associated with controlled processes) was larger in proselfs and negatively correlated with cooperation.

However, such a direct linkage may not hold in our case. In the producer-scrounger game, group production diminishes at the margin; the resulting negative frequency dependence in individual payoffs (Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002, 2003) may engage all players in strategic deliberations about their choices. In other words, the seemingly minor difference in the shape of group-production functions (i.e., linear vs. non-linear) may trigger different cognitive strategies for group cooperation. Furthermore, different cooperation norms may also be evoked in these two cases. While a dominant social norm in traditional (linear) social dilemmas is full cooperation by all members (Fehr & Fischbacher, 2004), such a norm may not necessarily work in the (non-linear) producer-scrounger game, where full cooperation yields redundancy (and thus inefficiency) at the group level. We are currently investigating this possibility empirically, which we hope may provide a useful insight about social evolution of cooperation norms in humans.

Overall, our results suggest that human cooperation in group production may be more context-dependent than previously thought. Future research examining core dimensions underlying human behavioral plasticity, including individual risk tolerance and social norms, seems critical to understanding the large-scale cooperation unique to our species and possibly extending its natural and cultural boundaries toward the betterment of our societies (Bowles & Gintis, 2011).

Ethics

This study was approved by the Institutional Review Board of the Centre for Experimental Research in Social Science at Hokkaido University. Written informed consent was obtained from all participants before beginning the task.

Data accessibility

All data are available from the corresponding author upon request.

Competing interest

We have no competing interest.

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