Activity in the Nucleus Accumbens and Amygdala Underlies Individual Differences in Prosocial and Individualistic Economic Choices

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Abstract

■ Much decision-making requires balancing benefits to the self with benefits to the group. There are marked individual differences in this balance such that individualists tend to favor themselves whereas prosocials tend to favor the group. Understanding the mechanisms underlying this difference has important implications for society and its institutions. Using behavioral and fMRI data collected during the performance of the ultimatum game, we show that individual differences in social preferences for resource allocation, so-called "social value orientation," is linked with activity in the nucleus accumbens and amygdala elicited by inequity, rather than activity in insula, ACC, and dorsolateral pFC. Importantly, the presence of cognitive load made prosocials behave more prosocially and individualists more individualistically, suggesting that social value orientation is driven more by intuition than reflection. In parallel, activity in the nucleus accumbens and amygdala, in response to inequity, tracked this behavioral pattern of prosocials and individualists. In addition, we conducted an impunity game experiment with different participants where they could not punish unfair behavior and found that the inequity-correlated activity seen in prosocials during the ultimatum game disappeared. This result suggests that the accumbens and amygdala activity of prosocials encodes "outcome-oriented emotion" designed to change situations (i.e., achieve equity or punish). Together, our results suggest a pivotal contribution of the nucleus accumbens and amygdala to individual differences in sociality. ■

INTRODUCTION

A desire for fairness plays a critical role in our social behavior (Fehr & Schmidt, 1999), often taking the form of a preference for equity, that is, an aversion to receiving more as well as less than others. However, there are striking individual differences (Fehr, Bernhard, & Rockenbach, 2008; Fehr & Schmidt, 1999; Van Lange, 1999; Kelley & Stahelski, 1970; Messick & McClintock, 1968) in preference for equity (Haruno & Frith, 2010; Fehr et al., 2008; Van Lange, 1999; Kelley & Stahelski, 1970; Messick & McClintock, 1968). In some cases, a better-off participant is motivated to reduce a gap in wealth, whereas in other cases, people will pay to maintain or even increase their relative status (Tricomi, Rangel, Camerer, & O'Doherty, 2011). These differences are captured in the concept of "social value orientation" (Van Lange, 1999; Kelley & Stahelski, 1970; Messick & McClintock, 1968). Prosocials are defined as those who like to maximize the sum of resources for the self and the other, while simultaneously minimizing the difference between the two. By contrast, individualists like to maximize resources for the self, regardless of the amount available for the other. Social value orientation is linked with real-world social behaviors and is hypothesized to emerge from rapid and intuitive preferences (Van Lange, Bekkers, Chirumbolo, & Leone, 2011; Joireman, Lasane, Bennett, Richards, & Solaimani, 2009).

Although behavioral characteristics of social value orientation have been well recognized and each person's particular social value orientation is known to be stable for at least 6 months (Bogaert, Boone, & Declerck, 2008), knowledge about its computational and neural mechanism is still very limited. The observation that TMS to the right dorsolateral prefrontal cortex (DLPFC) during the ultimatum game increases participants' acceptance of unfair offers (Baumgartner, Koch, Hotz, Eisenegger, & Fehr, 2011; Knoch & Fehr, 2007) is consistent with the view that prosocial preference may depend on and reflective, cortically based suppression of a selfish emotional system possibly through consideration of the other's intentions.

On the other hand, an fMRI study showed that activity in the amygdala was correlated with the degree to which each prosocial disliked inequity during passive evaluation of rewards divided between self and an other (Haruno & Frith, 2010), and a recent large-scale behavioral study showed that participants were more cooperative in dilemma games when they reached their decisions more quickly (Rand, Greene, & Nowak, 2012). These results

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raise the possibility that a rapid subcortical system contributes to the choice of prosocial behavior.

These two streams of studies indicate the coexistence of reflective and intuitive (Haidt, 2001) social systems. However, the relative importance and neural substrates of these two systems for determining prosocial or individualistic decision-making are not known.

To address this issue, we conducted behavioral and fMRI studies of the ultimatum game (Camerer, 2003; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Guth, Schmittberger, & Schwarze, 1982) and also examined the effects of cognitive load on rejection rates of prosocials and individualistic participants as responders. Cognitive load was introduced to reduce the availability of reflective process for responder's decision-making (Valdesolo & DeSteno, 2008), and we hypothesized that if the rapid and automatic system is central to social value orientation, then prosocials and individualists should become more prosocial and more individualistic, respectively, in the presence of cognitive load.

Finally, we examined how prosocial rejection rates changed in the impunity game where responders can reject an unfair offer, but proposers are not punished (i.e., they always receive what they proposed). This task allows us to clarify whether rejection behavior and neural activity of prosocials identified in ultimatum game is simply the response to an unfair offer or also takes account of the effect of their rejection of the offer.

METHODS

Tasks

Categorizing Participants by the Triple-dominance Measure Task

The degree of the prosocial, individualistic, or competitive orientation was measured in all participants using the triple-dominance measure (Van Lange, 1999) of social value. Ten to 22 participants at a time were invited into a room. First, they were numbered randomly (e.g., 1–16 for 16 participants), and each participant received a sheet of paper on which two numbers were written, one number for identification of the participant and the other for assigning the participant's pair. They did not know who the pair number corresponded to.

Before starting the task, the participants were asked to write their own number and that of their partner on their answer sheet. Then the participants were presented with eight triple-dominance measure tasks (Haruno & Frith, 2010; Van Lange, 1999; Figure 1A), one at a time, and requested to select the most preferable reward condition from the three options within 10 sec. They were instructed that the amount of reward written in the selected option would be paid to them and their assigned pair and such payments were subsequently made. There were at least 3 days between the social value orientation categorization and the subsequent fMRI experiments (i.e., ultimatum game or impunity game).

The Ultimatum Game with Cognitive Load

In each trial (Figure 1B), the participant was first required to remember a five-digit number. Either a random or a constant (01234) string of digits was shown in loaded and unloaded conditions, respectively, which were conducted as different fMRI sessions, and their order was counterbalanced within both prosocial and individualistic groups. In each session, after a name and a face of a proposer had been displayed for 1 sec, the participant was asked to decide whether to accept or reject an offered division of 500 yen within 1.5 sec. Offers were one of 250–250, 200–300, 150–350, or 100–400 divisions for responder and proposer (Figure 1B), and each division appeared 10 times in one session. Therefore, one session comprised 40 trials.

The name and face was utilized once for each individual participant and its association with an offer was counterbalanced across participants, and thus this ultimatum game is a sequential one-shot game. All faces were taken from the ATR facial expression database (Ogawa & Oda, 1998) and had neutral facial expressions. Participants were instructed that the proposers had been recruited from a college nearby and asked to choose one of four divisions of 500 yen (Figure 1B) with unknown university students. Participants were also told that the proposers would be paid later in accordance with responders' decisions. Although this involved deception, no participant had doubts on the existence of proposers in the post-experiment briefing session.

After the offer had been responded to, a digit from the (memorized or "01234") sequence was presented and the participant had to indicate the next digit by a button press initiated by a beep (11 ± 2 sec after the presentation of an offer). This query was designed to control the availability of cognitive resources, and the correct answer ranged from 1 to 4. Participants were shown the correct digit after 3 sec. One trial lasted 20.5 ± 1.5 sec, and one session (20.5 × 40) lasted 820 sec.

The following are the English-translated instructions for the ultimatum game.

1. A student of a college nearby was asked to choose a money division and the choice is being used as an offer.
2. The offer is shown after the name and face of the proposer is displayed. Decide whether to accept or reject the offer and press a corresponding button (accept: right index finger and reject: right middle finger) within 1.5 sec.
3. If you accept an offer, money is split as offered; otherwise, both of the two receive zero yen.
4. Before face presentation, a five-digit number sequence is displayed, and please memorize it. After you respond, a digit in the number sequence (random or constant ["01234"] sessions) is shown, then press a button corresponding the next number in the sequence.

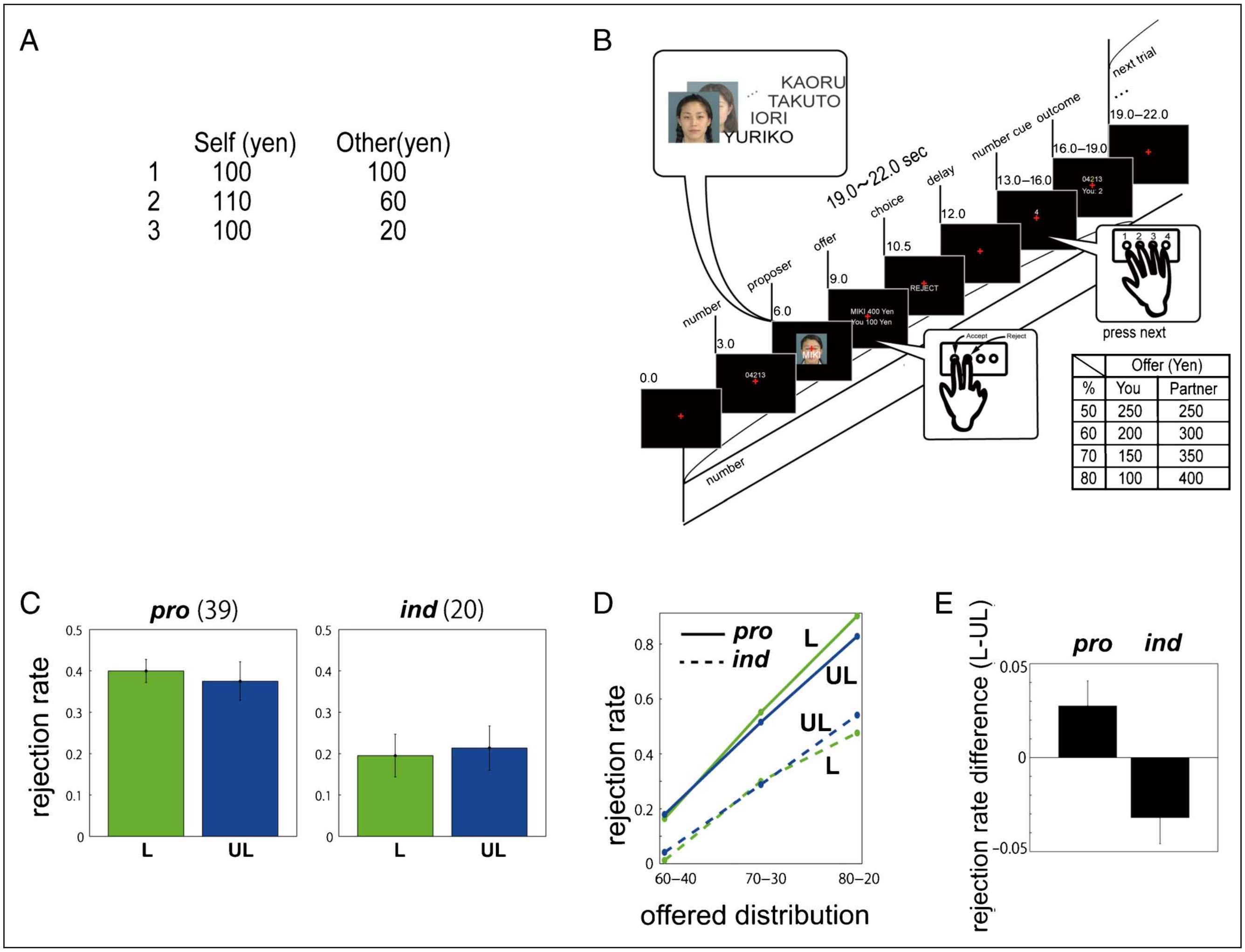

Figure 1. Task design and behaviors. (A) Triple-dominance measure task. Participants chose one of three alternatives: prosocial (1), individualistic (2), and competitive (3) distributions of money between the self and the unknown other. (B) Ultimatum game with cognitive load. In each trial, the participant was first required to remember a five-digit number. Either a random or a constant (01234) string of digits was shown in loaded and unloaded conditions, respectively. The participant was then asked to decide whether to accept or reject an offered division of 500 yen. Finally, a single digit from the remembered string was presented, and the participant had to indicate the next digit by a button press initiated by a beep (11 ± 2 sec after the pair presentation). One trial lasted 20.5 ± 1.5 sec, and the entire task comprised 40 trials lasting 820 sec. (C) Prosocials (n = 39) exhibited a significantly higher rejection rate in both loaded (green) and unloaded (blue) conditions, $F(2, 58) = 18.2$, $p < .001$, than individualists (n = 20). (D) Prosocials rejected unfair proposals more in the loaded condition, whereas individualists accepted more. (E) Within-participant comparison of the loaded and unloaded conditions confirmed prosocials rejected more in the loaded condition, $t(38) = 2.1$, $p = .023$ (paired t test), whereas individualists accepted more, $t(19) = 2.3$, $p = .017$, and the groups were significantly different ($p = .007$).

5. The base salary is 2000 yen, and half of the total money you obtain in two sessions is topped up.

The Impunity Game with Cognitive Load

The impunity game (Bolton & Zwick, 1995) used the same time schedule as the ultimatum game with load. The only difference between the two games is that, in the impunity game, participants cannot affect the proposer's gain even if they reject the offer. In other words, proposers always take what they propose in this task. This rule of the impunity game was clearly explained to participants. The instructions for the impunity game were the same as the one for the ultimatum game, except the following Nos. 3 and 4:

3. If you accept an offer, money is split as offered; otherwise, only your gain becomes zero yen.
4. Before face presentation, a five-digit random number sequence is displayed, and please memorize it. After you respond, a digit in the number sequence is shown, then press a button corresponding the next number in the sequence.

Participants

The participants were categorized as having one of the three social value orientations (i.e., prosocial, individualistic or competitive) only when they made at least six consistent choices out of eight (Haruno & Frith, 2010). During the course of this study, we did not find any competitive participants, so only participants categorized as prosocial or individualist proceeded to the subsequent imaging experiments as summarized below. Informed consent was obtained from all the participants, and the experimental protocol was approved by the ethics committees of the National Institute of Information and Communication Technology and Tamagawa University.

Ultimatum Game

In the first experiment, 39 prosocials (16 men and 23 women, 21 ± 1.1 years old, all right-handed) and 20 individualists (10 men and 10 women, 20 ± 1.3 years old, all right-handed) participated in the ultimatum game experiment. The participants were all students of Tamagawa University.

Impunity Game

In the second experiment, we asked a different set of participants from the first experiment to perform both impunity and ultimatum games with cognitive load as two separate sessions. Cognitive load was applied in both sessions. The order of the sessions was counterbalanced within prosocial and individualistic participants. Nineteen prosocials (8 men and 11 women, 21 ± 1.0 years old, all right-handed) and 19 individualists (9 men and 10 women, 20 ± 1.4 years old, all right-handed) participated in the experiment, which was designed to compare the brain activity in impunity and ultimatum games. The participants of this experiment were all students of Tamagawa University. We have previously found a smaller number (2–3%) of competitors than average in this population of participants (5% in Japan), and this may explain why we did not identify any competitors in the experiments.

MRI Acquisition

MRI scanning was conducted with a Siemens Trio TIM 3T scanner (repetition time = 3 sec, echo time = 30 msec, flip angle = 90°, field of view = 192 mm, and resolution = 3 × 3 × 3 mm) at Tamagawa University. 23.5° oblique orientations from the x–y plane of the scanner's coordinate system were used to cover the whole brain signal, including the ventromedial pFC. In addition to the experimental trials, the session contained two preliminary dummy scans to allow for T1 equilibration effects. High-resolution (T1 [1 × 1 × 1 mm] and T2 [0.6 × 0.4 × 3 mm]) structural images were also acquired for each participant.

Statistical Analysis of fMRI Data

The data were analyzed using standard procedures for random effect models in Statistical Parametric Mapping (SPM8; Friston et al., 1995). Before the statistical analysis, we performed motion correction and nonlinear transformation into the standard space of the Montreal Neurological Institute (MNI) coordinates using the T2 template of SPM8. Data from all participants were included in the analysis as their head movements were all smaller than 2 mm. These normalized EPI images were resliced into 2 × 2 × 2 mm voxels and then smoothed with an 8-mm FWHM isotropic Gaussian kernel. The data were high-pass filtered (cut-off frequency: 128 sec) by using the default setting of SPM8.

In the main analysis, for each participant, seven regressors were included for general linear model analysis of fMRI data. Two event-related regressors (duration = 0) were constructed at the timing of an offer. The first was a constant representing the event of offer, and the second had the amplitude of the inequity: reward for proposer–reward for participant. The second played a central role in examining the effect of inequity on participant's decision-making. The remaining five were standard event-related regressors (duration = 0) of the timings of presentations of the digit string and name presentation, button press for decision-making, and digit presentation and button press for the memory task. In addition to these, six-dimension head movement regressors were included. We also conducted three additional analyses. The first two analyses replaced the inequity regressor with reward for participant or reward for proposer, keeping other regressors the same. The third additional analysis replaced the offer constant and inequity regressors with a binary regressor that represented rejection trials at the timing of offer, and this analysis was included to see whether prosocials and individualists had different neural substrates associated with rejection.

After the first-level analysis of individual data concerning inequity, we conducted group analysis using a 2 × 2 factorial design consisting of Social Value Orientation (between group: prosocial or individualist) and Cognitive Load (within group: loaded or unloaded). On the basis of the behavioral results, the order of the conditions was not entered into the fMRI analysis. We used one-sample and two-sample t test to reveal the main effect of Inequity and the difference between the two groups, respectively. As the amygdala was expected to be involved from our previous study (Haruno & Frith, 2010), we used an uncorrected statistical threshold ($p < .001$, uncorrected for multiple comparison) for the amygdala and other regions seen in previous studies of the ultimatum game, but the more suitable corrected threshold ($p < .05$, FWE) for other brain structures. Only clusters containing more than 15 consecutive voxels were reported. We also conducted three additional analyses. For the first two analyses, we did not find any significant activity related to reward for proposer, and Table 1 summarizes all the results for inequity and reward for participant (self-reward). The only brain structure that survived the corrected threshold was the right nucleus accumbens annotated by an asterisk in Table 1. Finally, the third additional analysis examined

Table 1. Results of fMRI Analysis for Ultimatum Game Showing Correlations with Inequity and Self-reward

	Inequity ($p < .001$)									*Self-reward* ($p < .001$)		
	SVO			*SVO × Load*			*Effect of Conditions*			*Effect of Conditions*		
	MNI	*T*	*Voxels*	*MNI*	*T*	*Voxels*	*MNI*	*T*	*Voxels*	*MNI*	*T*	*Voxels*
R. accumbens*	(10 10 −10)	4.77	132	(10 6 −8)	3.61	38						
L. accumbens	(−10 10 −12)	4.65	93									
R. amygdala	(34 −4 −24)	3.43	25									
R. insula							(30 20 −10)	4.03	37	(36 20 −8)	3.71	79
L. insula							(−34 18 −12)	4.21	307	(−34 20 6)	3.68	65
ACC							(−6 16 50)	4.72	655	(−4 18 50)	4.34	493
R. caudate										(8 8 −4)	4.07	59
L. caudate										(−10 18 2)	3.82	42
R. DLPFC							(26 48 22)	3.78	115			

*means the significance for multiple correction (for $p < .05$, FWE). No significant results were obtained for negative contrasts.

SVO = social value orientation.

whether prosocials and individualists had different neural substrates associated with rejection or acceptance. This analysis did not reveal any differences, even with a moderate threshold ($p = .01$, uncorrected).

RESULTS

We conducted an fMRI study of the ultimatum game (Camerer, 2003; Sanfey et al., 2003; Guth et al., 1982), where prosocial ($n = 39$) and individualistic ($n = 20$) participants, categorized by a conventional behavioral task (Haruno & Frith, 2010; Van Lange, 1999; Figure 1A), were requested to decide (within 1.5 sec) to “accept” or “reject” the division of 500 yen offered by the proposer (Figure 1C and Methods). To examine the extent to which the decision was intuitive, we manipulated the availability of cognitive resources by varying the cognitive load imposed on the participants. In the loaded session, participants had to remember a five-digit random number sequence (e.g., “03241”) displayed before the presentation of an offer, and after the decision to accept or reject, they had to answer which number (e.g., “4”) was the next to the presented number (e.g.,“2”). By contrast, in the unloaded condition, the sequence was constant (i.e., “01234”). The imposition of a high cognitive was expected to reduce the availability of reflective processes (Valdesolo & DeSteno, 2008), and the two sessions were done as separate scans and the order was counterbalanced within prosocials and individualists.

Behavioral Results

As expected, prosocials rejected more than individualists (Figure 1C), $F(2, 58) = 18.2, p < .001$. This observation is consistent with the idea that the prosocials avoid inequity whereas the individualists prioritize personal gain. More interestingly, load had a small but significant interaction effect for unfair offers, $F(2, 58) = 3.19, p < .05$, increasing the difference in rejection rate between the prosocial and individualistic groups (Figure 1D, 80–20 offer). In other words, under the influence of load, prosocials became more prosocial (Figure 1E, paired t test), $t(38) = 2.41, p < .05$, and individualists became more individualistic (paired t test), $t(19) = 2.56, p < .05$, respectively. This suggests that the differential responses of the prosocials and individualists to the offers largely depend on a rapid and automatic intuitive system (we will discuss this issue further). The main effects of Load and the Order of loaded and unloaded conditions were not significant, $F(2, 58) = 0, p = .99$ and $F(2, 58) = 0.21, p = .65$, respectively. Similarly, the interaction of Load and the Order was not significant, $F(2, 58) = 1.47, p = .23$.

fMRI Results

We then wished to identify the neural substrates for the behavioral responses of prosocials and individualists and analyzed fMRI data by focusing on brain areas where the correlation between BOLD activity and the inequity of the offer (i.e., reward for other minus reward for self) differed between prosocials and individualists. To achieve this, the first-level analysis was conducted for inequity (we also examined self-reward and other reward). On the basis of behavioral results, social value orientation (prosocial or individualist) and existence of load (loaded or unloaded) were included in the second-level factorial design of fMRI analysis. We used t tests to reveal the difference between prosocials and individualists and the main effect of

Inequity (see also Figure 3). Significant differences between prosocials and individualists were found in the nucleus accumbens (peak MNI: (10, 10, −10); $p < .05$, FWE) and amygdala (peak MNI: (34, −4, −24); $p < .001$, uncorrected; Figure 2A and B). All of the significant results from this analysis are summarized in Table 1.

Importantly, there was also a small but significant interactive effect of load and social value orientation (t test, $p < .05$) in the accumbens (Table 1). There was a correlation between increased activity in the accumbens with load and increased rejection rate with load in both groups ($p = .005$; red: prosocials and blue: individualists; Figure 2C). These results suggest that activity in the nucleus accumbens reflects not only the difference in rejection rate between prosocials and individualists (Figure 1B) but also the effect of load on rejection rate in both groups. (Note that prosocials and individualists tend to lie at different ends of the same regression line in Figure 2C). By contrast, the amygdala activity did not represent such detailed behavioral changes ($p = .51$). This observation suggests that the nucleus accumbens may be more related to selection of action in the implementation of social value orientation. However, a direct comparison of activity in these two regions did not reach an acceptable level of significance.

Inequity in Insula and DLPFC

It was notable that our exploration of the greater rejection rate by prosocials did not reveal any effects in the various prefrontal regions previously associated with responses to inequity in the ultimatum game (Wright, Symmonds, Fleming, & Dolan, 2011; Sanfey et al., 2003). We therefore searched for the brain structures where activity was correlated with inequity for both prosocials and individualists. Activity in the bilateral insula, ACC, and right DLPFC was identified ($p < .001$; uncorrected; Figure 3A and B; see also Table 1), consistent with the previous studies. However, if we examine prosocials and individualists more closely, individualists showed a somewhat larger response to inequity than prosocials, $t(58) = 2.16$, $p < .05$, with activity being greater in the unloaded condition in these three regions. The overall pattern of activity does not correspond to the associated rejection rates (see Figure 1C), and this suggests that activity in these brain areas might be associated with high-level, conscious

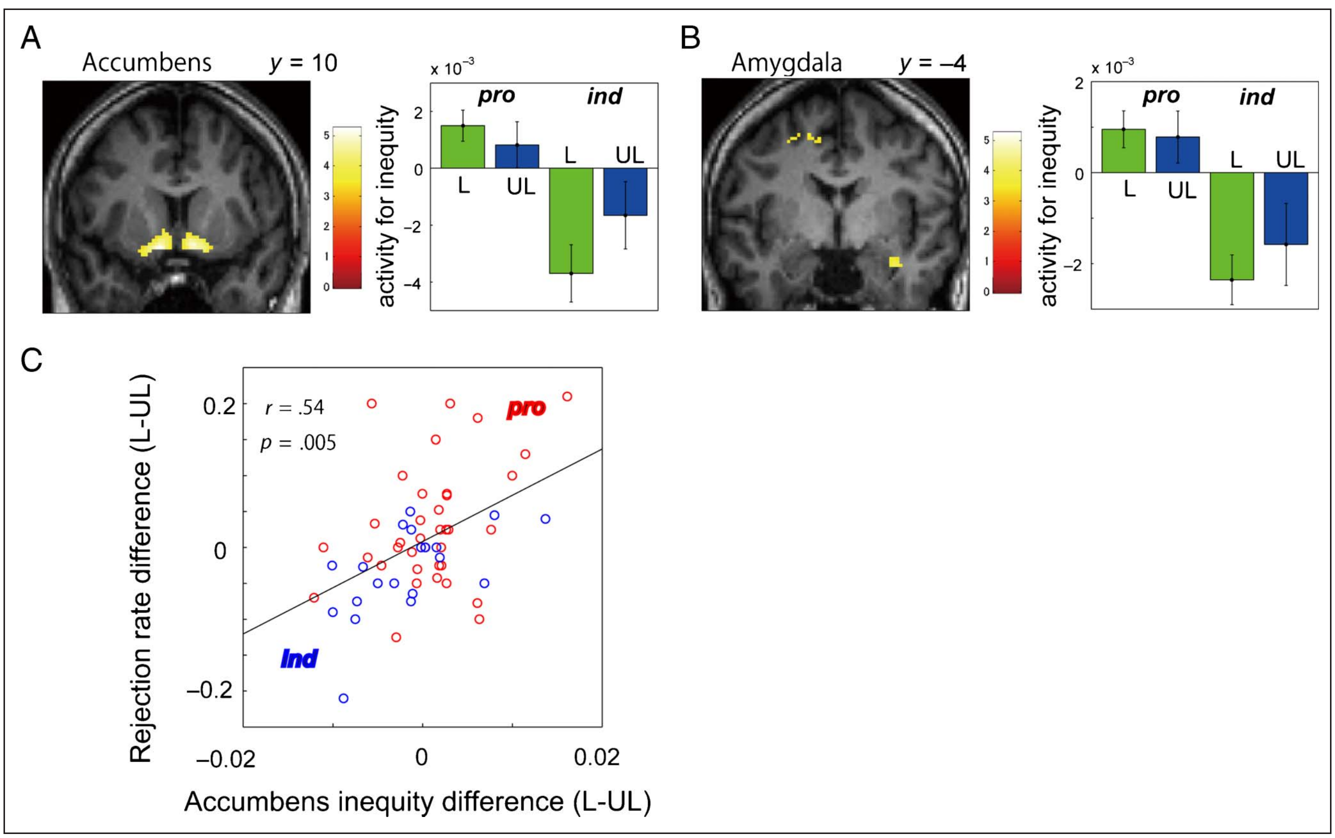

Figure 2. Activity in the accumbens and amygdala as the main effect of social value orientation (prosocials vs. individualist). Differences in the nucleus accumbens (A) (peak MNI: (10, 10, −10); $p < .05$, FWE) and amygdala (B) (peak MNI: (34, −4, −24); $p < .001$, uncorrected) were revealed. Throughout the figures, all brain activity is shown with the statistical threshold of 0.001 uncorrected, for display purposes, unless otherwise stated. (C) The difference in inequity (Ro − Rs) activity in the nucleus accumbens and the rejection rate difference between the loaded and unloaded conditions also showed a significantly positive correlation ($p = .005$; red: prosocials and blue: individualists). Prosocials and individualists tend to lie at different ends of the regression line as indicated in Figures 1C and 2A.

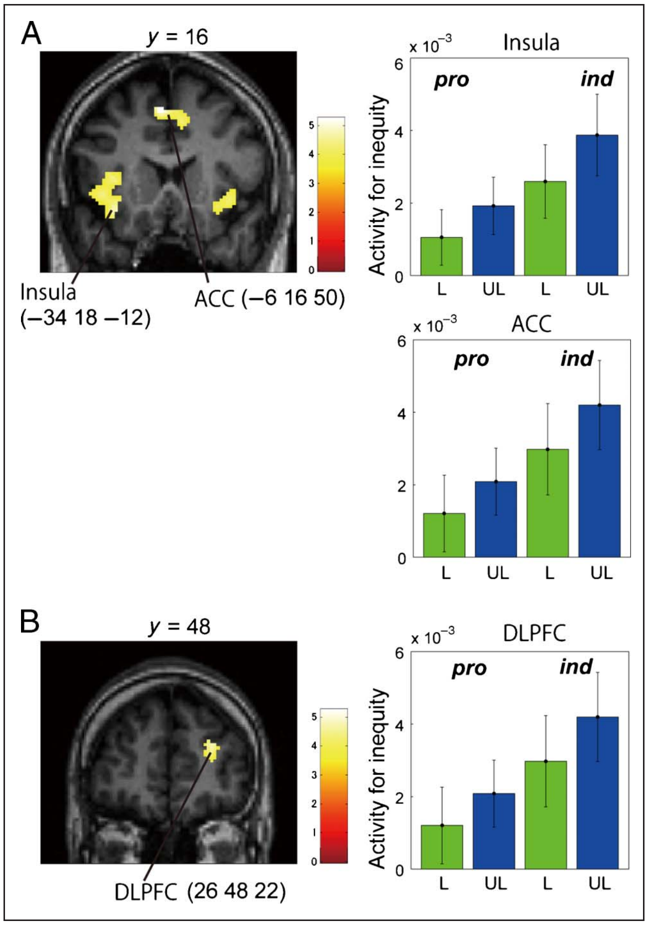

Figure 3. Correlation with inequity for all conditions. The ACC (A, peak MNI (−6, 16, 50)), insula (A, peak MNI (−34, 18, −12)), and DLPFC (B, peak MNI (26, 48, 22)) showed correlation with inequity for both prosocials and individualists ($p < .001$, uncorrected). Bar graphs show beta values averaged over participants.

reflection on the unfair offer (e.g., emotional awareness; Craig, 2009). Although the individualists responded more to unfair offers in this high-level system, they nevertheless chose to accept such offers.

Prosocials Have Outcome-oriented Intuition

The rejection of unfair offers in the ultimatum game can be seen as a form of altruistic punishment designed to increase equity by punishing the behavior of the unfair proposer (Fehr & Fishbacher, 2003). Altruistic punishment is an example of prosocial behavior, which changes the current situation, because the costly rejection by the responder may translate into advantages for the group if the proposer behaves more fairly in the future. However, it is also possible that the rejection of unfair offers is simply an emotional reaction to unfair treatment from others (e.g., see Koenigs & Tranel, 2007).

To distinguish between these possibilities, we contrasted the ultimatum game with the impunity game (Bolton & Zwick, 1995) where rejection makes the responder's payoff null but does not affect the proposer's. In this case rejection cannot have any effect on the proposer. Both games were played during the imposition of a cognitive load. Nineteen prosocials and nineteen individualistic participants who had not taken part in the first study participated in this experiment, with the order of the two games counterbalanced across the participants. The prosocials' rejection rate was significantly lower when playing the impunity game, $t(37) = 5.66, p < .0001$, paired t test (Figure 4A and B) than in the ultimatum game, whereas the rejection rate of individualists did not change. This suggests that rejection by the prosocial responders in the ultimatum game was not simply a response to an unfair offer but was designed to have an effect on the proposer and that this strategy was applied even in the presence of a cognitive load.

In a replication of the first experiment, rejection rate for prosocials was higher in ultimatum game than individualists (Figure 4A). Furthermore, activity in response to inequity in the nucleus accumbens and the amygdala (also caudate nucleus; Figure 4C, $p < .001$, uncorrected; see also Table 2) reflected the rejection rate for the two groups. For the prosocials, activity in these regions was higher in the ultimatum game than in the impunity game, whereas there was no difference in activity for the individualists. It is also notable that there was no such difference in response to unfair offers in ACC, DLPFC, and insula between the impunity and ultimatum games (even at $p = .1$, uncorrected). These results suggest that the high rejection rate of the prosocials is largely an aspect of their outcome-oriented attitude.

DISCUSSION

The results of this study suggest that the behavior of both prosocials and individualists in the ultimatum game largely reflects automatic and intuitive processes underpinned by activity in the nucleus accumbens and amygdala responding to inequity. By contrast, although activity in insula and ACC is elicited by inequity, this activity cannot explain the low rejection rate of individualists and is consistent with the hypothesis that this activty is associated with conscious reflection on the unfair offer and the emotional reaction elicited. By contrasting the impunity game with the ultimatum game, we also showed that the high rejection rate of the prosocials as responders is an aspect of their prosocial outcome-oriented attitude.

Nucleus Accumbens Tracks Behavioral Output

The nucleus accumbens has been implicated in diverse aspects of social interaction, such as the effects of the other's reward (Fliessbach et al., 2007), the effect of current endowment (Tricomi et al., 2011), and the closeness to the other (Fareri, Niznikiewicz, Lee, & Delgado, 2012) on reward processing. In our study, activity in the nucleus accumbens precisely reflected behavioral change between

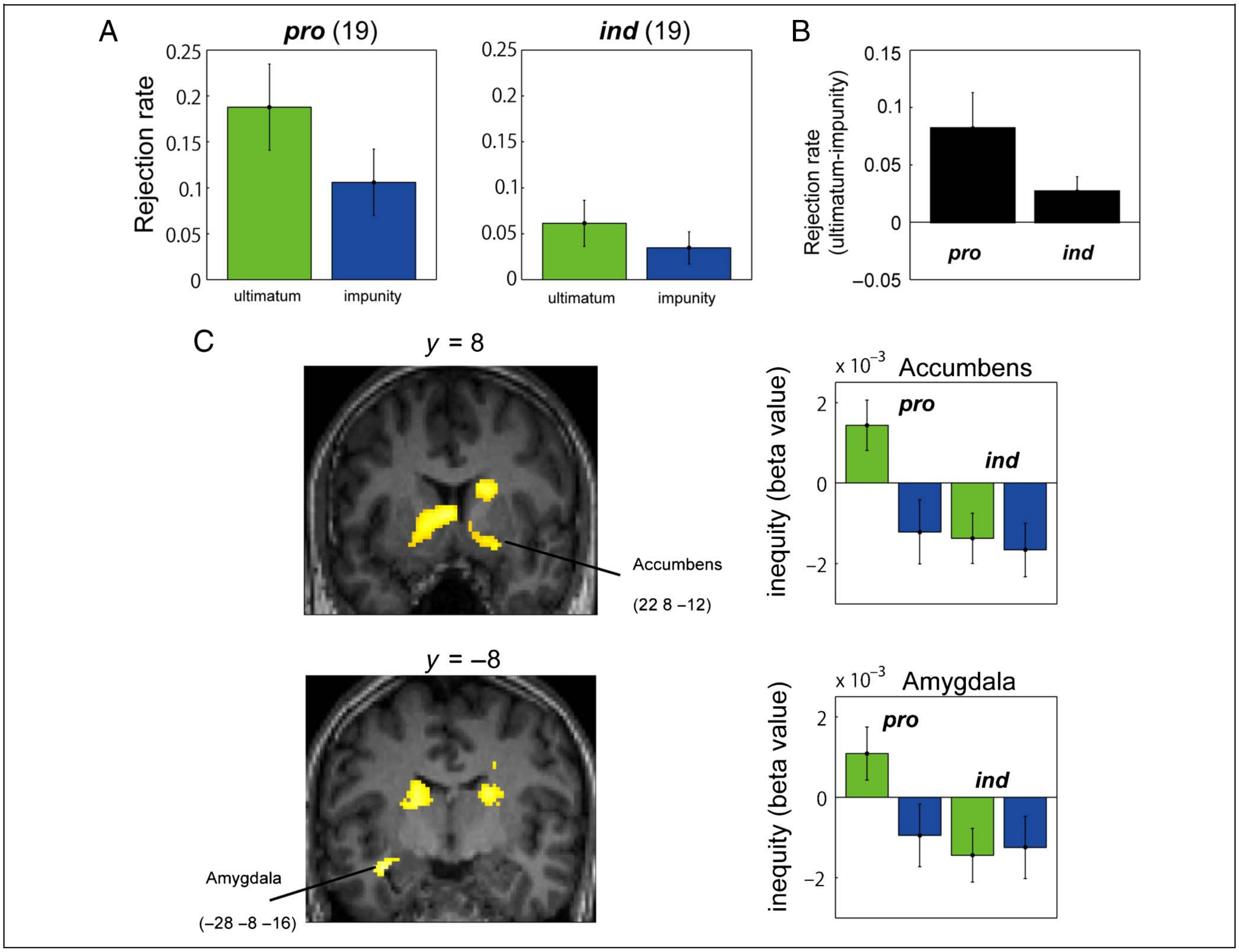

Figure 4. Comparison between ultimatum game and impunity game. (A, B) Prosocials (n = 19) exhibited a significantly higher rejection rate in the ultimatum game (green) than in the impunity game (blue) (paired t test; p = .021, B), whereas no such difference was observed in individualists (n = 19) (paired t test; p = .085, B). There was also a significant difference between ultimatum games of prosocials and individualists, $t(37)$ = 2.66 (two-sample t test; p = .023) and no such difference for impunity games (two-sample t test; p = .09). (C) Significantly higher correlation with inequity was found in the nucleus accumbens (peak MNI (22, 8, −12)), amygdala (peak MNI (−28, −8, −16)), and caudate nucleus (peak MNI (22, −2, 18)) when prosocials were playing the ultimatum game in comparison with other game conditions (p < .001; uncorrected).

Table 2. Results of fMRI Analysis for the Impunity Game in Correlation with Inequity

	Inequity (p < .001)		
	Pro(Ult) − [Pro(Imp) + Ind(Ult) + Ind(Imp)]		
	MNI	*T*	*Voxels*
R. accumbens	(22 8 −12)	5.14	118
L. accumbens	(−16 10 −8)	4.10	120
R. amygdala	(33 −12 −14)	4.18	39
L. amygdala	(−28 −8 −16)	4.53	187
R. caudate	(22 −2 18)	5.59	331
L. caudate	(−14 16 6)	4.96	262

the loaded and unloaded conditions for both prosocials and individualists. This property is likely to be different from that of the amygdala in intuitive detection of inequity and consistent with the view that the nucleus accumbens links motivation and emotion to action (Stuber et al., 2010; Reynolds & Berridge, 2008; Mogenson, Jones, & Yim, 1980).

It is also an interesting property of the nucleus accumbens that both prosocial and individualistic orientations, although seemingly opposite characteristics of human sociality, are encoded in a single structure (Reynolds & Berridge, 2008). A possible scenario might be that the accumbens activity indexes a framing effect for participants wherein prosocials encode the inequity as other–self (how much better are they?), whereas individualists encode it as self–other (how much better am I?).

Interestingly, when prosocial participants were exposed to the impunity game, the activity in the nucleus accumbens seen during the ultimatum game was not apparent, and the activity pattern was similar to that shown by individualists (Figure 4C). This may suggest that the nucleus accumbens has the ability to integrate different sources (Humphries & Prescott, 2010) of motivation and emotion and constitutes a hub for action selection, and is modulated by individual personality traits.

Amygdala Activity and Prosocial Orientation

Our finding that the amygdala plays a key role in prosocial attitudes is consistent with a recent pharmacology study of the ultimatum game with the enhancer of GABAa receptor benzodiazepine showing that diminished amygdala activity was associated with a decrease in rejection rates to unfair offers (Gospic et al., 2011). This treatment might reduce responsiveness in the amygdala, which would then make the participants' decision-making system less sensitive to the imbalance between the self and the other. Some recent studies report that serotonin, which also effects activity in the amygdala (Hariri et al., 2002), can also change rejection rates in the ultimatum game (Takahashi et al., 2012; Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008).

The ventromedial pFC is known to regulate activity in the amygdala. Our finding that amygdala response to inequity in prosocials is linked with rejection rate of unfair offers is consistent with a report of the increased rejection rate when human ventromedial prefrontal cortices were damaged (Koenigs & Tranel, 2007).

Conscious Reflection of Fairness and Emotion

Activity in the bilateral insula, ACC, and right DLPFC were correlated with inequity (Figure 3A and B) in both prosocials and individualist, in a manner highly consistent with previous studies of inequity aversion (Wright et al., 2011; Sanfey et al., 2003), which separately examined accept and reject behaviors. Considering the fact that these activities were stronger in the unloaded session, and for individualists, we suggest that they may represent conscious reflection on fairness and the emotional reaction to inequity. Related to this, it has recently been proposed that rejection behavior in one-shot ultimatum games arises mainly from an emotional reaction to an unfair situation rather than prosocial motivation (Yamagishi et al., 2012). The common component of rejection behavior seen for prosocials and individualists may well be explained by this emotional mechanism. On the basis of the observations of this study, we propose a two-level emotion hypothesis: an intuitive emotional system that mainly involves the amygdala and nucleus accumbens and a reflective emotional system that mainly involves the insula and prefrontal cortices.

In conclusion, the relative distribution of resources between self and other lies at the center of every aspect of human social endeavor including education, politics, economics, and even art and science. It might be counterintuitive at first glance that automatic and intuitive social preferences encoded in primitive structure such as the nucleus accumbens and amygdala play a major role in differentiating human social orientation. However, Fehr and colleagues have shown that prosocial behavior develops early, between the ages of 3 and 7 years, and is closely related to parochiality (Fehr et al., 2008). This result suggests that development of a prosocial attitude may not depend on high-level cognitive functions.

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