Honesty mediates the relationship between serotonin and reaction to unfairness

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How does one deal with unfair behaviors? This subject has long been investigated by various disciplines including philosophy, psychology, economics, and biology. However, our reactions to unfairness differ from one individual to another. Experimental economics studies using the ultimatum game (UG), in which players must decide whether to accept or reject fair or unfair offers, have also shown that there are substantial individual differences in reaction to unfairness. However, little is known about psychological as well as neurobiological mechanisms of this observation. We combined a molecular imaging technique, an economics game, and a personality inventory to elucidate the neurobiological mechanism of heterogeneous reactions to unfairness. Contrary to the common belief that aggressive personalities (impulsivity or hostility) are related to the high rejection rate of unfair offers in UG, we found that individuals with apparently peaceful personalities (straightforwardness and trust) rejected more often and were engaged in personally costly forms of retaliation. Furthermore, individuals with a low level of serotonin transporters in the dorsal raphe nucleus (DRN) are honest and trustful, and thus cannot tolerate unfairness, being candid in expressing their frustrations. In other words, higher central serotonin transmission might allow us to behave adroitly and opportunistically, being good at playing games while pursuing self-interest. We provide unique neurobiological evidence to account for individual differences of reaction to unfairness.

positron emission tomography | decision-making | fairness

How should one deal with line cutters? In the 2010 holiday season, Cable News Network (CNN; (http://edition.cnn.com/2010/LIVING/11/25/gift.etiquette.black.friday/index.html)) featured this topic. No one can help feeling frustrated in such a situation, but actual responses might differ among individuals. Some people would speak up, but others might say nothing because they either worry about causing a scene or conclude that a confrontation is not worth the trouble.

The fundamental question underlying this specific topic is: What would you do if you faced unfair or wrong behavior? This question has been dealt with by various disciplines such as philosophy, psychology, economics, and biology. Experimental studies using the ultimatum game (UG) have also shown that there are substantial individual differences in reaction to unfairness (1). In UG, the first player (proposer) proposes how to divide the sum between the two players, and the second player (responder) can either accept or reject this proposal. If the responder rejects, neither player receives anything. If the responder accepts, the money is split according to the proposal. The theoretical solution for responders is that they should accept any unfair offer because it is better than nothing. However, responders frequently reject unfair offers (less than 30% of available stake). In other words, they show willingness to pay to resist or punish unfairness. The source of this behavior can be explained by aversion to inequity, meaning that the player is motivated to maintain equity (2) and/or desires to retaliate against wrong intention (negative reciprocity) (3, 4).

Given the substantial individual differences in the behavior of responders, it is reasonable to investigate the relation between personality and behavior of responders in UG. However, surprisingly few studies have been reported (5). Intuitive prediction is that impulsive or hostile personality is related to higher rejection of unfairness (6–8). However, some combination of emotional reactions, lack of control, and norms is considered to contribute to the rejection of unfair behavior (6). Lack of control (impulsivity) might be related to the rejection of unfair offers (9), but if responders do not feel indignation or moral outrage, they do not have to control these emotions no matter how impulsive they are. Thus, one's own moral standards or sense of justice should be a prerequisite to the rejection of unfair offers. In this sense, rejecting unfair offers can be regarded as behaving faithfully to one's own principles as well as behaving honestly with indignation, and accepting unfair offers can be interpreted as behaving in a realistic and opportunistic manner. We predict that apparently peaceful personality (straightforwardness or honesty) with high moral standards rather than aggressive personality (impulsivity or hostility) is related to retaliation.

Crockett et al. (10) demonstrated that serotonin (5-HT) played a role in modulating reaction to unfair offers in UG. A decreasing central 5-HT level increased rejection to unfairness. In other words, low level 5-HT makes us less tolerant of unfairness and more candid in expressing our frustration. Using an in vivo molecular imaging technique, positron emission tomography (PET), we directly measured 5-HT transporters (5-HTT) and 5-HT1A receptors and investigated their relation to personality and reaction to unfairness. Because dishonest behaviors are known to recruit brain regions associated with cognitive control, including the dorsal lateral prefrontal cortex (DLPFC) (11, 12), and 5-HT transmission in prefrontal cortex (PFC) is important for cognitive control (13, 14), we hypothesized that low 5-HT transmission in DLPFC or the dorsal raphe nucleus (DRN), a major source of

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5-HT, would be associated with higher rejection of unfair offers in UG, and that the personality trait of honesty would mediate this possible relationship.

Results

Mean rejection rates for unfair and fair offers were 78.8 ± 25.1 and 16.9 ± 22.3, respectively. Participants were more likely to reject unfair offers than fair offers ($t = 10.4$, $P < 0.001$). Mean of T scores of overall neuroticism and agreeableness scores were 54.1 ± 12.6 and 46.4 ± 15.4, respectively. As we expected, the rejection rate for unfair offers was positively correlated with straightforwardness ($R = 0.59$, $P = 0.006$) and trust ($R = 0.54$, $P = 0.015$) facets (Fig. S1 *A* and *B*), subscales of agreeableness, but not with the overall agreeableness score ($R = 0.35$, $P = 0.13$). That is, honest and trustful people are more likely to reject unfair offers. However, importantly, the rejection rate for unfair offers was neither correlated with the overall neuroticism score ($R = -0.15$, $P = 0.52$) nor with subscales such as anger–hostility ($R = -0.20$, $P = 0.40$) and impulsivity ($R = 0.21$, $P = 0.37$). The rejection rate for fair offers did not correlate with any personality scales.

Voxel-wise statistical parametric mapping (SPM) (Fig. 1 *A* and *B*) analysis revealed significant negative correlation between the rejection rate for unfair offers and the binding potential for nondisplaceable radioligand in tissue (BP_{ND}) (15) of [^{11}C]DASB in the midbrain regions including DRN (Fig. 2*A*). Confirmatory region-of-interest (ROI) analysis revealed identical results (Fig. 2*B*). The mean BP_{ND} of [^{11}C]DASB in the midbrain including DRN was 3.05 ± 0.86. There were no significant correlations between the rejection rate of fair offers and [^{11}C]DASB binding of any of the brain regions, nor were the rejection rates of unfair and fair offers correlated with [^{11}C]WAY100635 binding. SPM and ROI analyses also revealed that straightforwardness ($R = -0.54$, $P = 0.013$) (Fig. S2 *A* and *B*) and trust ($R = -0.51$, $P = 0.022$) (Fig. S3 *A* and *B*) were negatively correlated with BP_{ND} of [^{11}C]DASB in the midbrain regions including DRN. Finally, to examine whether personalities mediated the relationship between 5-HTT and rejection to unfairness, we conducted mediation analyses. They revealed that straightforwardness was a significant mediator of the relationship between 5-HTT binding in DRN and rejection of unfair offers in UG (Sobel test = −1.70, $P = 0.04$, one tailed) (Fig. 3). The mediation effect of trust approached significance (Sobel test = −1.47, $P = 0.07$, one tailed) (Fig. S4). Because straightforwardness and trust were highly correlated ($R = 0.58$, $P = 0.008$), we averaged these indices to enhance the robustness of the mediation model. The analysis revealed a more robust mediation effect (Sobel test = −1.91, $P = 0.03$, one tailed). We also tested an alternative model in which personality drives 5-HTT in DRN, which then mediates the relationship between personality and rejection to unfair offers. This model showed that 5-HTT in DRN was not a significant mediator of the relationship between personality and rejection to unfair offers in UG (straightforwardness: Sobel test = 1.09, $P = 0.14$,one tailed and trust: Sobel test = 1.25, $P = 0.11$, one tailed).

Discussion

Contrary to the common belief that aggressive personalities (impulsivity and anger–hostility) are related to a high rejection rate of unfair offers in UG (6–8), we found that individuals with apparently peaceful personalities (straightforwardness and trust) are more likely to reject and retaliate against unfairness. Furthermore, straightforwardness and, to a lesser extent, trust personalities mediated our finding that individuals with low 5-HTT in DRN were more likely to reject unfair offers.

Straightforwardness is similar to honesty and implies directness and frankness in dealing with others. Trust can be defined as the general expectation of others (16, 17). Honesty is correlated with trust (18, 19), and honest and trustful persons tend to believe that most people are honest, decent, and trustworthy (17). Thus, honest and trustful persons have a higher normative expectation, a standard of behavior that they believe people should comply with. Perception of fairness depends on normative expectations, and in fact, people with higher normative expectations tend to reject more unfair offers in UG (20).

The opposite pole of straightforwardness/honesty and trust is Machiavellianism (17, 19). Machiavellian individuals are cunning, unscrupulous, and opportunistic and behave adroitly to attain particular goals. They are generally more likely to suspect others of dishonesty (cynicism) (1). Machiavellian intelligence (also known as political intelligence or social intelligence) is hypothesized to have evolved through social complexity, in which individuals developed sophisticated strategies with a balance of competition and cooperation to achieve higher social and reproductive success (21–23). It has been shown that Machiavellian individuals accept unfair offers more in UG (24). This means that Machiavellian people with realism and opportunism behave to maximize their self-interest. However, honest and trustful persons cannot easily separate themselves from moral precepts and tend to adhere to a norm of fairness and consequently show lower tolerance of unfairness (24, 25). It should be noted that, because we did not measure Machiavellianism, our extrapolative arguments on it should be directly tested in future studies.

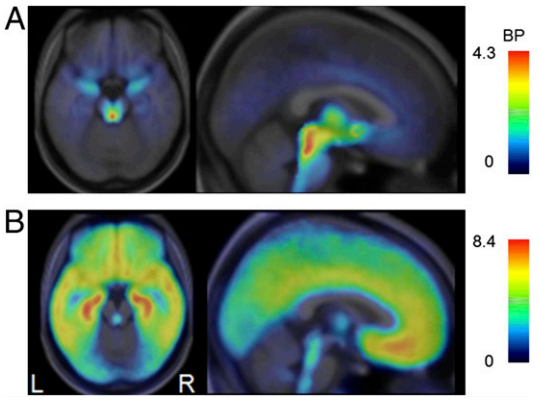

Fig. 1. Maps of 5-HTT and 5-HT1A receptor BP, averaged across participants. (*A*) [^{11}C]DASB image fused with MRI. (*B*) [^{11}C]WAY100635 image fused with MRI. Bar indicates the range of BP. In *Left* to *Right* columns, axial and sagittal planes of the brain are displayed. R, right; L, left.

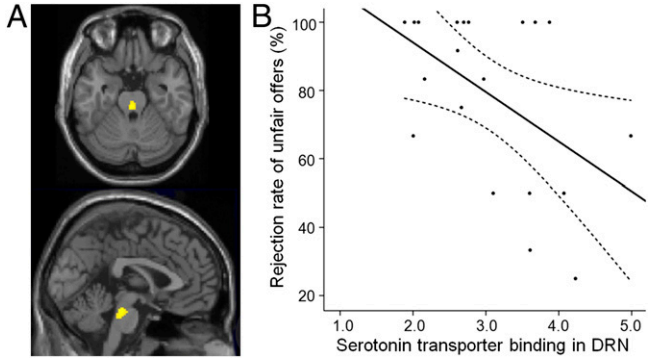

Fig. 2. Correlation between rejection rate of unfair offers in UG and 5-HTT binding in DRN. (*A*) SPM image showing regions of negative correlation between rejection rate of unfair offers and 5-HTT binding in DRN. (*B*) Plots and regression line of correlation between rejection rate of unfair offers and 5-HTT binding in DRN ($R = -0.50$, $P = 0.026$). Dashed lines are 95% confidence interval boundaries.

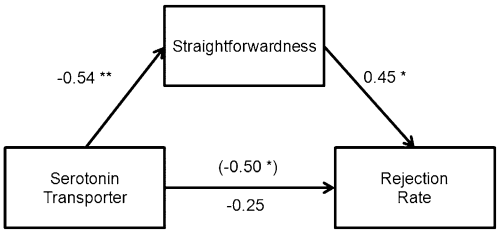

Fig. 3. Result of mediation analysis including straightforwardness as a mediator. The effect of 5HTT binding on the rejection rate of unfair offers became nonsignificant when the mediator was introduced. Analysis revealed that straightforwardness was a significant mediator of the relationship between 5-HTT binding in DRN and rejection of unfair offers in UG (Sobel test = −1.70, $P = 0.04$, one tailed). *$P < 0.05$, **$P < 0.01$.

Interestingly, we found that low 5-HTT in DRN was associated with straightforwardness and trust personality traits and therefore predicted higher rejection rates of unfair offers in UG. 5-HTT is primarily located in the soma and dendrites of 5-HT neurons in the raphe nuclei (26), and 5-HTT binding in DRN measured by PET reflects 5-HT neurons (27). Another possible interpretation is that low 5-HTT in DRN might indicate higher extrasynaptic serotonin, which could agonize autoreceptors, decreasing serotonin availability at the terminals. It has been shown that administration of a serotonin reuptake inhibitor decreased negative affect (hostility) (28), and induced negative emotions can increase rejections of unfair offers (29). In fact, lack of control (impulsivity) is reported to be related to rejection of unfair offers in UG (9). Impulsivity is a complex construct and we do not mean to imply that impulsivity does not play a role in rejecting unfair offers. However, our findings suggest one's own moral standards or sense of justice should be a prerequisite to the rejection of unfair offers, and that individuals with low 5-HT neurons in DRN or low serotonin availability at the terminals are more likely to be honest and trustful, cannot tolerate unfair offers, and are more likely to engage in personally costly forms of retaliation. In other words, individuals with high 5-HT neurons in DRN are more likely to be Machiavellian and should be good game players in terms of pursuing self-interest, accepting any offer even if it is unfair.

Using the acute tryptophan depletion method, Crockett and her colleagues (10) elegantly demonstrated that lowering the central 5-HT level caused an increase in the rejection rate of unfair offers in UG. It can be said that 5-HT prevents us from behaving with hot passion and promotes us to behave with a cool mind to attain particular goals. On the basis of their own result and previous studies showing that the 5-HT system promotes the acquisition of social dominance in monkeys (30, 31), they suggested that central 5-HT transmission plays a role in increasing social skills and intelligence (32).

As for the introductory example of line cutters in a crowded store, customers in line with low 5-HTT in DRN might not be able to tolerate unfair line cutters and are more likely to candidly speak up and express their frustration. On the other hand, customers in line with high 5-HTT in DRN might say nothing and perform their shopping composedly because they conclude that the cost of causing a scene is greater than waiting a couple of minutes longer.

The current study has several limitations. First, although the number of subjects is moderate for a PET study, it is relatively small for a study of individual differences. Second, sex, generation, and culture could influence the reaction to unfairness (33). Thus, any generalization should be approached with caution until the findings are replicated. Notwithstanding with these limitations, the present study demonstrated that individuals with low 5-HTT in DRN contend with and retaliate more against unfairness, and it also illustrated that honesty and to a lesser extent trust personalities mediate this behavioral phenomenon. Thus, our findings propose a neurobiological mechanism of the heterogeneity of reaction to unfairness and contribute to a better understanding of the molecular mechanism of extreme or impaired reaction to unfairness.

Materials and Methods

Subjects. Twenty healthy male volunteers [mean age 24.1 ± (SD) 5.2 y] were studied. They did not meet the criteria for any psychiatric disorder on the basis of unstructured psychiatric screening interviews. None of the controls were taking alcohol at the time, nor did they have a history of psychiatric disorder, significant physical illness, head injury, neurological disorder, or alcohol or drug dependence. All subjects were right-handed according to the Edinburgh Handedness Inventory. All subjects underwent MRI to rule out cerebral anatomic abnormalities. After complete explanation of the study, written informed consent was obtained from all subjects, and the study was approved by the ethics and radiation safety committee of the National Institute of Radiological Sciences, Chiba, Japan.

Experimental Procedure. Participants were told a cover story, that they would be playing the role of responder with volunteers who had submitted their offers previously. Participants were instructed as follows:

"Another male volunteer arrived at the institute earlier and is now in a different building. He does not and will not know who you are. He was informed of the fact that you also did not and would not know who he is." He was then explained the rules of the economics game. The rules were the following: "He (the proposer) proposes a way to split a sum of money (1,000 yen) with you (the responder). If you accept the offer, both you and he are paid accordingly. If you reject the offer, neither you nor he is paid. He understood the rules and decided his 20 offers. Now the computer in front of you will show his 20 offers. You can decide whether to accept or reject each offer."

In reality, there were no actual proposers, and 8 fair and 12 unfair offers were randomly presented. Like a previous study (10), offers of 500 and 400 yen (50 and 40% of 1,000 yen) were regarded as fair offers, and those of 300, 200, and 100 yen (30, 20, and 10% of 1,000 yen) were regarded as unfair offers. Participants were told that they would receive a bonus with a maximum limit, according to the financial outcomes of the games, in addition to a fixed base payment for participation. In reality, all participants received the maximum bonus. We calculated the rejection rates for unfair and fair offers.

Personality Assessment. Personality traits were assessed by the Japanese version of the Revised NEO Personality Inventory (34, 35) on the same day as the performance of the first PET scans. This test is composed of 240 items and contains five dimensional scales (neuroticism, extraversion, openness, agreeableness, and conscientiousness) corresponding to a five-factor model of personality trait. Revised NEO Personality Inventory results are presented as *T* scores with a mean of 50 and a SD of 10. Because our focuses are honesty/straightforwardness, anger–hostility, and impulsivity, we used neuroticism and agreeableness traits. Within the neuroticism dimension, there are six underlying personality trait facets: anxiety, anger–hostility, depression, self-consciousness, impulsivity, and vulnerability. Within the agreeableness dimension, there are six facets: trust, straightforwardness, altruism, compliance, modesty, and tender-mindedness.

PET Scanning. PET studies were performed on ECAT EXACT HR+ (CTI-Siemens). The system provides 63 planes and a 15.5-cm field of view. To minimize head movement, a head fixation device (Fixster) was used. A transmission scan for attenuation correction was performed using a ^{68}Ge-^{68}Ga source. Data were acquired in 3D mode for [^{11}C]WAY100635 and in 2D mode for [^{11}C]DASB, because [^{11}C]DASB is substantially trapped at first pass through human lungs due to the high expression of 5-HTT on the pulmonary membrane, leading to excessive random counts from 3D head recordings (36).

For evaluation of 5-HTT, a bolus of 754.8 ± 37.0 MBq of [^{11}C]DASB with specific radioactivities (302.3 ± 93.3 GBq/μmol) was injected intravenously. For evaluation of 5-HT1A receptors, a bolus of 222.0 ± 3.7 MBq of [^{11}C]WAY100635 with high specific radioactivities (162.1 ± 57.9 GBq/μmol) was injected in the same way. Dynamic scans were performed for 90 min for each of the radioligands immediately after the injection. All emission scans were reconstructed with a Hanning filter cutoff frequency of 0.4 (full width at half maximum, 7.5 mm). MRI was performed on Gyroscan NT (Philips Medical Systems) (1.5 tesla). T1-weighted images of the brain were obtained for all subjects. Scan parameters were 1-mm-thick, 3-dimensional T1 images with

a transverse plane (repetition time/echo time, 19/10 ms; flip angle, 30°; scan matrix, 256 × 256 pixels; field of view, 256 × 256 mm; number of excitations, 1).

Quantification of 5-HTT and 5-HT1A Receptors. A PET summation image of all frames and dynamic images was coregistered to each individual MR image by using PMOD (PMOD Technologies). The individual MR image was spatially normalized to the Montreal Neurological Institute (MNI) stereotaxic brain, and the transformation parameters were subsequently applied to the co-registered PET dynamic images. Thus, the PET and MR images of all subjects were anatomically standardized to the MNI template.

For the PET study with [^{11}C]WAY100635, BP_{ND} was calculated using a simplified reference tissue model (37). The cerebellum was used as reference region because a postmortem study indicated that the cerebellum cortex is almost devoid of 5-HT_{1A} receptors (38). On the basis of this model, we created parametric images of BP_{ND} using the basis function method (39) to conduct voxel-wise SPM analysis (Fig. 1 *A* and *B*).

For the PET study with [^{11}C]DASB, we created parametric images of BP_{ND} using a multilinear reference tissue model 2 (MRTM2) (40). The cerebellum was used as reference region because a postmortem study indicated that the cerebellum cortex is almost devoid of 5-HTT (38). The BP_{ND} estimation procedures for both radiotracers have been described in detail previously (41).

Statistical Analysis. ***SPM analysis.*** Parametric images of BP_{ND} of [^{11}C]DASB and [^{11}C]WAY100635 were analyzed using the SPM5 software package (Wellcome Department of Cognitive Neurology, London) running with MATLAB (Mathworks). Normalized BP_{ND} images were smoothed with a Gaussian filter to 8 mm full width half maximum. Using rejection rates for unfair and fair offers of each subject as covariates, regression analyses with the BP_{ND} images and the covariates were performed. Significant correlation recognized at a statistical threshold of false discovery rate corrected, $P < 0.05$, was used, except for a priori hypothesized regions, which were thresholded at $P < 0.001$ uncorrected (only clusters involving 10 or more contiguous voxels were reported). On the basis of previous literature (42–44), a priori ROIs included the insula and DLPFC in addition to the midbrain region including DRN, a major source of 5-HT.

ROI analysis. To confirm the SPM results, we conducted an independent ROI analysis. The detailed definition of ROI was described elsewhere (41). Tissue concentrations of the radioactivities of [^{11}C]WAY100635 and [^{11}C]DASB were obtained from ROIs defined on the averaged and standardized PET summations and MR images by using the PMOD fusion tool. The same ROI was used for both [^{11}C]WAY100635 and [^{11}C]DASB in all subjects. Pearson's correlation coefficient between BP_{ND} of [^{11}C]DASB and [^{11}C]WAY100635 in the ROIs and rejection rates for unfair and fair offers were calculated using SPSS. To examine whether the relationship between 5-HTT binding and rejection of unfairness was mediated by personality traits, we conducted mediation analyses. The mediation effect was tested by Sobel test (45).

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