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Processing of Social and Monetary Rewards in the Human Striatum

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SUMMARY

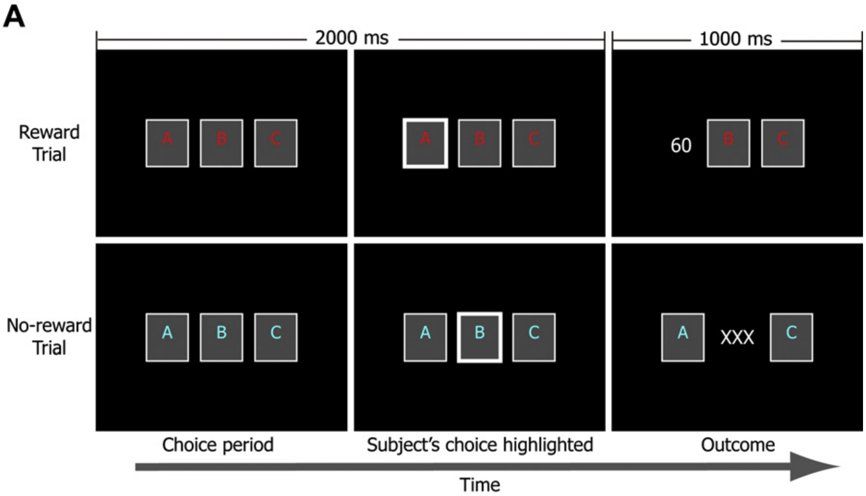
Despite an increasing focus on the neural basis of human decision making in neuroscience, relatively little attention has been paid to decision making in social settings. Moreover, although human social decision making has been explored in a social psychology context, few neural explanations for the observed findings have been considered. To bridge this gap and improve models of human social decision making, we investigated whether acquiring a good reputation, which is an important incentive in human social behaviors, activates the same reward circuitry as monetary rewards. In total, 19 subjects participated in functional magnetic resonance imaging (fMRI) experiments involving monetary and social rewards. The acquisition of one's good reputation robustly activated reward-related brain areas, notably the striatum, and these overlapped with the areas activated by monetary rewards. Our findings support the idea of a "common neural currency" for rewards and represent an important first step toward a neural explanation for complex human social behaviors.

INTRODUCTION

The decision-making process has recently attracted the attention of researchers from various disciplines, and considerable progress has been made in understanding its neural basis (Daw and Doya, 2006; Montague et al., 2006; Sanfey et al., 2006). However, the neural basis of human decision making in social situations is relatively less well understood because of its complexity. During the mid-twentieth century, in an effort to explain human social decision-making behaviors, psychologists incorporated the "rational agent" model, which is a basic economic theory, into the model of human social decision making. The social exchange theory (Homans, 1958; Lawler and Thye, 1999; Thibaut and Kelley, 1959) argues that social behaviors largely stem from the desire to maximize the ratio of social rewards to social costs, as is the case for monetary rewards and costs in economic settings. According to this theory, an individual engages in a certain social behavior (e.g., helping others) only when the benefits of doing so outweigh the costs. Importantly, the benefits in such a case take the form not only of material rewards, such as food and money, but also of more abstract rewards, such as social approval from others. This theory provides a base from which to explore complex human social decision making and behaviors in the simple terms of "reward."

In the present study, from among the many possible rewards in human social interactions, we focused on an individual's reputation or the impression of an individual formed by others. The importance of processing one's own reputation in human social decision making has been highlighted by the theoretical research on the evolution of human cooperation (Fehr and Fischbacher, 2003). It has been shown that cooperation in iterated games is significantly affected by the concern for reputation (Kreps and Wilson, 1982), and that an individual's motivation to acquire a good reputation or "image score" (Milinski et al., 2001; Wedekind and Milinski, 2000) might drive cooperation through indirect reciprocity. Social psychological studies have also shown that social approval has a profound impact on everyday decision making (Benabou and Tirole, 2006). The recognition that one has a good reputation can induce a feeling of happiness (i.e., a hedonic component of reward or "liking"), and individuals are often motivated to seek such social approval (i.e., a motivational component of reward or "wanting") according to behavioral evidence. For example, human subjects were motivated to present themselves in a positive manner or to engage in prosocial behaviors when their perception of being watched by others was enhanced (Bateson et al., 2006; Haley and Fessler, 2005; Kurzban et al., 2007; Paulhus, 1984). Thus, although social exchange theory assumes that gaining a good reputation is a reward and ample behavioral evidence supports its significant role in human decision making in a social context, the way in which its reward value is represented in the human brain remains unclear. Furthermore, while previous neuroimaging studies have shown that activities in the reward-related area, the striatum, are modulated by the perception of the moral character (or reputation) of others (Delgado et al., 2005; Singer et al., 2004) and that the striatum is involved in developing the reputation of other players during an economic game (King-Casas et al., 2005), to our knowledge, there has been no study investigating how the brain processes one's own positive reputation. Understanding this process is an essential step in constructing a neural model of human social decision making based on social reward.

A



B

	Monetary Reward Level		
	High Monetary Reward (HMR) block	Low Monetary Reward (LMR) block	No Monetary Reward (NoMR) block
the average amount of money obtained	330 yen (270 - 390 yen)	150 yen (90 - 210 yen)	Non

Figure 1. Experimental Paradigm for the Monetary Reward Experiment

(A) The sequences of events during a single reward trial (top) and during a no-reward trial (bottom). In each reward trial, subjects were asked to choose one card within 2 s, and the outcome of the chosen card (0, 30, or 60 yen) was shown for 1 s. Each block consisted of eight reward or no-reward trials (24 s). In each no-reward trial, subjects were similarly asked to choose one card, but the outcome was always "XXX," indicating no reward.

(B) Study design of the monetary reward experiment. The amount of money each subject could earn in each block was predetermined in order to manipulate the monetary reward level.

The goals of the present study were to investigate whether the acquisition of a good reputation activated reward-related brain areas, specifically the striatum, and, if so, whether this social reward activated the same reward circuitry as monetary rewards, as predicted by social exchange theory. The striatum is known to be involved in reward processing. Striatal neurons were reported to show activity in response to liquid and food rewards in nonhuman primates and were activated by both the anticipation and delivery of the reward (Schultz, 2000; Schultz et al., 2000). Using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), similar findings have been reported in humans: the striatum showed increased activation in response not only to primary rewards such as liquid or food (Berns et al., 2001; McClure et al., 2003; Pagnoni et al., 2002) and sexual stimuli (Arnow et al., 2002; Redoute et al., 2000) but also to money, which is a secondary reward (Breiter et al., 2001; Delgado et al., 2000, 2004; Elliott et al., 2000; Knutson et al., 2000, 2001; Nieuwenhuis et al., 2005; Thut et al., 1997). We therefore predicted that when individuals perceived themselves to have a good reputation among others, the striatum would be activated, and the activated areas would overlap with those activated by monetary rewards.

Nineteen subjects participated in two fMRI experiments (i.e., monetary and social reward experiments) on two separate days. In the monetary reward experiment, the subjects performed a simple gambling task (Figure 1A). In each trial, they were asked to choose one of three cards and were given 0, 30, or 60 yen depending upon the card chosen. Unknown to the subjects, the amount that they could earn in each block of eight trials was predetermined; thus, the monetary reward each subject received during each block was systematically manipulated (Figure 1B). After the subjects completed the monetary reward experiment, they were asked to respond to several personality questionnaires and to introduce themselves in front of a video camera. They were told that others would evaluate them based on their responses to these questionnaires and the video-taped self-introduction and that they would be shown the results in the next fMRI experiment. In the social reward experiment, the same 19 subjects were presented with a picture of themselves and a word or phrase indicating the impression of them formed by others (Figure 2A). However, in reality, the items that they were presented with were predetermined, such that all subjects had the same social reward experience. By systematically grouping six items (into one block) based on desirability ratings provided by another group of participants (n = 33), the level of social reward experienced by subjects in each block was also manipulated. The impressions of other people were also presented (Figure 2B), to exclude the possibility that seeing a positive word per se might be rewarding, as was suggested by a previous study (Hamann and Mao, 2002).

RESULTS

Behavioral Results in the Monetary Reward Experiment

Performance

There were few trials in which the subjects did not press a button to choose a card (an average of 0.7% per subject), and there were no significant differences in the number of failed trials among the three conditions.

Reaction Time

The result of a 1 × 3 (high monetary reward [HMR], low monetary reward [LMR], or no monetary reward [NoMR]) repeated-measures analysis of variance (ANOVA) revealed a significant difference in reaction time among the conditions. Multiple comparisons with a Bonferroni correction showed that the mean reaction time for the HMR condition (490 ms) was slower than that for the NoMR condition (448 ms; $p < 0.05$), whereas the mean reaction time for the LMR condition (451 ms) did not differ significantly from the other two conditions.

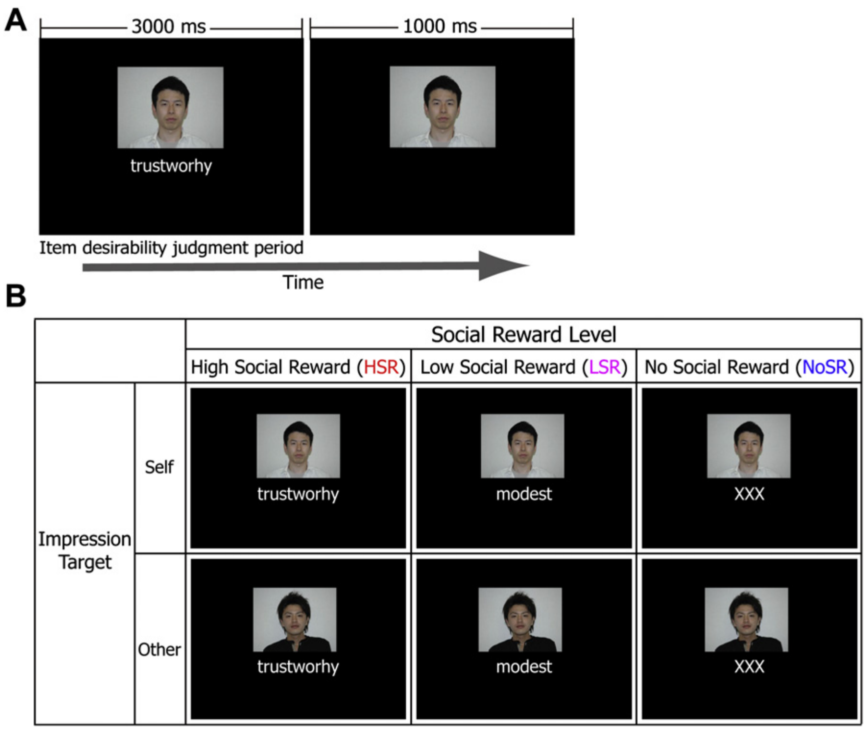


Figure 2. Experimental Paradigm for the Social Reward Experiment

(A) The sequence of events during an HSR-Self trial. In a single HSR-Self trial (4 s), a picture of each subject was shown continuously and an item indicating the impressions of himself/herself made by others was shown below the picture for 3 s, during which each subject was asked to rate the desirability of the item. The item was removed for 1 s until the next item was displayed. Six items were presented in each block (24 s).

(B) Study design of the social reward experiment. A 2 × 3 factorial design was used (plus fixation rest blocks). In HSR blocks, the items presented were all clearly positive and desirable traits, whereas in LSR blocks the items were positive but less desirable, and some negative items (e.g., "selfish") were included. Subjects viewed each item not only as impressions of themselves but also as impressions of other people. Regardless of the impression targets, the subjects were asked to rate the desirability of each item during scanning. In NoSR blocks, "XXX" was presented instead of an item, and the subjects were asked to press a button each time they saw it.

Behavioral Results in the Social Reward Experiment

Performance

There were few trials in which the subjects did not press a button (an average of 1% per subject). The result of a 2 (impression target: Self or Other) × 3 (reward level: high social reward [HSR], low social reward [LSR], or no social reward [NoSR]) repeated-measures ANOVA revealed no significant differences in the number of failed trials among the conditions.

Item Desirability Ratings during and after Scanning and Subjective Happiness Ratings

An analysis of the item desirability judgment on a three-point scale in the fMRI scanner revealed that, as predicted, regardless of whether the items were presented as impressions of oneself or others, those in the HSR conditions were rated as significantly more desirable than those in the LSR conditions (HSR versus LSR in Self and Other conditions, both p values <0.001, paired t tests; Figure 3A). When these ratings were submitted to a 2 (impression target: Self or Other) × 2 (reward level: HSR or LSR) repeated-measures ANOVA, the main effects of both the impression target and the reward level were significant (both p values <0.001), and their interaction was also significant ($p < 0.01$). Two paired t tests (Self versus Other in each of the HSR and LSR conditions) showed that, although subjects were presented with the same items between the Self and Other conditions, they tended to rate them as significantly less desirable when they were presented as impressions of themselves; this tendency was somewhat stronger for the LSR condition ($p < 0.01$) than the HSR condition ($p < 0.05$). Notably, however, the mean ratings of the HSR items in the Self and Other conditions were close to the maximum value (i.e., three), indicating a ceiling effect, and when a paired-sample Wilcoxon test was used, the difference between the HSR-Self and HSR-Other conditions was not significant ($p = 0.067$). The desirability ratings of the same items after fMRI scanning with a seven-point scale also showed that subjects rated items in the HSR condition as significantly more desirable than those in the LSR condition (paired t test, $p < 0.001$; Figure 3B).

An analysis of happiness ratings revealed that subjects felt significantly happier when seeing impressions of themselves in the HSR condition than in the LSR condition (paired t test, $p < 0.001$; Figure 3C). Thus, as we predicted, the subjects rated items in the HSR condition as more desirable both during and after scanning and felt much happier in the HSR-Self condition than the LSR-Self condition, indicating that our manipulation of the social reward level was successful.

Reaction Time

The results of a 2 (impression target; Self or Other) × 3 (reward level; HSR, LSR, or NoSR) repeated-measures ANOVA of reaction time revealed significant main effects of both impression target ($p < 0.01$) and reward level ($p < 0.001$) as well as their interaction ($p < 0.05$; Figure 3D). The mean reaction time in the NoSR condition (681 ms) was the fastest, and the subjects were slowest to respond in the LSR condition (1337 ms), probably because of ambiguity regarding the desirability of the items used in this condition. The reaction time for the HSR condition fell between the two, with a mean of 1124 ms, and the differences among the three conditions were all significant (multiple comparisons with a Bonferroni correction, all p values <0.001). When conditions with the same reward level were directly compared between Self versus Other using a paired t test, the mean reaction times for the Self condition were slower than for the Other condition when the social reward level was high ($p < 0.01$) or low ($p < 0.05$), while there was no significant difference between the Self versus Other conditions in the NoSR condition ($p = 0.48$).

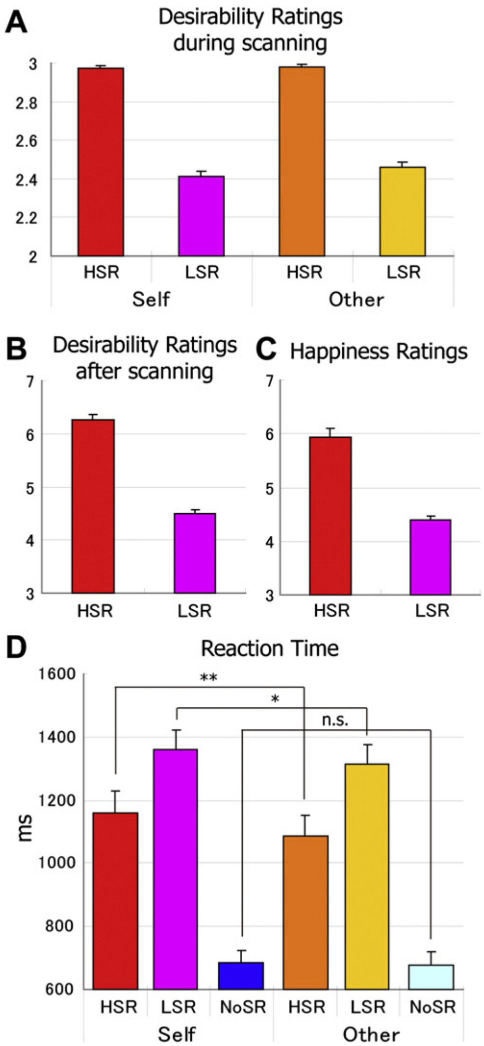


Figure 3. Behavioral Assessment of the Validity of the Social Reward Level Manipulation and Mean Reaction Times

(A) Item desirability ratings for HSR and LSR blocks in both the Self and Other conditions during fMRI scanning. The subjects used a three-point scale (1 = undesirable, 2 = neutral, and 3 = desirable).

(B) Desirability ratings for the same items after scanning. The subjects used a seven-point scale (1 = highly undesirable, 4 = neutral, and 7 = highly desirable).

(C) Subjective judgment of how happy the subjects felt upon seeing each item as an impressions of themselves formed by others, using a seven-point scale (1 = very unhappy, 4 = neutral, and 7 = very happy).

(D) Mean reaction times for all conditions in the social reward experiment. Subjects judged the desirability of each item presented in the HSR and LSR conditions and pressed a button each time "XXX" was presented in the NoSR condition.

Error bars indicate the standard error of the mean (SEM). $^{**}p < 0.01$, $^{*}p < 0.05$ (paired t test, two-tailed).

Imaging Results in the Monetary Reward Experiment

To broadly depict the brain areas related to monetary reward, we contrasted the HMR condition with the NoMR condition. This revealed significant activations in several brain areas, notably the striatum, insula, midbrain, and orbitofrontal cortex (OFC) (see Figure S1 available online), which was in agreement with previous findings on monetary reward processing (Breiter et al., 2001; Delgado et al., 2000, 2004; Elliott et al., 2000; Knutson et al., 2000, 2001; Nieuwenhuis et al., 2005; Thut et al., 1997). The areas activated in this contrast are shown in Table S1. The subsequent analyses of the social reward experiment used the contrast of HMR versus NoMR as a mask to explore the overlap between monetary and social rewards.

Imaging Results in the Social Reward Experiment

To specify the brain areas involved in the processing of social reward, we used the interaction contrast of (Self – Other) (HSR – NoSR). This was intended to identify the areas where activity was specifically enhanced when a high social reward was directed toward the self. This contrast was explored within the above-mentioned monetary reward-related areas. As predicted, we found significant activations in the striatum (Figure 4 and Table 1), indicating that social reward shares the same neural basis as monetary reward (all of the areas activated in this interaction contrast without the mask of the monetary reward experiment are listed in Table S2). Besides the striatum, only the thalamus and cerebellum showed common activations for both types of rewards. Within the striatum, the commonly activated areas included the bilateral caudate nucleus and bilateral putamen (Figure 5A). In addition, the activated areas in the main effects of self face (the Self – Other contrast) and other face (the Other – Self contrast) are listed in Table S3.

The percent signal changes were extracted from the peak voxels in these four regions of the striatum for all conditions of the social reward and monetary reward experiments. Initially, using only the data from the social reward experiment, four separate 2 (impression target: Self or Other) × 3 (reward level: HSR, LSR, or NoSR) repeated-measures ANOVAs were conducted. As predicted, we found significant interactions in all four regions (all p values <0.05), indicating that the positivity of the items alone (i.e., seeing positive words per se) could not explain these results. Furthermore, within each region, the three social reward levels for the Self conditions were compared with the three Monetary Reward levels by 2 (reward types: Monetary or Social) × 3 (reward level: high reward, low reward, or no reward) repeated-measures ANOVAs. Although the interactions were significant in the caudate nucleus and putamen in the right hemisphere (both p values <0.05), the corresponding regions in the left hemisphere both showed nonsignificant interactions (both p values >0.41) and highly significant main effects of reward level (both p values <0.001; Figure 5B). These results suggested that social reward was processed in a similar manner to monetary reward, especially in the left caudate nucleus and putamen.

DISCUSSION

The goals of the present study were to determine neurophysiologically whether a good reputation has a reward value and, if so, to verify whether this important social reward is processed in a neurally similar manner to monetary rewards. Our experimental paradigm was carefully designed so that subjects believed that they were being informed of their own reputation as

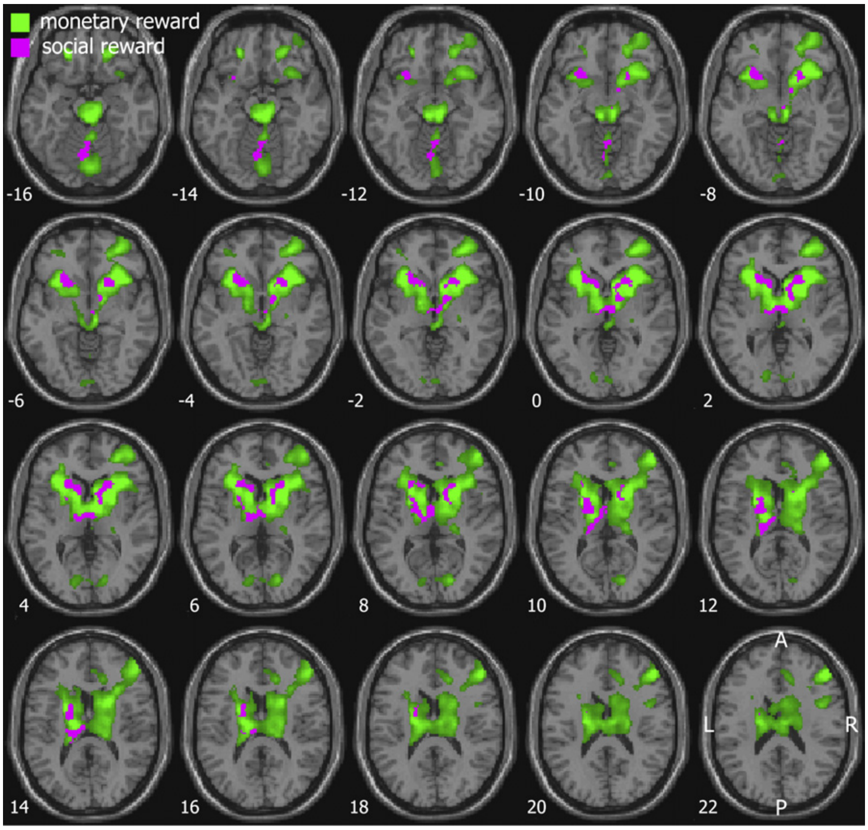


Figure 4. Axial Slices Showing Areas Commonly Activated by Monetary and Social Rewards

In the slices (2 mm thick, z = −16 to 22), areas activated by monetary rewards are shown in green, and areas activated by social reward are shown in magenta. The contrast of HMR versus NoMR was used for the monetary reward activation map. The interaction contrast of (Self – Other) (HSR – NoSR) masked by (HMR – NoMR) was used for the social reward activation map. For both contrasts, the statistical threshold was $p < 0.005$ uncorrected for multiple comparisons for height, and cluster $p < 0.05$ corrected for multiple comparisons.

formed by other people, while in reality the level of the social reward was systematically manipulated. Our reaction-time data in the social reward experiment first confirmed the significance of personal reputation, as suggested by theoretical research (Fehr and Fischbacher, 2003). Although the impression target (Self or Other) was irrelevant to the tasks performed during scanning (i.e., a desirability judgment task in the HSR and LSR conditions and a simple button press task in the NoSR condition), the subjects' reaction times were significantly influenced by it. The task difficulty could not explain the differences in reaction time (as the tasks the subjects performed and the items used in the Self and Other conditions were identical); this suggested that the subjects differentiated their own and others' reputations and could be interpreted as showing that one's own reputation as formed by others automatically captured a subject's attention and induced emotional reactions, which in turn disrupted his or her performance (delayed reaction time) on the item desirability judgment task.

Table 1. Areas Commonly Activated by Both Types of Reward

Location	Side	MNI Coordinate x	y	z	Z	Voxel	Cluster p
(Self – Other) (HSR – NoSR)							
Striatum/thalamus						866	<0.001
Putamen	R	22	16	−4	4.08		
Caudate nucleus	R	12	12	4	2.95		
Thalamus	L	−18	−6	12	3.61		
Thalamus	R	4	−14	0	3.89		
Striatum						361	0.031
Putamen	L	−22	20	−2	3.60		
Caudate nucleus	L	−8	14	2	3.52		
Cerebellum	R	10	−52	−34	3.29	451	0.012
Cerebellum	L	−4	−64	−12	3.90		

The interaction contrast of (Self − Other) (HSR − NoSR) was explored within the monetary reward-related areas (HMR − NoMR). The statistical threshold for both contrasts was $p < 0.005$ uncorrected for height and cluster $p < 0.05$ corrected for multiple comparisons.

We demonstrated that previously reported reward-related areas, such as the striatum, insula, midbrain, and OFC, were activated in the monetary reward experiment. Our fMRI data in the social reward experiment showed that, as predicted, the acquisition of a good reputation activated the striatum and that the activated areas overlapped with those activated by monetary rewards (HMR versus NoMR). Furthermore, despite differences in the experimental paradigm between monetary and social experiments (e.g., the fact that contingency was present between the button press response and the outcome in the monetary reward experiment but not the social reward experiment), an analysis of the percent signal changes in each region of the striatum indicated that both types of reward were characterized by similar activation patterns, especially in the left striatum, indicating that the reward value of both money and a good reputation is represented in this region.

The activations of the striatum in response to one's own reputation in the present study was interesting because the social approval gained during the experiment was from unfamiliar individuals whom the subjects had never met before (this was explicitly verified before the social reward experiment for all subjects). Thus, there had been no prior opportunity to create an association between social approval specifically from these people and other rewards. Although this suggests the possibility that a good reputation might be a primary reward, we believe that this is unlikely, as understanding one's own reputation requires higher

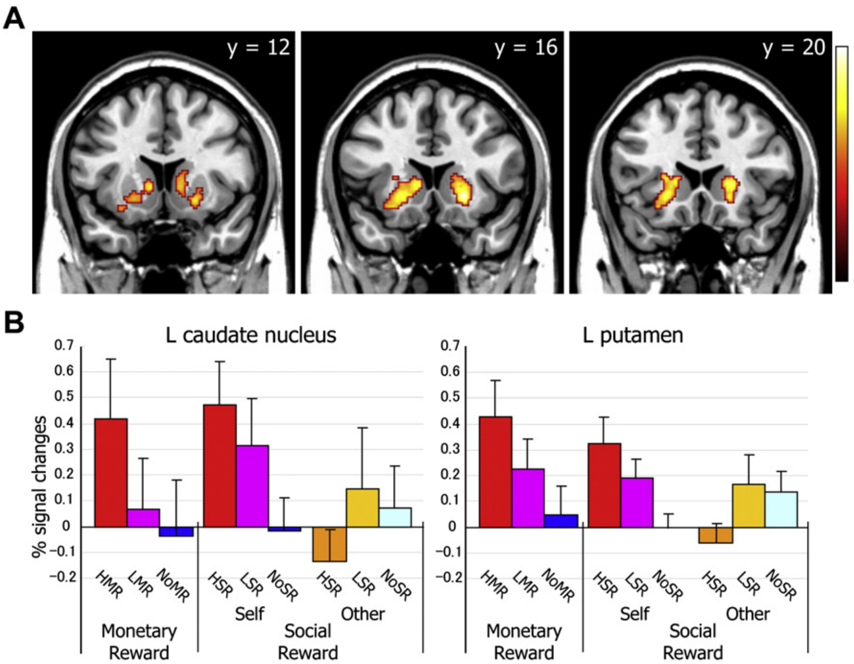


Figure 5. Activation Patterns in Areas Commonly Activated by Social and Monetary Rewards in the Striatum

(A) Coronal slices (4 mm thick, y = 12–20) showing significant activations in the striatum for both types of reward. The caudate nucleus and putamen were activated bilaterally. The scale shows the t values.

(B) Bar graphs indicating the task-related activation (percent signal change) in the left caudate nucleus [−8 14 2] and left putamen [−22 20 −2] for all three conditions during the monetary reward experiment and all six conditions during the social reward experiments. Error bars indicate the SEM.

cognitive functions, such as a theory of mind (see below). Instead, our findings illustrate how consistently social approval from other people is associated with other rewards during healthy development and that, through such associations, a good reputation might function as a conditioned stimulus (i.e., a secondary reinforcer) for typically developing healthy individuals.

By directly contrasting the brain activities of the same subjects in relation to the delivery of social and monetary rewards, our results clearly show that social approval shares the same neural basis as monetary rewards, thus providing strong support for the idea of a ''common neural currency'' of reward (Montague and Berns, 2002). Furthermore, our findings indicated that a good reputation is another example of a higher cognitive reward. Because the question was initially raised of whether higher cognitive rewards, such as beauty, social joy, and love, share the same neural mechanisms and structures as more basic rewards (Berridge, 2003; Schultz, 2000), several neuroimaging studies have reported activation in reward-related brain areas in response to rewards, such as humor (Mobbs et al., 2003), attractive faces (Aharon et al., 2001), maternal and romantic love (Bartels and Zeki, 2004), emotionally positive words (Hamann and Mao, 2002), beautiful paintings (Kawabata and Zeki, 2004), and pleasant music (Blood and Zatorre, 2001; Blood et al., 1999). However, among such cognitive rewards, a good reputation is of special importance because it is highly relevant to everyday social decision making.

The present findings indicate that the social reward of a good reputation should be incorporated into the neural model of human decision making in a similar manner to monetary rewards. Previous neuroimaging studies on human decision making in social situations used economic games as an experimental paradigm, in which subjects exchanged money with each other (de Quervain et al., 2004; King-Casas et al., 2005; McCabe et al., 2001; Rilling et al., 2002; Sanfey et al., 2003). However, as suggested by social exchange theory, in real social interactions individuals exchange not only material goods, such as money, but also nonmaterial goods (e.g., exchanging help for approval or a good reputation). Moreover, even during monetary exchange in an economics-based game, how one player is viewed by others (i.e., reputation) is an important factor influencing cooperation rates (Fehr and Fischbacher, 2003). Thus, in accordance with the argument of Montague and Berns, our findings suggest that the striatum plays a pivotal role in converting different types of rewarding stimuli, specifically money and good reputation, into a ''common currency'' (Montague and Berns, 2002) that is used to value each possible action on a common scale and to select the best option in a given social situation. This could explain why people sometimes engage in prosocial behaviors while giving up monetary benefits (Bateson et al., 2006; Haley and Fessler, 2005; Kurzban et al., 2007).

Although the present study focused on the similarities between monetary and social rewards, differences in brain activations between the two should be noted. Although variations in the paradigms of our two experiments (e.g., a difference in action contingency) made it difficult to authenticate differences in the neural representation of the two types of reward, the medial prefrontal cortex (mPFC) is one brain area that might be uniquely activated by social rewards. The mPFC has been implicated in higher cognitive functions, such as theory of mind (Gallagher and Frith, 2003), self-reflection (Johnson et al., 2002; Kelley et al., 2002), and reflected self-knowledge (Ochsner et al., 2005), and could be essential for processing one's own reputation (either good or bad), because this involves forming a representation of how other persons represent us (Amodio and Frith, 2006). In accordance with this idea, our data showed mPFC involvement in the representation of self-reputation regardless of the reward level (Figure 6), a pattern which greatly differed from that related to monetary rewards. This result was consistent with a previous study that showed that the mPFC was activated when trait adjectives were judged to be self-descriptive regardless of trait valence (Moran et al., 2006). However, an important difference was that, while their focus was on the self-attribution of personality traits, our study showed mPFC involvement in

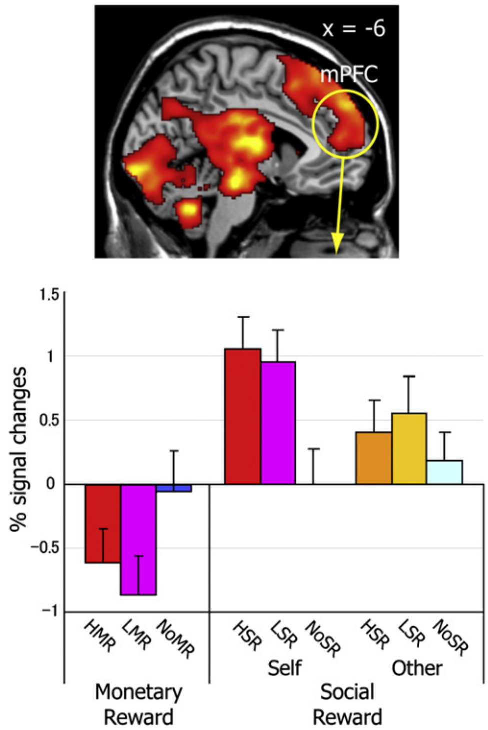


Figure 6. Activation Patterns in mPFC [−6 50 14]
Group activation map for the ([HSR-Self + LSR-Self] − 2 NoSR-Self) contrast ($p < 0.005$ uncorrected for height, and cluster $p < 0.05$ corrected for multiple comparisons). mPFC activity was significantly enhanced when a subject's own reputation was presented (regardless of the reward level) (top). Percent signal changes extracted from the mPFC during the social reward and monetary reward experiments (bottom). Error bars indicate the SEM.

self-reflection in the context of attributions made by others. Thus, the present study provides preliminary evidence suggesting that the neural basis of social reward processing involves the valuation process in striatal regions and the representation of one's own reputation in the mPFC.

While the present study has clearly contributed to the neural basis of social reward processing, several issues will need to be resolved in order to create a comprehensive neural model of social decision making. First, following on from the present findings, the next question that should be addressed is whether the striatum activity really predicts prosocial behaviors. This is an important issue for testing an integrated model of human social behavior (from brain activity to actual behaviors). Although predicting human social behaviors from patterns of brain activity might seem unrealistic, it was previously demonstrated in the context of economic behaviors that activities in the ventral striatum, especially the nucleus accumbens (which represented product preference), insula, and mesial prefrontal cortex (which represented price differentials) predicted subsequent economic decision making (i.e., whether to purchase a certain product) (Knutson et al., 2007). Second, although we focused on the positive reward value of a good reputation, how and where the negative reward value of a bad reputation is represented remains to be explored. One candidate area is the insula. Insula has been suggested to play a role in loss prediction (Paulus and Stein, 2006), and this view has been supported by studies involving monetary rewards (Knutson et al., 2007; Kuhnen and Knutson, 2005). Another candidate area is the lateral OFC, which is activated by a range of punishment stimuli (Kringelbach and Rolls, 2004). Third, although the neurotransmitter dopamine is well known to play a pivotal role in reward processing in animals (Bayer and Glimcher, 2005; Schultz, 2002; Wise, 2004), it is yet to be shown which neurotransmitter functions in social reward processing in humans. PET studies revealed that levels of endogenous dopamine in the human striatum were implicated in food motivation (Volkow et al., 2002), playing a video game for monetary reward (Koepp et al., 1998), and playing a card selection task for monetary reward (Zald et al., 2004). Its involvement in processing monetary reward in humans was also demonstrated in a study combining pharmacological and imaging techniques (Pessiglione et al., 2006). Taken together, these findings suggest that the neurotransmitter dopamine might also play a role in processing social reward.

Furthermore, because the influence of social reward can be seen in our everyday social interactions, the present study highlights several interesting areas for future research in various disciplines. First, social reward is also of interest in terms of its role in learning, and the present findings have implications for our understanding of the neural basis of children's moral development. Along with "wanting" and "liking," "learning" is a basic component of reward (Berridge and Robinson, 2003). Moreover, social rewards such as praise from parents, friends, and teachers, seem to be the most important reinforcers during a child's upbringing and learning of moral values (Bandura, 1977). Thus, building on previous knowledge of reinforcement learning and monetary rewards, future studies might identify the most efficient method of educating children through social rewards. Second, it would also be interesting to address individual and cultural differences in brain activity in response to social rewards, such as how people with different self-enhancement tendencies (Kwan et al., 2004) differ in their brain responses to evaluations made by others. These approaches should improve our understanding of human personality and cultural differences in various psychological tendencies (Markus and Kitayama, 1991).

As a final point, a methodological limitation of the present study should be noted. Because our study was an initial attempt to test whether good reputation activates the reward-related brain areas beyond the possible reward value of positive words per se (Hamann and Mao, 2002), we employed a block design, which was the most efficient way in which to detect activation (Friston et al., 1999b). For the monetary reward, evidence has accumulated indicating that activity in the striatum varies as a linear function of expected reward (e.g., Preuschoff et al., 2006). Although our results showed not only that the striatum was activated by both monetary and social rewards but also that the striatum was sensitive to the magnitude of both types of reward, it will be necessary to establish the reward magnitude sensitivity in detail on a trial-by-trial basis using an event-related design, in order to further support the common currency view of neural valuation.

In conclusion, the current study examined the neural basis of processing the reward value of a good reputation. To fully understand how the human brain works in social interactions or the social brain (Brothers, 1990), it is not sufficient to investigate brain activity in subjects while they perceive social stimuli (e.g., the face, gaze, and thoughts of others); yet, the majority of human imaging studies on social cognition have adopted this approach (for a review, see Adolphs, 2003). In real social interactions, each participant is both a perceive (i.e., a target of the perception of others) and a perceiver, and how individuals are viewed by others has considerable influence on their behaviors. Our findings indicate that the social reward of a good reputation in the eyes of others is processed in an anatomically and functionally similar manner to monetary rewards, and these results represent an essential step toward a complete neural understanding of human social behaviors.

EXPERIMENTAL PROCEDURES

Subjects

In total, 23 healthy right-handed subjects participated in the study. The reported analyses were based on 19 subjects (9 male; mean age = 21.6 ± 1.5 years). After the 23 subjects participated in the monetary reward experiment, they were asked to take part in the social reward experiment. After the general procedure of the second experiment was explained, 21 of the subjects agreed to participate and returned to complete the social reward experiment after an average of 15 days (range = 5–45 days). Two subjects were further excluded from the analyses because they indicated during the interview after the social reward experiment that they did not believe their impressions had been evaluated by the other people (they both reported that the impressions presented during the scanning were "too good"). None of the subjects had a history of neurological or psychiatric illness. All subjects gave written informed consent for participation, and the study was approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan.

Experimental Paradigm in the Monetary Reward Experiment

In the monetary reward experiment, the subjects performed a simple gambling task, as described in Figure 1A, which was a block-design version of the task used in a previous study (Nieuwenhuis et al., 2005). They were encouraged to try to earn as much money as possible and were told that one session would be randomly chosen at the end of the experiment and that their earnings in that session would be given to them. In each trial (3 s), the subjects were presented with three cards labeled as "A," "B," or "C" and were asked to choose one card within 2 s by pressing a button with the right index, middle, or ring finger, which spatially corresponded to the location of the cards. Soon after the button press, the chosen card was highlighted with a thick white border, and the outcome was displayed for 1 s. If the subject did not press any button within the choice period (2 s), the card they had chosen in one previous trial was automatically chosen, and its outcome was displayed.

When the letters on each card were written in red, the trial was a "reward trial" in which each card was randomly associated with 0, 30, or 60 yen. Each block consisted of eight trials (24 s). However, unknown to the subjects, the total reward that they could earn in each block was predetermined (Figure 1B). In the HMR blocks, the subjects earned an average of 330 yen each (range = 270–390 yen), which was consistently higher than the expected value of the eight reward trials (240 yen). In the LMR blocks, the subjects earned an average of 150 yen each (range = 90–210 yen), which was consistently lower than the expected value (note that 1 US dollar is equal to approximately 120 Japanese yen). The subjects also participated in NoMR trials, indicated by blue letters, in which they chose one card, but the outcome presented was always "XXX," indicating that there was no reward. A NoMR block or a fixation rest block (also 24 s) was always inserted between two reward blocks, so that the start and end of the reward manipulations could be clearly defined. For half of the subjects, the colors (red and blue) used for the reward and nonreward trials were switched. All subjects completed a 2 min practice task before scanning. During scanning, they performed a total of four 8 min sessions (20 blocks for each of the four conditions [HMR, LMR, NoMR, and fixation rest]) within which the HMR and LMR blocks were ordered differently, and the order of these four sessions was counterbalanced across subjects. All subjects were paid a fixed amount for their participation at the end of the experiment.

Experimental Paradigm in the Social Reward Experiment

The social reward experiment was divided into two parts performed on two separate days: a self-introduction phase and a social reward acquisition phase.

In the self-introduction phase, after the subjects finished the monetary reward experiment, they were asked to complete a survey questionnaire booklet that included several personality questionnaires and some open-ended questions. The questionnaires included the Social Desirability Scale (Crowne and Marlowe, 1960), the Impression Management scale, a subscale of the Balanced Inventory of Desirable Responding measure (Paulhus, 1984), the Rosenberg Self-Esteem Scale (Rosengerg, 1965), and the NEO Five Factor Inventory (NEO-FFI) (Costa and McCrae, 1989). The open-ended questions were as follows: "What do you do in your free time"? "Briefly describe your own personality." "What is your goal for the future"? And "Please pick one problem that modern Japanese society faces and briefly state your opinion of that issue." After the subjects had completed the booklets, they were asked to introduce themselves for at least 1 min while being video-recorded. During this self-introductory talk in front of a video camera, the subjects were instructed to say anything that they liked about themselves. Digital photographs were also taken of the subjects and were used in the subsequent social reward experiment. The subjects were told that eight people (four male and four female) would form impressions of them based on their answers to the personality questionnaires and the video-taped self-introduction, by selecting personality trait adjectives. The subjects were asked to return to participate in the social reward experiment some days later (individually scheduled).

In the social reward acquisition phase, the subjects were presented with the results of the impression evaluations made during scanning (Figure 2). In reality, the items that they were presented with were predetermined, and the level of social reward experienced in each block was systematically manipulated. For the items used in the HSR and LSR conditions, we initially picked 96 items from an adjective list (Anderson, 1968), and a sample of 33 subjects (ten female; mean age = 23.5 ± 3.7 years) rated the desirability of these items (after being translated into Japanese) using a nine-point scale (1 = highly undesirable, 5 = neutral, and 9 = highly desirable). After excluding some items, 84 were selected for the fMRI experiment (42 items each for the HSR and LSR conditions). The mean desirability rating of the items selected for the HSR condition was 7.52 and that for the LSR condition was 5.55; this difference was highly significant (paired t test, $p < 0.001$). The items in the LSR condition were rated higher than 5 (the midpoint), indicating that most of items were positive, but were less desirable than the items in the HSR condition. Furthermore, eight negative items (with a mean desirability rating of less than 4) were also included only in the LSR condition, in order to maintain the impression that the subjects were being evaluated by others and also to maintain the attention of the subjects by making their evaluations less predictable. None of the LSR blocks contained more than one negative item. See Table S4 for examples of the items used in each condition.

To make the results of the impression evaluation appear more believable and meaningful, all subjects were shown pictures of eight unfamiliar individuals and were told that they would be evaluated by these people and would meet and engage in tasks with them after scanning. Furthermore, each subject was told that he or she would not be evaluated by these people individually, but rather by two groups of four evaluators. Thirty of the 42 items for both the HSR and LSR conditions were presented twice, as they were said to have been commonly and independently selected by both groups of evaluators. Thus, the impressions the subjects were presented with were consistent both among individual evaluators and among the two groups of four evaluators.

To rule out the possibility that seeing positive words per se might be rewarding, we included conditions in which the subjects viewed the same items but were told that the items represented the impressions of people other than themselves. Images of six unfamiliar people (three male and three female) were used in these conditions, and the subjects were told that the eight assessors were also evaluating these individuals. Each image of the six individuals was equally associated with the HSR and LSR conditions. Regardless of the impression targets, the subjects were asked to rate the desirability of each item presented during scanning using a three-point scale with the index, middle, or ring finger of the right hand and to press a button with the right index finger each time "XXX" was presented in an NoSR trial (the responses for one subject were not collected due to a technical fault). A fixation rest block was also included, during which only a fixation cross was presented at the center of the screen for 24 s. The HSR-Self and LSR-Self blocks (and the HSR-Other and LSR-Other block) were never presented in succession, so the start and end of the reward level manipulations for each impression target were clearly defined. All subjects completed a 2 min practice task before scanning, in which no picture was included, and the subjects were asked to evaluate the desirability of each item presented (these items were not used in the main paradigm). During scanning, the subjects performed a total of four sessions (each lasting 8 min 24 s, with 12 blocks for each of 7 conditions including fixation rest blocks). Within each session, the blocks were ordered differently, and the order of the four sessions was counterbalanced across subjects. Also, while keeping the order of item presentation constant within each session, the images of the subjects themselves and those of six other people were switched for half of the subjects.

After scanning, the subjects completed a postexperimental questionnaire in which they were asked to rate the subjective happiness they felt when each of 84 items was presented as an impression of themselves using a seven-point scale (1 = very unhappy, 4 = neutral, and 7 = very happy). The subjects also rated the desirability of each item again, but this time using a seven-point scale (1 = highly undesirable, 4 = neutral, and 7 = highly desirable). Finally, the subjects were interviewed to ascertain whether they had any doubt about the impressions they saw during scanning. At the end of the social reward experiment, all subjects were fully debriefed and paid a fixed amount for their participation.

All of the stimuli for the monetary and social reward experiments were prepared and presented using Presentation software (Neurobehavioral Systems, CA) on a microcomputer (Dimension 8200, Dell Computer Co., TX). The visual stimuli were projected onto a half-transparent viewing screen using a liquid crystal display (LCD) projector (DLA-M200L, Victor, Yokohama, Japan). The screen was located behind the head coil, and the subjects viewed the stimuli through a mirror. All of the stimuli for the tasks were written in Japanese and presented as white letters against a black background.

Imaging Acquisition and Analysis

Images were acquired using a 3 Tesla MR imager (Allegra, Siemens, Erlangen, Germany). For functional imaging during the sessions in both experiments, interleaved T2*-weighted gradient-echo echo-planar imaging (EPI) sequences were used to produce 44 continuous 3 mm thick transaxial slices covering the entire cerebrum and cerebellum (repetition time [TR] = 3000 ms; echo time [TE] = 25 ms; flip angle [FA] = 85°; field of view [FOV] = 192 mm; 64 × 64 matrix; voxel dimensions = 3.0 × 3.0 × 3.0 mm). A high-resolution anatomical T1-weighted image was also acquired by magnetization-prepared rapid gradient-echo (MPRAGE) imaging (TR = 2.5 s; TE = 4.38 ms; FA = 8°; 256 × 256 matrix; 192 slices; voxel dimensions = 0.75 × 0.75 × 1 mm) for each subject.

After discarding the first six volumes to allow for stabilization of the magnetization, the remaining 160 volumes per session in the monetary reward experiment (a total of 640 volumes per subject for four sessions) and 168 volumes per session in the social reward experiment (a total of 672 volumes per subject for four sessions) were used for analysis. The data were analyzed using Statistical Parametric Mapping 5 (SPM5, Wellcome Department of Cognitive Neurology, London, UK) software implemented in Matlab 7.1 (Mathworks, Sherborn, MA). Head motion was corrected using the realignment program of SPM5. Head motion was not correlated with the task. Following realignment, the volumes were normalized to the Montreal Neurological Institute (MNI) space (Evans et al., 1994) using a transformation matrix obtained from the normalization process of the first EPI image of each individual subject to the EPI template. The normalized fMRI data were spatially smoothed with a Gaussian kernel of 8 mm (full-width at half-maximum) in the x, y, and z axes.

Statistical Analysis

Statistical analysis was conducted at two levels. First, the individual task-related activation was evaluated. Second, the summary data for each individual were incorporated into a second-level analysis using a random-effect model (Friston et al., 1999a) to make inferences at a population level.

In the individual analysis, the signal was scaled proportionally by setting the whole-brain mean value to 100 arbitrary units. The signal time course for each subject was modeled with a general linear model. Regressors of interest (condition effects) were generated using a box-car function convolved with a hemodynamic-response function. Regressors that were of no interest, such as the session effect, and high-pass filtering (128 s) were also included. To test hypotheses about regionally specific effects, the estimates for each model parameter were compared with the linear contrasts shown in Table S5 (monetary reward experiment) and Table S6 (social reward experiment).

The weighted sum of the parameters estimated in the individual analysis consisted of "contrast" images, which were used for the group analyses. The contrast images obtained by individual analysis represented the normalized increment of the fMRI signal for each subject. The SPM{t} and SPM{Z} for the contrast images were created as described above. Significant signal changes for each contrast were assessed by means of t statistics on a voxel-by-voxel basis. The threshold for the SPM{Z} of group analyses was set at $p < 0.005$ (uncorrected for multiple comparisons) for height, and cluster $p < 0.05$ (corrected for multiple comparisons).

SUPPLEMENTAL DATA

The Supplemental Data for this article, including a figure and tables, can be found online at http://www.neuron.org/cgi/content/full/58/2/284/DC1/.

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