Title: Neural basis of decision-making guided by emotional outcomes

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Abstract

Emotional events resulting from a choice influence an individual’s subsequent decision-making. Although the relationship between emotion and decision-making has been widely discussed, previous studies have mainly investigated decision outcomes that can easily be mapped to reward and punishment, including monetary gain/loss, gustatory stimuli, and pain. These studies regard emotion as a modulator of decision-making that can be made rationally in the absence of emotions. In our daily lives, however, we often encounter various emotional events that affect decisions by themselves, and mapping the events to a reward or punishment is often not straightforward. In this study, we investigated the neural substrates of how such emotional decision outcomes affect subsequent decision-making. By using functional magnetic resonance imaging (fMRI), we measured brain activities of humans during a stochastic decision-making task in which various emotional pictures were presented as decision outcomes. We found that pleasant pictures differentially activated the midbrain, the fusiform gyrus, and the parahippocampal gyrus, whereas unpleasant pictures differentially activated the ventral striatum, compared to neutral pictures. We assumed that the emotional decision outcomes affect the subsequent decision by updating the value of the options, a process modeled by reinforcement learning models, and that the
brain regions representing the prediction error that drives the reinforcement learning
are involved in guiding subsequent decisions. We found that some regions of the
striatum and the insula were separately correlated with the prediction error for either
pleasant pictures or unpleasant pictures, whereas the precuneus was correlated with
prediction errors for both pleasant and unpleasant pictures.

Keywords: Emotional pictures; Reinforcement learning; Valence; Striatum; Insula
Introduction

Emotion influences decision-making in humans and other animals. The process underlying this influence has generated interest because it can explain the various aspects of decision-making that are regarded as either rational or irrational (Loewenstein et al., 2001; Bechara et al., 2005; Cohen, 2005; Shiv et al., 2005; Seymour and Dolan, 2008). Previous studies have used monetary gain/loss or gustatory stimuli (e.g., juice) as decision outcomes that guide subsequent decision-making. The value or magnitude of these stimuli can be manipulated and quantified in an experimental environment relatively easily. However, such reward or punishment not only induces an emotional response but can also be objectively quantified: thus, it can be subject to the rational calculations of the decision-maker.

To address the pure impact of emotion induced by a decision outcome, we discuss the decision-making task in which the decision outcomes induce emotion with values that are difficult to compute in a straightforward manner. Emotional pictures have been used for investigating behavioral, physiological or neural reactions to emotional events (e.g., Lang et al., 1998a; Bradley et al., 2001). For example, brain activities during the passive viewing of emotional pictures have been studied using imaging techniques, and studies have found that emotional (pleasant and unpleasant) pictures activate several brain
regions, such as the occipital cortex, medial prefrontal cortex, thalamus, hypothalamus and midbrain, to a greater extent than neutral pictures (Lane et al., 1997; Lang et al., 1998).

In the main task of the current study, the emotional pictures and neutral pictures were presented as outcomes of choice, and the valence of the pictures was stochastically contingent on the participants' choices (Katahira et al., 2011, 2014). The neural basis of decision-making and associative learning based on reward or punishment have been intensively studied, and several brain regions, such as the striatum and the insula, are known to be involved in the learning processes (O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; O'Doherty et al., 2004; Seymour et al., 2004, 2005; Tanaka et al., 2004). We hypothesized that emotional pictures recruit the striatum and the insula in contexts in which the participants have to learn and make decisions.

According to the reinforcement learning theory, the reward prediction error that quantifies the discrepancy between what was expected and what is actually observed is a key variable that drives learning (Niv et al., 2005; Niv and Schoenbaum, 2008; Niv, 2009). Numerous studies have reported that the blood oxygenation level-dependent (BOLD) signal in several regions in the striatum and the insula is correlated with the prediction error (O'Doherty et al., 2003b; Seymour et al., 2004; Daw et al., 2006; Daw,
We derived the prediction error signal by fitting the reinforcement learning model to the subjects' behavioral data. We assumed that the emotional decision outcomes affected subsequent decisions by updating the values of the options and that the brain regions representing the prediction error that drives the reinforcement learning play a pivotal role in emotion-guided decision-making.

**Materials and Methods**

**Participants**

Thirty healthy volunteers participated in this study. All participants were neurologically normal and had normal or corrected-to-normal vision. Data from five participants were excluded because of incomplete data acquisition (one participant), excessive head motion (one participant), or poor behavioral performance that did not exceed the chance level (two participants). The data from the 25 remaining participants (13 males and 12 females aged 24.44 ± 5.28 years, mean ± SD) were analyzed. All participants provided informed consent according to the procedures approved by the RIKEN Ethics Committee and the RIKEN Functional MRI Safety and Ethics Committee.
Behavioral task

The task consisted of 80 decision-picture trials, 80 decision-money trials, and 40 no-decision-picture trials (Figure 1). The no-decision-picture trial was a control trial used to investigate the effects of choice (in decision-picture trials) on the response to picture stimuli. On the two decision trial types, participants were faced with the choice between two possible actions that were represented by affectively neutral fractal images (cues). Two different cue sets were assigned to two decision trial types. Then, on the decision-picture trial, a picture with its valence (pleasant, neutral, or unpleasant) dependent on the choice was presented. On the decision-money trial, a resulting monetary outcome (+500 yen, 0 yen, or -500 yen) was presented. On the no-decision-picture trials, two cues, marked with “?” and “×,” were first presented. The participants were asked to press the button corresponding to the position of “?”. Then, a picture whose valence was randomly determined was presented. All three trial types were pseudo-randomly inter-mixed throughout the task. The choice-outcome contingency (in the decision-picture trials and the money trials) was as follows. For each decision trial, one fractal image was an “advantageous” or “optimal” option, which was associated with a pleasant picture/+500 yen with a probability of 65%, a neutral picture/0 yen with a probability of 20%, or an unpleasant picture/-500 yen with a
probability of 15%. Another fractal image was a “disadvantageous” or “non-optimal”
option, which was associated with a pleasant picture/+500 yen with a probability of 15 %,
a neutral picture/0 yen with a probability of 20 %, or an unpleasant picture/-500 yen
with a probability of 65 %. The advantageous option and disadvantageous option
switched between two fractal images for each trial type without any signal at the 20th,
35th, and 45th trials of the decision-picture trials and at the 15th, 30th, and 50th trials
of the decision-money trials. The assignment of the fractal images to options was
counterbalanced across participants. The locations of the fractal images were also
randomized across trials. If a response was not made within the time limit of 1.5 s, a
response omission was indicated to the participants, and the trial was aborted. The
mean/maximum fractions of aborted trials across the participants were 0.019/0.062 for
the decision-picture trials, 0.020/0.088 for the decision-money trials, and 0.014/0.075 for
the no-decision-picture trials. After a white frame indicating the choice had been
presented for 4.0 s, an outcome image (a picture or an image of a monetary outcome) was
presented. The outcome image lasted 2 s and was followed by a jittered inter-trial
interval whose duration was 4-5 s (drawn from the uniform distribution).

For each picture category (pleasant, unpleasant, neutral), 20 pictures were
selected from the International Affective Picture System (IAPS) (Lang, Bradley, &
Cuthbert, 2008) [Footnote 1]. IAPS has been commonly used in emotion studies (e.g., Bradley, Codispoti, Sabatinelli, Lang, & Cuthbert, 2001; Codispoti, Bradley, & Lang, 2001; Peter & Bradley, 2010). We avoided using sexual pictures and pictures that included attractive faces or smiling faces because previous imaging studies have reported that these stimuli evoked the reward system by themselves (O’Doherty et al., 2003a; Bray and O’Doherty, 2007; Sabatinelli et al., 2007). Examples of pleasant pictures include beautiful scenes, such as gardens, sunsets, and beaches; cute living systems, such as dolphins, puppies, and human children; exciting scenes, such as sky divers; and appetizing objects, such as pancakes. Examples of unpleasant pictures include violent scenes; tragic scenes; and harmful objects, such as heroin, cockroaches, and dirty garbage. Examples of neutral pictures include simple objects, such as spoons, buttons, umbrellas, and scenes from daily living, such as a girl sitting in front of a computer screen. The pleasant and unpleasant pictures were selected to be equidistant from the neutral pictures in terms of valence and arousal. The normative valence/arousal ratings of these pictures were as follows (mean ± SD, 1 = most unpleasant/least arousing, 9 = most pleasant/most arousing): 5.03 ± 0.21/2.92 ± 0.85 for the neutral pictures, 7.37 ± 0.59/5.06 ± 0.71 for the pleasant pictures, and 2.70 ± 0.36/5.26 ± 0.79 for the unpleasant pictures. Pictures in the decision-picture trials and
the no-decision-picture trials were randomly sampled from the same set of pictures.

Before entering the scanner, the participants experienced one training session consisting of 30 trials (ten trials per trial type) with a different picture set from the main experiment. Prior to the training session, the participants were told that there were two pairs of stimuli for choice trials, and on each trial, one of these pairs would be displayed. They were instructed to select one of the stimuli on each trial by pressing the left or right response button. The participants were told that following their choices, they would be shown a picture or an image indicating the monetary outcome. The participants were instructed to carefully look at the picture to answer questions about the scenes and individuals in the picture after the entire experimental session had finished. The participants were not told which stimulus was associated with which particular outcome, but they were told that one option was associated with a higher probability of obtaining an outcome than the other, and the probability might change without any cue. The participants were encouraged to (1) try to make a choice so that they could see a picture they wanted to see and avoid seeing a picture they did not want to see for the decision-picture trials and (2) try to maximize the gain for the decision-money trials. In our previous study that used emotional pictures as the decision outcome (Katahira et al., 2011), we found that pleasant pictures act as appetitive stimuli and that unpleasant
pictures act as aversive stimuli. This result supports the assumption that normal participants have a tendency to want to see pleasant pictures and to not want to see unpleasant pictures. The participants underwent two sessions, each consisting of 100 trials. The participants were informed that they would receive compensation proportional to the total money earned in the decision-money trials although minimum compensation (approximately 5000 yen) was guaranteed regardless of performance. The actual compensation in yen equaled $5500 + 7.5 \times \min(\max[\text{average gain per decision-money trial}, 0], 200)$.

The participants first performed the practice session outside the scanner and then performed the two main sessions in the scanner. After completing the experimental task, the participants rated all pictures for valence on a scale from 1 (most unpleasant) to 9 (most pleasant) on a paper-based questionnaire. They were asked to rate how the images made them feel during the decision-making experiment. A paper-based recognition test in which the participants were asked whether each picture had appeared in the task was also administered. The mean fraction of pictures presented in the task was 0.84 ($SD = 0.04$). The mean correct recognition rate (including correct hit and correct rejection) across the participants was 0.94 ($SD = 0.05$), suggesting that the participants had a satisfactory attendance to the picture stimulus.
Reinforcement learning models

To model the participants’ choice behaviors, we employed the Q-learning models (Watkins and Dayan, 1992; Sutton and Barto, 1998). Because of the independence of the decision-picture trials and the decision-money trials (i.e., a non-overlapping and independent reward schedule was used for the two tasks), we could independently treat the data for these two tasks. Here, we first describe the standard Q-learning model (with valence-mixed representation) and then the valence-separated representation of the Q-learning model.

Standard Q-learning model (with valence-mixed representation). The standard Q-learning model represents the value of each action (selecting one option) as Q-values (action-values). Let $Q_i(t)$ denote the Q-value for option $i$ ($i = 1, 2$) on trial $t$. The Q-values are updated according to the choice and the resulting outcome (the outcome in this study corresponded to a picture or monetary feedback). Let $a(t)$ denote the option the participant chooses on trial $t$. If $a(t) = i$, then the Q-value corresponding to the selected option is updated as follows:

$$Q_i(t + 1) = Q_i(t) + \alpha \cdot \delta(t),$$
\[ \delta(t) = v(t) - Q(t), \]

whereas the Q-value for the unselected option does not change. Here, \( \alpha (0 \leq \alpha \leq 1) \) is the learning rate that determines the degree of the update and \( v(t) \) is the motivational value, or the reward value, for the picture or monetary feedback presented in trial \( t \), which is specified below. \( \delta(t) \) is called the reward-prediction error. Given a Q-value set, a choice is assumed to be made according to the probability of choosing option 1 \( (P(a(t) = 1)) \) given by the soft-max function:

\[
P(a(t) = 1) = \frac{\exp(Q_1(t))}{\exp(Q_1(t)) + \exp(Q_2(t))},
\]

with \( P(a(t) = 2) = 1 - P(a(t) = 1) \). The model set motivational value \( v(t) \) as follows:

For the \( t \)-th trial of decision-picture trials,

\[
v(t) = \begin{cases} 
\kappa^p_{\text{pict}} & \text{if a pleasant picture was presented} \\
0 & \text{if a neutral picture was presented} \\
\kappa^N_{\text{pict}} & \text{if a unpleasant picture was presented}
\end{cases}
\]

For the \( t \)-th trial of the decision-money trial,

\[
v(t) = \begin{cases} 
\kappa^p_{\text{money}} & \text{if the outcome was + 500 yen} \\
0 & \text{if the outcome was 0 yen} \\
\kappa^N_{\text{money}} & \text{if the outcome was - 500 yen}
\end{cases}
\]

Because we do not know the motivational value of each outcome category a priori, \( \kappa^p \) and \( \kappa^N \) are free parameters that should be estimated based on the participants’ choice data.

To quantify the relative motivational value of emotional outcomes versus neutral outcomes, we set the value of neutral outcome to zero and then estimated the
motivational value parameters for pleasant pictures and unpleasant pictures. Although neutral pictures may have effectively non-zero motivational value, including the free parameter for neutral outcome complicates the interpretation of the model. The absolute values of motivational value parameters are only meaningful when we compare them to the initial values of the action value. Thus, the effective motivational value of the neutral outcome (used as reference point) can be offset by adjusting the initial action values \( Q^0 \) \((= Q_1(1) = Q_2(1))\): setting \( Q^0 \) to a negative value while setting the value of neutral outcomes to zero represents the effective positive motivational value of neutral outcomes. To examine whether the effective motivational value of neutral outcomes was non zero, we compared the results obtained from the standard Q-learning model when \( Q^0 \) was either set to 0 or left as a free parameter. We used the model for the decision-picture trials and the decision-money trials separately; thus, all the parameters and Q-values were independently used for each trial type, and the trial index \( t \) was counted separately.

Valence-separated representation of the Q-learning model. The aforementioned standard-Q learning model expresses positive and negative valence in one dimension; that is, negative valence takes an opposite sign of positive valence. Therefore, we refer to
this model as a standard Q-learning model with valence-mixed representation. However, several reports suggest that the activities of our regions of interest (ROIs), the insula and the striatum, are correlated with negative valence with a positively signed value (Seymour et al., 2004, 2005, 2007). In our task, neutral options (fractal images) were related to bivalent outcomes. Here, to represent the positive-valence value and negative-valence value separately, we propose a valence-separated representation of the Q-learning model. In this representation, Q-values for option \( i \) are decomposed as follows:

\[
Q_i(t) = Q_i^+(t) + Q_i^-(t),
\]

where \( Q_i^+(t) \) represents the Q-value related to positive (appetitive) valence and \( Q_i^-(t) \) represents the Q-value related to negative (aversive) valence. Accordingly, the update rule and prediction error are divided into the appetitive component and the aversive component as follows:

\[
Q_i^+(t + 1) = Q_i^+(t) + \alpha^+ \cdot \delta^+(t),
\]

\[
Q_i^-(t + 1) = Q_i^-(t) + \alpha^- \cdot \delta^-(t),
\]

where the appetitive prediction error \( \delta^+(t) \) and the aversive prediction error \( \delta^-(t) \) are calculated depending on the outcome valence as follows:

For an appetitive or neutral outcome case (\( \nu(t) \geq 0 \),
\[ \delta^+(t) = v(t) - Q^+(t), \]
\[ \delta^-(t) = -Q^-(t), \]

and for an aversive outcome case \((v(t) < 0)\),
\[ \delta^+(t) = -Q^+(t), \]
\[ \delta^-(t) = v(t) - Q^-(t). \]

For the special case \(\alpha^+ = \alpha^-\), the valence-separated representation of the Q-learning model provides the equivalent prediction for the choice as the standard Q-learning model. We simply assumed the initial Q-values to be \(Q^+(1) = Q^-(2) = Q^0/2\).

We tested whether the learning rate should differ between appetitive and aversive components, and we compared the model with the common learning rate model \((\alpha^+ = \alpha^-)\) and the different learning rate model (both \(\alpha^+\) and \(\alpha^-\) are independent free parameters). In addition, to check whether both the positive and negative outcomes indeed worked as appetitive and aversive stimuli, respectively, we compared these models with simpler models in which either value parameters \(\kappa^p\) or \(\kappa^N\) were set to zero (equal to the neutral outcome). An example of the behavior of the Q-learning model is depicted in Figure 2A.

Parameter fit and model comparison. We used the maximum likelihood
approach to estimate the model parameter from the participants’ choice data. For each model and each trial type, a single parameter set was estimated for the participants as a whole to obtain a stable parametric regressor (Daw, 2009). The model parameters were optimized by minimizing the negative log likelihood using the Matlab function “fmincon.” To compare the models, we used the likelihood-ratio test of the null hypothesis that the improvement in the likelihood of more complicated models relative to the simpler ones occurred by chance alone. Under the null hypothesis, the likelihood-ratio statistic would obey the chi-square distribution with the degree of freedom being the difference in the number of model parameters between the two models. The degree of freedom does not depend on the number of participants because a single model parameter set was estimated for each model using the pooled data from all participants.

fMRI data acquisition

The functional imaging was conducted by using an Agilent 4-Tesla whole-body MRI system (Agilent Inc., Santa Clara, CA) with a circularly polarized quadrature birdcage radio-frequency coil as a transmitter and 12 array coils as receivers (Nova Medical Inc., Wilmington, MA). Fifty axial slices (19.2 cm FOV, 64 × 64 matrix, 3 mm thickness, 0 mm gap) with 30° forward rotation from the AC-PC plane were acquired
using a four-shot Echo Planar Imaging (EPI) pulse sequence (volume TR 7.32 s, TE 25 ms, flip angle 76°) for the two functional runs, each consisting of 180 volumes. After TSENSE (Pruessmann et al., 1999; Kellman, 2001) reconstruction (acceleration factor 4), the sampling frequency was quadruplicated and the effective volume TR became 1.83 s. Before the functional runs, a whole-brain anatomical image (voxel size = $1 \times 1 \times 1$ mm$^3$) was acquired using a 3D MPRAGE pulse sequence.

fMRI data analysis

After EPI image reconstruction, the four-volume cycle intensity alternation caused by TSENSE reconstruction was removed. The four data sets (4n, 4n+1, 4n+2, and 4n+3 th volumes) were averaged on a voxel-by-voxel basis, and we calculated the multiplication factor between the volume sets. A pressure sensor was used to measure the respiration signal, and a pulse oximeter was used to measure the cardiac signal. The respiratory and cardiac signals were used to remove the physiological fluctuations from the functional images by using a retrospective estimation and correction method (Hu et al., 1995). The data were then preprocessed using SPM12 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). The preprocessing of the EPIs included slice-timing correction, which adjusted each slice to the middle of the scan,
and motion correction (rigid body realignment of all images to the first volume). The T1-weighted structural image of each participant was normalized to a standard T1 image template in Montreal Neurological Institute (MNI) space. The EPIs were then normalized according to transformed structural images and thus transformed into the standard MNI space. The EPIs were then spatially smoothed using a Gaussian kernel with a full-width at half-maximum of 8 mm.

Statistical analysis of the fMRI data was performed using a general linear model (GLM) with regressors composed of sets of delta (stick) functions. We analyzed the data separately with the three independent GLMs described below. The first GLM (GLM1) was composed of simple regressors without a reinforcement learning model. The other GLMs (GLM2 and GLM3) included TD-errors as parametric modulators. All regressors were convolved with a standard two-gamma hemodynamic response function. For each GLM, the six scan-to-scan motion parameters were also included to account for the residual effects of movement.

1) GLM1 – regressors with stimulus identity. The GLM1 included the regressors at the time of the cue onset for three trial types: the decision-picture trial cue, the decision-money-trial cue, and the no-decision picture trial cue. The GLM1 also included the regressors at the time of outcome onset for the three valence groups for each of the
three trial types (nine regressors in total). Here, we were especially interested in how decision-making modulates the neural response to emotional pictures. Brain regions that were specifically activated in response to emotional pictures in the decision-trials compared with those in the no-decision trials were assumed to be involved in the emotional outcome-guided decision-making process. To observe this effect, we constructed the following two contrast images: (i) \[(\text{decision-pleasant picture} - \text{decision-neutral picture}) - (\text{no-decision-pleasant picture} - \text{no-decision-neutral picture})\] and (ii) \[(\text{decision-unpleasant picture} - \text{decision-neutral picture}) - (\text{no-decision-unpleasant picture} - \text{no-decision-neutral picture})\].

2) GLM2 – TD-error with valence-mixed representation. We used the Q-learning model to analyze the fMRI data. With valence-mixed representation, a temporal-difference (TD) error was derived from the Q-learning model. To include the TD error, the chosen option $Q_i(t)$ was set at the onset of the cue, and the reward-prediction error $\delta(t)$ was used at the onset of the outcome (“valence-mixed TD error” in Figure 2B).

3) GLM3 – TD-errors with valence-separated representation. We also constructed a regressor set with a valence-separated representation of the Q-learning model. Two distinct temporal-difference (TD) errors, i.e., the appetitive TD errors and
the aversive TD errors, were derived from the Q-learning model. To include the appetitive TD error, the chosen option $Q^+(t)$ was set at the onset of the cue and the appetitive reward-prediction error $\delta^+(t)$ was used at the onset of the outcome (Figure 2C). For the aversive TD error, sign-flipped values, $-Q^-(t)$ and $-\delta^-(t)$, were used for the cue onset and the outcome onset, respectively. We used the sign-flipped TD error because previous studies using punishment reported that greater punishment compared to prediction induced positively greater BOLD signals in the striatum and the insula (Seymour et al., 2004, 2005).

The individual contrast images were then entered into a second-level analysis using a one-sample t test. The resulting summary statistical map was initially given a threshold at $p < 0.005$ (uncorrected for multiple comparisons); a small volume correction (SVC) was then applied to our ROIs. The anatomically defined ROIs were extracted from ALL ROI libraries distributed with MarsBaR (Brett et al., 2002) for the bilateral insula, the putamen, and the caudate. For the nucleus accumbens (NAcc), we used 6 mm radius spherical ROIs centered at the locations with MNI coordinates $(x,y,z)$: right NAcc, 12, 8, -8; left NAcc, -12, 8, -8. Clusters that reached a threshold ($p < 0.005$ or 0.001, uncorrected) are shown overlaid on the average of all participants’ normalized structural images.
Results

The participants carried out two decision-making tasks in which they selected one fractal neutral image and a picture-viewing task without a decision (no-decision picture trials). On the decision-picture trial, which was our main task, an emotional picture or an emotionally neutral picture was presented as an outcome of the decision. In the decision-money trial, a monetary feedback was presented similar to a conventional value-based decision-making task.

Behavioral results

The valence rating for pictures (1 = the most unpleasant, 5 = neutral, and 9 = most pleasant) were collected after the fMRI scan. Here, we report the results only for the pictures that were actually presented in the experiment. The mean valence rating for the neutral pictures (mean ± SD across participants) was 5.08 ± 0.28, which did not significantly differ from neutral (=5: t(24) = 1.336, p = 0.19). The mean valence rating for the pleasant pictures was 7.53 ±0.63, and the valence rating for the unpleasant pictures was 2.51 ± 0.58, both of which significantly differed from neutral (ps < 10^{-10}; t(24) = 20.17 and t(24) = −21.07, respectively). These results indicate that the picture categories
assigned to each picture were valid. In addition, the absolute deviations from neutral for
rating the pleasant and unpleasant pictures did not significantly differ ($t(24) = 0.108, p$
$= 0.914$), implying the symmetry of subjective valence for our picture set.

The decision-making tasks were challenging because the participants were
required to continue learning due to the abrupt changes of the cue assignment to the
advantageous/disadvantageous option. The fractions of trials in which the participants
chose the advantageous option were $0.68 \pm 0.11$ for the decision-picture trials and $0.69 \pm$
$0.09$ for the decision-money trials. These values were significantly above the chance
level, i.e., $0.5$ ($p < 10^{-5}; t(24) = 7.98$ and $t(24) = 10.21$, respectively). As the time courses
of the proportions of choosing the advantageous options indicated, after the
contingencies (which options were advantageous) were changed, the participants
quickly changed their preferences for the advantageous option, with a few trials for all
switching position in both trial types (Figure 3).

We fit several variants of the reinforcement learning models to the choice data
of the decision trials and compared their goodness of fit. First, we examined whether the
motivational value of neutral pictures, which was used as a reference point ($=0$), differed
from the initial value of each action ($Q_0$). To achieve this, we compared the standard
$Q$-learning model in which the initial value $Q_0$ was fixed at zero with the standard
Q-learning model in which $Q_0$ was parameterized (see Material and Methods). The standard Q-learning model with a parameterized initial value (the estimated parameters were $\alpha = 0.663$, $\kappa^p = 0.710$, $\kappa^N = -1.714$, and $Q_0 = -1.666$ for the decision-picture trials and $\alpha = 0.698$, $\kappa^p = 1.602$, $\kappa^N = -1.707$, and $Q_0 = -0.766$ for the decision-money trials) provided a significantly better fit to the data than the restricted Q-learning model with $Q_0 = 0$ ($\chi^2(1) = 31.49$, $p < 10^{-7}$ for the decision-picture trials and $\chi^2(1) = 4.56$, $p = 0.032$ for the decision-money trials, likelihood ratio test), suggesting that the neutral outcomes have appetitive motivational values both in the decision-picture trials and in the decision-money trials. Next, to confirm that the pleasant pictures had a positive motivational value (relative to neutral pictures) and that unpleasant pictures had a negative motivational value in the decision-picture trial, we compared the standard Q-learning model with parameterized initial value and restricted models in which either the motivational value of pleasant or unpleasant pictures was set at zero ($\kappa^p = 0$ or $\kappa^N = 0$). For the data from the decision-picture trials, the unrestricted standard Q-learning model provided a significantly better fit to the data in the decision-picture trials than the restricted models in which $\kappa^p = 0$ ($\chi^2(1) = 109.8$, $p < 10^{-10}$, likelihood ratio test) and $\kappa^N = 0$ ($\chi^2(1) = 14.63$, $p < 0.001$), suggesting that the pleasant pictures had a more positive motivational value and the unpleasant
pictures had a more negative motivational value compared to the neutral pictures. The models for the decision-money trials showed similar results, that is, setting either the motivational value for a gain or loss at zero significantly decreased the likelihood ($\chi^2(1) = 102.38, p < 10^{-10}$ or $\chi^2(1) = 63.22, p < 10^{-10}$, respectively). Next, we examined the Q-learning model in which the model had two different learning rates for the appetitive value and the aversive value in the valence-separated representation (see Materials and Methods). For the decision-picture trials, the different learning rate model (estimated parameters: $\alpha^+ = 0.647$, $\alpha^- = 0.669$, $\kappa^p = 0.719$, $\kappa^N = -1.704$, and $Q_0 = -1.661$) did not provide a significantly better fit than the standard Q-learning model with a common learning rate ($\chi^2(1) = 0.01, p = 0.943$). Also for the decision-money trials, the different learning rate model (estimated parameters $\alpha^+ = 0.618$, $\alpha^- = 0.795$, $\kappa^p = 1.739$, $\kappa^N = -1.545$, and $Q_0 = -0.647$) did not provide a significantly better fit than the standard Q-learning model ($\chi^2(1) = 0.87, p = 0.350$). Taken together, the Q-learning model with a non-zero (negative) initial value, different motivational values for outcome valence, and a single learning rate was the best model for both the decision-picture and the decision-money trials. Thus, in the fMRI analysis, we used this model to generate prediction errors as parametric modulators of regressors.
Neural activities reflecting the stimulus identity

We first investigated several contrast images derived from the GLM in which stimulus identities were included as regressors (GLM1). Abundant studies have examined the brain activity in response to emotional pictures selected from the same database as ours (Britton, Taylor, Sudheimer, & Liberzon, 2006; Lang et al., 1998; Lang & Bradley, 2010; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Sabatinelli et al., 2007). The basic contrast image analysis for BOLD responses to outcome in the decision-picture trials is shown in Figure 4. The presentation of emotional (pleasant and unpleasant) pictures activated the occipital cortex more compared to neutral pictures (Figure 4A,B, Table 1), which might be caused in part by the differences in the visual properties of the pictures between the three picture categories. In addition, unpleasant pictures activated the fusiform gyrus and thalamus (Figure 4B, Table 1), which is in agreement with previous studies (e.g., Lane et al., 1997). However, our primary interest involved determining how presenting those pictures as the outcomes of decisions would influence neural activities in response to the pictures. Thus, we tested the differences between the pleasant/unpleasant pictures and the neutral pictures in the decision-picture trials with a similar contrast for the no-decision trials being subtracted.
(see Materials and Methods for details). For the pleasant picture contrast (i), there were no significant regions in our ROIs, i.e., the insula and the striatum. Instead, the whole-brain analysis revealed differential activations in the midbrain, the left fusiform gyrus, and the right parahippocampal gyrus ($p < 0.001$, uncorrected: Figure 5A, Table 2). For the unpleasant picture contrast (ii), there were significant activations in our ROIs, i.e., the left anterior insula ($x = -30, y = 26, z = -2$) and the right ventral striatum, including the putamen ($x = 18, y = 10, z = -6$) and the NAcc ($x = 16, y = 10, z = -6$) ($p < 0.01$, small volume corrected (SVC) for multiple comparisons within anatomically defined masks: Figure 5B). The estimated parameter (beta-value) for each outcome condition indicated that these significant contrasts were mainly driven by decreases in activity in response to the neutral pictures in the decision trial rather than by increases in activity in response to the pleasant or unpleasant pictures (Figure 5C).

The results of other contrasts between the decision-picture trials and the no-decision-picture trials are shown in Figure 4C, D. Several regions, such as the right dorsolateral prefrontal cortex (dIPFC), the dorsomedial prefrontal cortex (dmPFC), the right inferior parietal lobule (IPL), and the precuneus, showed differential activations (Figure 4C). Subsequent analyses that separated the data depending on the valence revealed that pictures with all valences activated the dIPFC and the right IPL, although
The regions activated by neutral pictures were smaller than those activated by emotional pictures (Figure 4D). The precuneus was activated only by emotional (pleasant and unpleasant) pictures, and the dmPFC was activated only by unpleasant pictures. As the basic neural responses to monetary rewards were not our primary aim, we did not include a no-decision control condition for monetary trials. Thus, the same analyses as used with the picture trials were infeasible. Instead, we analyzed basic contrasts, such as Gain (+500 yen) vs. No gain (0 yen) and Loss (-500 yen) vs. No gain (0 yen) (Table 3). These contrasts revealed significant activations primarily in the occipital regions (visual cortex), perhaps reflecting the differences in the visual properties among monetary feedbacks.

Neural activities reflecting TD errors

To investigate the brain regions that represented the learning signal, i.e., the TD error, we entered the TD errors into the GLM as parametric modulators (GLM2 and GLM3). The TD errors were derived on a trial-by-trial basis from the fitted Q-learning model with both the valence-separated representation (for GLM2) and the valence-mixed representation (for GLM3). With the valence-mixed representation, unpleasant outcomes and pleasant outcomes are assumed to have opposite values and a
single TD-error is assumed. In the valence-separated representation, two types of
learning signals are assumed: the appetitive TD error that is related to the appetitive
value of the cues and the aversive TD error that is related to the aversive value of the
cues (Figure 2B; see Materials and Methods). The appetitive TD error is used to update
the expected value of the cues related to the appetitive events (pleasant pictures or
monetary gain), whereas the aversive TD error is used for the expected value of the cues
related to the aversive events (unpleasant pictures or monetary loss). Because these two
representations are different representations of a single model (standard Q-learning
model with a non-zero initial value), both representations provide the statistically
identical prediction regarding choice behavior. Consequently, there is no reason for
favoring one representation from the viewpoint of statistical model fitting to behavioral
data. Thus, we used both representations for separate analyses.

No regions in our ROIs correlated with TD error derived from valence-mixed
representation (GLM2) even with a very weak threshold ($p < 0.01$, uncorrected) in both
the decision-picture and decision-money trials. In contrast, for the valence-separated
representation (GLM3), we found several regions in the ROIs that were correlated with
the TD errors. For the appetitive TD error in the decision-picture trials, there were
several regions in the ROI, including the insula and striatum, that showed significant
correlations after SVC (Figure 6A; left insula: x = -32, y = 14, z = 8, p < 0.01; right caudate: x = 8, y = 20, z = 6, p < 0.05). Whole-brain analysis revealed that the left precuneus showed the strongest correlation (Figure 6A, Table 4) with the appetitive TD error. In addition to the appetitive TD error, several brain ROIs showed significantly correlated activities with the aversive TD error (Figure 6B, Table 4; ps < 0.05, SVC, right NAcc: x = 16, y = 10, z = 4; right insula: x = 34, y = 16, z = 6; left insula: x = 42, y = 2, z = 8; right caudate: x = 8, y = 18, z = 4; right putamen: x = 18, y = 10, z = 2). The bilateral precuneus was also correlated with the aversive TD error (left: x = -6, y = -61, z = 40; right: x = 9, y = -73, z = 61).

With respect to the decision-money trials, the striatum regions were significantly correlated with the appetitive TD error (Figure 6C, Table 5; ps < 0.05; SVC, left caudate: x = -8, y = 6, z = 16; right NAcc: x = 12, y = 14, z = 8; right insula, x = 42, y = 10, z = 4). The right NAcc also correlated with the aversive TD error (ps < 0.05, right NAcc: x = 16, y = 8, -10). Other regions in our ROI showed a tendency to correlate with the aversive TD error but failed to reach the level of significance. (Figure 6C, Table 5: SVC, left caudate: x = -10, y = 10, z = 8, p = 0.055; right insula: x = 38, y = 14, z = 4, p = 0.077).
We investigated how emotional stimuli drive subsequent decision-making processes via learning processes. Although previous studies have investigated how emotional facial stimuli modulate financial-reward-based decision-making (Evans et al., 2011), to date, no study has addressed how purely emotional stimuli, presented solely as decision outcomes, guide decision-making. In addition, we used general emotion-evoking pictures, including emotional scenes adopted from a standard emotional picture set, rather than pictures of facial expressions. The reinforcement learning model in which motivational value parameters were free parameters allowed us to quantify the impact of the emotional images on the subsequent choice behavior: this model also provided trial-by-trial learning signals, i.e., prediction errors (TD errors), which were correlated with the BOLD signal.

The analysis with basic stimulus identity contrasts revealed significant differential activations (compared to neutral pictures) in the ventral striatum (including the putamen and the NAcc) for unpleasant pictures. As shown in Figure 5C, the differences were mainly driven by a decrease in activity in response to the neutral images in the decision trial rather than an increase in activity in response to the unpleasant pictures. This decreased activity in response to neutral pictures was not observed in the
no-decision trials. Thus, the decrease specifically occurred in the decision-making context, possibly reflecting different attitudes of the participants toward the task. One possible explanation for the decrease in activity in response to neutral images is the negative prediction error, which is caused by expecting pleasant or unpleasant pictures with a non-zero probability. Consistent with this interpretation, the model-based analysis showed significant correlations between the aversive prediction errors (aversive TD error) and activities in these regions. Similar to appetitive rewards, several studies have reported that the prediction error for aversive stimuli, such as electrical shock and monetary loss, are positively correlated with the BOLD signal in the ventral striatum (Seymour et al., 2007; Li et al., 2011). In addition, activity in the insula has been shown to correlate with TD error, particularly for aversive events, which is consistent with the present study if we regard seeing an unpleasant picture as an aversive event (Seymour et al., 2004, 2005). Our results showed that negative emotion induced by the unpleasant pictures similarly induced avoidance behavior through common neural systems with other aversive stimuli. In addition, our results are consistent with Levita et al. (2012), who reported that the BOLD responses from the ventral striatum are higher in active avoidance conditions compared to passive avoidance conditions. A series of fMRI studies reported that the BOLD responses in
striatum are dominated by action requirements (e.g., go vs. no-go) rather than by valence, in accord with the view that dopamine has a role in modulating vigor or motivation for actions independent of valence (Guitart-Masip et al., 2011, 2014).

We considered two types of action-value representations: One was a valence-mixed representation, which is a straightforward representation employed in standard reinforcement learning models, that expresses positive and negative valence in one continuous dimension, with negative valences having negative values. The other representation was a valence-separated representation, which we proposed in the present study, that represents the action value by decomposing it into an appetitive component and an aversive component: the more aversive events an action induces, the more positive the value of the aversive component. Our results showed that the striatum and insula mainly correlated with TD errors in the valence-separated representation. This result suggests that at least these regions separately represent positive and negative valences rather than representing both valences in one continuous dimension.

TD errors computed in the present study consist of a cue-induced anticipated value and a prediction error regarding the outcome value (Figure 2B). Previous studies have reported that the anticipation of emotional pictures was activated during the anticipation phase (Grupe et al., 2013). This anticipatory-related activation of the insula
can be interpreted as a part of TD-error-related activity and was incorporated in our analysis. Similar neural substrates might underlie the anticipation of aversive stimuli and TD-error-based action-value updates.

We previously found that the magnitude of motivational values was larger for unpleasant pictures than for pleasant pictures (Katahira et al., 2011). In the present study, this asymmetry was also observed as a difference in the estimated motivational value parameters. Significant correlations were found in both the ventral and dorsal parts of the striatum and insula with respect to the aversive TD errors. On the other hand, the activities of the ventral part of the striatum (NAcc and putamen) did not significantly correlate with the appetitive TD error, whereas the activities of the caudate correlated with the appetitive TD error. These differences in activation patterns may account for the asymmetry between the effects of the pleasant and unpleasant pictures on decision making. As the ventral striatum activity is directly related to motivation, the activity in response to unpleasant pictures may have a larger influence (for avoidance) on the subsequent choice behavior.

Besides the brain regions in our ROIs, pleasant pictures in the decision-making task activated the fusiform gyrus, the parahippocampal gyrus (compared to neutral pictures, as revealed by the analysis with GLM1) and the bilateral precuneus, which
were correlated with appetitive TD errors. The precuneus was also activated by the
aversive prediction error in the decision-picture trials. Previous functional imaging
studies have suggested that the precuneus is involved in self-processing operations,
mental imagery, and episodic memory retrieval (for a review, see Cavanna & Trimble,
2006). One fMRI study employing an empathic judgment task during the viewing of
emotional pictures reported that the attribution of emotions to the self and other
individuals commonly activated the precuneus (Ochsner et al., 2004). The activation of
the precuneus for both appetitive and aversive prediction errors in our decision-making
task may be accounted for by emotional pictures affecting the value of options through a
mental imagery process, such as “how do I feel if I am placed in this situation” or “how
does the person in the picture feel.” Some pictures used in our study were not
biologically or directly pleasant (such as sexual images) or unpleasant (such as pictures
of a snake or spiders) but were endowed with emotional valence only through
interpretations of the situation of the scenes. The fusiform gyrus, the parahippocampal
gyrus and the precuneus may engage in such interpretation processes. The precuneus
has anatomical projections to the dorsolateral caudate nucleus and the putamen,
possibly allowing its direct influence on updating the value of choices (Cavanna &
Trimble, 2006).
The TD errors for both monetary gain and monetary loss in the decision-money trials activated a region of the striatum, in agreement with previous fMRI studies (O'Doherty, Dayan, Schultz, & Deichmann, 2004; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Seymour et al., 2007). However, we found no significantly increased activation of the ventral striatum or orbitofrontal cortex to gain vs. no-gain contrast (Table 3), in contrast to previous studies that employed basic tasks that used monetary feedback. This inconsistency might be because of a weaker detection power of our experimental design for monetary outcome compared to pictures and because the ventral striatum activities are more sensitive to reward prediction error than to simple differences in outcome values. The weak detection power for monetary reward may arise from two factors. First, the picture trials and money trials were inter-mixed in our experiment; thus, the picture trials may have dampened the saliency of the monetary outcome. Saliency is a key factor for the activation of the striatum (Zink et al., 2003, 2004). Second, as the participants were informed that the minimum payment was guaranteed for participation in the experiment and it was sufficiently high (approximately 5000 yen), participants might be indifferent to the monetary feedback.

After we conducted the present experiment, we became aware of the study by Lin et al. (2012) investigating the neural substrates of social reward learning, in which smiling,
angry, or neutral faces paired with emotional words were used as decision-outcomes. They found substantial overlap between regions that correlated with the prediction errors for the social rewards and those that correlated with the prediction errors for monetary rewards in the ventral striatum. Our experimental design was apparently similar to theirs but differed in several aspects. First, they used emotional facial expressions as decision-outcomes while we used general emotional pictures, including natural scenes, rather than social rewards. This difference might have resulted in the disparities in the activated regions: our results showed remarkable correlations with prediction error in the precuneus, the insula, and the ventral striatum. Second, the association rules between cues and outcomes were different. In Lin et al. (2012), the target cues produced either a positive or a negative outcome in addition to a neutral outcome, while control cues produced all valences with equal probability (=1/3). In contrast, in our experimental cues always produced both positive and negative outcomes, which enabled us to evaluate how the brain learns the values of cues incorporating both valences. Third, we separated the influence of appetitive and aversive outcomes by using the valence-separated representation or the Q-learning model while Lin et al. (2012) collapsed them, as their model expressed both valences in one dimension in such a way that the motivational values of appetitive outcomes were set to 1, those of neutral
outcomes were set to 0.5, and those of aversive outcomes were set to 0. Furthermore, in our experimental design, the contingency was switched without any cue, which made the tasks difficult to learn and produced sufficient variability in the prediction error.

In conclusion, the present study examined the neural basis of decision-making guided by emotional events rather than a quantifiable reward or punishment. We found that brain regions correlated with prediction error related to emotional pictures overlapped, in part, with reward/motivation systems (the striatum and the insula). In addition, these regions appear to encode positive and negative valence separately, rather than on one continuous dimension. As we restricted our interest to the most basic dimension of emotion, i.e., valence, other important features, such as arousal and dominance, remain unexplored in the context of decision-making. Our experimental and modeling paradigm is the first step in exploring how more complex aspects of emotion guide decision-making.

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The authors declare no competing financial interests.

Footnote 1: The IAPS slide numbers (and descriptions) used in this study were 2411 (Girl), 7004 (Spoon), 7217 (Clothes Rack), 7491 (Building), 2840 (Chess), 7010 (Basket), 7175 (Lamp), 7500 (Building), 7950 (Tissue), 5740 (Plant), 7014 (Scissors), 7077 (Stove), 7018 (Screw), 7021 (Whistle), 7001 (Buttons), 7590 (Traffic), 7006 (Bowl), 5395 (Boat), 7150 (Umbrella), and 7026 (Picnic Table) for the neutral pictures; 1440 (Seal), 5199 (Garden), 5910 (Fireworks), 5994 (Skyline), 7470 (Pancakes), 1710 (Puppies), 5833 (Beach), 7502 (Castle), 8031 (Skier), 5301 (Galaxy), 1920 (Dolphins), 2655 (Child), 5890 (Earth), 1410 (Ferret), 5829 (Sunset), 2314 (Binoculars), 7508 (Ferris Wheel), 5825 (Sea), 1720 (Lion), and 5621 (Sky Divers) for the pleasant pictures; and 6550 (Attack), 3230
(Dying Man), 9041 (Scared Child), 9295 (Garbage), 9419 (Assault), 1271 (Roaches), 6231
(Aimed Gun), 9421 (Soldier), 9530 (Boys), 9610 (Accident), 2750 (Bum), 9280 (Smoke),
6242 (Gang), 7380 (Roach On Pizza), 9290 (Garbage), 1111 (Snakes), 9102 (Heroin), 2301,
(Kid Crying), 2276 (Girl), and 6560 (Attack) for the unpleasant pictures.

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Figure Captions

Figure 1.

Schematic of the flow of the three types of trials. On two decision-trials, the participant chose one of two fractal images and indicated his/her choice by pressing a corresponding key. After the choice, a white frame surrounding the chosen stimulus was presented for 4 s. Then, for a decision-picture trial, a picture whose valence (neutral, pleasant, or unpleasant) depended on the choice was presented for 2.0 s. For a decision-money trial, a resulting monetary outcome (0 yen, +500 yen, or -500 yen) was presented for 2.0 s. On no-decision-picture trials, the participant had to press a key corresponding to the position of a square marked with “?”.

Figure 2.

Illustration of the reinforcement learning model and the model-based fMRI analysis. A, An example of choice data from a single participant and the prediction of the reinforcement learning model. The first half of the decision-picture trials were shown. The vertical bars in the top panel indicate the chosen option for each trial. Their color and length represent the valence of the outcome pictures. The probability of choosing
option 1 (green line) was calculated from the fitted Q-learning model with a parameterized initial value and a single learning rate. The valence-separated representation of Q-values and the prediction error (for the outcome picture), as well as their valence-mixed representation, were derived from the same model (bottom panels). Note that for aversive components, the prediction errors (PEs) were sign-flipped so that PE = PE+ - PE-. B, Estimated TD errors for the 37th trial in the example. Options (fractal images) appear unpredictably and thus induce prediction errors approximately equal to the Q-values of the chosen option. Predicted BOLD responses (dotted line) were obtained by convolving the TD errors with the hemodynamic response function.

Figure 3.

The learning time courses of our participants for decision-picture trials and decision-money trials. The solid lines depict the fractions, across participants, who choose the advantageous options. The vertical solid lines indicate the points at which contingencies changed (thus, the advantageous options flipped). For the intervals with the same color bar (on each panel), the same option was advantageous. The broken lines indicate the 95% confidence intervals of the optimal choice (choosing the advantageous option) for each trial, computed by assuming that a choice obeys a binomial distribution.
Figure 4.

Regions showing significant statistical contrast at the outcome onsets. A, Pleasant > Neutral for decision-picture trials. B, Unpleasant > Neutral for decision-picture trials. C, decision-picture trials > no-decision-picture trials (valence-collapsed). D, decision-picture trials > no-decision-picture trials (valence-separated). Colors indicate valence. Thresholds for the maps have been set at p < 0.001 for all panels. dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; IPL, inferior parietal lobule.

Figure 5.

Regions differentially activated by emotional pictures specifically in the decision-picture trials. A, Pleasant-pictures, the right parahippocampal gyrus, midbrain, and fusiform gyrus. B, Unpleasant-pictures, the right ventral striatum (putamen) and the left anterior insula. The thresholds for the maps have been set at p < 0.001 or 0.005, uncorrected. Estimated parameter values (beta) for the right parahippocampal gyrus, fusiform gyrus, left anterior insula, and the right ventral striatum. Vtr Str, ventral striatum; Parahippocampal, parahippocampal gyrus; Fusiform, fusiform gyrus.
Figure 6.

Regions correlated with TD errors derived from the Q-learning model with valence-separated representation. **A**, The appetitive TD error for decision-picture trials was correlated with the bilateral precuneus, the right caudate and the left middle insula. **B**, The aversive TD error for decision-picture trials was also correlated with the bilateral precuneus, the right caudate, the right ventral striatum, and the right middle insula. **C**, The appetitive- and aversive- TD error for decision-money trials were correlated with the left caudate and right ventral striatum. The thresholds for the maps have been set at $p < 0.001$ or 0.005, uncorrected. Vtr Str, ventral striatum.
**Table 1. The fMRI peak voxels for emotional vs neutral picture contrasts**

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The uncorrected p-value threshold was $p < 0.001$, and the cluster size threshold was 15 voxels. $k$ represents the cluster size. Empty cluster size ($k$) means that the peak is in the same cluster with the above peak.
Table 2. The fMRI peak voxels for decision vs. no-decision contrasts

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**A - Pleasant pictures**

(Decision-pleasant  – Decision-neutral )

> (No-decision-pleasant  – No-decision-neutral )

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**B - Unpleasant pictures**

(Decision-unpleasant  – Decision-neutral )

> (No-decision-unpleasant  – No-decision-neutral )

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The threshold was $p < 0.001$, and the cluster size threshold was 15 voxels.
Table 3. The fMRI peak voxels for outcome of decision-money trials

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The uncorrected p-value threshold was p < 0.001, and the cluster size threshold was 15 voxels.
## Table 4. The fMRI peak voxels for TD-errors in decision-picture trials

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The threshold was $p < 0.001$, and the cluster size threshold was 15 voxels.
Table 5. The fMRI peak voxels for TD-errors in decision-money trials

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<th>Area</th>
<th>L/R</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>k</th>
<th>t-value</th>
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<td><strong>Appetitive TD-error for decision-money trials</strong></td>
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</tbody>
</table>
The threshold was $p < 0.001$, and the cluster size threshold was 15 voxels.
Figure 1.
Figure 2

(A) Trial index (in decision-picture trials)

(B) Cue onset

Cue onset

Picture onset

Prediction error

Valence-separated

Q-values

Prediction error

Valence-mixed

Q-values

Prediction error

Appetitive PE

Aversive PE

Valence-mixed TD error

Appetitive TD error

Aversive TD error

Predicted BOLD response

Prediction error

Time (second)
Figure 3

(A) Decision-picture trials

(B) Decision-money trials
A Pleasant > Neutral (Decision-picture trials)

B Unpleasant > Neutral (Decision-picture trials)

C Decision-picture trials > No-decision-picture trials (Valence collapsed)

D Decision-picture trials > No-decision-picture trials (Valence separated)

Figure 4
Figure 5

A

Parahippocampal
x = 34

y = 48

R

B

Midbrain
x = 2

y = 10

R

C

Parahippocampal gyrus

Estimated parameter (beta)

Decision trial  No-decision trials

Pleasant Neutral Unpleasant

Fusiform gyrus

Estimated parameter (beta)

Decision trial  No-decision trials

Pleasant Neutral Unpleasant

Ventral striatum (Putamen)

Estimated parameter (beta)

Decision trial  No-decision trials

Pleasant Neutral Unpleasant

Anterior insula

Estimated parameter (beta)

Decision trial  No-decision trials

Pleasant Neutral Unpleasant

Pleasant - Neutral (decision)>

Pleasant - Neutral (no-decision)

Unpleasant - Neutral (decision)>

Unpleasant - Neutral (no-decision)

p < 0.001

p < 0.001

p < 0.005
Figure 6

A
Appetitive TD error
(Decision-picture trial)

Appetitive TD error
(Decision-picture trial)

B
Aversive TD error
(Decision-picture trial)

Aversive TD error
(Decision-picture trial)

C
Appetitive TD-error
(Decision-money trial)

Aversive TD-error
(Decision-money trial)

p < 0.001

p < 0.001

p < 0.005

p < 0.005