

How Self-Determined Choice Facilitates Performance: A Key Role of the Ventromedial Prefrontal Cortex

Kou Murayama¹, Madoka Matsumoto², Keise Izuma^{3,4}, Ayaka Sugiura⁵, Richard M. Ryan⁶, Edward L. Deci⁶ and Kenji Matsumoto²

¹School of Psychology and Clinical Language Sciences, University of Reading, Whiteknights, Reading RG6 6AL, UK, ²Tamagawa University Brain Science Institute, Tokyo 194-8610, Japan, ³Division of Humanities and Social Sciences, California Institute of Technology, Pasadena, CA 91125, USA, ⁴Japan Society for the Promotion of Science, Tokyo 102-8471, Japan, ⁵Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo 153-8902, Japan and ⁶Department of Clinical and Social Sciences in Psychology, University of Rochester, Meliora Hall, Rochester, NY 14627, USA

Address correspondence to Dr Kenji Matsumoto, Tamagawa University Brain Science Institute, 6-1-1, Tamagawa-gakuen, Machida, Tokyo 194-8610, Japan. Email: matsumot@lab.tamagawa.ac.jp

Recent studies have documented that self-determined choice does indeed enhance performance. However, the precise neural mechanisms underlying this effect are not well understood. We examined the neural correlates of the facilitative effects of self-determined choice using functional magnetic resonance imaging (fMRI). Participants played a game-like task involving a stopwatch with either a stopwatch they selected (self-determined-choice condition) or one they were assigned without choice (forced-choice condition). Our results showed that self-determined choice enhanced performance on the stopwatch task, despite the fact that the choices were clearly irrelevant to task difficulty. Neuroimaging results showed that failure feedback, compared with success feedback, elicited a drop in the vmPFC activation in the forced-choice condition, but not in the self-determined-choice condition, indicating that negative reward value associated with the failure feedback vanished in the self-determined-choice condition. Moreover, the vmPFC resilience to failure in the self-determined-choice condition was significantly correlated with the increased performance. Striatal responses to failure and success feedback were not modulated by the choice condition, indicating the dissociation between the vmPFC and striatal activation pattern. These findings suggest that the vmPFC plays a unique and critical role in the facilitative effects of self-determined choice on performance.

Keywords: autonomy, intrinsic motivation, orbitofrontal cortex, striatum, value representation

Introduction

Many believe that when people can make personal choices in accord with their interests and values they have both improved experience and performance. In accord with this view, psychological experiments have robustly revealed the advantage of self-determined choice: When participants could choose a task from multiple ones available in accord with their own interest or value (i.e., self-determined choice), their task performance were improved as compared to when they were assigned a task without choice (i.e., forced choice), even if task difficulty was not different (Patallet al. 2008; Leottiet al. 2010). The practical implications of this facilitative effect of self-determined choice cannot be overemphasized. In fact, the effect of self-determined choice has been investigated in a variety of areas, such as education (e.g., Cordova and Lepper 1996), organizations (e.g., Van den Broeck et al. 2008), and creativity (e.g., Amabile 1996). The beneficial effect of self-determined choice also has theoretical implications in a wide range of human

models such as normative economic theories or reinforcement learning theory (Montague and Berns 2002), because these normative theories are basically indifferent to whether the choice was made out of one's own will (self-determined choice) or by others (i.e., forced choice).

Despite the broad significance, however, surprisingly little neuroscience research has been conducted to examine the neural mechanisms underlying the self-determined choice. In addition, the limited number of previous research has a restricted focus in two respects. First, previous research in neuroscience has not employed an achievement task (i.e., a task that involves one's skill and competence to obtain high performance) and, therefore, these studies did not address the possible performance enhancement in self-determined choice. For example, several researchers investigated the neural correlates of self-generated motor action (Haggard 2008; Passingham et al. 2010), but these studies focused primarily on identifying the brain areas that cause self-generated action of a simple motor task, and its resultant performance has never been questioned. One recent study investigated the neural responses to the anticipation of personal choice (Leotti and Delgado 2011), but this study used a pure probabilistic task and did not target the consequential performance caused by self-determined choice.

Second, these previous studies have focused only on the initiation of self-determined choice (Haggard 2008; Passingham et al. 2010) or the anticipation of self-determined choice (Leotti and Delgado 2011), but overlooked another important aspect of task engagement: Processing of outcome feedback. Outcome processing is one of the fundamental and key psychological processes underlying effective performance in achievement tasks (Carver and Scheier 1998; Kluger and DeNisi 1996). Accordingly, it is possible that self-determined choice modulates the neural activity during the outcome feedback period. In fact, a number of behavioral studies indicated that the psychological process of outcome feedback is one prominent factor underlying the facilitative effects of self-determined choice (e.g., Mikulincer 1988; Molleret al. 2006; see also Legault and Inzlicht 2013, for a study using electroencephalogram).

Thus, the goal of the current study is to examine the neural correlates of the beneficial effects of self-determined choice on task performance, especially focusing on the outcome feedback period. Two primary brain regions have been implicated in processing outcome feedback for an achievement task (Tricomi et al. 2006; Daniel and Pollmann 2010; Murayama et al. 2010; Shohamy 2011)—the striatum and the ventromedial prefrontal

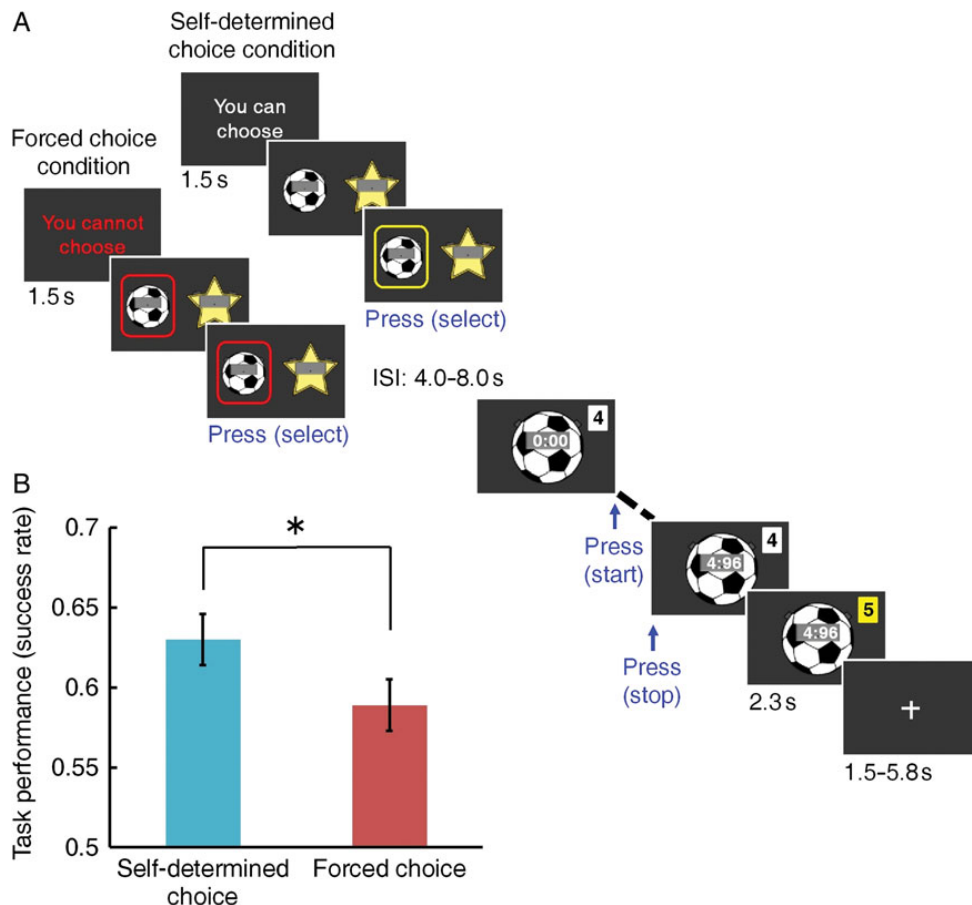


Figure 1. Experimental procedure, materials, and behavioral results. (A) Depiction of the experimental procedure. (B) Means and standard errors of the performance of the stopwatch task (success rate). Self-determined-choice condition significantly enhanced task performance in comparison to forced-choice condition ($t_{30} = 2.49, P = 0.018$).

cortex (vmPFC). Previous studies have indicated the flexible role of both the striatum and the vmPFC (and the adjacent subgenual anterior cingulate cortex, ACC) in representing task values that are regulated by cognitive states and nuanced contexts (Coricelli et al. 2005; Fliessbach et al. 2007; Hare et al. 2008; Plassmann et al. 2008; De Martino et al. 2009; Weber et al. 2009). In fact, the value representation in the striatum and the vmPFC has been shown to be influenced by various factors, such as intertemporal choice (Kable and Glimcher 2007; Sellitto et al. 2010), social norms (Koenigs et al. 2007; Izuma et al. 2008), and emotion regulation (Delgado et al. 2008; Wageret al. 2008). Accordingly, we expect that the effect of self-determined choice would manifest as brain activity change in the striatum and/or the vmPFC in response to outcome feedback.

In this study, participants played a stopwatch game (Murayama et al. 2010) where the goal was to press a button to stop a stopwatch within a specific time window. On each trial (Fig. 1A), participants were presented with a pair of stopwatches, and they were told they could freely choose the one they wished to use in the 'self-determined-choice condition'. In the 'forced-choice condition', they were told to play with a stopwatch that was assigned by a computer. After a stopwatch was selected, it appeared in the center of the screen. Then participants played the stopwatch task and received feedback. Using functional magnetic resonance imaging (fMRI), we investigated how self-determined choice modulates the activation of the striatum

and vmPFC in responses to outcome feedback in the stopwatch task.

Materials and Methods

Participants

A total of 35 healthy participants were recruited from Tamagawa University (Tokyo, Japan). One participant could not finish the experiment; 3 indicated they were distracted and did not follow instructions (in fact, more than 60% of the total error trials were produced by these participants). Accordingly, these 4 participants were excluded prior to fMRI data analysis, resulting in the final sample of 31 [mean age = 20.7 (SD = 2.4), 14 males and 17 females]. All participants gave informed consent for the study and the protocol was approved by the Ethics Committee of Tamagawa University. Four of the 31 participants took part in the experiment without fMRI scanning. These participants were included only in behavioral results.

Experimental Tasks and Procedure

We used a stopwatch task that has been proven to be a useful achievement task in fMRI experiments (Murayama et al. 2010). In this task, participants were presented with a stopwatch, and the goal was to press a button with the right thumb so that the button press fell within 50 ms of the 5-s time point. This time window was the same across the participants. A series of pilot studies were conducted to determine the time window (i.e., difficulty) of the task so that participants could succeed on approximately half of the trials. We took this procedure because 1) previous literature indicated that people obtain the greatest

sense of achievement for the tasks of intermediate difficulty (Atkinson 1957), and 2) this rate of success allows a sufficient number of success or failure trials to be obtained for proper fMRI statistical analysis.

The experiment was composed of 3 scanning sessions, each session consisting of 36 main trials (~14 min each). In addition, 3 catch trials were included at the beginning of the experiment. Each trial (see Fig. 1A) started with a task cue (1500 ms) signaling either the self-determined-choice or forced-choice condition, followed by a presentation of a pair of stopwatches. In the self-determined-choice condition, participants were able to freely choose one of the stopwatches to play in that trial by pressing 1 of the 2 buttons. In the forced-choice condition, a rounded rectangle that encloses one of the stopwatches appeared 800–1200 ms (pseudorandomized) after the stimuli presentation, and participants had to select that stopwatch by pressing the corresponding button. In this condition, responses were not allowed until a rounded rectangle suggested one of the stopwatches. This procedure was intended to expose participants to the choice options almost equally in both self-determined-choice and forced-choice conditions. As a result, reaction time to make a choice (counting from the moment of stimuli presentation) was not statistically different between these 2 conditions ($M = 1443.0$ ms across the conditions). A trial-based linear mixed-effects modeling (Baayen et al. 2008) did not find a significant relationship between the reaction time to make a choice and task performance ($P = 0.46$). On making a choice, the stopwatch that participants had just selected appeared in the center of the screen, where participants could start playing the stopwatch task by pressing a button. When a stopwatch was displayed, the participant's total score was also displayed in the upper-right corner of the display area. A point was added to his or her score (800 ms after the button press) and the updated score panel flashed for 1,500 ms; no point was added when they failed. The points accumulated throughout the experimental session, but no tangible reward such as money was associated with success. Critically, the difficulty of all the stopwatches was identical—they were different only in their appearance. Participants were explicitly instructed about this fact.

An error message was presented when 1) participants pressed the button before a suggested choice was presented, 2) participants selected a stopwatch that was not suggested, 3) participants had not pressed the button 10 000 ms after choice options were presented, 4) participants had not pressed the button 10 000 ms after the chosen stopwatch was ready to start, or 5) participants had not pressed the button 8 s after the stopwatch started. In those cases, the same trial started again.

We randomly intermixed the self-determined-choice trials (36 trials) and forced-choice trials (72 trials) for each participant (details about the trial numbers will be described later) with the constraint that there were no more than 3 successive trials of the same condition. The inter-trial interval (ITI) was jittered between 1500 and 5800 ms (average = 3500 ms). In addition to the ITI, after participants made a choice (both in the self-determined-choice and forced-choice conditions), there followed a variable interval between 4000 and 8000 ms (average = 6000 ms), after which participants could start the stopwatch by pressing a button. This variable interval allowed us to efficiently separate the choice-evoked brain activation from the activity associated with the initiation of the stopwatch task. The stimulus presentation and response recording were controlled by Cogent 2000 (<http://www.vislab.ucl.ac.uk/cogent.php>) running on Matlab. The instruction was provided through a computer program to prevent possible experimenter bias, and participants were thoroughly trained in advance to familiarize them with the task sequence.

After the last scanning session, participants were asked to indicate whether they enjoyed self-determined-choice or forced-choice trials (You had 2 types of trials, one where you could determine which stopwatch to play with, and the other where you were asked to choose a specific stopwatch to play with. Which trials did you enjoy more?).

Trial Matching

We prepared a total of 9 moderately attractive stopwatches from a larger set of stimuli (see Fig. 2). We presented all the possible pairs of different stopwatches 3 times to every participant (i.e., 108 main trials



Figure 2. Nine types of stopwatches used in the current experiment. They are different in their appearance, but the difficulty of the task was identical.

in total with 36 pairs)—one trial per pair of options when the participants were making self-determined choices and 2 trials per pair of options when the participants were making forced choices. In the 2 forced-choice trials within a pair, the experimental program made a different choice. With this procedure, it is assured for every participant that each of the self-determined-choice trials has a corresponding forced-choice trial that selected the same stopwatch from the same pair (forced-choice-matching trials). Importantly, in order to match self-determined-choice and forced-choice conditions as close as possible, unless otherwise noted, our statistical analysis included only the forced-choice matching trials (a within-participant yoked-control design; Peele et al. 1984). This way, we could compare the self-determined-choice condition and forced-choice condition with the identical pairs and choices within participants, achieving a perfect control for any confounding effects. Conceptually, forced-choice matching trials represent the situation where participants were externally forced to play with the stopwatch they like, which provides comparison without the confounding influence of differential emotional commitment to the task. Nonetheless, analyses focusing on forced-choice trials involving a different stopwatch (forced-choice nonmatching trials) will be also reported.

fMRI Data Acquisition

The functional imaging was conducted using a 3-Tesla Siemens Trio A Tim MRI scanner to acquire gradient echo T_2^* -weighted echo-planar images (EPI) with blood oxygen level-dependent (BOLD) contrast. Forty-two contiguous interleaved transversal slices of EPI images were acquired in each volume, with a slice thickness of 3 mm and no gap (repetition time, 2500 ms; echo time, 25 ms; flip angle, 90°; field of view, 192 mm²; matrix, 64 × 64). Slice orientation was tilted 0.30° from the AC-PC line. We discarded the first 3 images before data processing and statistical analysis to compensate for the T_1 saturation effects.

fMRI Data Analysis

Image analysis was performed using Statistical Parametric Mapping 8 (SPM8; <http://www.fil.ion.ucl.ac.uk>). Images were corrected for slice acquisition time within each volume, motion-corrected with realignment to the first volume, spatially normalized to the standard Montreal

Neurological Institute (MNI) EPI template, and spatially smoothed using a Gaussian kernel with a full width at half-maximum of 8 mm.

For each participant, the BOLD responses across the scanning sessions were modeled with a general linear model (GLM). The analysis was intended to model the following effects: Presentation of cue in the self-determined-choice condition, presentation of cue in the forced-choice condition, task initiation in the self-determined-choice condition (success and failure trials were combined), task initiation in the forced-choice condition (success and failure trials were combined), success feedback in the self-determined-choice condition, success feedback in the forced-choice condition, failure feedback in the self-determined-choice condition, and failure feedback in the forced-choice condition. The onset of task initiation was set 1000 ms before the button press, because previous studies showed that preparatory brain activity begins about 1000 ms before action takes place (Haggard 2008). It should be noted that, in the regressors of forced-choice condition in task initiation and feedback periods, we only included the trials that suggested the option that the participants selected in the corresponding self-determined-choice condition (i.e., forced-choice matching trials). As indicated earlier, this procedure allowed us to control for any confounding factors associated with stopwatch selection. Both for task initiation and feedback periods, forced-choice trials that suggested the other option (i.e., forced-choice nonmatching trials) were coded as separate regressors. Choice period (i.e., between presentation of choice options and button press to make a choice), motion parameters, error trials, and session effects were also modeled as regressors of no interest. All the regressors (except for the motion parameters and the session effects) were calculated using a box-car function convolved with a hemodynamic-response function. Estimates were corrected for temporal autocorrelation using a first-order autoregressive model. The obtained parameter estimates were then taken to the second level, and a random effects analysis was performed.

In an additional GLM that aimed to control for the total number of failure (or success) experiences that individuals had on each trial, we added the cumulative number of failure trials as a trial-specific parametric modulator to the failure-feedback periods. The cumulative number of failure trials was computed and included in the model separately for the self-determined-choice and forced-choice conditions.

Analysis for the cue presentation period was a region of interest (ROI) analysis focusing on the ACC, insular cortex, striatum/pallidum, and midbrain (for reasons, see Results), with a priori anatomical ROIs defined by using the WFU-Pickatlas SPM tool (Maldjian et al. 2003): Using the AAL atlas, the ACC ROI consisted of the bilateral anterior cingulum; The anterior insula ROI consisted of the bilateral insula; and the striatum/pallidum ROI consisted of the bilateral caudate, putamen, and pallidum. The midbrain ROI was defined by the Talairach Daemon database. A familywise error-corrected significance threshold of $P < 0.05$ ($k \geq 5$ voxels) within these ROIs were used (the reported significant voxels also survived at $P < 0.001$, uncorrected, $k \geq 30$ voxels).

Analysis for the feedback period (i.e., our main analysis) was also a ROI analysis focusing on the striatum and vmPFC, with a priori anatomical ROIs defined by using the WFU-Pickatlas SPM tool (Maldjian et al. 2003). The striatum ROI consisted of the bilateral caudate and putamen, and the vmPFC ROI consisted of the bilateral gyrus rectus and medial orbitofrontal gyrus in the AAL atlas. A familywise error-corrected significance threshold of $P < 0.05$ ($k \geq 5$ voxels) within these ROIs were used (the reported significant voxels also survived at $P < 0.001$, uncorrected, $k \geq 30$ voxels). A preliminary exploration of the data indicated that there is a strong outlier in vmPFC activation in response to feedback [more than 3.8SD outside the mean value. Grubb's test for outliers (Grubbs 1950) was significant, $P < 0.01$]. Accordingly, we excluded this participant from the vmPFC analysis.

To quantify the pattern of effects in the ROI analyses, we further conducted a series of post hoc analyses using a cross-validation leave-one-out procedure to avoid a nonindependence bias in the post hoc analyses. Specifically, we re-estimated our second-level analysis (i.e., 2×2 ANOVA, see results), always leaving out one subject. We selected the peak voxel within the ROI (i.e., striatum or vmPFC) in these cross-validation second-level analyses. From that new voxel we extracted the β value from the left-out subject and used these β values in the series of post hoc t -tests. This procedure is akin to an independent

functional localizer, and ensures the independence of the post hoc analyses (Esterman et al. 2010; Gläscher et al. 2010). All the post hoc analyses were conducted with this procedure. The brain-behavior correlation analysis was also performed based on these extracted β values.

For task initiation period, an exploratory whole-brain analysis was conducted ($P < 0.001$, uncorrected, $k \geq 5$ voxels). Moreover, we ran additional GLM that added the response time to initiate the stopwatch as a trial-specific parametric modulator to explore how the response time is correlated with brain activation.

For exploratory purpose, we also conducted a within-subject functional connectivity analysis between choice period and feedback period. This exploratory analysis was conducted in order to examine which brain activation during the choice period is related to the modulation effect of the vmPFC activation observed during the feedback period. The procedure took the following steps. First, a new GLM design file was constructed where each individual trial of the feedback period was coded with a unique independent variable. This allowed us to estimate the trial-by-trial brain activation (i.e., β values) from a seed region during the feedback period (Rissman et al. 2004). Next, the extracted β values from a seed region (using individual peaks) were included in the main GLM as a trial-specific parametric modulator during cue period. The parametric modulators were included in the model separately for the self-determined-choice and forced-choice conditions and for the success and failure trials, resulting in 4 different parametric modulators. With this procedure, β values associated with each parametric modulator represent the association between the brain activation during the cue period and seed-region activation during the feedback period in respective conditions (self-determined-choice/success, self-determined-choice/failure, forced-choice/success, and forced-choice/failure). Finally, to investigate condition-dependent change in functional connectivity, second-level random-effects analysis (e.g., ANOVA) was performed.

Results

Behavioral Results

Our data revealed that performance on the stopwatch task was significantly better in self-determined-choice condition ($M = 0.63$, $SD = 0.15$, range = 0.33–0.92) than in forced-choice condition ($M = 0.59$, $SD = 0.14$, range = 0.31–0.89; $t_{30} = 2.49$, $P = 0.018$; Fig. 1B). This provides the evidence that self-determined choice indeed enhances task performance. This effect was not moderated by gender difference ($P = 0.23$). In addition, the analysis on the post-session question showed that participants preferred self-determined-choice trials (94%) to forced-choice trials (6%; binomial test; $P < 0.0001$), suggesting that participants were indeed motivated for the self-determined-choice trials over the forced-choice trials.

To further validate our findings, we conducted additional controlling analyses. First, a latent growth curve modeling of task performance trajectory (McArdle et al. 1990) indicated that there is a linear increasing trend in task performance over trials, perhaps due to a practice effect, $\text{Exp}(B) = 1.003$, $P < 0.05$ (note that quadratic effect was not statistically significant, $P = 0.31$). Accordingly, to address the possibility that this linear trend may have influenced our findings, we computed the mean position (range is 1–108 and smaller number indicates earlier presentation) of the self-determined choice and the corresponding forced-choice (matching) trials. If a specific experimental condition tends to be positioned later in trials, this condition should benefit the practice effect. The results showed that forced-choice matching trials were positioned slightly later ($M = 56.0$, $SD = 30.2$) than self-determined choice trials ($M = 54.5$, $SD = 30.4$), and this difference was not statistically significant, $t_{30} = 1.64$, $P = 0.11$, suggesting that the practice effect is unlikely to bias our findings.

Second, we examined whether the performance in forced-choice trials influenced the choice of the self-determined choice trials within the same pair of stopwatches. For example, within a given specific pair of stopwatches, participants may have had a tendency to choose the stopwatch that they succeeded with in an earlier trial. This could potentially bias the findings (although in this case performance in forced-choice condition should be higher than that in self-determined-choice condition). Accordingly, we compared the task performance of forced-choice matching trials that were presented before the corresponding self-determined choice trials ($M=0.59$, $SD=0.49$) and those presented after the self-determined choice trials ($M=0.59$, $SD=0.49$). No statistically significant difference in performance was observed, $t_{30}=0.08$, $P=0.94$, indicating that performance in forced-choice trials did not influence the choice in the corresponding self-determined choice trials.

Finally, in order to examine how our matching procedure affected our findings, we examined performance of the forced-choice nonmatching trials. Interestingly, the performance comparison between forced-choice matching trials (trials used in the main analysis; $M=0.59$, $SD=0.14$; range = 0.31–0.89) and forced-choice nonmatching trials ($M=0.59$, $SD=0.16$; range = 0.31–0.92) did not reveal significant difference, $t_{30}=0.16$, $P=0.87$, indicating that selection bias may not have big impact on our behavioral findings. Self-determined-choice condition still showed better performance than forced-choice condition even when we collapsed these 2 forced-choice trials, $t_{30}=2.71$, $P<0.01$. Taken together, the set of controlling analyses indicated that the facilitative effects of self-determined choice on task performance cannot be attributable to methodological artifacts.

On the other hand, self-determined choice did not seem to influence task initiation time (e.g., reaction time between the onset of the chosen stopwatch and the button press to start the stop watch). Indeed, there was no significant difference between the self-determined-choice condition ($M=793$ ms, $SD=326$ ms) and forced-choice condition ($M=773$ ms, $SD=303$ ms), $t_{30}=0.98$, $P=0.33$. A trial-based generalized linear mixed-effects modeling (Baayen et al. 2008) further revealed that the task initiation time was not related to task success of the same trial ($P=0.54$) or the interaction between task success and choice condition ($P=0.64$).

Brain Activation in Response to Task Anticipation

A recent study showed that anticipation of self-determined choice activates a variety of brain regions, especially, the ACC, insula, striatum, and midbrain (Leotti and Delgado 2011). To confirm the validity of our experimental task for examining self-determined choice, we preliminarily investigated whether the self-determined-choice cue in our task (in comparison to the forced-choice cue) indeed activated those brain regions. We anatomically defined the ACC, insula, striatum/pallidum, and midbrain as ROI, and compared brain activation in response to the self-determined-choice cue with the forced-choice cue within these ROIs (see Fig. 3A; for completeness, Table 1 lists all regions displaying a significant effect in a whole-brain analysis). Because the cue was presented before the presentation of choice options (i.e., before the choice was suggested), all the forced-choice trials were included in the analysis. Consistent with the past study, the self-determined-choice cue activated the dorsal ACC (extending into the medial prefrontal cortex and

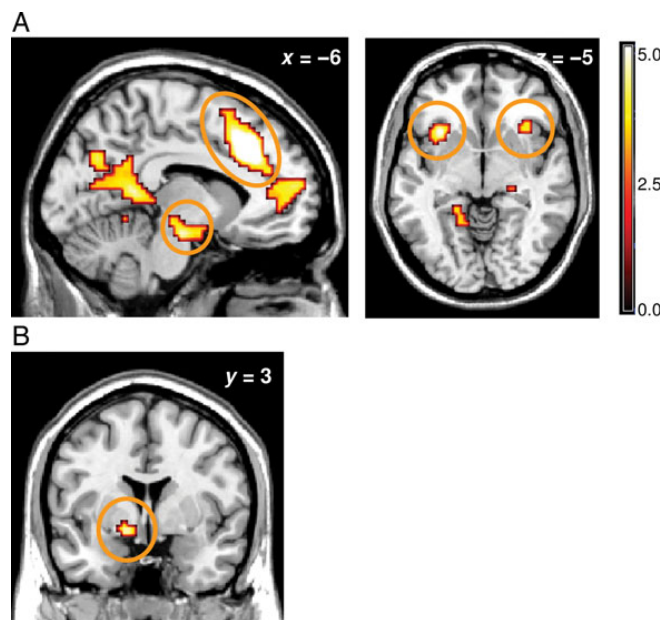


Figure 3. (A) Anterior cingulate cortex (left panel, upper circle), midbrain (left panel, bottom circle), and bilateral insula (right panel) activation elicited by self-determined-choice trials relative to forced-choice trials when participants were presented a task cue ($P < 0.05$, familywise error corrected; the image is shown at $P < 0.001$, uncorrected). Neural responses are displayed in sagittal and transaxial formats. (B) The ventral pallidum activation elicited by self-determined choice trials relative to forced choice trials when participants were presented a task cue ($P < 0.005$, uncorrected). Neural responses are displayed in coronal format.

Table 1
Effects of self-determined choice during cue presentation period

Region	Peak MNI coordinates			<i>t</i> value	<i>k</i>
	<i>x</i>	<i>y</i>	<i>z</i>		
Self-determined choice > forced choice					
L. Anterior cingulate cortex	-9	26	37	8.02	343
R. Anterior cingulate cortex	15	26	25	3.79	15
L. Medial prefrontal cortex	-9	56	13	4.35	223
R. Presupplementary motor area	12	14	67	3.87	14
L. Anterior insula	-33	17	-2	5.55	102
L. Anterior insula	-36	32	13	4.80	121
R. Anterior insula	36	23	-2	4.01	47
R/L. Midbrain	-9	-16	-17	4.86	97
R. Parahippocampal gyrus	27	-25	-17	5.22	103
L. Parahippocampal gyrus	-21	-25	-17	4.61	27
R. Isthmus	12	-43	10	4.75	42
L. Isthmus	-15	-43	4	4.66	51
R/L. Midcingulate cortex	-3	-4	31	4.00	58
L. Ventromedial prefrontal cortex	-9	29	-11	3.88	15
R. Superior frontal gyrus	12	14	67	3.70	11
R. Inferior frontal gyrus	48	8	25	4.28	37
L. Angular gyrus	-42	-64	46	3.60	7
R. Lateral prefrontal cortex	48	35	16	3.58	14
Forced choice > self-determined choice					
L. Supramarginal gyrus	-57	-46	40	4.80	61
L. Angular gyrus	-51	-55	28	4.45	57
L. Occipital cortex	-12	-100	16	4.21	53
R. Occipital cortex	12	-97	13	4.35	45
L. Supramarginal gyrus	-57	-25	22	3.66	10
L. Middle temporal gyrus	-54	-46	-5	3.77	10
L. Middle temporal gyrus	-54	-67	7	3.65	12
R. Fusiform gyrus	33	-73	-17	3.54	18
L. Cerebellum	-27	-79	-23	3.38	5

A whole-brain analysis results showing significant difference between the self-determined-choice condition and the forced-choice condition during the cue presentation period ($P < 0.001$, uncorrected, $k \geq 5$ voxels). *k*, number of significant voxels.

presupplementary motor area, pre-SMA), anterior insula, and midbrain more strongly than did the forced-choice cue ($P < 0.05$, family-wise error corrected). In the striatum, BOLD activity was greater when anticipating self-determined-choice relative to forced choice, but this difference was somewhat weaker and not statistically significant with family-wise error control. With a more lenient threshold used in the same previous study (Leotti and Delgado 2011; $P < 0.005$, uncorrected; Fig. 3B), however, the self-determined-choice cue did significantly increase activation in the ventral pallidum. In sum, these findings are consistent with previous work (Leotti and Delgado 2011) and support the validity of our experimental task for examining the neural correlates of the self-determined choice.

Brain Activation in Response to Outcome Feedback

Our primary interest was whether the brain activation in the striatum and vmPFC in response to outcome feedback would be modulated by the choice manipulation. Thus, we anatomically defined the striatum and vmPFC as ROIs, and conducted a 2×2 analysis of variance (ANOVA) with choice condition (self-determined choice or forced choice) and outcome feedback (success or failure) as factors within each ROI (for completeness, Table 2 lists all regions displaying a significant effect in a whole-brain ANOVA).

Table 2

Brain structures showing a significant effect in the 2 (choice condition; self-determined choice vs. forced choice) \times 2 outcome feedback; success or failure) analysis of variance in response to feedback

Region	Peak MNI coordinates			<i>t</i> value	<i>k</i>
	<i>x</i>	<i>y</i>	<i>z</i>		
Success feedback > Failure feedback					
R. Ventral striatum	21	14	-5	4.99	299
L. Ventral striatum	-15	-1	-14	4.86	302
L. Occipital cortex	-45	-67	7	4.13	81
L. Dorsal prefrontal cortex	-18	32	61	4.05	56
L. Middle temporal gyrus	-57	-49	-8	3.76	17
R. Inferior temporal gyrus	45	-52	-14	3.61	15
R. Superior temporal gyrus	69	-31	7	3.60	5
L. Angular gyrus	-45	-70	34	3.62	35
L. Medial prefrontal cortex	-12	56	7	3.45	12
R. Primary motor cortex	30	-19	64	3.34	6
L. Precuneus	-3	-49	37	3.30	7
L. Inferior frontal gyrus	-48	5	25	3.23	5
Failure feedback > Success feedback					
(No significant activation)					
Self-determined choice > forced choice					
(No significant activation)					
Forced choice > self-determined choice					
(No significant activation)					
Interaction					
R. Ventromedial prefrontal cortex	6	26	-14	3.96	32
L. Ventromedial prefrontal cortex	-12	32	-11	4.02	18
L. Ventromedial prefrontal cortex	-15	23	-20	3.72	10
R. Cerebellum	27	-70	-35	4.27	200
L. Cerebellum	-18	-55	-41	4.06	72
L. Cerebellum	-9	-55	-14	3.53	10
R. Anterior temporal cortex	48	-7	-23	4.07	25
R. Occipital cortex	27	-85	7	3.92	58
L. Occipital cortex	-30	-85	7	3.80	189
L. Posterior temporal cortex	-48	-43	1	3.72	20
R. Posterior temporal cortex	42	-55	1	3.61	8
R. Fusiform gyrus	30	-58	-11	3.88	22
R. Fusiform gyrus	42	-28	-14	3.43	6
L. Angular gyrus	-36	-67	31	3.41	12
L. Precuneus	-3	-58	31	3.31	8
L. Occipital cortex	-9	-70	25	3.30	5

A whole-brain analysis results showing a significant effect in the 2 (choice condition; self-determined choice vs. forced choice) \times 2 outcome feedback; success or failure) analysis of variance in response to feedback ($P < 0.001$, uncorrected, $k \geq 5$ voxels). All the significant interactions have the same direction with the ventromedial prefrontal cortex as presented in Figure 5.

Activation in the striatum showed a significant main effect of outcome feedback ($P < 0.05$, familywise error corrected), indicating greater striatal activity in response to success (relative to failure) feedback. This is consistent with the previous findings that showed the striatum being sensitive to the valence of feedback even without any monetary incentives (Tricomi et al. 2006; Izuma et al. 2008; Murayama et al. 2010). However, no significant interaction was observed between choice condition and outcome feedback (Fig. 4). Indeed, the striatal activation in the self-determined-choice condition is not different from that in the forced-choice condition in response to either success or failure feedback (P 's > 0.19); the greater activation in the striatum in response to success feedback (relative to failure feedback) was observed both in the self-determined-choice and forced-choice conditions (P 's < 0.01).

In contrast, we found that self-determined choice modulated the brain activation in the vmPFC. Specifically, in the 2×2 ANOVA, the right vmPFC activation showed a significant interaction between choice condition and outcome feedback (Fig. 5; $P < 0.05$, familywise error corrected). Neither the main effect of choice condition nor outcome feedback revealed significant activation in the vmPFC. Post hoc analyses showed that, in response to success feedback, the vmPFC activation in the self-determined-choice condition was not different from that in the forced-choice condition ($F_{1,50} = 0.70$, $P = 0.41$). On the other hand, however, the self-determined-choice condition showed higher vmPFC activation in response to failure feedback than did the forced-choice condition ($F_{1,50} = 14.11$,

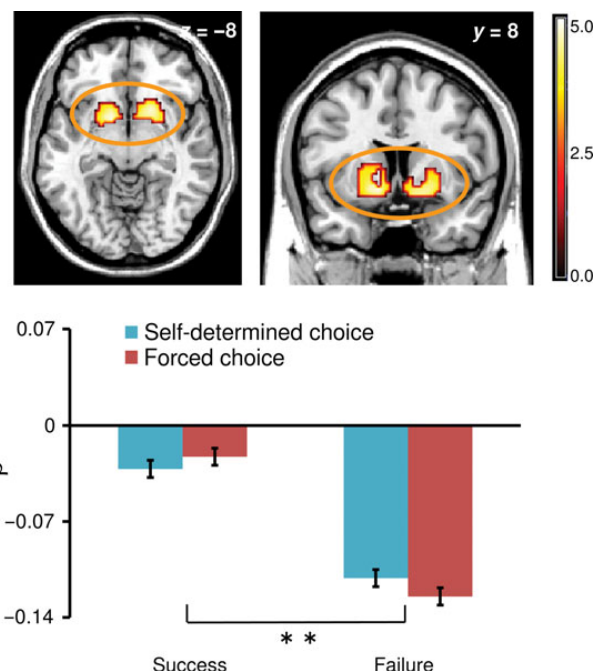


Figure 4. Bilateral striatum activation (peak at 21, 14, -5, and -12, 8, -8) showing a significant main effect of outcome feedback ($P < 0.05$, familywise error corrected; the image is shown at $P < 0.001$, uncorrected). Neural responses are displayed in transaxial and coronal formats. The bottom panel represents the mean β values (a 6-mm sphere centered on the peak) and corresponding SEs in the striatum as a function of choice condition (self-determined choice vs. forced choice) and outcome feedback (success vs. failure). Note that the graph plotted the activation in the right striatum to allow for reasonable comparison with Figure 5. The plot indicated that the striatum was strongly influenced by outcome feedback (positive vs. negative), but this effect was not modulated by choice condition.

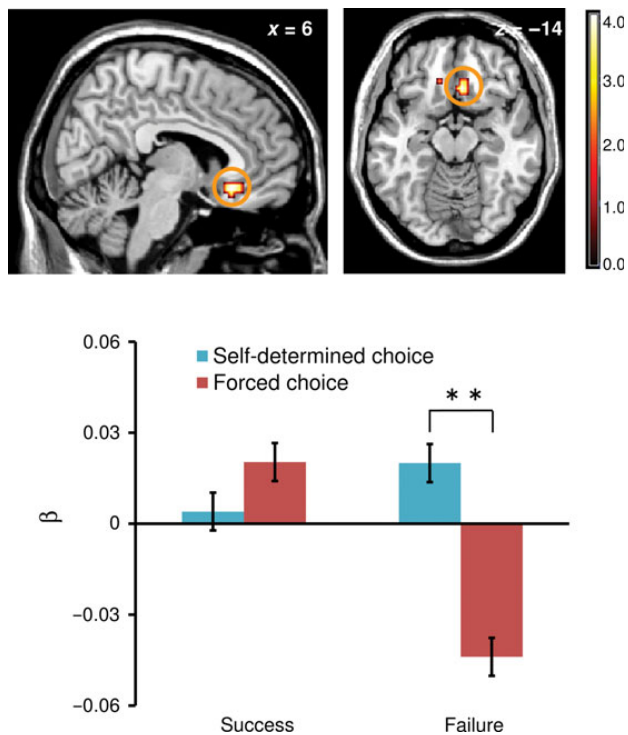


Figure 5. Right vmPFC activation (peak at 6, 26, -14) showing a significant choice condition by outcome feedback interaction in response to task feedback ($P < 0.05$, familywise error corrected; the image is shown at $P < 0.001$, uncorrected). Neural responses are displayed in sagittal and transaxial formats. The bottom panel represents the mean β values (a 6-mm sphere centered on the peak) and corresponding SEs as a function of choice condition (self-determined choice vs. forced choice) and outcome feedback (success vs. failure). The plot indicated that, in response to success feedback, the vmPFC activation in the self-determined-choice condition was not different from that in the forced-choice condition ($F_{1,50} = 0.70$, $P = 0.41$). On the other hand, the self-determined-choice condition showed higher vmPFC activation when compared with the forced-choice condition in response to failure feedback ($F_{1,50} = 14.11$, $P < 0.01$).

$P < 0.01$). That is, whereas vmPFC activation in the forced-choice condition decreases in response to failure when compared with success feedback ($F_{1,50} = 6.58$, $P = 0.01$), which is consistent with the previous literature (Hare et al. 2008; Noonan et al. 2011), this pattern was not observed in the self-determined-choice condition ($F_{1,50} = 0.58$, $P = 0.45$). In other words, the self-determined choice, relative to forced choice, buffered the decreased activation in the vmPFC in response to the negative feedback.

In our experiment, the forced-choice condition had a larger number of trials and produced more failure trials (see Behavioral results). Therefore, the decrease in the vmPFC in response to failure in the forced-choice condition might merely reflect the habituation to failure that was specific to the forced-choice condition. To address this possibility, we ran another GLM that included the cumulative number of failure experiences for each condition as a trial-specific parametric modulator. This parametric modulator was separately modeled for self-determined-choice and forced-choice conditions in response to failure feedback. The number of failure experiences was not significantly related to the vmPFC deactivation in either condition ($P < 0.05$, familywise error corrected), even with a more lenient criterion ($P < 0.005$, uncorrected). We also conducted a $2 \times 2 \times 3$ ANOVA with choice condition (self-determined choice or forced choice), outcome feedback

(success or failure), and session (sessions 1–3) as factors within each ROI, in order to investigate whether our findings were moderated by practice effect (see our behavioral analysis). None of our main findings in the striatum and the vmPFC significantly interacted with the session.

Finally, to confirm that the activation pattern in the striatum and vmPFC were statistically different, we further conducted a $2 \times 2 \times 2$ ANOVA with choice condition, outcome feedback, and brain region (striatum vs. vmPFC) as factors. The analysis showed a three-way interaction ($F_{1,25} = 4.09$, $P = 0.05$), indicating that the striatum and vmPFC functioned differently in self-determined-choice and forced-choice conditions in response to outcome feedback.

The vmPFC result is in marked contrast with the striatum findings, and suggests the possibility that the enhanced task performance in the self-determined-choice condition may be related to this modulation effect in the vmPFC activation in response to failure feedback. To examine whether the differential vmPFC activation in response to failure feedback was indeed related to the enhanced task performance, we further conducted a brain-behavior correlation analysis. Specifically, we indexed the magnitude of brain resilience in the self-determined-choice condition by subtracting the β value in the forced-choice condition from the β value in the self-determined-choice condition in response to failure feedback. We also indexed the performance advantage in the self-determined-choice condition by subtracting the task performance in the forced-choice condition from that in the self-determined-choice condition. The performance advantage was uncorrelated with overall task performance ($r = 0.06$, $P = 0.75$), indicating that this index does not merely reflect overall task performance or general motivation for the task. Our analysis revealed a significant positive correlation between these 2 indices ($r = 0.40$, $P < 0.05$), indicating that those who showed less drop in the failure-induced brain activity in the self-determined-choice condition (when compared with the forced-choice condition) exhibited a larger performance enhancement effect caused by self-determined choice (Fig. 6B).

We then conducted the same correlational analysis for the striatum activation, but the correlation was not significant ($r = 0.03$, $P = 0.89$; see Fig. 6A). This finding provides further evidence for the functional dissociation between the striatum and the vmPFC. We also performed the same correlational analysis focusing on the brain activation in responses to success feedback. Neither the vmPFC nor striatum showed significant correlation ($r = -0.21$ and 0.10 , $P_s > 0.31$), suggesting that the observed correlation is specific to failure feedback.

Brain Activation in Response to Task Initiation

For exploratory purpose, we also examined the brain activation associated with self-determined choice during task initiation (when they pressed a button to start the stopwatch; see Fig. 1A). A whole-brain analysis showed that task initiation in the self-determined-choice condition (in comparison to the forced-choice condition) increased brain activation in the pre-SMA (extending into the superior frontal gyrus; $P < 0.001$ uncorrected), which is implicated in the initiation of self-generated (or voluntary) action (Fig. 7; Haggard 2008; Passingham et al. 2010). This comparison also revealed other areas of significant activation, including superior frontal gyrus, mid-brain, and cerebellum ($P < 0.001$ uncorrected; see Table 3). No

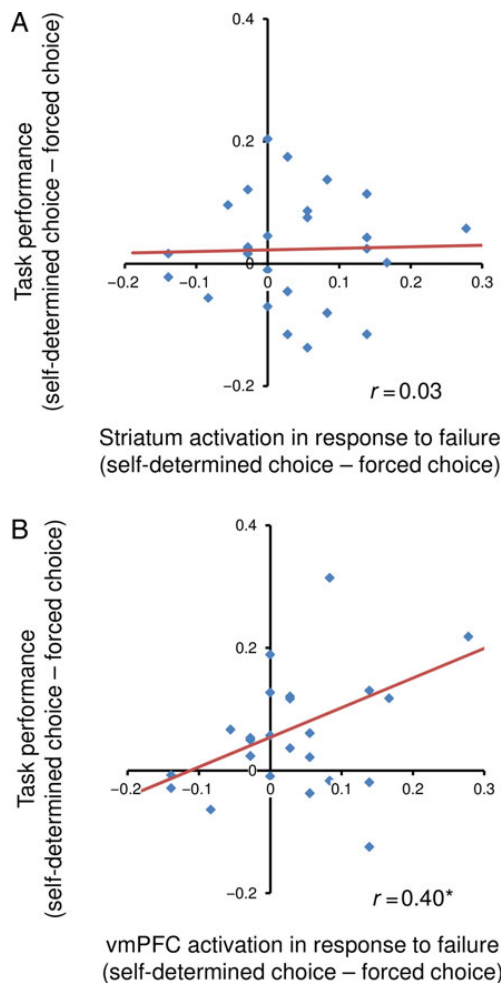


Figure 6. (A) Correlation between the promoted task performance due to self-determined choice (y-axis) and the magnitude of the striatum resilience in the self-determined-choice condition (computed by subtracting the β values in the forced-choice condition from the β values in the self-determined-choice condition in response to failure feedback; x-axis). No significant positive correlation was observed ($r = 0.03$, $P = 0.89$), indicating that the striatum may be unrelated to promoted performance and motivation due to self-determined choice. (B) Correlation between the promoted task performance due to self-determined choice (y-axis) and the magnitude of the vmPFC resilience in the self-determined-choice condition (computed by subtracting the β values in the forced-choice condition from the β value in the self-determined-choice condition in response to failure feedback; x-axis). Significant positive correlation was observed ($r = 0.40$, $P < 0.05$), indicating that those who showed less activation drop in the self-determined-choice condition in response to failure feedback tended to show enhanced task performance in the self-determined-choice condition.

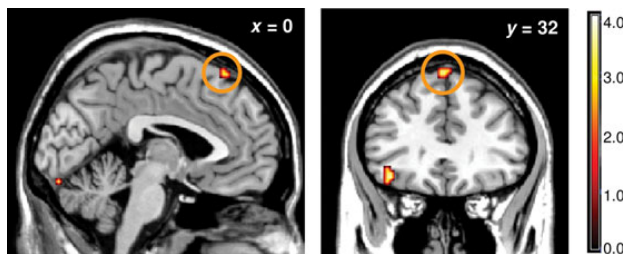


Figure 7. Pre-SMA responses elicited by self-determined-choice trials relative to forced-choice trials when participants initiated the task (i.e., when participants pressed a button; $P < 0.001$, uncorrected). Neural responses are displayed in coronal and transaxial formats.

Table 3
Effects of self-determined choice during task initiation period

Region	Peak MNI coordinates			t value	k
	x	y	z		
Self-determined choice > forced choice					
R/L. Presupplementary motor area	0	35	61	3.48	8
R. Middle temporal gyrus	66	-19	-17	4.98	30
R. Central orbitofrontal cortex	36	41	-11	3.84	10
L. Central orbitofrontal cortex	-39	32	-14	3.68	12
L. Middle temporal gyrus	-60	-10	-26	3.47	6
Forced choice > self-determined choice (No significant activation)					

Results of a whole-brain analysis showing higher activation in the self-determined-choice condition than in the forced-choice condition during the task initiation period (i.e., when participants started a stopwatch task; $P < 0.001$, uncorrected, $k \geq 5$ voxels). No areas showed significantly higher activation in the forced-choice condition than in the self-determined-choice condition. k , number of significant voxels.

brain region showed stronger activation in the forced-choice condition than in the self-determined-choice condition. Additional GLM model including task initiation time as a parametric modulator did not show any significant brain activations associated with the task initiation time ($P < 0.001$ uncorrected).

Functional Connectivity Analysis Between Cue and Feedback Periods

Finally, to explore possible mechanisms underlying the buffering effect of the self-determined choice in response to failure feedback, we conducted a functional connectivity analysis between the brain activation during the cue period and the vmPFC activation during the feedback period. We were especially interested in the connectivity in the self-determined-choice condition in response to failure feedback. Accordingly, we examined the brain areas whose activation during the cue period showed stronger functional connectivity with the vmPFC activation in response to feedback in the self-determined-choice/failure condition than in the other 3 conditions (i.e., self-determined-choice/success, forced-choice/success, and forced-choice/failure). We used the peak voxel from the vmPFC region that exhibited a significant interaction (Fig. 5) as the seed of the connectivity analysis. Given the exploratory nature of the analysis and relatively low statistical power to detect difference in functional connectivity across conditions, we used a relatively lenient threshold ($P < 0.01$, uncorrected, $k \geq 10$). Only 3 brain areas survived the statistical test, including the central orbitofrontal cortex, a brain area closely related to the vmPFC (Table 4). These results indicate that, when participants received negative feedback in the self-determined-choice condition, the within-person fluctuation of the OFC activation during the cue period is more positively correlated with that of the vmPFC activation during the outcome feedback period, than when participants received feedback in the forced-choice condition or when participants received positive feedback in the self-determined-choice condition.

Discussion

The current study provides the evidence that activation in the vmPFC in response to failure feedback for an achievement task is modulated by self-determined choice. More specifically, our neuroimaging results showed that self-determined choice (when compared with forced choice) prevented the drop in

Table 4

Brain areas that showed stronger functional connectivity with the vmPFC activation in response to negative feedback in the self-determined-choice condition (cue period)

Region	Peak MNI coordinates			<i>t</i> value	<i>k</i>
	<i>x</i>	<i>y</i>	<i>z</i>		
Self-determined choice > forced choice					
R. Central orbitofrontal cortex	21	29	-17	3.18	19
R. Superior frontal gyrus	24	14	67	3.12	39
L. anterior cingulate cortex	-6	20	-11	2.75	10

This functional connectivity analysis examined the brain activation during the cue period which has trial-by-trial connectivity with the vmPFC activation during the outcome feedback period. Results show a whole-brain analysis indicating stronger functional connectivity in the self-determined-choice condition with negative feedback than in the self-determined-choice condition with positive feedback and in the forced-choice condition with positive and negative feedback ($P < 0.01$, $k \geq 10$ voxels). *k*, number of significant voxels.

the vmPFC activation (i.e., negative reward value) in the face of failure feedback, and this was related to the enhanced task performance in the self-determined-choice condition. It is worth noting that participants knew that choice options were different only in their physical appearance, which is clearly irrelevant to task difficulty. Despite this subtle manipulation, we found that self-determined choice promoted task performance and modulated the vmPFC activation.

A critical question that arises is why the vmPFC activation did not drop in response to negative feedback in the self-determined-choice condition. When people ongoingly work on an achievement task, some failure is essentially unavoidable. Most literature in decision neuroscience assumes that such failures have immediate negative reward value, and in fact, failure has been regarded as the source of many psychiatric symptoms (e.g., depression; Seligman 1975). Studies which observed the drop in the vmPFC activation in response to negative feedback (relative to positive feedback) interpreted their findings based on this scheme (e.g., Daniel and Pollmann 2010). Yet negative feedback can serve to provide important information that may minimize further errors and improve people's performance in the long run (Carver and Scheier 1998). In other words, people can treat the negative feedback as useful information for improving their own future performance—this is referred to as interpreting feedback informationally (Ryan 1982; Deci and Ryan 1985). As such, to maintain optimal performance, it would appear that it is critical for people to offset the negative emotional value of failure by treating the feedback informationally and thus embracing the positive experience of using the feedback on their own behalf.

We speculate that this informational processing of negative feedback to be a critical mechanism underlying the facilitative effect of self-determined choice on performance. In fact, several behavioral studies have shown that self-determined choice reduces individuals' vulnerability to failure experiences (Mikulincer 1988; Moller et al. 2006; see also Legault and Inzlicht 2013). Thus, the absence of the drop in the vmPFC activation in response to failure may reflect the possibility that self-determined choice oriented people toward experiencing the negative feedback informationally, interpreting it in terms of its value for enhancing future performance and attaining future positive outcomes. In accord with this interpretation, there is substantial body of research indicating the role of the vmPFC in updating outcome value (Rolls 2004) or future outcome expectations (Schoenbaum et al. 2009). Our functional connectivity analysis also implied that trial-by-trial

fluctuation of choice value (as reflected in the OFC activation) predicted the extent to which participants were resilient to failure feedback in the self-determined-choice condition (as indicated by the smaller vmPFC decrease) more than it did in the other conditions.

It is important to note that our data showed the modulation effect of self-determined choice only in the vmPFC, and not in the striatum. The vmPFC and striatum are directly connected brain structures that have been strongly implicated in reward-related processing (Haber and Knutson 2010), but their functional dissociation has not been well documented in the literature, except for a relatively few cases (Hare et al. 2008; Knutson et al. 2001). We speculate that, in contrast to the vmPFC, the striatum may entail crude and automatic valuation processes that are relatively insensitive to the context. It has been well established in the psychological literature that the human evaluation process is supported by 2 qualitatively different systems—an automatic, general process and an elaborative, context-specific process (dual process model; Cacioppo and Petty 1985; Kahneman 2003; this dichotomy may possibly be related to the distinction between model-free and model-based mechanisms in reinforcement learning, which attracts recent attention in decision neuroscience; Daw et al. 2011; O'Doherty 2012). It is possible that this distinction may map onto the functional dissociation between the striatum and vmPFC observed in the present experiment. In fact, previous research indicated that initial crude evaluation is made in the ventral striatum/pallidum, whereas the vmPFC is involved in the re-organization of already formed evaluations initially mediated by the striatum (Kim et al. 2007; but see also Lieberman 2007). Another line of research also suggests a relation between the vmPFC and impulse control (Bechara et al. 2000). This idea is also consistent with the fact that the vmPFC has strong anatomical connection with the medial prefrontal cortex and ACC, both of which have been implicated in top-down modulation in the cognitive and affective value computation (Matsumoto et al. 2003; Botvinick et al. 2004). Although researchers have agreed that vmPFC activation is correlated with reward value, the precise nature of value representation in the vmPFC is still debated (Rushworth et al. 2011). At least, accumulating evidence suggests that the vmPFC represents more than a passive assessment of objective value (e.g., Boorman et al. 2009). Our findings may have potential to contribute to this ongoing discussion.

The insensitivity of the striatum to the outcome of self-determined choice, however, should be interpreted with caution. On the one hand, this insensitivity nicely corroborates with a recent study (Kool et al., 2013) examining the neural correlates of the classic phenomenon "illusion of control" (Langer 1975). In this study, participants showed higher estimates of reward probability for gambles they had chosen than for identical gambles that were imposed. Despite the increase in subjective reward probability, however, the striatal activation in response to outcome was unaffected by whether participants made a choice or not. On the other hand, there is a line of research showing that the striatal activation to outcome feedback is modulated by the perceived connection between action and outcome (Tricomi et al. 2004, 2006). For example, Tricomi et al. (2004) showed that, using a probabilistic task, the striatal activation decreased in response to punishment more in choice condition (i.e., participants could choose an option which they believe to lead to reward) than in no-choice

condition. Further studies are needed to examine the effects of self-determined choice on the striatal activation in response to outcome feedback.

Our experiment also replicated a previous study showing that anticipation of choice recruits activity in the dorsal ACC, insula, ventral pallidum, and midbrain (Leotti and Delgado 2011). Both the dorsal ACC and anterior insula have been implicated in a variety of cognitive and motivational functioning, such as cognitive control, conflict monitoring, and emotional awareness (Botvinick et al. 2004; Craig 2009). This suggests that self-determined choice requires emotional and cognitive commitment to the task. This conjecture is also consistent with a recent fMRI study showing that the anterior insula is related to self-determined reasons for behavior (Lee and Reeve 2013). The ventral pallidum and midbrain have been related to reward processing (Pessiglione et al. 2007; Mobbs et al. 2009), and as such, our findings suggest that there is inherent reward value in self-determined choice (Leotti and Delgado 2011). It should be noted, however, that our experiment has fewer self-determined-choice trials than forced-choice trials to control for item selection bias, and it is possible that the observed activation in response to the self-determined choice trials represents cue saliency (Litt et al. 2011). Although our findings were consistent with the previous study that controlled for cue saliency (Leotti and Delgado 2011), this issue should be addressed in future research. As another side note, we observed somewhat weaker activation in the ventral pallidum. This may reflect the fact that our experimental task has smaller incentive value than the task used in the previous study. Indeed, unlike the previous study, participants were not provided with any monetary rewards and were explicitly instructed that choice of stopwatch is irrelevant with task difficulty. Thus, self-determined choice did not convey any information about the immediate reward value in our experimental task.

An interesting finding for our exploratory analysis in the task initiation period (i.e., when participants press a button to start the task) is the pre-SMA activation in the self-determined-choice condition. Previous studies have indicated that the pre-SMA is involved in the initiation of self-generated action—action that people choose to perform without any external cues (Rushworth et al. 2004; Haggard 2008; Passingham et al. 2010). At a glance, this may lead people to think that the pre-SMA activation reflects self-generated action, as self-generated action seems to bear close resemblance to self-determined choice. Yet, the interpretation may not be as straightforward as it seems, because the task initiation was actually voluntary regardless of the choice conditions in our experiment—participants could freely determine the time to start the stopwatch in both the self-determined choice and forced-choice conditions. Perhaps our results indicate that not all the self-generated actions are equal: Even when people can determine the timing to initiate the same task, the subjective sense of freedom to initiate the task may be different depending on contextual factors such as task instructions. Future work would do well to examine factors that elicit subjective sense of self-determination in self-generated action.

The present study provided evidence that self-determined choice has beneficial effects on performance. Yet it is not entirely clear why self-determined choice has such an effect, even when people know that their choice is irrelevant to the ultimate outcome. This may reflect an evolutionarily innate human need for autonomy (Deci and Ryan 1985) or prior learning experiences in which self-determined choice led to

positive outcomes (learned belief in personal control; Huys and Dayan 2009). Work on separating these effects, although conceivably difficult, would greatly contribute to theoretical advancement in the fields of motivation and neuroscience.

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Notes

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References

- Amabile KM. 1996. Creativity in context: update to the social psychology of creativity. Boulder (CO): Westview Press.
- Atkinson JW. 1957. Motivational determinants of risk-taking behavior. *Psych Rev.* 64:359–372.
- Baayen RH, Davidson DJ, Bates DM. 2008. Mixed-effects modeling with crossed random effects for subjects and items. *J Mem Lang.* 59:390–412.
- Bechara A, Tranel D, Damasio H. 2000. Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain.* 123:2189–2202.
- Boorman ED, Behrens TE, Woolrich MW, Rushworth MFS. 2009. How green is the grass on the other side? Frontopolar cortex and the evidence in favour of alternative courses of action. *Neuron.* 62:733–743.
- Botvinick MM, Cohen JD, Carter CS. 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci.* 8:539–546.
- Cacioppo JT, Petty RE. 1985. Central and peripheral routes to persuasion: the role of message repetition. In: Alwitt L, Mitchell A, editors. *Psychological processes and advertising effects.* Hillsdale (NJ): Lawrence Erlbaum Associates. p. 91–111.
- Carver CS, Scheier MF. 1998. *On the self-regulation of behavior.* New York (NY): Cambridge University Press.
- Cordova D, Lepper M. 1996. Intrinsic motivation and the process of learning: beneficial effects of contextualization, personalization, and choice. *J Educ Psychol.* 88:715–730.
- Coricelli G, Critchley HD, Joffily M, O’Doherty JP, Sirigu A, Dolan RJ. 2005. Regret and its avoidance: a neuroimaging study of choice behavior. *Nat Neurosci.* 8:1255–1262.
- Craig AD. 2009. How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci.* 10:59–70.
- Daniel R, Pollmann S. 2010. Comparing the neural basis of monetary reward and cognitive feedback during information-integration category learning. *J Neurosci.* 30:47–55.
- Daw ND, Gershman SJ, Seymour B, Dayan P, Dolan RJ. 2011. Model-based influences on humans’ choices and striatal prediction errors. *Neuron.* 69:1204–1215.
- Deci EL, Ryan RM. 1985. *Intrinsic motivation and self-determination in human behavior.* New York (NY): Plenum.
- Delgado MR, Nearing KI, LeDoux JE, Phelps EA. 2008. Neural circuitry underlying the regulation of conditioned fear and its relation to extinction. *Neuron.* 59:829–838.

- De Martino B, Kumaran D, Holt B, Dolan RJ. 2009. The neurobiology of reference-dependent value computations. *J Neurosci*. 29:3833–3842.
- Esterman M, Tamber-Rosenau BJ, Chiu YC, Yantis S. 2010. Avoiding non-independence in fMRI data analysis: leave one subject out. *NeuroImage*. 50:572–576.
- Fliessbach K, Weber B, Trautner P, Dohmen T, Sunde U, Elger CE, Falk A. 2007. Social comparison affects reward-related brain activity in the human ventral striatum. *Science*. 318:1305–1308.
- Gläscher I, Daw N, Dayan P, O'Doherty JP. 2010. States versus rewards: dissociable neural prediction error signals underlying model-based and model-free reinforcement learning. *Neuron*. 66:585–595.
- Grubbs FE. 1950. Sample criteria for testing outlying observations. *Ann Math Stat*. 21:27–58.
- Haber SN, Knutson B. 2010. The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*. 35:4–26.
- Haggard P. 2008. Human volition: towards a neuroscience of will. *Nat Rev Neurosci*. 9:934–946.
- Hare TA, O'Doherty J, Camerer CF, Schultz W, Rangel A. 2008. Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *J Neurosci*. 28:5623–5630.
- Huys QJM, Dayan P. 2009. A Bayesian formulation of behavioral control. *Cognition*. 113:314–328.
- Izuma K, Saito DN, Sadato N. 2008. Processing of social and monetary rewards in the human striatum. *Neuron*. 58:284–294.
- Kable JW, Glimcher PW. 2007. The neural correlates of subjective value during intertemporal choice. *Nat Neurosci*. 10:1625–1633.
- Kahneman D. 2003. A perspective on judgment and choice: mapping bounded rationality. *Am Psychol*. 58:697–720.
- Kim H, Adolphs R, O'Doherty JP, Shimojo S. 2007. Temporal isolation of neural processes underlying face preference decisions. *Proc Natl Acad Sci USA*. 104:18253–18258.
- Kluger AN, DeNisi A. 1996. The effects of feedback interventions on performance: a historical review, a meta-analysis, and a preliminary feedback intervention theory. *Psychol Bull*. 119:254–284.
- Knutson B, Fong GW, Adams CM, Varner JL, Hommer D. 2001. Dissociation of reward anticipation and outcome with event-related fMRI. *Neuroreport*. 12:3683–3687.
- Koenigs M, Young L, Adolphs R, Tranel D, Cushman F, Hauser M, Damasio A. 2007. Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature*. 446:908–911.
- Kool W, Getz SJ, Botvinick MM. Forthcoming 2013. Neural representation of probability: evidence from the illusion of control. *J Cogn Neurosci*. 25:852–861.
- Langer EJ. 1975. The illusion of control. *J Pers Soc Psychol*. 32:311–328.
- Lee W, Reeve J. 2013. Self-determined, but not non-self-determined, motivation predicts activations in the anterior insular cortex: an fMRI study of personal agency. *Soc Cogn Affect Neurosci*. 8:538–545.
- Legault L, Inzlicht M. 2013. Self-determination, self-regulation, and the brain: autonomy improves performance by enhancing neuroaffective responsiveness to self-regulation failure. *J Pers Soc Psychol*. 105:123–138.
- Leotti LA, Delgado MR. 2011. The inherent reward of choice. *Psychol Sci*. 22:1310–1318.
- Leotti LA, Iyengar SS, Ochsner KN. 2010. Born to choose: the origins and value of the need for control. *Trends Cogn Sci*. 14:457–463.
- Lieberman M. 2007. Social cognitive neuroscience: a review of core processes. *Annu Rev Psychol*. 58:259–289.
- Litt A, Plassmann H, Shiv B, Rangel A. 2011. Dissociating valuation and saliency signals during decision-making. *Cereb Cortex*. 21:95–102.
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH. 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage*. 19:1233–1239.
- Matsumoto K, Suzuki W, Tanaka K. 2003. Neuronal correlates of goal-based motor selection in the prefrontal cortex. *Science*. 301:229–232.
- McArdle JJ, Anderson E, Birren JE, Schaie KW. 1990. Latent variable growth models for research on aging. In: Birren JE, Schaie KW, editors. *Handbook of the psychology of aging*. 3rd ed. San Diego (CA): Academic Press. p. 21–44.
- Mikulincer M. 1988. Freedom of choice, control, and learned helplessness. *J Soc Clin Psychol*. 7:203–213.
- Mobbs D, Hassabis D, Seymour B, Marchant JL, Weiskopf N, Dolan RJ, Frith CD. 2009. Choking on the money: reward-based performance decrements are associated with midbrain activity. *Psychol Sci*. 20:955–962.
- Moller AC, Deci EL, Ryan RM. 2006. Choice and ego-depletion: the moderating role of autonomy. *Pers Soc Psychol Bull*. 32:1024–1036.
- Montague PR, Berns GS. 2002. Neural economics and the biological substrates of valuation. *Neuron*. 36:265–284.
- Murayama K, Matsumoto M, Izuma K, Matsumoto K. 2010. Neural basis of the undermining effect of monetary reward on intrinsic motivation. *Proc Natl Acad Sci USA*. 107:20911–20916.
- Noonan MP, Mars RB, Rushworth MFS. 2011. Distinct roles of three frontal cortical areas in reward-guided behavior. *J Neurosci*. 31:14399–14412.
- O'Doherty JP. 2012. Beyond simple reinforcement learning: the computational neurobiology of reward-learning and valuation. *Eur J Neurosci*. 35:987–990.
- Passingham RE, Bengtsson SL, Lau HC. 2010. Medial frontal cortex: from self-generated action to reflection on one's own performance. *Trends Cogn Sci*. 14:16–21.
- Patall EA, Cooper H, Robinson JC. 2008. The effects of choice on intrinsic motivation and related outcomes: a meta-analysis of research findings. *Psychol Bull*. 134:270–300.
- Peele DB, Casey J, Silberberg A. 1984. Primacy of interresponse-time reinforcement in accounting for rate differences under variable-ratio and variable-interval schedules. *J Exp Psychol Anim B*. 10:149–167.
- Pessiglione M, Schmidt L, Draganski B, Kalisch R, Lau H, Dolan RJ, Frith CD. 2007. How the brain translates money into force: a neuroimaging study of subliminal motivation. *Science*. 316:904–906.
- Plassmann H, O'Doherty JP, Shiv B, Rangel A. 2008. Marketing actions can modulate neural representations of experienced pleasantness. *Proc Natl Acad Sci USA*. 105:1050–1054.
- Rissman J, Gazzaley A, D'Esposito M. 2004. Measuring functional connectivity during distinct stages of a cognitive task. *Neuroimage*. 23:752–763.
- Rolls ET. 2004. The functions of the orbitofrontal cortex. *Brain Cogn*. 55:11–29.
- Rushworth MFS, Noonan MP, Boorman ED, Walton ME, Behrens TE. 2011. Frontal cortex and reward-guided learning and decision-making. *Neuron*. 70:1054–1069.
- Rushworth MFS, Walton ME, Kennerley SW, Bannerman DM. 2004. Action sets and decisions in the medial frontal cortex. *Trends Cogn Sci*. 8:410–417.
- Ryan RM. 1982. Control and information in the intrapersonal sphere: an extension of cognitive evaluation theory. *J Pers Soc Psychol*. 43:450–461.
- Schoenbaum G, Roesch MR, Stalnaker TA, Takahashi YK. 2009. A new perspective on the role of the orbitofrontal cortex in adaptive behaviour. *Nat Rev Neurosci*. 10:885–892.
- Seligman MPE. 1975. *Helplessness: on depression, development, and death*. San Francisco (CA): Freeman.
- Sellitto M, Ciaramelli E, di Pellegrino G. 2010. Myopic discounting of future rewards after medial orbitofrontal damage in humans. *J Neurosci*. 30:16429–16436.
- Shohamy D. 2011. Learning and motivation in the human striatum. *Curr Opin Neurobiol*. 21:408–414.
- Tricomi EM, Delgado MR, Fiez JA. 2004. Modulation of caudate activity by action contingency. *Neuron*. 41:281–292.
- Tricomi EM, Delgado MR, McClelland BD, McClelland JL, Fiez JA. 2006. Performance feedback drives caudate activation in a phonological learning task. *J Cogn Neurosci*. 18:1029–1043.
- Van den Broeck A, Vansteenkiste M, De Witte H, Lens W. 2008. Explaining the relationships between job characteristics, burnout and engagement: the role of basic psychological need satisfaction. *Work Stress*. 22:277–294.
- Wager TD, Davidson ML, Hughes BL, Lindquist MA, Ochsner KN. 2008. Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*. 59:1037–1059.
- Weber B, Rangel A, Wibral M, Falk A. 2009. The medial prefrontal cortex exhibits money illusion. *Proc Natl Acad Sci USA*. 106:5025–5028.