

Striatal sensitivity to personal responsibility in a regret-based decision-making task

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Regret and relief are complex emotional states associated with the counterfactual processing of nonobtained outcomes in a decision-making situation. In the “actor effect,” a sense of agency and personal responsibility is thought to heighten these emotions. Using fMRI, we scanned volunteers ($n = 22$) as they played a task involving choices between two wheel-of-fortune gambles. We examined how neural responses to counterfactual outcomes were modulated by giving subjects the opportunity to change their minds, as a manipulation of personal responsibility. Satisfaction ratings to the outcomes were highly sensitive to the difference between the obtained and nonobtained outcome, and ratings following losses were lower on trials with the opportunity to change one’s mind. Outcome-related activity in the striatum and orbitofrontal cortex was positively related to the satisfaction ratings. The striatal response was modulated by the agency manipulation: Following losses, the striatal signal was significantly lower when the subject had the opportunity to change his/her mind. These results support the involvement of frontostriatal mechanisms in counterfactual thinking and highlight the sensitivity of the striatum to the effects of personal responsibility.

There is a growing appreciation that emotional responses and mood states have an impact on human decision making, and the neural substrates that underpin these interactions are an area of intense interest (Mellers, Schwartz, & Ritov, 1999; Slovic, Peters, Finucane, & MacGregor, 2005; Weber & Johnson, 2009). Decision making occurs in situations where the individual is required to choose one of a number of response options. In arriving at a deliberative decision, the individual must not only select one option, but reject the alternatives. If the outcomes on these alternative options become known to the subject, this information can modulate the evaluation of the obtained outcome. This phenomenon is known as *counterfactual thinking* (Roese, 1994, 1997; Zeelenberg, van Dijk, van der Pligt, et al., 1998). Specifically, when the subject has lost a gamble (i.e., obtained outcome is negative) and it is revealed that the alternative choice would have led to a better outcome (e.g., a win), negative affect is intensified. In processing this additional information, disappointment has become tainted by *regret*. Conversely, when the subject has won a gamble (i.e., obtained outcome is positive) and discovers that the alternative choice would have led to an inferior outcome (e.g., a loss), his/her positive affect is accentuated by *relief*. Counterfactual thinking requires one to mentally juxtapose

the representations of “what might have been” and the factual states of affairs, and its use confers a considerable advantage to individuals attempting to identify the optimal choice among an array of options (Bell, 1982; Zeelenberg, 1999).

Cognitive neuroscience has begun to explore the brain basis of these counterfactual processes. In healthy individuals, presentation of the nonobtained outcome is shown to modulate not just the self-report ratings of affect, but also psychophysiological indices of emotional processing, such as galvanic skin responses (Camille et al., 2004). Behavioral data indicate that these emotional responses feed back to influence ongoing choice; individuals select options that serve to minimize anticipated regret (Zeelenberg, 1999; Zeelenberg & Beattie, 1997; Zeelenberg & Pieters, 2004), and a neural network model showed improved performance if regret-based comparisons were incorporated (Marchiori & Warglien, 2008). In a group of patients with focal brain lesions affecting the orbitofrontal cortex (OFC), these counterfactual processes were abolished (Camille et al., 2004). This task involved repeated choices between two wheel-of-fortune gambles, where each wheel offered loss and gain outcomes at varying probabilities. On “partial feedback” trials, only the outcomes on the chosen wheel were revealed (eliciting

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disappointment and elation), and on “complete feedback” trials, the outcomes on both the chosen and nonchosen wheels were also revealed to the subject. The lesion patients experienced normal responses of elation and disappointment to obtained outcomes of winning and losing, respectively, but, unlike healthy controls, these responses were not modulated by the nonobtained outcome. The OFC patients also failed to alter their decisions in order to minimize regret outcomes. This was interpreted as evidence for a higher level role of the OFC in the integration of emotional responses with decisional processes.

The involvement of the OFC in regret has been supported by subsequent functional imaging studies. In adapting the Camille et al. (2004) task for fMRI, Coricelli et al. (2005) showed that the contrast of complete feedback and partial feedback trials detected a medial OFC response, which correlated with the objective difference between the nonobtained and obtained outcomes. Using a similar gambling task, Chua, Gonzalez, Taylor, Welsh, and Liberzon (2009) found no differences between trials expected to elicit relief and elation. However, regret, compared with disappointment, was associated with lateral OFC activation, where the response also correlated with the objective difference between the nonobtained and obtained outcomes. OFC responses were also observed in a modified task using avoidance of electric shocks rather than monetary gains and losses (Chandrasekhar, Capra, Moore, Noussair, & Berns, 2008).

The existing studies on the neural basis of regret have not thoroughly explored the close links between counterfactual processing and the attribution of personal responsibility. The experience of regret is greater when we feel responsible for making the decision that led to the outcome in question, with the degree of regret reflecting the extent to which we see ourselves as causal agents. This was initially highlighted in Kahneman and Tversky’s (1982) “actor effect.” In the paradigmatic example, subjects were presented with two scenarios involving a stockbroker sustaining a dramatic loss in his share portfolio. In Scenario A, the stockbroker has moved his stock from one company to another, whereas in Scenario B he considers moving his stock but decides against it. Subjects judge that the stockbroker in Scenario A will experience more regret, presumably because of his more active role in precipitating the negative outcome. Personal agency and self-blame are thus the critical elements in distinguishing regret from related emotions such as disappointment (Zeelenberg, van Dijk, & Manstead, 1998, 2000).

The previous study by Coricelli et al. (2005) contained a general manipulation of agency by including choice trials and “follow” trials, where the computer selected one gamble automatically. Although the ventral striatal responses to winning and losing (obtained) outcomes were significantly stronger on the choice trials than on the follow trials, their examination of regret effects was restricted to the choice trials, so the agency interactions with regret were not reported. The later experiment by Chua et al. (2009) did not manipulate agency but used trial-by-trial ratings to gauge subjects’ desire to reverse their decisions. These ratings were higher on regret trials and correlated with

outcome-related brain activity in the frontal polar region. The present experiment sought to characterize the effects of agency across choice trials by manipulating personal responsibility for the decision: We compared trials on which subjects had a brief window of opportunity to change their minds with trials that had no such opportunity, in order to evaluate the effects of nonobtained outcomes across both levels of personal responsibility. On the basis of previous research showing that the “degree of volition” for the action taken enhances the personal feeling of responsibility for the outcome (Lagnado & Channon, 2008; Shaver & Drown, 1986), we reasoned that the opportunity to change one’s mind in this way would modulate perceived responsibility for the decision. We hypothesized that on trials where the subjects had an option to change their minds, the subjective experience of regret and relief outcomes would be enhanced.

An apparent role for the OFC in counterfactual processing, as indicated by the human lesion and neuroimaging data, is consistent with broader functions of this region in representing goal values (Hare, Camerer, & Rangel, 2009; Hare, O’Doherty, Camerer, Schultz, & Rangel, 2008) and in emotion regulation (Beer, Heerey, Keltner, Scabini, & Knight, 2003; Koenigs & Tranel, 2007). However, there is also much evidence to indicate striatal sensitivity to the subjective impact of decision outcomes (Kable & Glimcher, 2007; Nieuwenhuis et al., 2005), and sectors of the striatum communicate extensively with the orbitofrontal region (Alexander, DeLong, & Strick, 1986; Haber, Kunishio, Mizobuchi, & Lynd-Balta, 1995). In considering the relative contributions of the OFC and striatum, one possibility is that the striatum performs a lower level function of encoding obtained outcomes (Coricelli et al., 2005) and/or errors of reward prediction (Hare et al., 2008). An alternative hypothesis is that the component of personal responsibility in regret processing may be instantiated at the level of the striatum, based on evidence that striatal responses are dependent on instrumentality (O’Doherty et al., 2004; Tricomi, Delgado, & Fiez, 2004). For example, an experiment by Tricomi et al. employed an oddball task in order to compare the neural response to monetary wins that were delivered at a fixed delay after a predictive stimulus versus a second condition where the volunteer was told that wins were dependent on a binary choice response. The dorsal striatum was selectively activated by monetary wins under the choice condition. This is compatible with animal studies showing striatal involvement in instrumental-action–outcome learning, contrasting with a role for the OFC in Pavlovian stimulus–outcome learning (Ostlund & Balleine, 2007). On the basis of this evidence for striatal involvement in coding instrumentality, we hypothesized that the modulatory effect of the personal responsibility manipulation would be instantiated at the level of the striatum.

In addition to the direct manipulation of personal responsibility across choice trials, there were two further methodological strengths of the present experiment. First, in contrast to the previous studies that regressed outcome-related brain responses against the objective difference between the nonobtained and obtained outcomes (Cori-

celli et al., 2005), we acquired self-report ratings during the scanning procedure itself, in order to regress brain activity onto subjective measures of counterfactual processing. Second, given evidence that regret is stronger on difficult decisions than on easy choices (Janis & Mann, 1977; Sugden, 1985; Zeelenberg & Pieters, 2007), where the subject has a high degree of confidence that he has picked the better choice, we constrained our decision trials to pairs of gambles that were rated as low certainty in behavioral piloting, in order to optimize the sensitivity of our task to regret-related neural changes.

METHOD

Subjects

Twenty-two healthy right-handed volunteers (7 males and 15 females; mean age = 36.7; SD = 16; age range = 20–65) were recruited from a volunteer panel. This sample was selected from a prior pilot study, involving 44 subjects, in which all subjects performed a similar version of the regret task. The 22 subjects selected from the pilot study were screened to exclude (1) history of psychiatric/neurological disorders according to DSM IV-TR, and (2) contraindications for MRI scanning. All subjects gave written informed consent, and the study was approved by the local research ethics committee (Rec 06/Q0102/51).

Experimental Design and Task

Subjects performed 112 trials of a gambling task involving real monetary wins and losses that were dependent on points acquired during the task. For ethical reasons, we paid the same amount to each subject by programming the computer to always assign £5 in total. Subjects were required to choose between two wheels displayed on a computer screen, involving combinations of four possible values (-210, -70, +70, +210) and two probabilities (0.5/0.5 and 0.25/0.75) (see Figure 1). On the basis of pilot data, 28 pairs of wheels were selected, involving decisions rated as difficult on the question “How sure are you that you made the best choice?” Each of these

pairs was presented four times in a pseudorandom order (hence, 112 trials total), with gamble position (left/right) also counterbalanced. The trial outcomes were rigged, so that the gambles were fair. However, the exact sequence of experienced *outcomes* varied according to individual choices on each trial. The gamble pairings with four values gave rise to 16 possible combinations of obtained and nonobtained outcomes. Two of these combinations (+210/+210 and +70/+70) were excluded from the model due to an insufficient number of ratings across all subjects, leaving 14 trial types with ratings data that were included in our parametric fMRI model (see below).

Subjects were instructed to select one of the two wheels by pressing the first or third button on a three-button box. On selection (max. 6 sec), the chosen gamble was highlighted with a red surround and gray background. Within the 6 sec, subjects could unselect and reselect either wheel by pressing the left or right key. To confirm their decision, subjects pressed the central key on the button box. If no response was detected within 6 sec, the computer selected the less optimal choice according to the expected value. On half of the trials, we asked the subjects to reevaluate their choices before the feedback was displayed, by giving them the opportunity to change their mind by pressing the central button. On trials on which the subject switched, the gray background moved to the new choice, but the red surround remained to highlight the original choice. Subjects had 3 sec to switch their choice, after which time the currently selected wheel would remain chosen. Following the selection phase, a small ball appeared within each of the wheels. The nonchosen wheel darkened, so that only the ball within the chosen wheel was visible. The balls then started bouncing randomly within the wheels and slowly came to a stop at an unpredictable area of each wheel within 5 sec, at which point the obtained outcome was revealed. This random method of “spinning” was designed to attenuate anticipatory processing. The obtained outcome was displayed for 1.5 sec, at which point the nonobtained outcome on the unchosen wheel was revealed, for a further 4 sec.

On 50% of trials, subjects were asked to provide satisfaction ratings after presentation of the obtained and nonobtained outcomes. A rating scale was presented below the pair of wheels, ranging from *very disappointed* (0, left of scale) to *very pleased* (1, right of scale). The cursor was initially placed at the middle of the scale, and the

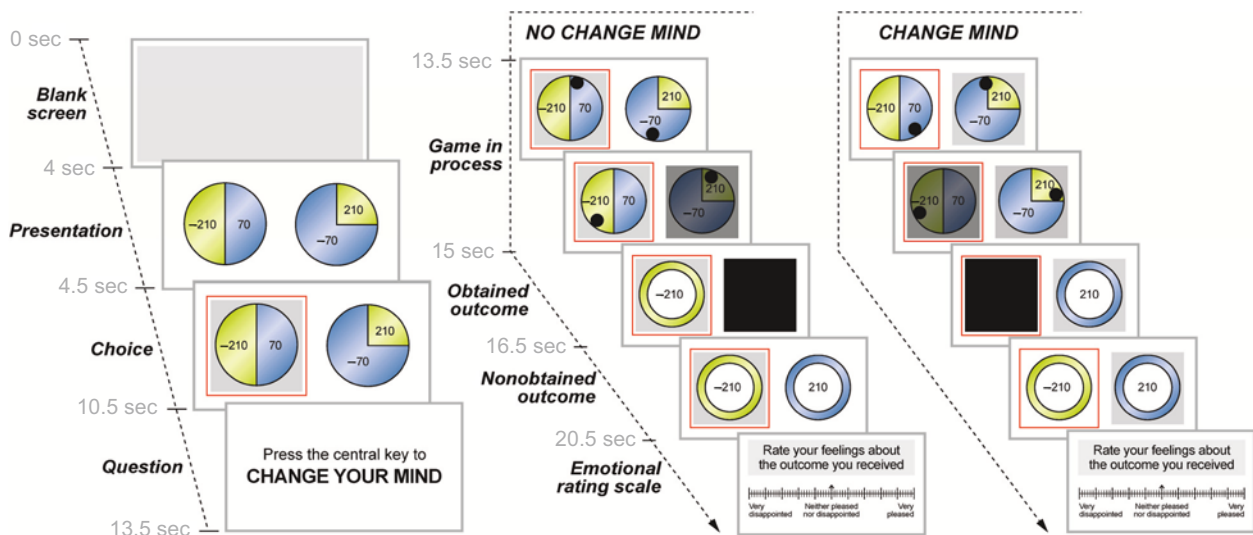


Figure 1. Two trials from the experimental task. On both trials, the subject initially selected the wheel on the left, indicated by the gray background and red surround (left column). On a “no-change” trial (middle column), the subject was given the opportunity to change his/her mind but maintained his/her original choice. The obtained outcome for this trial was -210, and the nonobtained outcome was +210 (i.e., a regret trial). On the “change mind” trial (right column), the subject was given the opportunity to change his/her mind and switched to the right wheel. The red surround remains with the original choice, but the gray background moves to the newly selected wheel. The obtained outcome for this trial was +210, and the nonobtained outcome was -210 (i.e., a relief trial).

subjects used a buttonpress (left or right) to move the cursor. The next trial commenced after an intertrial interval of 4 sec, during which time the cumulative points total was displayed.

Imaging Acquisition and Data Analysis

MR measurements were obtained using a Siemens MAGNETOM Trio, 3 Tesla scanner. After the acquisition of a T1-weighted scan, T2*-weighted echoplanar images, optimized for BOLD contrast, were acquired (32 transversal slices per volume were acquired with 30° anterior posterior angulation, TE 30 msec, TR 2,000 msec, flip angle 78°, matrix 64 × 64, field of view 192 × 192 mm, resolution 3 × 3 mm, slice thickness 3 mm, slice gap 25%). A preparation pulse (duration 1 msec, amplitude -2 mT/m) was used in the slice selection direction to compensate for through-plane susceptibility gradients for enhancement of imaging of OFC and medial temporal lobe regions (Deichmann, Gottfried, Hutton, & Turner, 2003). Data were analyzed using SPM5 (Wellcome Department of Imaging Neuroscience, University College London). Each subject's data were preprocessed using a standard procedure, which included motion and slice-timing correction, realignment, coregistration to a skull-stripped (using the Brain Extraction Tool; Smith, 2002) high-resolution structural scan (field of view 256 × 240 × 160 mm, matrix 256 × 240 × 160, resolution 1-mm isotropic, TR 2,250 msec, TI 900 msec, TE 2.99 msec, flip angle 9°), normalization into stereotaxic Montreal Neurological Institute (MNI) space, and smoothing with a Gaussian 8-mm full-width half-maximum filter. The time series were high-pass filtered (128 sec).

Three models were created at the first level. A first design matrix assessed brain responses to the obtained outcomes, distinguishing winning and losing outcomes. In the second model, brain activity was modeled to the onset of the nonobtained outcome, using two factors: whether the obtained outcome was positive or negative ("outcome") and whether the subjects were given the chance to change their minds or not ("personal responsibility"). Thus, four different trial types were modeled: wins where subjects had the opportunity to change their minds; wins where subjects did not have the opportunity to change their minds; losses where subjects had the opportunity to change their minds; and losses where subjects did not have the opportunity to change their minds. The following contrasts were performed at the first level: outcome positive versus outcome negative; outcome negative versus outcome positive; and the interaction between outcome and personal responsibility. In the third model, the brain response to the nonobtained outcome was modeled as a single condition of interest, and a parametric modulator was added to the single-subject design matrices. The aim of this analysis was to examine whether there was a linear relationship between subjective ratings for the outcome and BOLD signal. The parametric modulator was obtained in two steps. First, we averaged the ratings at the single-subject level for each of the 14 combinations of obtained and nonobtained outcomes (see above). We then used these 14 values to calculate a mean rating for each condition, across all subjects. We applied these numbers as a parametric modulator for each of the 14 conditions individually, obtaining a first-level matrix for every subject. A one-sample *t* test on the parametric modulator produced for each subject a contrast image, which was taken to a second-level analysis involving a one-sample *t* test in order to test for an effect at the group level.

In each of the three models, the contrast images from the first-level comparisons were taken into a second-level analysis involving one-sample *t* tests, in order to test for effects at the group level. For the whole-brain analyses, the threshold set for statistical significance was $p < .05$, corrected for familywise error rate (FWE). Region of interest (ROI) analyses were performed using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002). In order to examine the effects of personal responsibility on BOLD signal in reward-related circuitry, an ROI was defined on the basis of the right striatum cluster in Model 2 (size 443 voxels, peak in putamen, thresholded at $p < .05$ FWE), and two further ROIs were selected from the peak voxels in the article by Coricelli et al. (2005) in medial OFC ($x, y, z = -8,$

$32, -14$) and lateral OFC ($x, y, z = 42, 42, -18$) and defined as 5-mm spheres.

RESULTS

Behavioral Data

In order to examine the impact of the obtained and nonobtained outcomes on the associated subjective feeling, ratings obtained during the scanning session were subjected to a 2 × 2 repeated measures ANOVA with the factors obtained outcome (positive or negative) and nonobtained outcome (positive or negative). This revealed a significant main effect of obtained outcome [$F(1,21) = 71.4, p < .001$], due to higher ratings following a positive obtained outcome ($M = .66$) compared with a negative obtained outcome ($M = .38$). We also found a significant main effect of nonobtained outcome [$F(1,21) = 126, p < .001$], due to higher ratings following negative nonobtained outcomes ($M = .65$) compared with positive nonobtained outcomes ($M = .40$). There was no interaction between obtained outcome and nonobtained outcome [$F(1,21) = 0.45, p = .508$]. Thus, ratings were modulated by both the obtained (wins > losses) and the nonobtained outcomes. This analysis can also be expressed as a correlation between the ratings of satisfaction and the objective difference between the obtained and the nonobtained outcomes ($r = .93, p < .001$) (see Figure 2).

To test the hypothesis that personal responsibility influenced the subjective value attached to the outcomes, we performed an ANOVA with obtained outcome (positive vs. negative) and personal responsibility (opportunity to change mind vs. no opportunity) as factors. This analysis revealed main effects of obtained outcome [$F(1,21) = 2886, p < .001$] and personal responsibility [$F(1,21) = 14.5, p = .001$], but no significant interaction between these two factors [$F(1,21) = 1.75, p = .2$]. Post hoc analyses revealed a significant effect of personal responsibility in the loss condition [mean obtained negative/opportunity to change mind, .25; mean obtained negative/no opportunity, .27; $t(21) = -3.889, p = .001$], whereas the effect of personal responsibility in the win condition was not statistically significant [mean obtained positive/opportunity to change mind: .74; mean obtained positive/no opportunity, .75; $t(21) = -1.99, p = .06$]. Thus, subjective ratings were significantly modulated by personal responsibility in the loss condition, such that subjects reported feeling worse after a loss when they had been given the opportunity to change their mind.

fMRI Data

Effects of winning and losing on BOLD signal.

The contrast of all trials with a positive outcome against all trials with a negative outcome (Model 1) revealed significant increases in activation for wins compared with losses in the bilateral striatum, focused on the putamen (see Table 1). In the second model, testing brain responses modeled to the nonobtained outcome, the contrast of wins minus losses also revealed significant signal change in several striatal regions, including right putamen, left caudate, and left pallidum (see Figure 3).

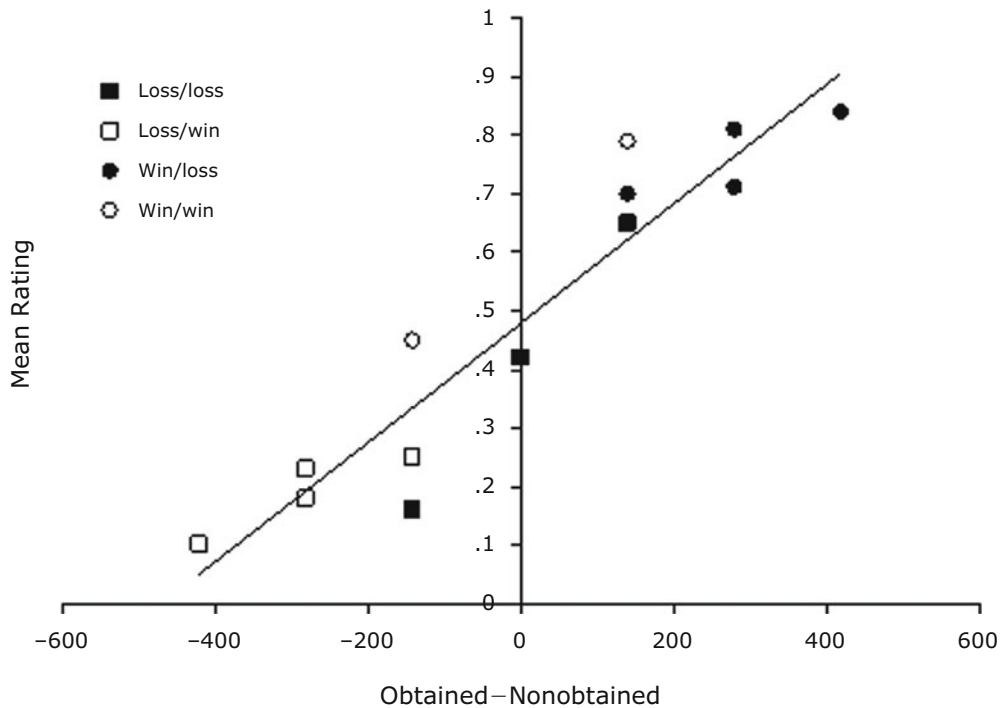


Figure 2. Scatterplot showing the effect of counterfactual reasoning on subjective ratings of satisfaction, as a function of the magnitude of the difference between the obtained and nonobtained outcome. There is a linear positive correlation between average subjective rating and the difference between the obtained and nonobtained outcomes across the 14 trial types. The four types of data point indicate the four combinations of obtained and nonobtained outcomes, respectively. Both the $-210/-210$ and $-70/-70$ conditions were rated equally (.42).

There were no regions sensitive to the interaction between outcome and personal responsibility at the whole-brain level. There were no areas in either model where signal change was significantly greater on losses compared with wins.

Next, we explored whether the satisfaction ratings predicted variation in BOLD response in a whole-brain analysis. Several areas showed a significant positive correlation between subjective rating and BOLD response (Model 3), including several clusters in the bilateral striatum (caudate and putamen) and the left OFC ($x, y, z = -28, 40, -10$) (Table 2 and Figure 4). There were no significant regions in the reverse contrast—that is, areas showing a signifi-

cant negative correlation between subjective rating and BOLD signal.

Effect of personal responsibility on reward-related BOLD signal. In order to examine the effect of personal responsibility on win- and loss-related BOLD signal in reward-related circuitry, we examined the interaction between the factors personal responsibility (opportunity to change mind vs. no opportunity) and outcome (positive or negative) in three ROIs in the striatum, the medial OFC, and the lateral OFC. The striatal ROI was a functional cluster with a peak in the putamen (MNI 12, 10, -2) (but extending into adjacent subdivisions of the striatum) defined from the win-minus-loss con-

Table 1
Brain Areas Where BOLD Signal Was Greater on Winning Outcomes Compared With Losing Outcomes

Brain Region	Side	x	y	z	Z Score	Cluster Size
A. Responses Modeled to the Onset of the Obtained Outcome (Model 1)						
Putamen	R	24	10	-6	5.49	247
	L	-22	6	-8	4.99	44
B. Responses Modeled to the Onset of the Nonobtained Outcome (Model 2)						
Hippocampus	R	32	-16	-12	5.61	33
Superior temporal pole	R	58	2	-8	5.57	36
Putamen	R	12	10	-2	5.48	443
Pallidum	L	-10	4	-2	5.16	35
Superior frontal gyrus	L	-24	-12	60	5.09	12
Caudate	L	-20	6	26	5.06	30

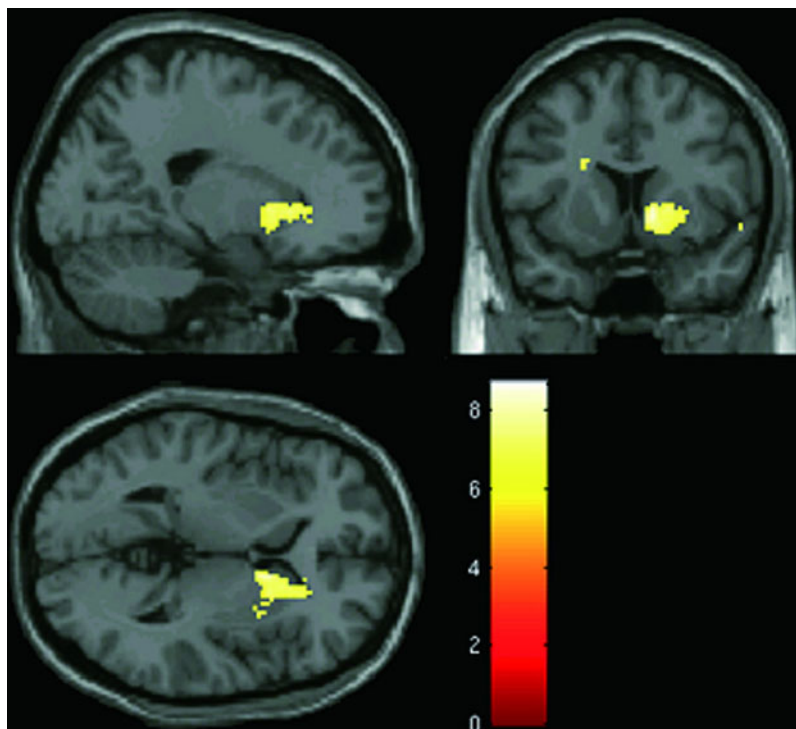


Figure 3. Areas showing significantly increased activation for wins relative to losses (Model 2). The cluster displayed here is located in the right putamen (MNI coordinates 20, 10, 2; whole-brain analysis, $p < .05$ FWE corrected).

trast in the model fitted to the presentation of the non-obtained outcome ROI. The ANOVA model revealed a significant interaction between personal responsibility and obtained outcome [$F(1,21) = 11.8, p < .05$]. There was no significant main effect of personal responsibility [$F(1,21) = 3.00, p = .098$], and there was a significant main effect of outcome [$F(1,21) = 68.3, p < .001$] that is inherent, given the contrast used to define the ROI. To qualify the interaction effect, we performed two post hoc *t* tests comparing the difference in BOLD signal in the striatum across the two levels of personal responsibility, separately for positive and negative obtained outcomes. These tests revealed a significant effect of personal responsibility for negative obtained outcomes [$t(21) = -2.99, p < .01$] but no significant effect of personal responsibility for positive obtained outcomes [$t(21) = 0.396, p = .696$]. On loss trials, signal change in the putamen was exacerbated (i.e., more negative) on trials when subjects had the opportunity to change their mind relative to trials with no opportunity (Figure 5). In the signal extracted from medial OFC, the main effect of outcome approached significance [$F(1,21) = 4.11, p = .055$], with a higher signal on average on wins than on losses, but there was no main effect of personal responsibility [$F(1,21) = 0.799, p = .381$] and no personal responsibility \times outcome interaction [$F(1,21) = 1.04, p = .319$]. In the signal extracted from lateral OFC, there was a significant main effect of outcome in the lateral OFC [$F(1,21) = 6.66, p = .017$], due to higher signal on wins than on losses, but there was no main effect of personal

responsibility [$F(1,21) = 0.520, p = .479$] and no interaction between personal responsibility and outcome [$F(1,21) = 1.45, p = .242$].

DISCUSSION

The present study aimed to characterize the neurophysiological mechanisms supporting counterfactual thinking, using fMRI. More specifically, we sought to identify brain regions sensitive to Kahneman and Tversky's (1982) "actor effect" by using a manipulation of personal responsibility (giving subjects the opportunity to change their minds on some trials) to isolate brain regions where counterfactual processing was modulated by agency. Two strengths of our task design were that we constrained our gamble decisions to difficult pairings, in order to maximize our task's sensitivity to regret and relief, and we obtained satisfaction ratings on a proportion of trials in order to regress brain activity onto the subjective impact of the nonobtained outcomes. These emotional ratings demonstrated that the affect associated with winning and losing outcomes was significantly modulated by the nonobtained outcome, and satisfaction ratings were highly correlated with the difference between the obtained and nonobtained outcomes. Thus, our task was successful in eliciting counterfactual processing consistent with the phenomena of regret and relief. Furthermore, our manipulation of personal responsibility significantly modulated subjective ratings of regret, such that subjects reported feeling worse after losing when they had been given the opportunity to

Table 2
Brain Areas Where BOLD Signal Was Predicted
by the Subjective Satisfaction Ratings (Model 3)

Brain Region	Side	x	y	z	Z Score	Cluster Size
Superior temporal gyrus	R	56	4	-8	5.98	74
	L	-56	-2	-6	5.21	17
Hippocampus	R	34	-16	-10	5.96	1,112
	L	-30	-14	-12	5.34	83
Caudate	L	-22	12	22	5.80	263
	R	22	32	-4	5.38	109
Putamen	R	36	-6	-2	5.73	632
	L	-20	16	-10	5.13	60
Postcentral gyrus	R	34	-36	38	5.70	42
	R	48	-22	36	5.37	20
	R	20	-74	2	5.32	28
	R	14	-34	68	5.12	15
	L	-46	-10	40	4.98	12
Middle temporal gyrus	L	-40	-70	18	5.56	237
Superior occipital gyrus	L	-18	-70	36	5.46	89
Fusiform gyrus	R	26	-78	-16	5.45	81
	R	24	-80	-4	4.91	13
Inferior frontal gyrus	L	-42	32	14	5.23	31
Inferior temporal gyrus	R	46	-42	-20	5.17	15
Thalamus	R	22	-22	12	5.12	41
Cerebellum	R	0	-74	-34	5.11	37
Middle frontal gyrus	R	28	46	24	5.06	14
Inferior occipital gyrus	R	48	-76	-6	5.03	31
Superior parietal gyrus	R	24	-58	60	5.03	12
	L	-26	-50	58	4.99	14
Middle occipital gyrus	L	-24	-82	18	4.99	11
Middle frontal gyrus (orbital)	L	-28	40	-10	4.97	21

change their mind, relative to when they did not have the opportunity to revise their decision.

In the fMRI data, the direct contrasts of winning and losing outcomes (Models 1 and 2) identified substantial signal change in the striatal region, focused on the putamen, but with no significant activation in the OFC region. These striatal effects support a range of previous neuroimaging studies identifying differential responses to winning and losing outcomes in the striatum (see Delgado, 2007, for a review) and serve as a proof-of-concept finding for our (more complex) decision-making task. A model that utilized the subjective ratings as a parametric modulator of brain activity identified a more distributed network, including both the striatum (putamen, caudate) and the OFC, where activity correlated positively with the satisfaction ratings. In addition, signal change in the putamen was sensitive to the manipulation of personal responsibility: After losing, apparent deactivations in a right putamen ROI were significantly greater on trials on which subjects were given the opportunity to change their minds, compared with loss trials without this opportunity. Notably, we did not find modulatory effects of personal responsibility in ROIs in the medial or lateral OFC, or when the obtained outcomes were positive. Thus, the modulatory effects of personal responsibility on counterfactual processing were primarily detected under conditions of regret (rather than relief) and were instantiated at the neural level in the striatum.

Obtained outcomes in decision making can inform future choice via (at least) two distinct mechanisms. The first is an evaluation of the difference between the observed and the expected outcome, known as *prediction error*. Striatal involvement in coding prediction errors has been demonstrated in human studies with fMRI (McClure, Berns, & Montague, 2003; Seymour, Daw, Dayan, Singer, & Dolan, 2007) as well as electrophysiological recording from midbrain dopamine neurons that project into striatum (Hollerman & Schultz, 1998; Schultz, 2002). The second mechanism is a counterfactual comparison of whether choice of the alternative option would have led to a better or worse obtained value. Experiences of regret and relief facilitate future decisions between similar options (Bell, 1982; Zeelenberg, 1999). The findings of the present article highlight a role of the striatum in these counterfactual thinking mechanisms that support value estimation. On the one hand, our results indicate both striatal and OFC involvement in the subjective impact of nonobtained outcomes; on the other hand, according to ROI analysis, the brain signal in the striatum but not in the OFC was modulated by personal responsibility.

Our observed effect of loss outcomes in the putamen is consistent with previous data showing striatal deactivations to negative outcomes (Delgado, Locke, Stenger, & Fiez, 2003; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Liu et al., 2007), including studies that have reported loss-related deactivation compared with a neutral feedback

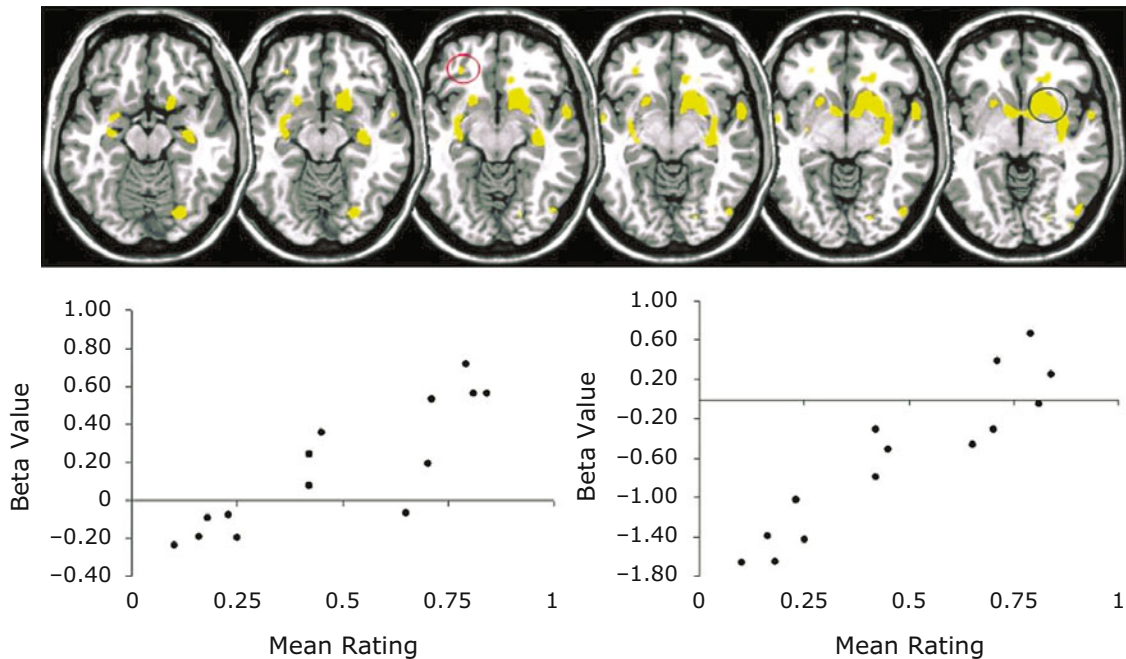


Figure 4. Statistical parametric map (SPM) showing areas in which BOLD signal was significantly positively modulated by subjective ratings (whole-brain analysis, $p < .05$ FWE corrected). The SPM shows activation in the left orbito-frontal cortex (OFC) (red circle, MNI coordinates $-28, 40, -10$) and the right putamen (black circle, MNI coordinates $16, 12, -4$). The scatterplots display the positive linear relationship between average subjective ratings and parameter estimates in the left OFC (left graph) and right putamen (right graph). The mean subjective rating for each condition (each combination of obtained and nonobtained outcomes) is plotted on the x -axis. The mean parameter estimate for each condition is plotted on the y -axis. To obtain the mean parameter estimates, first-level models were created in which each condition was modeled separately, and parameter estimates (beta values) were extracted using MarsBaR and averaged across all subjects.

baseline (Delgado et al., 2000). These striatal responses are closely linked to the subjective impact of the outcomes. For example, striatal responses are sensitive to individual discount functions—that is, the subjective value of delayed monetary rewards (Kable & Glimcher, 2007)—and

to the framing context in which a reward or punishment is presented (Nieuwenhuis et al., 2005). Moreover, these striatal responses are dependent on instrumental action: Reward-related responses in caudate were observed only when subjects believed that their actions were linked to

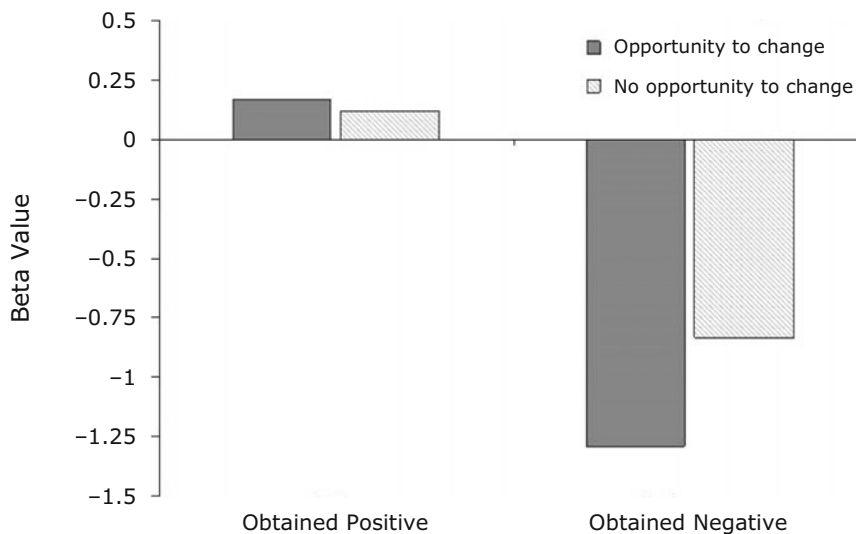


Figure 5. Mean parameter estimates in the right putamen ROI for wins (positive obtained outcomes) and losses (negative obtained outcomes) according to agency (whether subjects were given the opportunity to change their mind).

their obtained outcome (Elliott, Friston, & Dolan, 2000; O'Doherty et al., 2004; Tricomi et al., 2004). For example, the study by Liu et al. reported stronger *deactivation* of the striatum to losing outcomes that occurred as a result of a response omission. Our findings are also congruent with previous work showing that the hedonic response to gambling outcomes is modulated by choice and agency. For example, on a modified slot-machine task involving win and no-win outcomes (but not losses), subjects reported greater pleasure at winning outcomes that derived from the subject's own choice compared with wins of identical financial magnitude, selected automatically by the computer (Clark, Lawrence, Astley-Jones, & Gray, 2009). No correlates of this effect were observed in an fMRI experiment using the same task. However, the previous fMRI study of regret by Coricelli et al. (2005) used an elegant 2×2 factorial design to assess a similar manipulation of agency (choose vs. follow trials) crossed with the effect of the nonobtained outcome (complete feedback vs. partial feedback). The comparison of "choose" and "follow" trials detected significant modulation of the ventral striatal response to obtained outcomes, such that ventral striatal activation to wins, and deactivation to losses, were primarily observed in the choose condition. The present data support this striatal sensitivity to a different agency manipulation, but this was statistically significant only on loss outcomes. Other studies indicate stronger psychological, and neural, effects of losses compared with gains of similar magnitude (Chua et al., 2009; Rao, Korczykowski, Pluta, Hoang, & Detre, 2008).

In the Coricelli et al. (2005) study, the follow-up analyses of the counterfactual outcomes (complete feedback vs. partial feedback trials) were confined to the choice trials, using the value of the nonobtained outcome as a parametric regressor. Regret and relief were associated with signal in the medial OFC: This region showed increasing activation on loss trials as a function of the size of the nonobtained outcome (i.e., regret) and increasing deactivation on gain trials as a function of the size of the forgone outcome (i.e., relief). The present data failed to confirm a response in the medial OFC region, using an ROI sphere derived from the peak voxel in the Coricelli et al. study. The statistical comparisons are considerably different, given that we focused on a more subtle agency manipulation (of personal responsibility for the decision) and did not include the partial feedback condition. The medial OFC is also susceptible to signal drop-out in fMRI studies at 3 Tesla, and although we took steps to minimize these artifacts (Deichmann et al., 2003), it remains possible that this underlies our failure to replicate. We did detect a more lateral ($x = -28$) OFC cluster (as well as activity elsewhere), correlated positively with the difference between the obtained and nonobtained outcomes. We assume that this OFC response is at least partly consistent with a lateral OFC response in the Coricelli et al. study, in a separate analysis of outcome-related activity on win and loss trials, regressed against the difference between the nonobtained and obtained outcomes. The study by Chua et al. (2009) also detected a lateral OFC response in the contrast of regret and disappointment trials (but no differ-

ence between relief and elation), and activity in this region also correlated with the difference between nonobtained and obtained outcomes.

Counterfactual reasoning and the experience of regret play an adaptive role in decision-making processes, both by guiding one's selection toward the optimal choice and by helping one to learn from past experience. Previous evidence from lesion neuropsychology (Camille et al., 2004) and functional imaging (Coricelli et al., 2005) has implicated the OFC in regret. The present data show that the striatum, like the OFC, is also sensitive to the comparison of obtained and nonobtained outcomes. The relative involvement of these two regions in regret-related decision making is not known, but our data highlight a more selective sensitivity of the striatum to personal responsibility for the decision. The striatum is widely implicated in reinforcement learning mechanisms, an involvement more obvious in the dorsal striatum (i.e., caudate, putamen) when learning involves actions rather than simply passive events. One interpretation might be that the activity in the striatum following a nonoptimal decision plays a key role in guiding future action selection toward more valuable options, or in inhibiting the selection of less valuable options. Striatal activity may be modulated more or less strongly, depending on whether the context is action oriented or not (Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008). Our manipulation of personal responsibility also modulated subjective ratings in the present data, and in the absence of data on the effects of focal basal ganglia damage we cannot be sure of the causal role of the striatum in the effects of agency in this form of decision making. Nevertheless, by combining fMRI and subjective measures of regret, we have been able to establish an association of this emotional state with activity in frontostriatal pathways.

AUTHOR NOTE

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