Distinct Orbitofrontal Regions Encode Stimulus and Choice Valuation

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Abstract

■ The weak axiom of revealed preferences suggests that the value of an object can be understood through the simple examination of choices. Although this axiom has driven economic theory, the assumption of equation between value and choice is often violated. fMRI was used to decouple the processes associated with evaluating stimuli from evaluating one's actions. Whereas activity in left posterior areas of the orbitofrontal cortex (OFC) was associated with processing the objective value of stimuli, activity in medial anterior areas of the OFC was associated with accepting high value gambles and rejecting low value gambles; that is, making correct decisions. These data demonstrate that distinct areas of the OFC provide dissociated representations for use in adaptive decision-making and suggest an important processing distinction between the concepts of good/bad and right/wrong. ■

INTRODUCTION

The analysis of choice is at the heart of behavioral economics. Informed by the weak axiom of revealed preferences, it is often assumed that the analysis of choice behavior can be used to determine the values that people attribute to various objects and situations (Varian, 1992; Samuelson, 1938); that is, a comprehensive understanding of how costs and benefits are weighed and how preferences develop can be achieved by studying instances when people choose one option over another. However, the conceptual mapping between preferences and behavior is far from perfect. For example, classic research on preference reversals suggests that there is a discrepancy between how much people would be willing to pay to play each of two gambles and their response when they are asked which of the two gambles they would prefer to play. People are willing to pay more for one gamble but prefer to play the other (Grether & Plott, 1979; Lichtenstein & Slovic, 1971). Although these inconsistencies can be attributed to differences in the information participants attend to during different tasks (Slovic & Lichtenstein, 1968), they suggest that the processes by which people evaluate stimuli may be qualitatively different from the ones used to evaluate the actions associated with their decisions (Tversky, Slovic, & Kahneman, 1990). From this perspective, decision-making involves two conceptually related, but distinct, aspects: the evaluation of stimuli and the evaluation of one's actions with respect to the options available.

Although the neural processes underlying decision-making are diffuse, areas of the orbitofrontal cortex (OFC) appear to play a critical role in processing rewards and punishments (Knutson, Fong, Bennett, Adams, & Hommer, 2003; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). For example, similar patterns of OFC activation are observed for both the anticipation and prediction of rewards and for the actual receipt of rewards (Rolls, McCabe, & Redoute, 2008; Gottfried, O'Doherty, & Dolan, 2003). This OFC activity is evident for primary rewards such as food or drink (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Rolls, 2000), as well as symbolic rewards, such as money (Tom, Fox, Trepel, & Poldrack, 2007; Elliott, Newman, Longe, & William Deakin, 2003; Knutson et al., 2003). OFC activity has also been linked to the evaluation of the relative appropriateness of one's responses, activating both to receiving rewards and avoiding punishments (Kim, Shimojo, & O'Doherty, 2006). Although it is difficult to determine from existing data whether this activity reflects affective and goal-directed aspects of decision-making (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Plassmann, O'Doherty, & Rangel, 2007; Bechara, Damasio, Damasio, & Lee, 1999) or only the calculations of value (Fellows & Farah, 2007; Padoa-Schioppa, 2007; Padoa-Schioppa & Assad, 2006), these studies clearly suggest that the OFC provides a representation of a ''common currency'' that aids decision-making across stimulus modalities (Montague, King-Casas, & Cohen, 2006).

Although the OFC has traditionally been treated as a homogenous region (BA 11), recent work suggests this structure is composed of functionally distinct subregions that may be involved in different aspects of valuation

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(Öngür & Price, 2000). A recent meta-analysis has suggested that medial areas of the OFC are associated with reward monitoring, whereas lateral areas appear to play a role in evaluating punishment (Kringelbach & Rolls, 2004). Likewise, an anterior–posterior division has been proposed, suggesting that anterior regions of the OFC process more abstract representations of value than posterior regions (Kringelbach, 2004). The anatomical connections associated with the OFC provide further support for this functional division, with the anterior OFC sharing connections to higher-order prefrontal cortical regions and the posterior OFC more closely linked to subcortical structures such as the amygdala (Öngür & Price, 2000). If the anterior–posterior division represents differences in the relative abstractness of value, the evaluation of stimuli and actions may be computed in functionally distinct regions of the OFC. Whereas posterior OFC regions are well situated to represent stimulus value, anterior OFC regions are well placed to link these stimulus properties with response options and goals. In other words, posterior regions may provide a representation of the goodness/badness of stimuli, whereas anterior regions provide a representation of the rightness/wrongness of actions.

To examine the distinct processes involved in the evaluation of stimuli and the evaluation of actions, we constructed a series of 50/50 gambles (Tom et al., 2007) that manipulated expected reward and punishment. Gambles were presented as stimuli resembling vitamins, with two colors representing two equally probable outcomes, a gain and a loss. The magnitude of gains and losses was orthogonally manipulated such that the values reflected bivariate evaluative space (Cacioppo & Berntson, 1994). Although each gamble involved the potential for some degree of reward or punishment, some gambles were objectively better or worse than others. Unlike Tom et al. (2007), we constructed the magnitudes of these gambles such that half would be relatively good and half would be relatively bad so that, on average, participants would accept half the gambles and reject half the gambles. Further, some of the objectively better gambles were more clearly good and some of the objectively worse gambles were more clearly bad. In other words, some decisions were more clearly right and some were more clearly wrong. In accordance with anteriorization hypotheses of prefrontal function (Amodio & Frith, 2006; Kringelbach, 2004), we predicted that stimulus evaluation would recruit more posterior areas of the OFC, whereas action evaluation would recruit more anterior areas of the OFC.

METHODS

Participants

Data from 16 participants (5 men, mean age = 22.2 years, range = 18–29 years) were used for analysis. Participants reported no abnormal neurological history and had normal or corrected-to-normal vision. Two participants were excluded for not learning the evaluative dimensions up to criterion. An additional participant was removed for responding randomly in the second half of the task. Participants were compensated with $40.

Procedure

Prior to scanning, participants performed a 10-min computer task designed to provide experience with the gambling task to be used in the fMRI scanner. To promote engagement in the task, participants were presented with stimuli resembling multicolored vitamins and were instructed to ''eat'' (accept) or ''pass'' (reject) each vitamin with the goal of maximizing a running health score. The saturation of one color represented the magnitude of potential gains and the saturation of the other color represented the magnitude of potential losses. Potential gains were 1, 4, 7, or 10 points. Similarly, potential losses were 1, 4, 7, or 10 points (see Figure 1A). Although participants were encouraged to earn as many points as possible, monetary compensation was not contingent on performance. Color and gain/loss was counterbalanced across participants. Participants were informed that on each gamble there was a 50% chance of receiving the reward value (gaining points) and a 50% chance of receiving the punishment value (losing points). Furthermore, participants were informed that the color of the vitamin could be used to determine whether the value of the positive outcome was large enough to outweigh the risk of the negative outcome. Using this information, the participant's task was to determine whether the potential gain was worth risking the potential loss and decide whether to accept or reject the gamble. Participants began with 100 points. On each trial, a fixation cross appeared for 2500 msec followed by a gamble for 2000 msec. Participants had 2000 msec to decide whether they wanted to accept or reject the gamble. If the participant accepted the gamble, the number of points gained or lost was presented for 2000 msec, and this value was added to the participant's running tally. If the participant rejected the gamble, the number of points that would have been gained or lost was presented, but this value was not added to the running tally. After each trial, the running tally was presented. Following training, participants were able to articulate the rules governing the stimulus–outcome contingencies.

Following training, participants completed the gambling task in the scanner environment. The scanner task was nearly identical to the training task with a few minor adjustments. First, participants did not receive their updated score at the end of each trial, although this information was provided at the end of each functional scanning run. Second, the timing of fixation crosses was adjusted to allow for the estimation of the hemodynamic

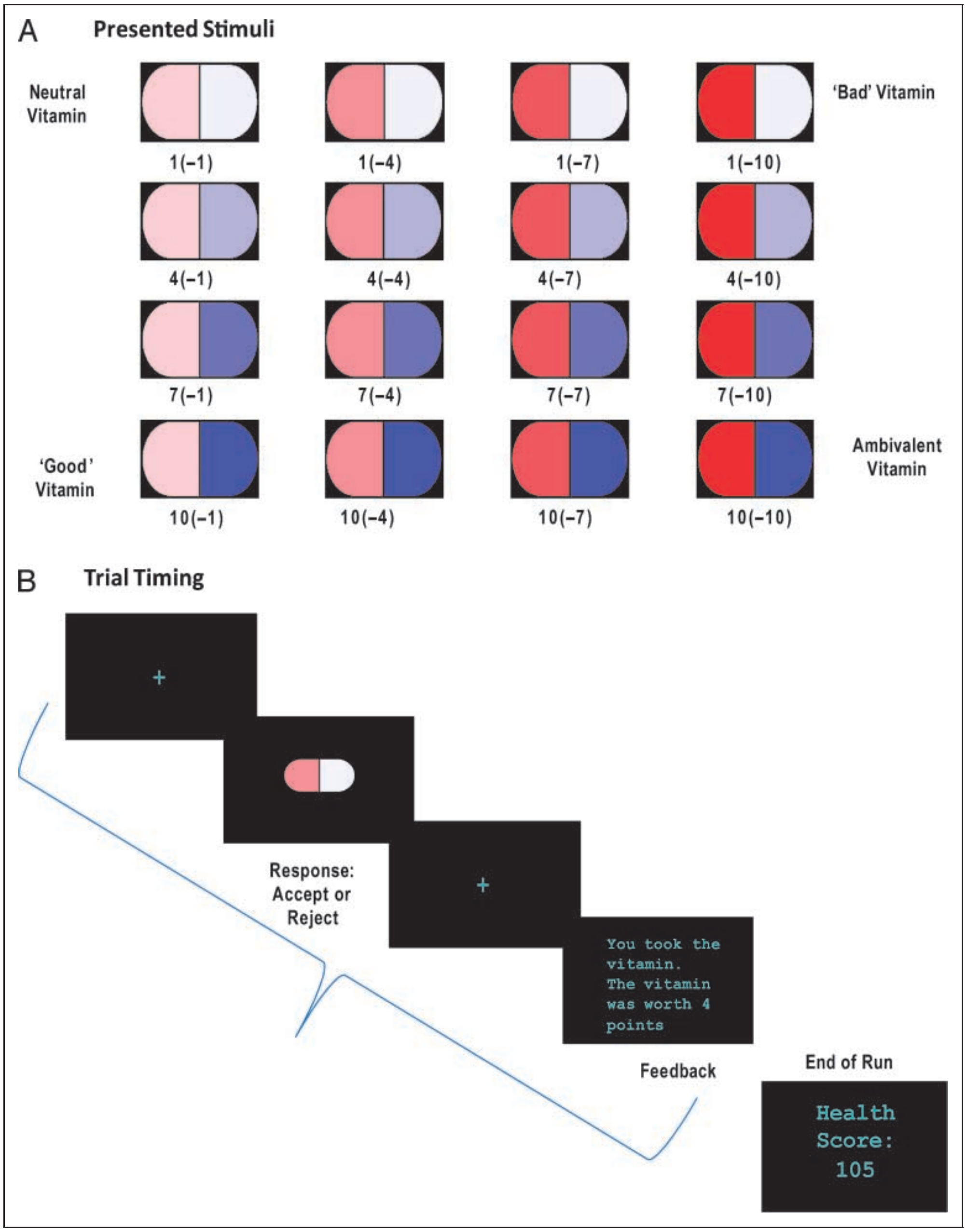


Figure 1. (A) Presented stimuli with associated gain and loss values. (B) Trial structure.

signal. Specifically, the fixation crosses between presented gambles and feedback appeared in a pseudorandom order for 2, 4, or 6 sec. Further, the fixation crosses between trials appeared in a pseudorandom order for 4, 6, or 8 sec (see Figure 1B). Eight functional runs of data were collected. In each run, participants made decisions regarding 16 gambles, providing 128 trials.

fMRI Parameters

All imaging was conducted with a Siemens 3-T scanner. For whole-brain functional coverage, 32 axial slices (slice thickness = 3.5 mm, 0.5 mm skip) were prescribed parallel to the AC–PC line. Nearly isotropic functional images were acquired from inferior to superior using a single-shot, gradient-echo, echo-planar pulse sequence (TE = 25 msec, TR = 2 sec, in-plane resolution = 3.5 × 3.5 mm, matrix size: 64 × 64, and FOV = 224 mm).

fMRI Processing

Data were prepared for analysis using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Data were first corrected for slice-acquisition time and motion (using the additional unwarping procedures) using SPM default settings. Data were then transformed to conform to the default EPI Montreal Neurological Institute (MNI) brain interpolated to 3 × 3 × 3 mm and were smoothed using an 8-mm full-width half-maximum kernel in SPM5. A high-pass filter of 128 sec was used during analysis.

To correct for multiple comparisons, an anatomical mask of the OFC (both BA 11 and BA 47) was generated in MRIcroN (www.mricro.com/mricron) and was used as an explicit mask for our primary analyses. It was determined that an FWE correction to $p < .05$ would be achieved by using an uncorrected voxelwise statistical threshold of $p < .001$ with a cluster size threshold of 11 contiguous voxels.[1] For secondary whole-brain analyses, it was determined that an FWE correction to $p < .05$ would be achieved by using an uncorrected voxelwise statistical threshold of $p < .001$ with a cluster size threshold of 33 contiguous voxels.

RESULTS

Behavioral Results

To ensure that participants adequately learned stimulus contingencies, the objective positive and negative values of the stimuli were regressed against choice behavior during the scanning task. Demonstrating the successful learning of the stimulus contingencies, the value of potential gains was positively associated [$F(1, 15) = 183.55$, $p < .0001$] and the value of potential losses was negatively associated [$F(1, 15) = 129.02$, $p < .0001$] with accepting a gamble (see Figure 2). These results were not moderated by stimulus trial, all *p*s = *ns*. Further, response latencies suggested that the best and worst decisions (i.e., gambles where the values of gains and losses were most differentiated) were made more quickly than gambles associated with the most conflict [i.e., where gains and losses were more closely matched; interaction of reward and punishment: $F(1, 15) = 9.67$, $p < .01$].

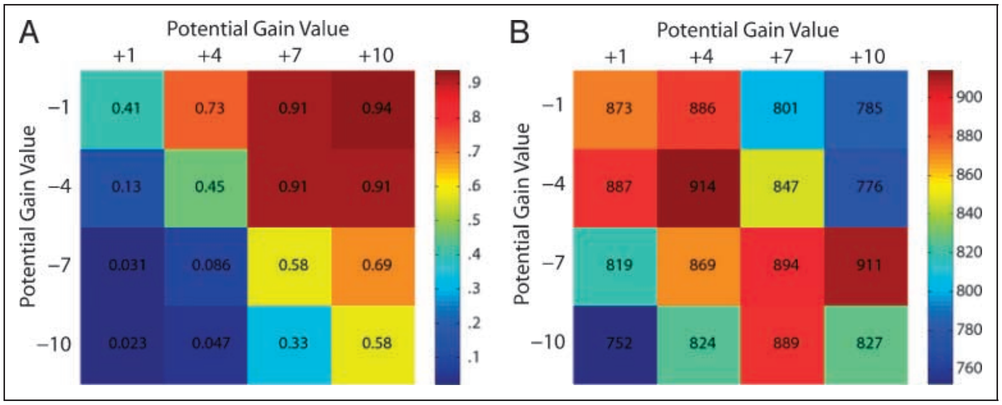
fMRI Results

Data were analyzed using the general linear model as implemented in SPM5. Because winning or losing was equally probable on each trial, the expected value (EV) of all gambles was computed as the potential gain value minus the potential loss value (divided by 2). A series of regressors was then constructed to examine BOLD brain activity for each trial. Specifically, activity for each trial was modeled using three parametric regressors:

$$\text{BOLD} = \text{EV} + \text{Response} + \text{Interaction}_{\text{EV*Response}}$$

To generate more robust parameter estimates, parametric regressors were zero-centered and orthogonalized to the onset regressor. The three parametric regressors, however, were not orthogonalized against one another.[2] Response was entered as 1 for accept and −1 for reject. The interaction of EV and response was created by multiplying the zero-centered values for each of the main effects. An additional regressor modeled the onset for feedback to account for this variance. Each regressor was convolved with an expected hemodynamic response function to model BOLD activity as well as a temporal derivative. Lastly, a series of regressors of no conceptual interest was estimated to account for the linear and quadratic effects of scanner signal drift. We used the unwarping procedure during the motion correction preprocessing stage and therefore did not explicitly model the motion parameters.

First-level contrast images associated with each parametric regressor were subjected to random effects second-level analyses. Of particular importance were the contrasts for the main effect of EV and the interaction of EV and response. Neural activity at decision was predicted by parametric regressors representing the EV of each stimulus, the response made, and the interaction of EV and response. The parametric regressor associated with the EV of each stimulus was associated with activity in a left posterior area of the OFC [$t(15) = 5.37$, $p < .001$; MNI: −21, 30, −12] (Table 1) such that the larger the EV of the stimulus, the greater the activation in the



	+1	+4	+7	+10
−1	0.41	0.73	0.91	0.94
−4	0.13	0.45	0.91	0.91
−7	0.031	0.086	0.58	0.69
−10	0.023	0.047	0.33	0.58

	+1	+4	+7	+10
−1	873	886	801	785
−4	887	914	847	776
−7	819	869	894	911
−10	752	824	889	827

Figure 2. (A) The proportion of each gamble accepted presented as a color-coded heatmap. The reddest areas represent gambles that were most likely to be accepted and the bluest areas represent gambles least likely to be accepted. As can be seen in the pattern of results, participants for the most part accepted the best gambles and rejected the worst gambles. Participants were, on average, at chance for accepting or rejecting gambles that were not clearly good or bad (gambles along the diagonal). (B) The average response latency associated with accepting or rejecting each gamble as a color-coded heatmap. The reddest areas represent gambles that took for which the participants took the longest to response and the bluest areas represent the gambles which the participants took the least time to respond. Corresponding to our idea that some gambles are clearly better than others, response latencies were the shortest for gambles with the clearest differentiation between the gain and loss value.

Table 1. Significant Regions of Activity: Expected Value

					MNI Coordinates		
Voxels	*Area*	*BA*	*L/R*	*t*	*x*	*y*	*z*
Expected Value (Positive Association)							
16	Superior OFC	11	L	5.37	−21	30	−12

region (Figure 3A). Providing further evidence for stimulus valuation, there was no interaction between EV and response in these voxels [$t(15) = 0.56, p = .58$.[3] This left posterior region has been found previously to be linearly and positively associated with self-reported taste preferences (Kringelbach et al., 2003) as well as self-reported liking for faces (Van Bavel, Packer, & Cunningham, 2008). In contrast to this finding, but consistent with the idea of differentiated evaluative processes in the OFC, a more medial anterior and dorsal region of the OFC was associated with the interaction of EV and response [$t(15) = 5.17, p < .001$; MNI: 12, 48, −6], such that the accepted gambles with the largest EVs and the rejected gambles with the smallest EVs showed the largest activity (Figure 3B). Further, these voxels did not demonstrate a main effect relationship to EV, as would be expected if this region was involved in the simple computation of stimulus value [$t(15) = 1.33, p = .20$]. In contrast to the posterior region, which may fall within BA 13 of the Öngür and Price (2000) cytoarchitecture map of the OFC, the medial anterior region clearly falls within BA 11.

In addition to decoding the value of a stimulus or action, decision-making requires monitoring conflict and recruiting executive resources to judge when one should seek or avoid risk (Miller, 2000). In this study, because some gambles involved more risk than others (e.g., a positive EV, with a 50% risk of a high negative outcome), we expected to find areas associated with negative affect, conflict, and cognitive control associated with these ''less right'' or evaluatively ''trickier'' decisions. An examination of this interaction revealed a large area of bilateral inferior the OFC (BA47) that responded the most to the more difficult decisions [right: $t(15) = 6.69, p < .001$; MNI: 33, 24, 0; left: $t(15) = 6.78$, $p < .001$; MNI: −30, 27, 0]. Specifically, activity was the greatest to stimuli with lower EV when participants

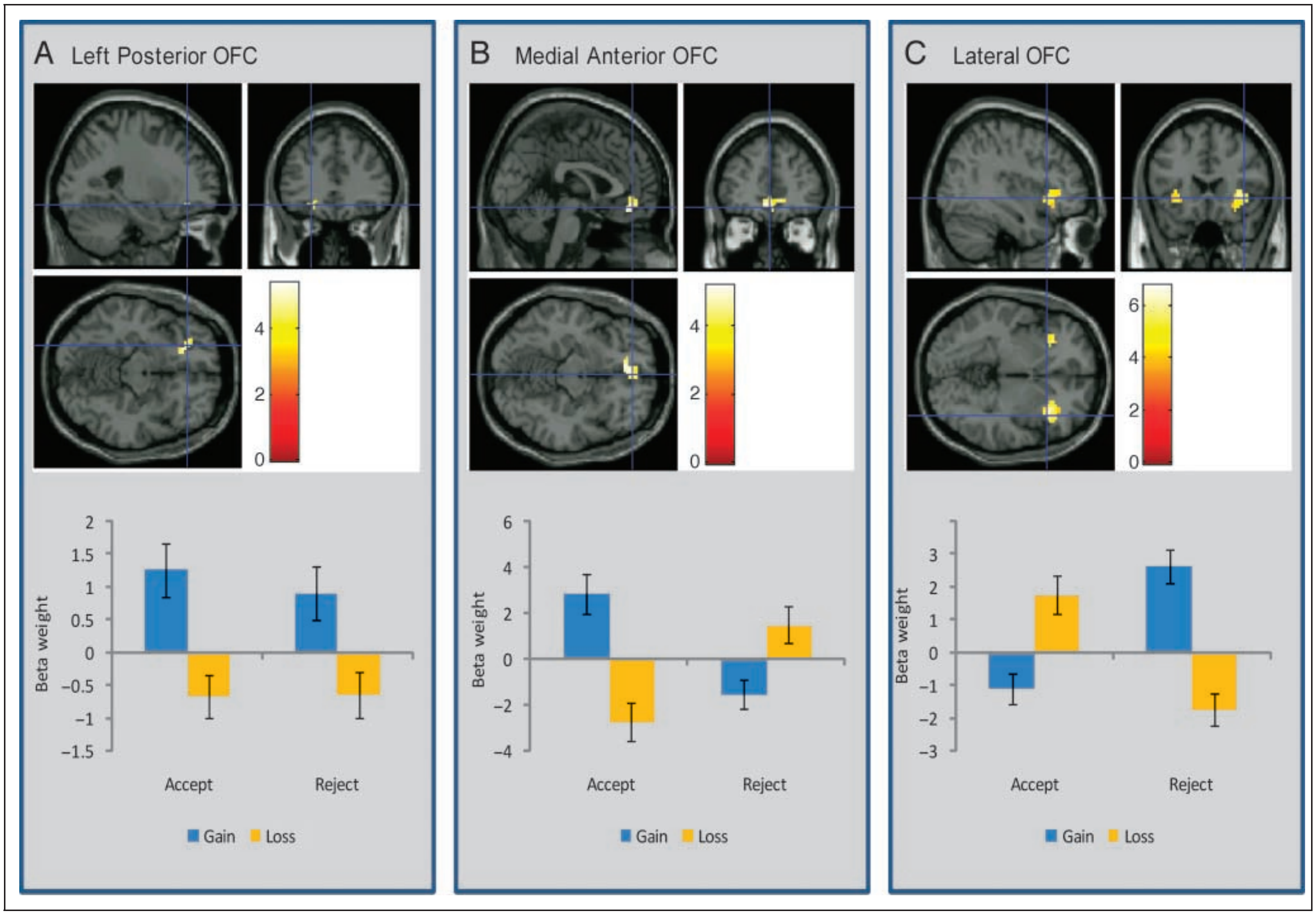


Figure 3. Overlaid regions of significant activity ($p < .001$) in each of the three areas of the OFC along with extracted mean beta vales for the interaction of response (accept/reject) and potential reward/punishment magnitude (gain/loss). (A) Left posterior OFC; (B) medial anterior OFC; (C) lateral OFC.

accepted the gamble, and to stimuli with higher EV when participants rejected the gamble (see Figure 3C). Additional whole-brain analyses indicated that this region extended into areas of the anterior insula. These data are consistent with hypotheses that suggest a medial/lateral distinction between reward and punishment processing in the OFC (O'Doherty et al., 2001) and the role of insula in decision-making (Damasio, Everitt, & Bishop, 1996). Interestingly, these regions did not respond to the potential stimulus punisher value, but rather the potential for punishment (or nonreward) that the participant's action afforded. The whole-brain analysis (see Table 2) of the interaction of EV and response additionally indicated that these decisions were related to activity in regions of the anterior cingulate [$t(15) = 8.06$, $p < .001$; MNI: 9, 27, 39] and the inferior frontal cortex [$t(15) = 5.24$, $p < .001$; MNI: 42, 27, 21], such that the most activation was observed for accepted gambles with lower EV and rejected gambles with higher EV. Previous work has implicated these regions in response conflict (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1998) and executive function

Table 2. Significant Regions of Activity: Interaction of Expected Value and Response

					MNI Coordinates		
Voxels	*Area*	*BA*	*L/R*	*T*	*x*	*y*	*z*
*Expected Value * Response (Positive Association: Better Decisions)*							
71	Middle OFC	11	R	5.17	12	48	−6
545	Superior parietal	2	L	7.57	−18	−39	57
	Superior parietal	5	L	6.17	−18	−51	60
	Paracentral lobe	6	L	6	−18	−21	75
182	Rolandic operculum	48	R	7.16	54	−12	12
	Superior temporal	48	R	6.27	66	−3	6
	Postcentral gyrus	43	R	5.91	66	−3	24
124	Superior temporal	48	L	6.97	−60	−3	3
153	Precuneus	23	R	6.13	6	−63	24
	Cuneus	18	L	5.54	−3	−72	30
96	Postcentral gyrus	3	R	5.78	24	−36	78
116	Precuneus	5	L	4.79	−3	−51	51
	Middle cingulate	23	L	4.71	−12	−48	36
*Expected Value * Response (Negative Association: Worse Decisions)*							
203	Insula	48	R	6.69	33	24	0
	Inferior OFC	47	R	6.03	48	21	−9
	Inferior OFC/insula	47/48	R	5.55	30	24	−9
56	Inferior OFC/insula	47/48	L	6.78	−30	27	0
	Insula	48	L	4.85	−33	18	6
251	Anterior cingulate	32	R	8.06	3	27	39
73	Inferior frontal gyrus	44	R	5.24	45	3	27
	Inferior frontal gyrus	44	R	4.55	48	15	33
39	Superior occipital	7	R	6.11	24	−63	39
69	Precentral gyrus	6	L	5.88	−36	0	36
91	Inferior occipital	37	L	5.41	−42	−66	−6
297	Brainstem		L	7.41	−6	−24	−6

Table shows local maxima $p < .001$ with an extent threshold of 36 voxels for areas not in BA 11 or BA 47. BA = Brodmann's area; R/L = right or left hemisphere; t = maximal t statistic for the statistical difference; x, y, z = 3-D coordinates of activation within normalized MNI space.

(Aron, Robbins, & Poldrack, 2004; Ochsner et al., 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Advantageous actions (whether accepting or rejecting) that carry the potential for undesirable consequences result in additional processing that seems to be involved in resolving this conflict and the associated negative affect.[4]

Although these analyses suggest that the left posterior region of the OFC is sensitive to stimulus value and the more medial anterior region is sensitive to action utility, it is possible that either accepted or rejected trials alone are responsible for these effects. To rule out this possibility, activity for accepted and rejected trials was modeled separately in a second analysis. Additional parametric regressors were added to model the relationship between each of the trial types and EV. As in the first analyses, BOLD activity for each regressor was modeled with a hemodynamic response function and a time derivative. All other parameters were modeled similarly to the first analysis, with the exception that because there was only one parametric regressor per trial type, we were able to use the standard SPM5 orthogonalization procedures. For the most part, participants made the correct response on each trial, resulting in a restriction of range of EVs per regressor and reducing the statistical power of this analysis. To compensate for this loss in power, we constructed functional regions of interest (ROIs) from the previous analyses to interrogate only the voxels that already showed either a main effect relationship with EV, or an interaction between EV and response.[5]

Results from within each response type confirmed the interpretations of the initial analyses. The relationship between EV and the posterior ROI was significant and positive for both the accepted [$t(15) = 3.07$, $p < .01$] and rejected [$t(15) = 2.21$, $p < .05$] trials. The difference between these two values was not significant [$t(15) = -0.60$, $p = .55$]. Further, the relationship between EV and activity in the more medial anterior region and the inferior lateral regions both significantly interacted with response. For the medial anterior region, there was a positive relationship with EV for accepted trials [$t(15) = 3.49$, $p < .01$], but a negative relationship for rejected trials [$t(15) = -2.15$, $p < .05$]. The difference between these two conditions was significant [$t(15) = 4.26$, $p < .001$]. The reverse relationship was found for the inferior lateral area of the OFC; there was a negative relationship with EV for accepted trials [$t(15) = -3.14$, $p < .001$] and a positive relationship with EV for rejected trials [$t(15) = 4.62$, $p < .001$]. To additionally confirm that the same voxels were contributing to these relationships, we ran a minimum-T conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) in order to determine the number of voxels within each ROI that were significant at a minimum of $p < .05$ for both accepted and rejected trials. To ensure that only voxels that were from the primary analysis were included, we generated and used a mask for this analysis that included voxels from only the left posterior, medial anterior, and bilateral lateral regions. Despite the power restriction, this analysis indicated that 45 of the medial anterior voxels, 11 of the left posterior voxels, and 131 of the lateral voxels (collapsing right and left) survived this criterion.

To further decompose the effects of evaluating stimuli from evaluating actions, in a secondary analysis, we predicted fMRI signal from two parametric regressors that represented the independent gain and loss values for each presented stimulus separately for accepted and rejected trials. As in the other analyses, an additional regressor modeled the onset for feedback and a series of regressors of no conceptual interest was estimated to account for the linear and quadratic effects of scanner signal drift. ROI masks for the medial anterior and left posterior OFC were generated from the regions identified in the primary analysis and mean signal was extracted for each of the four critical regression parameters ($\text{PotentialGain}_{\text{Accept}}$, $\text{PotentialLoss}_{\text{Accept}}$, $\text{PotentialGain}_{\text{Reject}}$, $\text{PotentialLoss}_{\text{Reject}}$). These parameters were analyzed with a 2 × 2 within-subjects ANOVA in SAS to estimate the main effects of valence (gain/loss) and response (accept/reject) and the interaction between valence and response.[6]

Consistent with the previous analysis, the posterior region of the OFC tracked stimulus value [main effect of valence: $F(1, 15) = 18.01$, $p < .001$; see Figure 3A, bottom], regardless of whether it was accepted or rejected [interaction of valence and response: $F(1, 15) = 0.48$, $p = .50$], and the medial anterior region of the OFC tracked the utility of the action [interaction of valence and response: $F(1, 15) = 17.02$, $p < .001$; see Figure 3B, bottom] and not the stimulus value per se [main effect of valence: $F(1, 15) = 1.01$, $p = .33$]. Specifically, the posterior region of the OFC responded to the relative "goodness" of a stimulus, regardless of the response for both the accepted [$t(15) = 3.33$, $p < .01$] and rejected trials [$t(15) = 2.61$, $p < .05$]. In contrast, although greater activation in the medial anterior region of the OFC was associated with larger potential rewards and smaller potential punishments when accepting a gamble [$t(15) = 3.03$, $p < .01$], this medial anterior region also showed increased activation to *rejected* gambles with larger potential punishments and smaller potential rewards [$t(15) = 2.04$, $p < .05$]. Lastly, the inferior lateral regions showed the reverse pattern as the medial anterior medial region [$F(1, 15) = 30.92$, $p < .0001$], such that greater activity was associated with smaller potential rewards and larger potential punishments for accept trials [$t(15) = 2.88$, $p < .01$], and larger potential rewards and smaller potential punishments for rejected trials [$t(15) = 4.38$, $p < .0001$; see Figure 3C, bottom]. Thus, whereas the posterior region activated to potential rewards (regardless of response), the medial anterior region responded most to advantageous actions or doing the "right" thing.

DISCUSSION

Multiple evaluative processes are necessary to aid the countless decisions made in the course of daily life (Cunningham & Zelazo, 2007). This research provides evidence for two interrelated, although conceptually distinct, neural processes involved in the evaluation of the EV of a stimulus and the utility of one's actions with regard to that stimulus. In line with current views of a functionally heterogeneous OFC, we found that distinct areas of the OFC were associated with the evaluation of the EV of a particular gamble and the evaluation of one's actions (i.e., whether accepting or rejecting the gamble was the right thing to do). This distinction provides support for the notion that valuation resulting from a decision depends not only on obtaining positive outcomes and avoiding negative outcomes but also on evaluations of the appropriateness of the actions leading to those outcomes. In other words, the reward system may be sensitive to both the ends and the means of the decision-making process. This consideration of separable stimulus and action evaluation processes has the potential to resolve conceptual discrepancies in theories of decision-making and may provide new interpretations of existing data.

Although it has guided research in behavioral economics, troubling violations of the weak axiom of revealed preferences have been documented. For example, how can it be that given two choices, under certain circumstances, people state that they would be willing to pay more for A than for B, but when given a choice between the options, often select B over A (Grether & Plott, 1979; Slovic & Lichtenstein, 1968)? Why is the value of an obtained outcome judged to be worth more when obtained through appropriate means? Because these studies involve identical outcomes, they provide powerful examples of how ''doing the right thing'' can be rewarding in its own right (Higgins, 2000). These results suggest a neural mechanism that may underlie the concept of ''value from fit,'' which compels individuals to value objects and outcomes more when the means and ends of behavioral are congruent with one's motivational frame (Higgins, Idson, Freitas, Spiegel, & Molden, 2003) and to be more persuaded by similarly congruent messages (Cesario, Grant, & Higgins, 2004). Thus, if hedonic experience attached to both internal and external stimuli is not simply a result of outcomes received and the objective calculated value of the stimuli (see Higgins, 2005 for a review), but also a function of the evaluation of the actions taken to obtain these outcomes, these findings demonstrate powerful violations of the axiom of revealed preferences. However, if we propose two separable evaluative processes, only one of which is directly tied to action, these violations can be explained. If actions and preferences involve dissociable neural circuitry, we should not expect to find perfect congruence.

These findings also help to resolve current debates within cognitive neuroscience concerning the functional and computational role of the OFC. In recent discussions, two dominant positions have emerged. First, it has been suggested, in accordance with the somatic marker hypothesis, that the OFC is critical for decision-making through linking actions with affective information (Bechara et al., 1999; Damasio et al., 1996). Conceptually, when decisions are made, we simulate the affective outcomes of the various possible actions and then select the one that has the best hedonic outcome. The OFC is thought to be involved in both processes. In contrast to this perspective, it has been suggested that the fundamental process underlying all OFC functions is the relatively more simple computation of determining the hedonic tone of a particular stimulus (Fellows & Farah, 2007). This computation is not linked to actions, but rather provides critical information needed to make adequate decisions. Although this debate has been important for developing models of OFC function, it is been largely informed by lesion data. Because OFC lesions are large, they typically extend between the subregions examined in the current study and could affect both stimulus and action evaluation processes. The present data suggest that both models may be true, with different processes associated with distinct areas of the OFC.

Conceptually, separate representations of stimulus and action value allow for psychological states and adaptive actions that would not be possible with a single representation. First, evaluations of stimuli can remain relatively stable across contexts even when decisions do not map directly onto stimulus value. These discrepancies can occur for various reasons, such as an individual's higher-order goals or the constraints on action associated with a given situation. For example, it is possible to believe that an object is of great value, even if obtaining it is not the best course of action in the current context. Second, decision rules can remain relatively stable even as the valuations of particular stimuli vary. For example, for a dieter, eating a piece of chocolate cake remains the wrong decision regardless of how delicious the cake is. Similarly, self-sacrifice is often thought of as a desirable action despite the significant and immediate costs to self. This interpretation of the data is consistent with two-factor learning theories that propose separate stimulus–reinforcer association learning speeds action learning or the instrumental learning of an operant response (Rolls, 2007).

Although these data demonstrate a dissociation between stimulus and action evaluation in the context of a gambling task, it is unlikely that activation in these regions only reflects stimulus or action evaluation. For example, the anterior region of the OFC, found to be associated with action evaluation in this study, has also been found to respond to the receipt of actual rewards (Rolls, McCabe, et al., 2008), even when participants do not need to make a behavioral response to obtain the reward (Rolls, Grabenhorst, & Parris, 2008). However, even in studies that have shown activation in this region to reward magnitude, activation has been modulated by cognitive and motivational influences. These results suggest that goals have the ability to shape anterior OFC activation (McCabe, Rolls, Bilderbeck, & McGlone, 2008). Together, these data suggest that the patterns of activity observed in this study may reflect the anticipation of an affective outcome following behavioral choice mediated through currently active goal representations.

An alternative explanation for these findings is that the anterior medial OFC responds to more arousing/intense stimuli; that is, stimuli with the highest potential for gains or the highest potential for losses. According to this account, the posterior OFC responds to valence, whereas the anterior medial OFC responds to arousal. In this case, the expected pattern of anterior medial OFC activity would be greatest for gains (vs. nongains) and losses (vs. nonlosses), which was not observed in the current study. Although it is difficult, based on the current data, to completely disentangle this explanation from the action evaluation explanation presented here, we believe that the arousal account is further challenged by existing literature implicating the medial OFC in goal-relevant processing with respect to one's actions. For example, Kim et al. (2006) found that there is larger activity in a similar area of the OFC when participants, having the option of losing money or not losing money on a particular trial, do not lose money. If this region was responding solely to intensity or valence independent arousal, then one would expect more activity to the loss trials than the nonloss trials (indeed, losses are often found to be even more arousing than equally valued gains). Further, Plassmann et al. (2007) showed that this region was more active when participants had the opportunity to choose between certain foods (as opposed to it being selected for them). Again, this suggests a role for the anterior OFC in goal-relevant processing as opposed to the decoding of stimulus properties alone. Other studies further suggest a role for the medial OFC in manipulating simple, stimulus-related information (e.g., valence, arousal, or EV) to guide goal-directed behaviors, signal desirable outcomes, and select the most appropriate means of goal pursuit (Schoenbaum & Roesch, 2005; Holland & Gallagher, 2004; Arana et al., 2003). Thus, to the extent that the medial anterior OFC could represent an arousal state, it is more likely to reflect an arousal state that is specific to the one's goals, or the expectation of gaining (and not losing), rather than simple stimulus intensity.

Beyond the narrow focus on decision-making, the distinction between good and bad stimuli, and right and wrong decisions and actions, may provide more speculative insights into the more social aspects of decision-making. Specifically, the medial anterior region associated with the appropriateness of actions has repeatedly been implicated in both self-relevant (Kelley et al., 2002) and moral (Greene & Haidt, 2002; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Greene, Sommerville, Nystrom, Darley, & Cohen, 2001) decision-making, especially for moral acts that are judged to be relatively more intentional (Borg, Hynes, Van Horn, Grafton, & Sinnott-Armstrong, 2006). For self-relevant decisions, as in this study, these activations appear to be more strongly associated with the affective than cognitive aspects of self-processing (Moran, Macrae, Heatherton, Wyland, & Kelley, 2006), suggesting that these activations may reflect aspects of self-evaluation (Beer, 2007). Thus, these data may suggest a basic neural computation that attaches affective meaning to particular actions within a particular goal state. As opposed to simply indicating that an external stimulus is good or bad, this computation allows for an understanding of right and wrong actions within a particular context. Because of the overlap in regions between this process and moral cognition, it is possible that our psychological understanding of moral right and wrong stems from the more simple computation of right and wrong actions in the context of decision-making.

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Notes

1. FWE correction was determined using CorrClusTh.m developed by Tom Nichols and downloaded from: www.sph.umich.edu/~nichols/JohnsGems5.html. Results were also obtained for $p < .005$ and $p < .01$. Results of these simulations indicated that a cluster threshold of 35 would be needed for a statistical threshold $p < .005$ and a cluster threshold of 59 would be required for a statistical threshold of $p < .01$ for analyses using the orbitofrontal explicit mask. All activity reported for the orbitofrontal activations are significant at all three of these thresholds.
2. SPM by default orthogonalizes parametric regressors in a serial fashion. Although this has some advantages for the estimation of parameters, it leads to the conceptual problem that the resulting beta weights differ as a function of order of entry. To deal with this issue, modified scripts were obtained from the Gabrieli lab to orthogonalize parametric regressors to onset regressors, but not to one another. Alternatively, orthogonalization can be simply commented out of the SPM code (www.jiscmail.ac.uk/cgi-bin/wa.exe?A2=ind04&L=SPM&P=R212032&I=-3). Nearly identical results are obtained using either orthogonalization procedure.
3. Comparisons between the strength of activation in two regions were conducted by extracting the mean signal from one contrast, using an explicit mask from another.
4. Follow-up analyses examining the separate contributions of the processing of gain and loss information separately provided evidence that each of these regions showed the expected crossover interaction pattern of results.

5. It is important to note that standard statistical thresholding resulted in identical conclusions from these analyses.

6. The 2 × 2 ANOVA was replicated using the flexible factorial 2nd level analysis option in SPM5 using the four parametric contrast weights generated from the 1st level analyses reported here as a within subject factor, and participant as a between subject factor. The main effects of participant, valence (possible gain/loss), response (accept/reject), and the interaction of valence and response were estimated. Results from this analysis (thresholded at $p < .001$) provided conceptually identical results to the ones reported from the ROI analysis. Main Effect of Valence: Posterior OFC; $F_{1,15} = 17.64$, $p < .001$; maximal voxel (MNI): −15, 30, −9. Interaction of Response and Valence: Anterior OFC; $F_{1,15} = 17.22$, $p < .001$; maximal voxel (MNI): −9, 36, −12. An analysis of simple effects indicated that these patterns emerged for both accept and reject trials, all $ps < .05$.

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