Neural correlates of dueling affective reactions to win–win choices

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Win–win choices cause anxiety, often more so than decisions lacking the opportunity for a highly desired outcome. These anxious feelings can paradoxically co-occur with positive feelings, raising important implications for individual decision styles and general well-being. Across three studies, people chose between products that varied in personal value. Participants reported feeling most positive and most anxious when choosing between similarly high-valued products. Behavioral and neural results suggested that this paradoxical experience resulted from parallel evaluations of the expected outcome (inducing positive affect) versus the cost of choosing a response (inducing anxiety). Positive feelings were reduced when there was no high-value option, and anxiety was reduced when only one option was highly valued. Dissociable regions within the striatum and the medial prefrontal cortex (mPFC) tracked these dueling affective reactions during choice. Ventral regions, associated with stimulus valuation, tracked positive feelings and the value of the best item. Dorsal regions, associated with response valuation, tracked anxiety. In addition to tracking anxiety, the dorsal mPFC was associated with conflict during the current choice, and activity levels across individual items predicted whether that choice would later be reversed during an unexpected reevaluation phase. By revealing how win–win decisions elicit responses in dissociable brain systems, these results help resolve the paradox of win–win choices. They also provide insight into behaviors that are associated with these two forms of affect, such as why we are pulled toward good options but may still decide to delay or avoid choosing among them.

reward | decision making | emotion | functional MRI

In a famous thought experiment, a hungry donkey is placed exactly between two equal bales of hay and, unable to decide which to approach, starves. Human decision makers face problems similar to the metaphorical donkey. Whether deciding between schools to attend or desserts to order, choices involving equally good outcomes ("win–win" choices) can generate anxiety along with the positive feelings one has about the rewarding prospects (1). Although the positive feelings may lead individuals to prefer having more good options, the anxiety can lead them to delay choosing, choose suboptimally, or make no choice at all (2–5). These seemingly contradictory preferences, particularly in situations where a "wrong" choice has negligible costs, represent a paradox for many decision scientists (6). The potential impact of negative choice experiences on important medical and financial decisions (7, 8) and on general well-being (6, 9, 10) gives the paradox far-reaching consequences. However, despite substantial research on the impact of choice conflict on behavior (2, 5, 7, 8) and postchoice feelings (1, 9, 11), little is known about the basis of the dueling affective reactions to the choice itself.

One possibility is that positive and anxious feelings to win–win choices are tied to separate components of the neural circuitry for decision making. Brain regions that determine how good an item is and the costs of performing the response required to obtain it are supported by separate corticostriatal circuits (12–16). Ventral regions of the striatum and the medial prefrontal cortex (mPFC) associate stimuli and contexts with their expected outcomes, whether or not those outcomes are directly relevant to one's response (17–20). Dorsal regions of the striatum and mPFC associate possible actions (including "internal actions": i.e., control signals) with their expected outcomes and modify these actions according to current demands (13, 14, 16, 21–24). One of the most well-studied demands encoded by the dorsal mPFC is response conflict (21, 25), including instances of choice conflict similar to those described at the outset (26–30). Whether dorsal mPFC activity correlates with the anxiety elicited by choice conflict and/or predicts future adjustments to prior choices remains an open question.

Here, we explored the neural systems underlying the dueling affective states evoked by win–win decisions. In two functional MRI (fMRI) experiments and one behavioral follow-up, participants made a series of decisions between real products that they cared about. Choices between similarly high-value options were rated as the most positive and anxiety-inducing. Activity in dissociable regions correlated with these competing experiences. Ventral mPFC and striatum correlated with the positive experience of the choice offers whereas dorsal mPFC and striatum correlated with the anxiety associated with making the choice. Activity within the dorsal mPFC also predicted postscan choice adjustment (i.e., changes of mind). These findings suggest that win–win choices give rise to separate assessments of the value of options versus the cost of choosing among them, leading to a paradoxical experience that is as anxiety-provoking as it is

Significance

Choices between multiple good prospects (e.g., job offers) are known to generate anxiety, even as the decision maker feels positivity toward their options. Here, we explored the basis for these (paradoxically) simultaneously occurring experiences. We evaluated brain activity during win–win choices relative to how positive and anxious the participant later reported having felt when encountering a set of options, and relative to subsequent choice reversals. Our participants felt increasingly positive and anxious with increasingly good options, and these two experiences were accounted for by dissociable neural circuits. Positivity-related circuits primarily tracked the value of the best item whereas anxiety-related circuits primarily tracked the level of competition between potential responses, and whether the participants would later decide to reverse their choice.

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positive. Our results may have broad implications for understanding the behavioral correlates of these affective experiences, such as indecisiveness and decision avoidance.

Results

Participants in study 1 were scanned during time-pressured choices between products of similar or dissimilar value (Fig. 1). The choices paired real products that each participant had earlier rated to be of similarly low value (low–low), similarly high value (high–high), or dissimilar value (low–high) (Figs. S1*C* and S2 and S3). After the scan, participants rated each choice pair for induced affect (positive and anxious feelings) and were given an opportunity to reevaluate (and switch) their earlier choice. Participants received one of their choices.

Positive Affect Increases with Expected Rewards and Anxiety with Overall Choice Conflict. Retrospective ratings in study 1 revealed that choice type influenced both positive affect (mixed-effects ANOVA $F_{2,82} = 203.6$, $P < 0.0001$) and anxiety ($F_{2,82} = 61.1$, $P < 0.0001$). Participants rated high–high trials as the most positive and paradoxically the most anxiety-inducing and rated low–low trials as lowest on both scales. Dissociating the two components of the experience, the low–high choices induced low levels of anxiety and high levels of positive affect (Fig. 2, *Left*). Ratings of positive affect and anxiety were positively correlated when choices were similarly valued (low–low, average $r = 0.25$, Wilcoxon signed-rank $P < 0.0001$; high–high, $r = 0.26$; $P < 0.005$), but not when they were differently valued (low–high, $r = 0.02$, $P = 0.86$).

These patterns of affective reactions to choices suggest that positive feelings were largely a function of the expected reward whereas feelings of anxiety were a function of the conflict between the potential responses (i.e., interaction between their value and degree of competition) (11, 25). This proposed dissociation predicts that maintaining the same expected outcome while increasing the number of options should increase anxiety (1), particularly for options of similarly high value (31), but it should not increase positive affect. An alternative account might interpret the patterns of anxiety described above as resulting from an experienced opportunity cost (i.e., a representation of the value of the foregone option) (32, 33) when making one's choice. This cost would be highest for high–high choices and lowest for the remaining conditions. Under this account, anxiety should be sensitive only to the value of the next best option and therefore should not increase with the value of additional options in the choice set (the third best, etc.).

A follow-up behavioral study (study S1) explicitly tested these predictions. Participants chose between two or six options at a time, with all options being similarly low value (all-low), similarly high value (all–high), or one option being high value and the remaining ones low value (low–high). Consistent with a conflict-based account, and weighing against the opportunity cost account above (see *Discussion*), anxiety increased as a function of condition ($F_{2,42} = 45.6$, $P < 0.0001$), choice size ($F_{1,21} = 37.5$, $P < 0.0001$), and their interaction ($F_{2,42} = 11.2$, $P < 0.0005$). The six-high choices were significantly more anxiety-provoking than would be predicted based on the choice type and number of options alone (Fig. 2, *Right*). Conversely, positive affect was not influenced by choice size ($F_{1,21} < 0.5$) but was again influenced by condition ($F_{2,42} = 30.5$, $P < 0.0001$, all pairwise $P < 0.05$). Choices involving a highly valued outcome (all–high and low–high) were rated significantly more positive than all–low. These findings also show that win–win choice anxiety does not rely on the presence of time pressure, as this study omitted a response deadline, but such pressure may serve to enhance anxiety for all choices (*SI Results*, section 1).

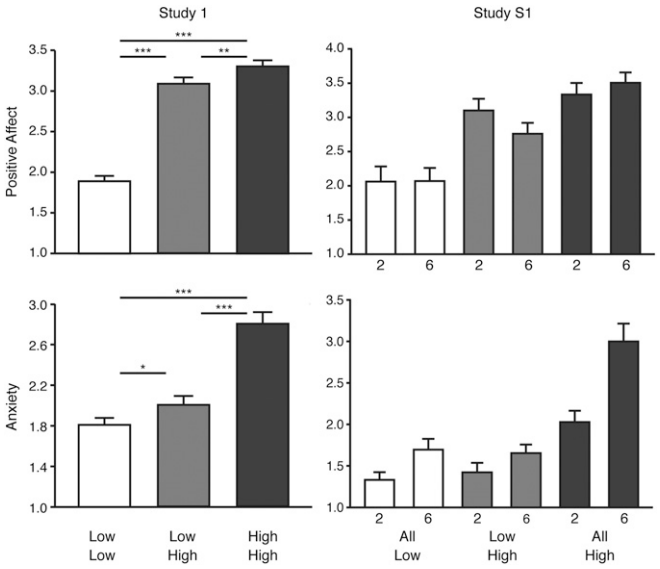

Fig. 2. Choices between similarly high-valued options generated the most positive affect and the most anxiety. Participants rated choices between all high-value options as significantly more positive (*Upper*) than choices between all low-value options and significantly more anxiety-inducing (*Lower*) than either of the other two conditions. Ratings from study S1 (*Right*) show that increasing the number of options from two to six substantially increases anxiety (interacting with the value of one's options) but has little impact on experienced positive affect. Error bars indicate SE. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

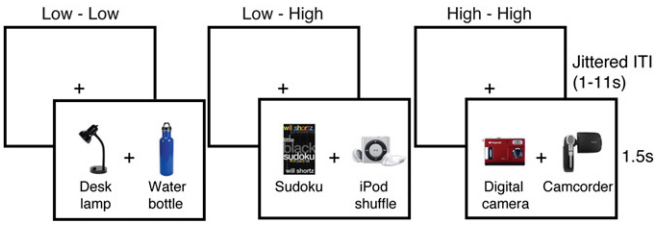

Fig. 1. Behavioral task performed in the scanner (study 1). Participants viewed pairs of products and pressed a button to indicate whether they preferred the item on the left or right side of the screen. Subjective values indicated in an earlier task were used to generate three kinds of choice pairs: products of similarly low value (low–low), similarly high value (high–high), or dissimilar values (low–high). Choices remained on the screen for 1.5 s and were followed by a jittered intertrial interval (ITI). Participants received their choice from one randomly selected trial.

Positive Affect and Anxiety Are Linked to Dissociable Corticostriatal Circuits. We examined brain regions where activity during the choice correlated with increasing positive affect and/or anxiety. We found that activity in bilateral regions of the ventral mPFC [particularly, the rostral anterior cingulate cortex (rACC)], the ventral striatum (vStr), and the posterior cingulate cortex (PCC) increased parametrically with positive feelings toward the choice being offered (Fig. 3*A*, green). Conversely, we found that activity in bilateral regions of the dorsal mPFC [particularly, the dorsal ACC (dACC)], the dorsomedial striatum (dmStr), and the anterior insula (aIns) were correlated with choice-related anxiety (Fig. 3*A*, red).

The ventral mPFC projects most densely to the ventral striatum whereas the dorsal mPFC preferentially projects to the dorsomedial striatum (reviewed in refs. 34 and 35). Given the differential involvement of these individual regions in distinct aspects of learning and decision making, these patterns of connectivity suggest a circuit-level explanation for functional

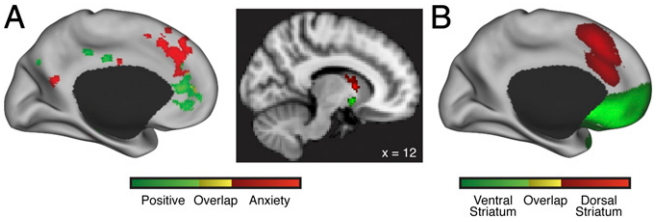

Fig. 3. Dissociable neural circuits simultaneously tracked positive and anxious feelings about a choice. (*A*) Whole-brain parametric analyses identifying regions where activity correlated with retrospective affective ratings (study 1). Activations in green correlated with how positive participants felt about the choice being offered. Activations in red correlated with how anxious participants felt about making their choice. Overlapping activations are shown in yellow. Ventral versus dorsal regions of the mPFC and striatum differentially tracked positive affect versus choice anxiety, respectively. Subcortical activations are masked to exclude significant voxels on the cortex. Unless otherwise noted, statistical maps (*t* values) are thresholded at voxel-wise $P < 0.001$, uncorrected. These effects replicated in study 2 (Fig. S4). (*B*) Regions with highest resting-state functional connectivity with ventral striatal peak for positive affect (green) and dorsal striatal peak for choice anxiety (red). Maps display *r* values derived from analyses performed by Yeo et al. (36), thresholded at $r \geq 0.10$ ($n = 1{,}000$).

differentiation between outcome associations linked to stimuli (ventral regions) versus responses (dorsomedial regions) (14, 15). We therefore tested whether the separate regions of the striatum identified by the positive affect and choice anxiety contrasts exhibited different levels of resting-state functional connectivity with regions of the mPFC identified by the corresponding contrasts. We seeded the vStr and dmStr (Fig. 3*A*, *Right*) in a large independent sample ($n = 1{,}000$) (36) and found that the two regions were differentially functionally coupled with ventral and dorsal regions of the mPFC, respectively, consistent with the regions identified by our task-based contrast (Fig. 3*B*; compare Fig. 3*A*, *Left*).

Because both the experience of anxiety and the regions we found to be associated with this experience have been previously linked to unpredictability of expected outcomes (37–39), we sought to confirm that our findings did not result simply from surprise about the values of objects appearing on a given trial. In study 1, both overall and relative outcome values were revealed along with the specific choice options. In study 2, participants made the same choices but were cued on each trial with the trial type that was forthcoming (low–low, low–high, or high–high) (Fig. S1*A*). Aside from reducing potential surprise when the options appeared, these cues helped to emphasize the objectively trivial cost of making the "wrong" choice on similarly valued trials, something that study 1 participants might not have fully appreciated given the short response window and the absence of information about the different choice types. Despite advance notice, study 2 participants reported the same patterns of anxiety and positive affect as observed in study 1 (Fig. S1*B*). Interestingly, we further found that choice type significantly influenced how positive ($F_{2,82} = 54.1$, $P < 0.0001$) and anxious ($F_{2,82} = 42.1$, $P < 0.0001$) participants felt in anticipation of a choice (i.e., when the choice-type cue appeared). Even knowing that they had valued the forthcoming options as similarly good, participants felt most anxious (and most positive) when anticipating high–high choices. Cue ratings were also significantly higher than average choice ratings, particularly when a high-value option was available (Fig. S1*B*) (main effect of cue, anxiety $F_{1,41} = 22.7$, $P < 0.0001$, positive affect $F_{1,41} = 0.82$, $P = 0.37$; cue × condition interaction, anxiety $F_{2,82} = 14.8$, positive affect $F_{2,82} = 8.68$, $P < 0.0005$). Although not predicted a priori, this finding may reflect a difference in affective responding to abstract relative to concrete choice contexts, or may relate to the difference in the number of data points included for each condition's estimate (i.e., 20 choices versus a single cue).

Study 2's neuroimaging findings replicated those observed in study 1 for anxiety and positive affect. Regions of interest (ROIs) were defined based on peak activations from study 1, and tested contrasts of interest on study 2 fMRI activity within these ROIs (Fig. S4 and *SI Methods*). For each region and contrast, activity differed significantly in the expected direction (anxiety, $t_{41\_dACC} = 2.72$, $P < 0.005$, $t_{41\_dmStr} = 3.32$, $P < 0.001$, $t_{41\_aIns} = 3.68$, $P < 0.001$; positive affect, $t_{41\_rACC} = 4.92$, $P < 0.001$, $t_{41\_vStr} = 7.78$, $P < 0.001$, $t_{41\_PCC} = 3.04$, $P < 0.005$; unless otherwise noted, all replications use paired *t* tests and one-tailed *P* values). Having established that ventral and dorsal regions of the striatum and mPFC differentiate experiences of positive affect and choice anxiety, respectively, we next tested whether the dorsal mPFC region that tracked anxiety (dACC) overlapped with those that track salient cognitive demands of choosing (for additional analyses probing the nature of ventral mPFC responses to these choices, see Figs. S5–S7, *SI Results*, section 2, and *SI Discussion*).

Dorsal ACC Tracked Anxiety and Choice Conflict and Predicts Future Choice Reversals. Two additional findings lend support to the possibility that choice anxiety ratings and dACC activation are both associated with the evaluation of potential response demands. First, consistent with previous findings implicating dACC in signaling conflict between potential responses/choices (23, 25–30, 40), dACC tracked choice conflict in the current study: activity was greater for high–high than low–high choices (trials that differed in conflict but guaranteed equally rewarding outcomes), in a region overlapping the one that tracked choice anxiety (Fig. 4*A*). This pattern was found even when participants knew in advance that either choice would yield similarly positive outcomes (Fig. 4*B*) ($t_{41} = 3.53$, $P = 0.001$). Additional regions elicited by this contrast included the medial orbitofrontal cortex (mOFC), the retrosplenial cortex (RSC), and the left superior frontal sulcus (SFS) (Figs. S5 and S6). The sensitivity of dACC and these other regions to our conflict contrast could not be accounted for by differences in response time (RT) (Fig. S1*D* and *SI Results*, section 4) or differences in combined option value (see legend to Fig. S7 and *SI Results*, section 2).

Second, dACC activity was consistent with a role in signaling demands for subsequent adjustments in behavior or cognitive control (e.g., response slowing, choice reversal) (22, 23, 41–44). Specifically, dACC activity during or immediately following a choice made in the scanner predicted whether that choice would be reversed during the unanticipated reevaluation period that took place after subjects left the scanner. dACC activity was greater for choices that would be reversed (switch trials) than those that would not (stay trials) in a region that overlapped regions of dACC tracking choice anxiety (Fig. 4 *C* and *D*) ($t_{38} = 2.56$, $P < 0.01$); similar overlap was found in the bilateral aIns (Fig. S8 and *SI Results*, section 3).

Anxiety is Associated with Subsequent Indecision and Reversal. Consistent with previous research linking anxiety and indecisiveness at the trait level (4, 45), we found that affective experiences during the choice process were associated with markers of continued wavering after the choice was made. Anxiety for high–high choices not only was correlated with later choice reversals (study 1, Wald *z*-statistic = 6.6; study 2, $z = 6.7$; $P < 10^{-10}$) but also was associated with longer time spent reevaluating (study 1, $F_{1,37.0} = 56.4$; study 2, $F_{1,34.5} = 29.3$; $P < 10^{-5}$) and lower final choice confidence (study 1, $z = 2.5$; study 2, $z = 3.0$; $P < 0.05$), after controlling for the decision whether to switch. We were also interested in whether experiences of choice anxiety and subsequent choice reversals for these high–high choices were modulated by individual differences in trait anxiety or decision-making style.

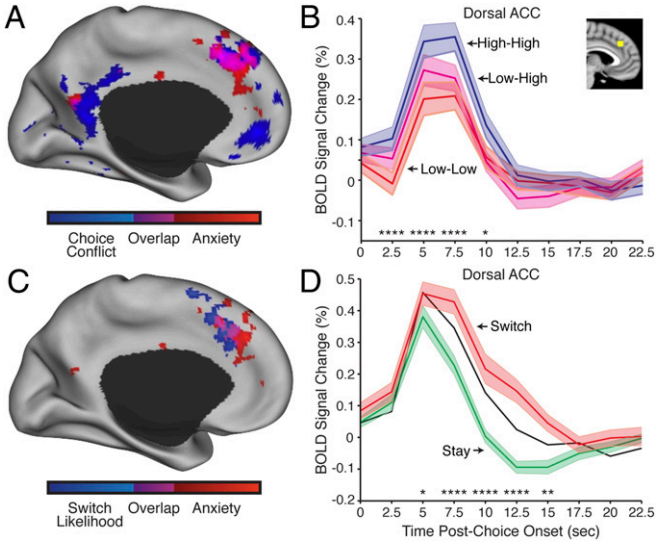

Fig. 4. Anxiety-related region of dorsal ACC tracks choice conflict and predicts postscan choice reversal. (*A*) Whole-brain contrast in study 1 for brain regions with greater activity during increased choice conflict, holding outcome value constant (high–high vs. low–high; blue), overlaid on parametric map of regions tracking increased anxiety (red) (Fig. 3), with substantial overlap seen in dACC (magenta). (*B*) Time courses extracted from the dACC peak in *A* [Montreal Neurological Institute (MNI) coordinates: −2, 34, 36] show that conflict-related effects replicated in study 2. For each time point, a significant main effect of condition is noted with asterisks. (*C*) Increased dACC activity predicted that the participant would later choose to switch the current choice (study 1; blue), again in a region overlapping anxiety-related activations (red). (*D*) Study 2 replicated switch-related findings in the dACC (peak from *C*: −6, 26, 40). Because of insufficient trials across participants, toss-up trials (where participants chose the midpoint of the stay/switch reevaluation scale) are excluded from these analyses, but their average time course is provided for visual reference (black line). Shaded error bars reflect between-subject SE. $*P < 0.05$, $**P < 0.01$, $****P < 0.001$.

Aggregating data across the two studies, a significant correlation was found between a composite measure of trait anxiety (*SI Methods*) and both choice anxiety ($r_{82} = 0.24$, $P < 0.05$) and frequency of choice reversal ($r_{82} = 0.29$, $P < 0.01$) for high–high trials. Controlling for trait anxiety, we further found that anxious experiences ($r_{81} = 0.26$, $P < 0.05$) but not reversals ($r_{81} = -0.04$, *ns*) were associated with the degree to which an individual generally tries to make the best choice (maximizing) rather than settling for a good enough choice (satisficing) (9). Trait anxiety was also marginally correlated with conflict-related differences in choice anxiety (high–high vs. low–high; $r_{82} = 0.19$, $P = 0.09$) and reversals ($r_{82} = 0.21$, $P = 0.05$); maximizing was not significantly correlated with either (($|r| < 0.085$, $P > 0.45$), suggesting that maximizers are generally more susceptible to choice anxiety but that this susceptibility is not necessarily modulated by choice type. Neither maximizing tendencies nor trait anxiety correlated with positive affective experiences of these choices ($|r| < 0.04$), or with an individual's average low- and high-value bids ($|r| < 0.05$).

We also performed exploratory analyses to test whether individual differences in conflict-induced choice anxiety or trait anxiety were associated with activity in anxiety or positive affect related regions of the mPFC and the striatum. Conflict-related variations in choice anxiety were significantly correlated with conflict-related activity (high–high > low–high) averaged across dorsal ($r_{82} = 0.23$, $P < 0.05$) but not ventral ($r_{82} = 0.12$, $P = 0.28$) regions of the mPFC/striatum. Because activity in these two circuits was correlated, we entered both into the same regression and found that dorsal regions maintained a trend for a correlation with conflict-related anxiety ($r_{8i} = 0.20$, $t_{81} = 1.8$, $P = 0.08$) and ventral regions exhibited no correlation ($r_{8i} = -0.01$, $t_{81} = -0.09$, $P = 0.93$). Using a similar regression, although the direction of effects trended toward the predicted directions, trait anxiety was not significantly correlated with conflict-related activity in dorsal ($r_{8i} = 0.09$, $t_{81} = 0.8$) or ventral regions ($r_{8i} = -0.16$, $t_{81} = -1.5$).

One possibility is that decision costs related to choice conflict—such as decision time and error likelihood—may themselves explain the relationship between conflict and anxiety. Further analyses ruled this possibility out for both our behavioral and neural findings (*SI Results*, section 4 and Figs. S1, S3, and S7*B*). Collectively, factors like decision time, likelihood of choice reversal, and likelihood of timing out were insufficient to account for the relationship between conflict and anxiety, or for the relationship between anxiety and dACC activity.

Discussion

Affect can guide choices between different products or choice strategies (3, 20, 46), including strategies for avoiding a choice altogether (2, 4, 5). Given the varied roles for affect in guiding behavior, it may not be surprising that different decision contexts can give rise to either positive or anxious feelings. What is striking is that humans are capable of experiencing both of these feelings simultaneously when choosing between only good options, and that both feelings grow with the value of those options. By probing the neural circuits that underlie this paradoxical experience, our studies were able to provide insight into the mechanisms that steer us toward good options but away from having to choose between them. Our data suggest that the two components of this affective experience may arise from distinct corticostriatal circuits separately specialized for determining the value of stimuli versus responses (12–14, 16).

Positive feelings about one's options were closely tied to the value of the best option, largely irrespective of the value and number of other options. These ratings were predicted by activity in ventral regions of the striatum and mPFC (specifically, the rACC), regions whose activity typically correlates with the level of reward associated with a stimulus (12, 17, 19). Representations of anticipated reward in these regions are primarily influenced by stimulus devaluation (e.g., increasing reward delay) but are less sensitive to response costs (e.g., increasing effort) (47, 48). Choice anxiety was also tied to the value of the best option; however, relative to positive affect, it was more sensitive to the alternative option(s), increasing substantially with both the value and number of similar options. Anxiety levels were predicted by activity in the dorsomedial striatum and dorsal mPFC (specifically, the dACC), regions where reward-related activity is contingent on the response required to obtain those rewards (15, 16, 21).

The dACC in particular is sensitive to the costs associated with responding, and activity in this region predicts the degree to which these costs make the reward less worth pursuing (21, 47, 49). In the case of win–win choices, the cost that the decision-maker must incur is not specific to one of the options but to conflict between all of the options. This and other forms of response conflict have been consistently associated with increased activity in the dACC (21, 25–28, 30). Conflict is also known to generate anxiety-like states (39, 50) and has been considered by some to be a central feature of clinical anxiety (51). Accordingly, in our study, regions of dACC that tracked anxiety also tracked current choice conflict and the likelihood that a choice would later be reversed (potentially consistent with its role in tracking conflict that persists after a choice is made) (44). Both anxious experiences and choice reversals were modulated by levels of trait anxiety.

We were able to rule out a number of potential confounding factors that often complicate the interpretation of conflict-related

findings. These factors include increased decision time, error likelihood, and surprise, effects that index but are not in and of themselves the phenomena of interest (52, 53). The behavioral and neural patterns associated with choice anxiety in our task were not mediated by RT (during choice or reevaluation), by correlates of error likelihood (choice confidence, switch likelihood, or likelihood of running out of time), or by ambiguity/unpredictability of option values (addressed by study 2). These findings were also unaccounted for by models of choice uncertainty that focus only on indifference (i.e., value similarity) without also taking account of the overall value of competing options (as recommended by, e.g., refs. 11, 25, and 31).

One alternative explanation for choice anxiety and its neural correlates is still difficult to rule out: perceived loss. It may be that, when making their choices, participants register the value of each foregone option as a form of subjective loss (50). If participants are experiencing a loss, it is not simply that of the next best option (i.e., the opportunity cost) because choice anxiety increased substantially with more options (Fig. 2*B*). This finding is important insofar as it weighs against a number of potential normative accounts of our data that have been offered to explain related phenomena (33, 54–56). Rather, to the extent participants were anxious because of a perceived loss, it would be explained only by a reaction to the total loss (i.e., the sum of the unchosen values), a possibility that could plausibly obtain if participants felt "endowed" with the options presented to them on each trial (57, 58). Because the predictions of this particular foregone value account are indistinguishable from those of a conflict-based account for any choice between similarly valued items, further experimental data and theoretical models (quantifying the conflict experienced as items vary in overall and relative values) are needed to better adjudicate between these two possibilities.

However, one piece of evidence suggests that loss may not explain our findings. Blair et al. (26) had participants choose between stimuli associated with reward or punishment and found that dACC was more active for more similarly valued stimuli. The dACC did not, however, differentiate between choices where the foregone option was associated with reward versus punishment.

We note that, similarly to previous studies (59, 60), our experiments rely on retrospective rather than instantaneous ratings of affect. Although the period between choosing and reporting affect was relatively short, these reports may still be noisier or may differ in intensity relative to whether they had been instantaneous (61). There is no clear reason to think that instantaneous ratings or alternative means of assaying affective responses would have produced qualitatively different patterns across our choice conditions, but this remains a possibility. At the same time, a clear benefit of our approach is that neural correlates of affect were measured covertly while the participant's explicit task was only to make a choice.

The observation that win–win choices induce anxiety underscores the question of whether trends in certain modern societies toward more attractive goods, and more options for each good, might have a detrimental impact on well-being in those societies (6, 10). For instance, the finding that people who spend longer considering their options score higher in depression and lower in overall life satisfaction (9) has led to the hypothesis that increased choice might be linked to increasing rates of depression and anxiety (6), though our own data provide somewhat limited support for this latter claim. Whether or not such a causal relationship exists, our results show that choice conflict can at least lead to substantial short-term anxiety, that this anxiety increases with the number and value of one's options (potentially enhanced by time pressure), and that it is not attenuated by awareness of the objectively negligible costs of a "bad" choice. To the degree that our surroundings are changing in ways that prompt us to make more win–win choices that induce positive but increasingly anxious states (and suboptimal behaviors aimed at avoiding such states) (2, 31), the present findings may help us better understand and counteract this paradoxical effect.

Methods

Participants. Right-handed native English speaking young adults were recruited to participate in imaging studies that involved evaluating products that they would have the opportunity to receive over and above a base payment. After an initial screening phase to assess for interest in a sufficient number of those products (*SI Methods*), 42 individuals completed MRI study 1 (25 female; M_{age} = 21.9, SD_{age} = 2.9) and 42 independent individuals completed MRI study 2 (24 female; M_{age} = 21.2, SD_{age} = 2.8). Seven participants were excluded a priori due to attrition (3), claustrophobia (1), incomplete session (1), or misunderstanding task instructions (2). None reported a history of neurological or psychiatric illness. Twenty-two independent individuals (11 female; M_{age} = 21.2, SD_{age} = 3.8) completed behavioral study S1 (details of this study's procedures are in *SI Methods*). Participants provided written informed consent in accordance with Harvard University's institutional review board.

Procedure. The experimental session for both fMRI studies proceeded in three parts: product valuation, product choice, and choice evaluation. Product valuation was completed 1–3 d before the MRI study, product choice during the MRI session, and choice evaluation immediately following the MRI session.

During product valuation, participants viewed over 300 products and indicated how much they would want to have each one, using an incentivized bidding procedure (62). During product choices, participants made a series of choices between pairs of products, knowing that they would receive a randomly selected choice (Fig. 1). Choice pairs were generated based on whether the items had been valued similarly high (high–high), similarly low (low–low), or dissimilarly (low–high), while guaranteeing that items within a value category (low vs. high) were matched for average value (Fig. S1*C*). Responses were given within a 1.5-s time window and followed by a variable intertrial interval (1–12 s). Participants completed 20 trials of each choice type, presented in a pseudorandomized order. Study 2 included an anticipatory cue that identified the forthcoming choice type before the appearance of each choice (Fig. S1*A*).

During choice evaluation, participants viewed each choice pair again (outside of the scanner) and rated it along each of the following five-point scales: (*i*) induced positive affect, (*ii*) induced choice anxiety, and (*iii*) preference to maintain the earlier choice or switch to the alternative (centered on "toss-up"). Ratings were blocked by rating type, given in the order listed, and were not foreshadowed earlier in the session. The first two ratings were given retrospectively (with reference to induced affect during earlier choices). The final reevaluative ratings directly influenced which item the participant received—choices made in the scanner were switched or made by a coin flip if the participant chose a "switch" or toss-up option, respectively, at this final stage. See *SI Methods* for additional details on each task.

fMRI Data Acquisition and Analysis. fMRI data were acquired on a Siemens 3T scanner. After standard preprocessing steps, a series of within-subject whole-brain general linear models (GLMs) were conducted using SPM8 (Wellcome Department of Imaging Neuroscience) to examine categorical effects of choice condition, parametric correlates of affective ratings, and binary contrasts predicting subsequent choice reversal (details in *SI Methods*). Group-level one-sample *t* tests were performed over contrasts of interest within these GLMs. Regions of interest (ROIs) for a given contrast were identified in study 1 using a voxel-wise uncorrected threshold of $P < 0.001$, and all findings were then tested for replication by examining independent time courses from study 2 within these ROIs. Unless otherwise noted, statistical reduction of these time courses was performed with paired *t* tests comparing normalized activity 5 s post-choice onset between conditions of interest, but figures show significant main effects of condition at each time point.

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Supporting Information

Shenhav and Buckner 10.1073/pnas.1405725111

SI Methods

Task Procedure: Part 1 (Product Valuation). Participants viewed individual products and were asked to indicate how much each item was worth to them. Products included food, electronics, housewares, kitchenware, clothing, and university/Boston paraphernalia, each shown with a brief label. Product sets were tailored slightly according to participant sex, and partially overlapped those used in previous studies (1, 2). We used the Becker–Degroot–Marschak auction method (BDM) (3) (slightly modified, as described below) to incentivize participants to provide an accurate estimate of subjective value for each of the items shown. Briefly, participants were asked to offer a bid for each item between $0 and $20 to indicate the amount they would be willing to put up to receive that item. They were told that one of the items would be randomly chosen at the end of their final session and that their bid would be compared with a random bid by the computer. If their bid was lower than the computer's, they would receive only the $20. If their bid was the same or higher than the computer's, they would receive $20 minus their bid, and the item would be delivered to them. (Note that this procedure deviates from a traditional, second-bid BDM in that "minus their bid" is not "minus the computer's bid". This modification simplified the instructions for participants but potentially increased the risk of participants' under-bidding relative to their true value.) Bidding $0 for a given product ensured that the participant would not get it if it were selected. To ensure full comprehension, participants were given written and verbal instructions and completed two short practice blocks, each followed by a simulated drawing and computer bid. Participants evaluated a total of 321–324 (study 1) or 338 (study 2) products, split into two blocks.

Products varied in market value from approximately $1.25 to $60.00 (approximate median: $20). Consistent with previous research (2), subjective values (bids) across study 1 and study 2 were on average 24% of these prices. Accordingly, the maximum of the bidding scale ($20) was used relatively infrequently (2.3% of bids), avoiding ceiling effects. We further found the correlation between subjective values and approximate market value to be relatively small (average $r = 0.24$), albeit highly reliable (sign-rank $P < 10^{-14}$).

Task Procedure: Part 2 (Product Choices). Subjective values from the product valuation were used to sort pairs of products into conditions of interest for each individual participant. Products were rank-ordered according to their subjective value (bids), and all $0 bid items were removed from the set. Fifty items were then removed around the median of the distribution, and the remaining items were classified as either high- or low-value items. Low–high choices paired items chosen at random from low and high bins. Low–low and high–high choices paired an item chosen at random from the appropriate bin with an item immediately adjacent to it (i.e., one with an identical or nearly identical bid) (Figs. S1*C* and S8). No product was included in more than one choice. Twenty pairs were generated for each condition, for a total of 60 trials. Participants who offered nonzero bids on too few products to generate this number of trials were dismissed following the product valuation portion of the study.

While undergoing functional MRI (fMRI), participants viewed each pair of products and pressed a button to indicate which of the two items they would prefer to receive (Fig. 1). Participants used a left or right index finger button press to indicate their choice of product (left or right side of screen; screen placement was randomized). They were given 1.5 s to respond, and the products remained on the screen for the entire response window. They were instructed that one trial would be chosen at random and that they would receive their choice on that trial, in addition to their winnings from part 1. To incentivize participants to respond on every trial (rather than only those they especially wanted to win), they were also told that each missed choice pair would be forfeited along with an additional randomly selected trial where they had successfully responded. Each choice was followed by a randomly varying intertrial interval (ITI) (study 1, 1–11 s, M = 5.1 s; study 2, 2–12 s, M = 6.1 s). Condition and ITI order were counterbalanced across participants. Participants performed a practice block (study 1, 5 trials; study 2, 6 trials), and two main blocks of 30 trials each.

Study 2 differed in that participants were instructed that they would be choosing between products they bid for similarly or dissimilarly and were taught anticipatory cues that would predict the choice type for each individual trial. The cues were pairs of upward or downward pointing arrows indicating which of the three kinds of choices the trial would be (Fig. S1*A*). The cues appeared at central fixation 4 s before the choice pair appeared and remained on the screen for 0.75 s before changing back into a fixation cross. The timing of the choices otherwise remained the same.

Task Procedure: Part 3 (Choice Evaluation). Immediately following the scans, participants evaluated the pairs of items they had seen during the MRI session on three dimensions using a five-point scale: (*i*) how positive they had felt to be offered those items (instructions specified that these should be ratings of the offer, not the choice process), (*ii*) how stressed/anxious they had felt making that choice, and (*iii*) whether they would like to change their previous choice (options: definitely stay, probably stay, toss-up, probably switch, or definitely switch). To ensure accurate responding, subjects were instructed that the third dimension (choice reevaluation) was binding. If the pair was selected, choosing either of the switch options would change what they received; choosing toss-up would have the computer select at random. For a given dimension, participants evaluated choices in the order they had viewed the choices earlier (excluding missed trials). Participants were made aware of each subsequent type of evaluation only after completing the previous one (i.e., participants were unaware of the opportunity to reevaluate until after giving positive affect and anxiety ratings). For study 2, participants rated their affective reactions for each anticipatory cue as well.

Task Procedure: Individual Difference Measures. During their initial session, before product valuation, participants completed a series of computerized self-report measures to assess individual differences in trait anxiety and decision style. The following scales were used to assess trait anxiety: (*i*) the Behavioral Inhibition (BIS) component of the Behavioral Inhibition/Behavioral Activation Scale (BIS/BAS) (4); (*ii*) the three-item version of the Penn State Worry Questionnaire (PSWQ) (5); (*iii*) the trait component of the Spielberger State-Trait Anxiety Inventory (STAI) (6); and (*iv*) the neuroticism subscale of the NEO Five-Factor Inventory (7). Scores on these individual scales were *z*-scored and averaged together to form a composite index of trait anxiety. Participants additionally completed the six-item version of the Maximization Scale (8, 9), which assesses the degree to which an individual tries to find the best choice

(maximizing) or only a good enough choice (satisficing) when making everyday decisions.

fMRI Data Acquisition. Scans were conducted on a Siemens TimTrio 3T scanner with a 12-channel phase-arrayed head coil. Both studies used the following gradient-echo planar imaging (EPI) sequence parameters: repetition time (TR) = 2,500 ms; echo time (TE) = 30 ms; flip angle (FA) = 90°; 2.5-mm voxels; 0.50-mm gap between slices; field of view (FOV): 210 × 210; interleaved acquisition; 37 slices. To reduce signal dropout in regions of the orbitofrontal cortex and the amygdala, slice prescriptions were rotated ∼30° relative to the anterior-posterior commissure plane, and the z-shim prepulse sequence was modified slightly (0.61mT/(m*ms) (10). This limited slice prescription included the ventralmost extent of frontal/temporal cortices but excluded the dorsalmost regions of the posterior parietal cortex for many participants. For each of two task blocks, either 88 (study 1) or 148 (study 2) functional volumes were acquired. Structural data were collected with T1-weighted multiecho magnetization prepared rapid acquisition gradient echo image (MEMPRAGE) sequences using the following parameters: TR = 2,200 ms; TE = 1.54 ms; FA = 7°; 1.2-mm isotropic voxels; FOV = 192 × 192. Head motion was restricted with a pillow and padded head clamps. Stimuli were generated on an Apple MacBook Pro (Apple Computers) running Matlab software (The Mathworks) with the Psychophysics Toolbox extension and were viewed through a mirror mounted on the head coil. Participants responded with MR-safe response keypads.

fMRI Data Preprocessing. After four functional volumes were discarded from the beginning of each task block (to correct for effects of T1 equilibration), fMRI data were preprocessed as follows: Functional volumes were spatially aligned (using a linear transform) to the first volume to correct for motion within and between task blocks; across functional volumes, slices were temporally aligned to the acquisition time of the first slice; data were resampled to 2-mm isotropic voxels and nonlinearly transformed to Montreal Neurological Institute (MNI) atlas space (using a T2-weighted template in SPM2); and normalized data were spatially smoothed with a 6-mm full-width at half-max (FWHM) Gaussian kernel.

Analysis: Behavior. Response times (RTs) for product choice and during choice reevaluation were analyzed as continuous variables relative to each choice type (for the reevaluation RTs, log-transformation was applied to correct for positive skew in their distribution). Due to limited trial numbers and choice reevaluation ratings being heavily skewed toward "definitely stay," we examined these ratings on a dichotomous basis, focusing on whether (*i*) the ratings expressed high confidence (definitely stay/switch) or low confidence (probably stay/switch or toss-up) in their final decision, and (*ii*) whether the participant chose to stay with or switch from their earlier choice. Unless otherwise stated, behavioral analyses involved mixed-effects ANOVAs/regressions, modeling subject-level intercepts and slopes as random effects.

Analysis: fMRI. fMRI data were analyzed in SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London) using a general linear model. Regressors of no interest were modeled for the mean of each task block, linear drift within each block, and overall volume displacement (relative to the previous volume, based on motion realignment). Additional regressors were added for time points identified as extreme motion outliers (greater than 5 SD outside of average between-scan movement and at least 0.25 mm). Individual trials were modeled as events (duration = 0 s) occurring at the time the choices were presented, convolved with a canonical hemodynamic response function. Any missed trials, which were infrequent (M_{study1} = 2.5%, M_{study2} = 1.8%) and did not vary significantly by condition (F_{study1} (2,82) < 1.0; F_{study2} (2,82) < 2.5; $P > 0.05$), were modeled as a separate condition.

Two kinds of analyses were performed over these data: Condition-wise analyses modeled the average of each condition with separate regressors; parametric analyses (e.g., focusing on post-scan ratings) modeled all trials as a single condition and examined effects of a given variable on neural activity [as indirectly measured through the blood oxygenation level-dependent (BOLD) response] by modeling it as a parametric modulator on that condition. For positive affect and anxiety, these modulators were continuous parameters; for switch likelihood, they were binary (1 for later switched, 0 otherwise; see *Analysis: Behavior*). Moreover, all analyses that involve the switch likelihood contrast (Fig. 4 and Figs. S7*B* and S8) exclude participants that did not switch on at least five trials, resulting in 37 and 39 included participants for study 1 and study 2, respectively [the average number of switches for included participants was 10.0 (study 1) and 10.6 (study 2)]. Additional analyses (reported in Fig. S7*B*) tested for parametric effects of a given variable (e.g., anxiety) after controlling for our conflict contrast (high–high > low–high). These models included serially orthogonalized regressors for RT, choice laterality, and regressors, modeling the difference between pairwise means of each of the three conditions. We then extracted beta estimates for the parameter of interest from a given region of interest (ROI) and tested their mean against zero (two-tailed *t* test).

To visualize the average time course for "toss-up" trials, Fig. 4*D* and Fig. S8 *B* and *D* exclude four additional study 2 participants who never gave this response. However, all statistical analyses associated with these figures excluded toss-up trials and therefore incorporate these four participants.

Unless otherwise noted, the parametric analyses focused on the effect of a given parameter after controlling for both RT on that trial and whether the participant made a left or right button press. Between-condition and parametric contrast maps were formed at the individual-subject (first) level and carried over to the group (second) level, where one-sample *t* tests were used to generate group whole-brain results.

Data were projected onto the Caret-inflated cortical surface (11) and an MNI average volume to display cortical and subcortical activations, respectively. Exploratory whole-brain analyses for study 1 were performed using a voxel-wise threshold of $P < 0.001$ (uncorrected), and a region-of-interest (ROI) approach was then used to test for replication of each of our findings in an unbiased manner. ROIs were generated by creating spheres around peak activations of interest in study 1 (radii: subcortical = 4 mm; insula = 5 mm; all other cortical = 6 mm). BOLD time courses were extracted from these ROIs within the independent dataset (study 2) by using Marsbar (12) to fit a finite impulse response (FIR) model with a length of 25 s, beginning at the time of choice presentation. For these analyses, continuous affective ratings were dichotomized according to a median split within each participant. For summary statistics, percent signal change estimates were derived by subtracting the mean of time points 1 and 10 from time point 3 (5 s post-choice onset). These signal-change estimates were also used to evaluate individual differences in neural reactivity to different choice conditions, which aggregated data across study 1 and study 2 but continued to extract data from ROIs identified by the equivalent contrast in the opposite study. For completeness, raw time courses are accompanied by asterisks indicating significant between-condition differences at each time point based on a mixed-effects ANOVA at that time point, performed after subtracting the average of the first and last time point (as above).

Resting-state functional connectivity maps were derived from an independent dataset (n = 1,000) collected and previously

analyzed by Yeo et al. (13). Using these data, we identified regions that were reliably functionally connected with our peak activation voxels of interest at rest.

Task Procedure: Study S1. Motivated by the results of the first two MRI studies, study S1 was conducted to explore the behavioral and affective consequences of having many similarly valued options in a choice. The procedures were very similar to those in study 1 and study 2 so we highlight here only the ways in which study S1's procedures diverge.

First, all three parts of study S1 were completed in a single session (rather than product valuation occurring on a previous day). For product choice, the same conditions from study 1 and study 2 remained, but three equivalent conditions were added with six options rather than two. These choice sets consisted of six options of similarly low (all–low) or high (all–high) value, or one high-value combined with five low-value items (low–high). Options were arranged in rows of either one or three options each, and participants responded by clicking on the product that they most preferred. Participants were not given a time limit to make their choices in this study, and no anticipatory cues were presented. Study S1 participants were not directly screened out from part 2 if they failed to provide a certain number of nonzero bids. Instead, the choice task generated up to 10 choices for each of the six conditions but dynamically adjusted the number of choices according to the number of products that were given a nonzero bid. A given participant completed the same number of choices per condition, but participants who ended up with fewer than five choices per condition were excluded from analysis. (Follow-up analyses confirmed that interindividual variability in number of choices offered did not influence the results reported.) Further, rather than always receiving the outcome of part 1 and part 2, study S1 participants were given a lottery number (between 1 and 8), and, if their number was drawn within a few weeks of the session, they received the items won during the session (all participants were told at the end of the session what they could receive). Finally, post-choice evaluation differed from study 1 and study 2 slightly in that choice reevaluation involved clicking on either the previous choice or another and then indicating confidence with staying or switching on a five-point scale.

SI Results

1. Average Choice Anxiety Is Greater for Study 1 and Study 2 than for Study S1. We tested whether affective ratings differed between our imaging studies and behavioral study S1. Focusing only on the binary choices made in the different studies, we found that average ratings of anxiety ($F_{1,104} = 27.8$, $P < 10^{-6}$) but not positive affect ($F < 0.10$, $P > 0.75$) were significantly higher for the two neuroimaging studies, relative to study S1. The difference in anxiety ratings may be due to the presence of time pressure or the difference between choice environments (inside versus outside the scanner). Importantly, however, the differences between the imaging and nonimaging studies did not interact with effects of condition on either form of affect ($Fs_{2,208} < 1.80$, $P > 0.15$).

2. Dissociable Regions of Ventral mPFC Track Positive Affect Versus Decision Conflict. Comparing activity related to positive affect versus choice conflict identified a surprising dissociation within regions of the ventral medial prefrontal cortex (mPFC) and the posterior midline (Fig. S5*A*). Although our earlier analyses showed that positive feelings toward one's options were tied to a posterior/dorsal portion of the ventral mPFC [rostral anterior cingulate cortex (rACC)], both studies identified a more anterior/ventral region in the medial orbitofrontal cortex (mOFC) that tracked choice conflict, holding outcomes constant. The same was true when comparing the posterior cingulate cortex (PCC) and the retrosplenial cortex (RSC), regions that share differential intrinsic connectivity with the rACC versus mOFC (Fig. S5*B*). Additional analyses aimed to clarify the potential functional basis of this dissociation.

We found that the mOFC and RSC were selectively responsive to high–high trials, and not more generally to forms of value previously associated with the ventromedial prefrontal cortex (vmPFC), such as total value (the only value-related factor along which high–high and low–high trials differed; see Figs. S6*B* and S7). By contrast, positive affect ratings and activity in associated regions [e.g., the rACC, PCC, and ventral striatum (vStr)] could be accounted for straightforwardly by the value of the chosen option (Fig. S6). The pattern of activity in the latter network may reflect a role in selecting the best outcome but may also be unrelated to the decision process and simply reflect the generation of automatic (e.g., Pavlovian) associations between the options and one's expected reward. Such associations could be generated before a choice is made between similarly valued options and could to some extent be generated before the specific options appear in study 2 (in which expected reward magnitude was cued before the choice). It is therefore notable that we found preliminary evidence that activity in the PCC and, to a lesser extent, rACC was sensitive to prechoice discriminative cues in study 2 (Fig. S6*B*), cues that we found to elicit similar patterns of affective ratings as the choices themselves (Fig. S1*B*). These anticipatory patterns of activity were weak or absent in choice conflict-associated regions (e.g., the RSC and mOFC). A possible interpretation of these findings is provided in *SI Discussion*.

3. Rostrolateral PFC Is Associated with Choice Reversal. Because activations that predict subsequent reversals could be strongest either immediately before or after a choice was made, an initial analysis was performed at the time the options were presented, but a secondary analysis was performed at the time the response was made. (Note that these studies were not designed to differentiate BOLD activity between these two periods so these analyses were intended to offer different power to two potential hypotheses rather than determine whether activity in a given region was time-locked to the onset of the choice offer or the response.) This follow-up analysis identified bilateral regions of the rostrolateral PFC (rlPFC) in study 1 that predicted future choice reversal (Fig. S7*C*). Study 2 replicated this effect, again finding a somewhat delayed onset relative to choice onset (Fig. 7*D*) (5 s – $t_{38} = 1.01$, *ns*; 7.5 s – $t_{38} = 2.91$, one-tailed $P < 0.005$).

This finding is potentially consistent with the rlPFC's proposed role in implementing control adjustments signaled by the dorsal ACC (dACC) (14–16). Whether or not rlPFC activity on switch trials does reflect the coordination of cognitive control exerted immediately after a choice was made (e.g., over internal representations of that preceding choice), it is notable that switch trials were not otherwise associated with adjustments to one's immediate behavior while performing the choice task in the scanner: trials that directly followed a switch trial did not differ in response time (RT) from those following a stay trial, nor were they more likely to be themselves switched.

4. Anxiety Is Not Accounted for by Objective Decision Costs. Our participants' anxious reactions to win–win choices appear at odds with an account of anxiety that is specific to potential negative outcomes. We therefore tested whether choice anxiety to these choices simply reflected an aversion to decision costs associated with conflict, such as longer decision times, higher error rates, and greater likelihood of running out of time and forfeiting all options. Although time-outs were infrequent and did not differ between conditions (see *SI Methods*; note also that study S1 had no deadline), choices between similarly valued options did lead to more choice reversals, lower final choice confidence, and longer reevaluation RTs (RTs for the choices themselves also differed by condition, but not purely based on value similarity;

see next paragraph). All of these effects were exacerbated with larger option sets (Fig. S3). However, even after controlling for all of these behavioral indicators of choice conflict/uncertainty, the effect of choice type on anxiety remained (study 1, $F_{2,84.3} = 60.3$; study 2, $F_{2,82.1} = 37.2$; $P < 0.0001$).

These controls also held up for our neuroimaging findings. All of our whole-brain analyses examined the effect of interest after controlling for RT, which notably did not differ significantly between high–high and low–high trials (only between low–low and other trials) (Fig. S1*D*). Further, despite the overlapping activations for switch likelihood and choice anxiety, we found that regions identified by the anxiety contrast were still sensitive to differences in anxiety even when all switch trials were removed ($t_{41\_dACC} = 2.30$, $P < 0.05$; $t_{41\_dmStr} = 2.46$, $P < 0.05$; $t_{41\_aIns} = 3.48$, $P < 0.005$; see also Fig. S7*B*). In other words, these regions tracked choice anxiety whether or not participants felt their response on that trial should be changed (i.e., potentially experienced these as error trials).

SI Discussion

The findings described in the main text may help explain how anxiety can arise simultaneous with positive feelings about a choice, but do not completely explain why positive feelings about high–high choices were undeterred (indeed, even enhanced) by the presence of additional high-value options (Fig. 2 and Fig. S1*B*). A second, and unexpected, dissociation observed within the ventral mPFC may offer some clues. Whereas ratings of positive affect correlated most strongly with activity in the rACC, a more ventral focus in the mOFC was found to be most strongly associated with whether participants were choosing between similarly high-value options (but not more generally with how anxious participants felt or the likelihood they would reverse their choice; Figs. S5 and S6*B*). These two regions were differentially coactivated with regions that are commonly found in studies of valuation (the vStr and PCC) (17, 18) and autobiographical/associative memory [e.g., the RSC and superior frontal sulcus (SFS)] (18–20) (*SI Results*, section 2). The fact that activation of the mOFC could not be straightforwardly explained by prominent accounts of value representation in this region (17, 21, 22) (Figs. S6 and S7) invites an interpretation of our mOFC findings in terms of both value and choice difficulty. This interpretation is consistent with a previous finding in which the mOFC tracked these two decision properties during hypothetical choices between options from a restaurant menu (23), and with a growing body of mOFC lesion studies that find impairments in decisions between similar and/or multiattribute options but not decisions between dissimilarly valued options (24, 25). These findings have led researchers to suggest that the mOFC does not play a role in simply representing value, but in the process of integrating and comparing value-relevant information over the course of a decision (18, 24, 26–29). Such information would be in particularly high demand when each choice requires a unique set of multiattribute tradeoffs, as in our studies.

A potential, albeit speculative, account for this second dissociation is therefore that the rACC and PCC are more involved in generating associations with potential rewards (thus tracking our participants' reflexive positive reactions toward a set of high-value options) whereas the mOFC is more involved in comparing values to arrive at the eventual choice. Such a circuit-level account—which has been previously proposed and given meta-analytic support by Grabenhorst and Rolls (22) —would help to further explain why individuals are able to experience positive feelings about the value of an expected outcome (e.g., getting a new house) before and even as they are in the difficult process of selecting which specific option they prefer.

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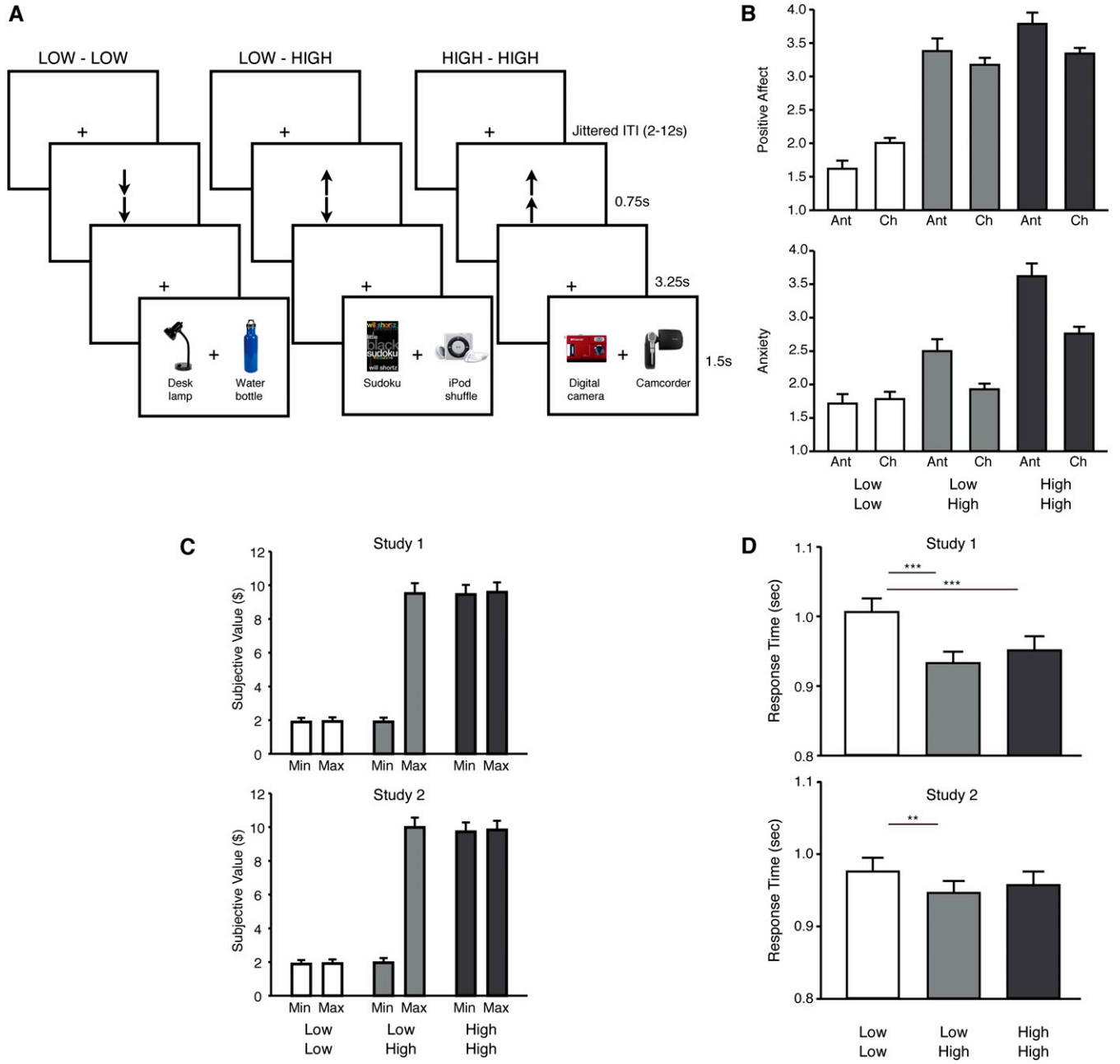

Fig. S1. (*A*) Behavioral task performed in the scanner (study 2). Trials were preceded by cues (arrows) indicating which type of choice they would be making on that trial. Cues were presented for 0.75 s, and choice options appeared following 3.25 s of additional fixation. Study 2's design was otherwise identical to study 1. (*B*) Condition-wise patterns of positive affect and anxiety in study 2 mirrored those in study 1 and study S1 (compare Fig. 2), both when rating the choice pairs themselves (Ch) and when rating how they felt when seeing the anticipatory cue associated with a given condition (Ant). (*C*) Average minimum and maximum (subjective) product value within each choice pair, by condition. Subjective value reflects amount bid for each product, irrespective of market value. See also Fig. S2. (*D*) Average response times for choices made in the scanner. Participants spent significantly longer choosing between two similarly low-valued options (low–low) than either of the other two conditions. The difference between high–high and low–high RTs did not reach significance in either study (study 1, $F_{1,82} = 3.0$, $P = 0.084$; study 2, $F_{1,82} = 1.0$, $P = 0.32$). Although more readily apparent when participants are under time pressure (compare Fig. S3, *Top Right*), this pattern of RTs may be explained by a combination of speeding and slowing influences of overall value and value similarity, respectively (1–3). Unless otherwise noted, error bars represent between-subject SE. $^{**}P < 0.01$, $^{***}P < 0.001$.

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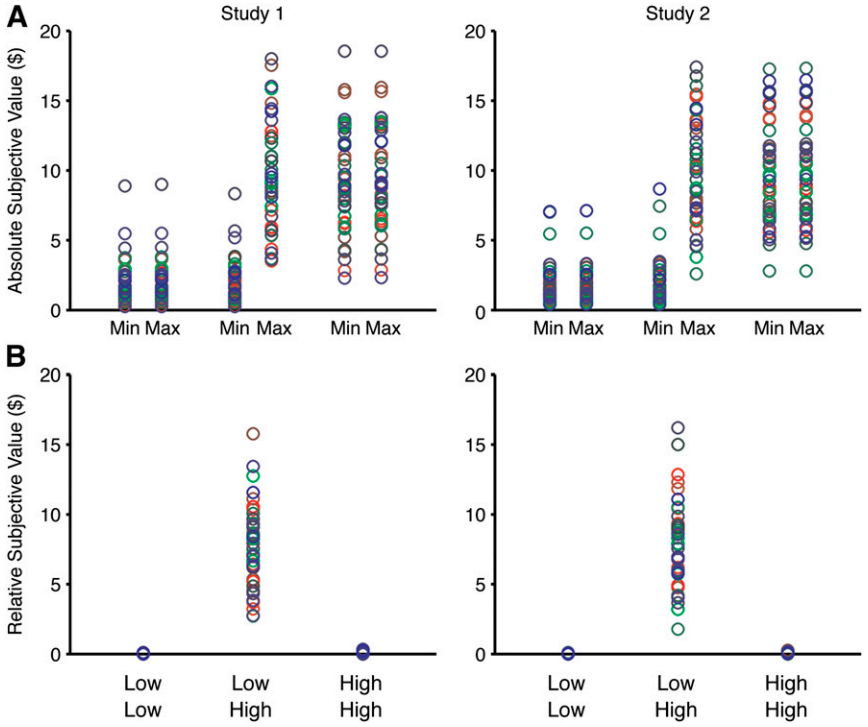

Fig. S2. Distributions of average bid values for low- and high-value items, by condition, for study 1 (*Left*) and study 2 (*Right*). (*A*) Average minimum and maximum subjective values (bids) for each condition. Each color represents a single participant. (*B*) Average value difference (i.e., max minus min) by condition.

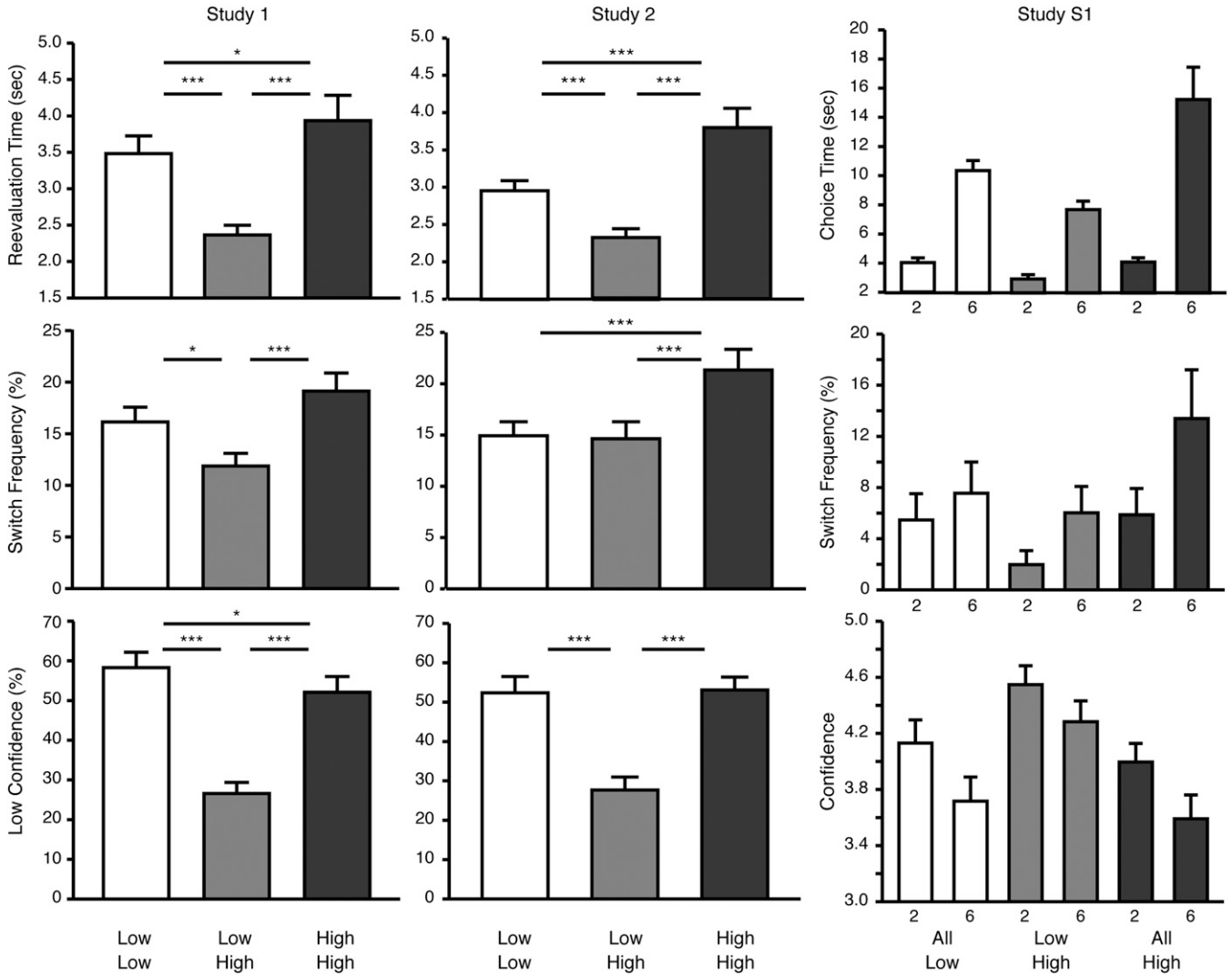

Fig. S3. Choosing between similarly valued options led to more reevaluation and choice reversal, and lower final-choice confidence. Participants performing postscan reevaluations (study 1 and study 2, *Left* and *Center*) for choices between similarly valued products (low–low or high–high) took longer to reevaluate (*Top*), were more likely to switch to the other product (*Middle*) (expressed as proportion of "probably switch" or "definitely switch" trials), and expressed lower confidence in their final decisions (*Bottom*) (expressed as proportion of "probably stay," "toss-up," or "probably switch" trials). Study S1 (*Right*) reveals the same pattern during the choice period (*Top*) if participants have no response deadline (as with reevaluation but not choice periods in study 1 and study 2) and shows that increasing the size of the option set particularly influences response times and ratings of confidence [note that higher values in the confidence plot (*Bottom*) for study S1 (*Right*) indicate higher choice confidence, whereas higher values in the study 1 (*Left*) and study 2 (*Center*) plots indicate lower confidence; see *SI Methods*]. $*P < 0.05$, $***P < 0.001$.

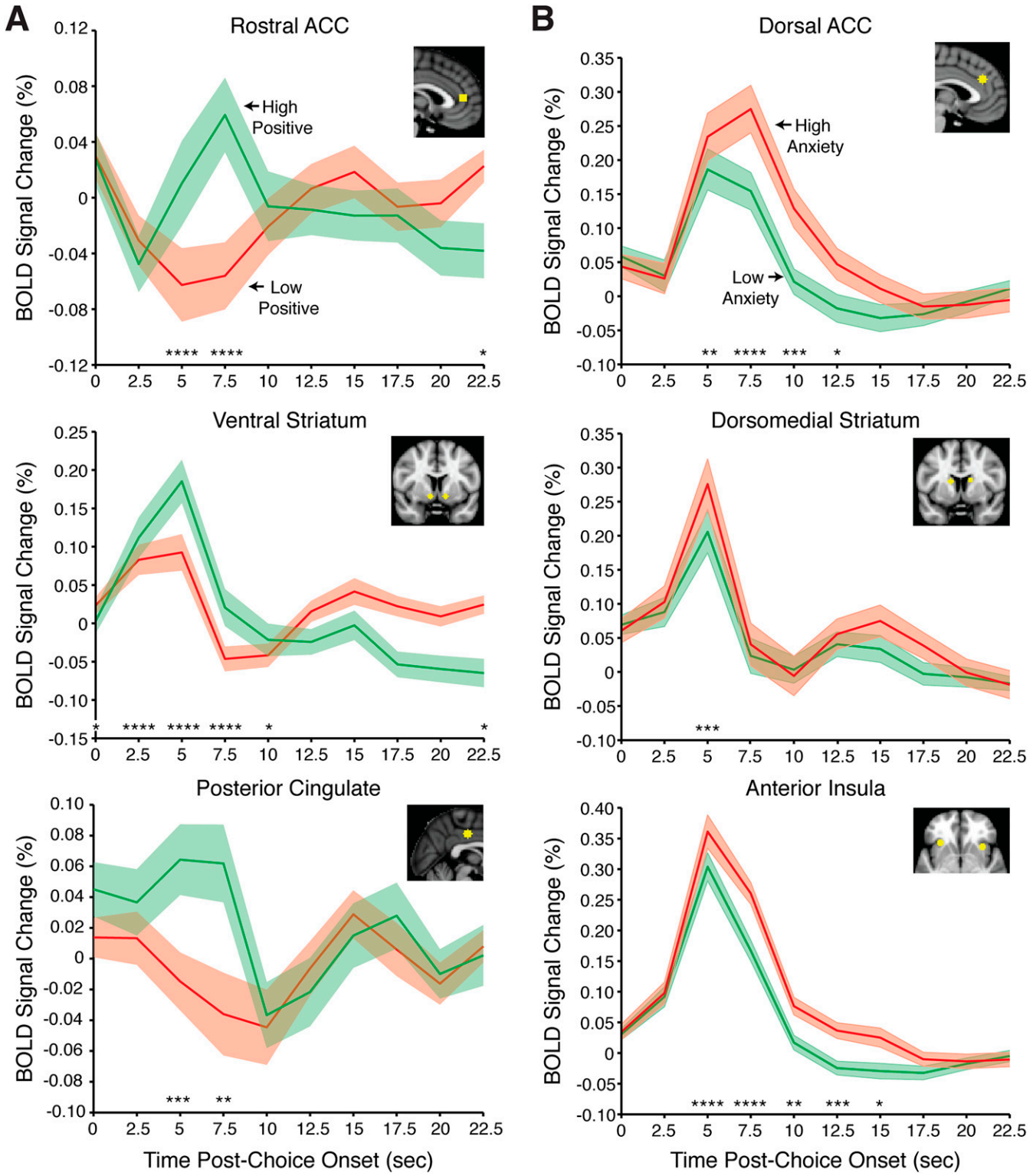

Fig. S4. Patterns of BOLD activity associated with positive affect and anxiety replicated in study 2. (*A*) Average BOLD time courses for levels of positive affect experienced during choices in study 2. Time courses are extracted from the rostral ACC (0, 44, 10), the bilateral ventral striatum (L, −12, 6, −8; R, 10, 6, −8, combined), and the PCC (2, −20, 40) ROIs based on peak positive affect activations in study 1. Unless otherwise noted, shaded error bars reflect between-subject SE. For each time point, a significant main effect of condition (based on a mixed-effects ANOVA) is noted with asterisks. (*B*) Average BOLD time courses for levels of anxiety experienced in study 2. Time courses are extracted from the dACC (−2, 36, 28), the bilateral dorsomedial striatum (caudate; L, −14, 6, 14; R, 14, 4, 16, combined), and the bilateral anterior insula (L, −30, 22, −8; R, 34, 16, −8, combined) ROIs based on peak choice anxiety activations in study 1. *$P < 0.05$, **$P < 0.01$, ***$P < 0.005$ ****$P < 0.001$.

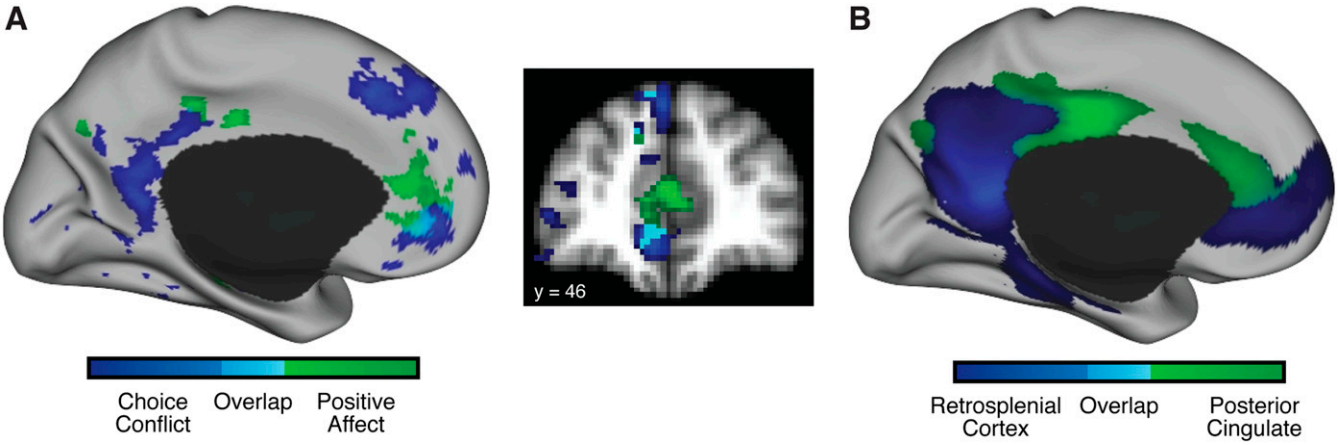

Fig. S5. Regions of ventral mPFC and posterior midline differentially tracked positive affect versus choice conflict. (*A*) Whole-brain maps for regions in study 1 tracking positive affect (green; Fig. 3) and choice conflict (blue; Fig. 4*A*; overlap in cyan). In both studies, regions of PCC and rACC track more closely with positive affect, and more generally with the value of the best option (Fig. S6). Conversely, regions of RSC and mOFC are selectively more active for high–high choices than the other conditions, consistent with a potential role in tracking both the value and the difficulty of the decision. (*B*) Regions with highest resting-state functional connectivity with PCC peak for positive affect (green) and RSC peak for choice conflict (blue). To emphasize differences within ventral mPFC, maps are thresholded more conservatively than those shown in Fig. 3 ($r \geq 0.20$, $n = 1{,}000$).

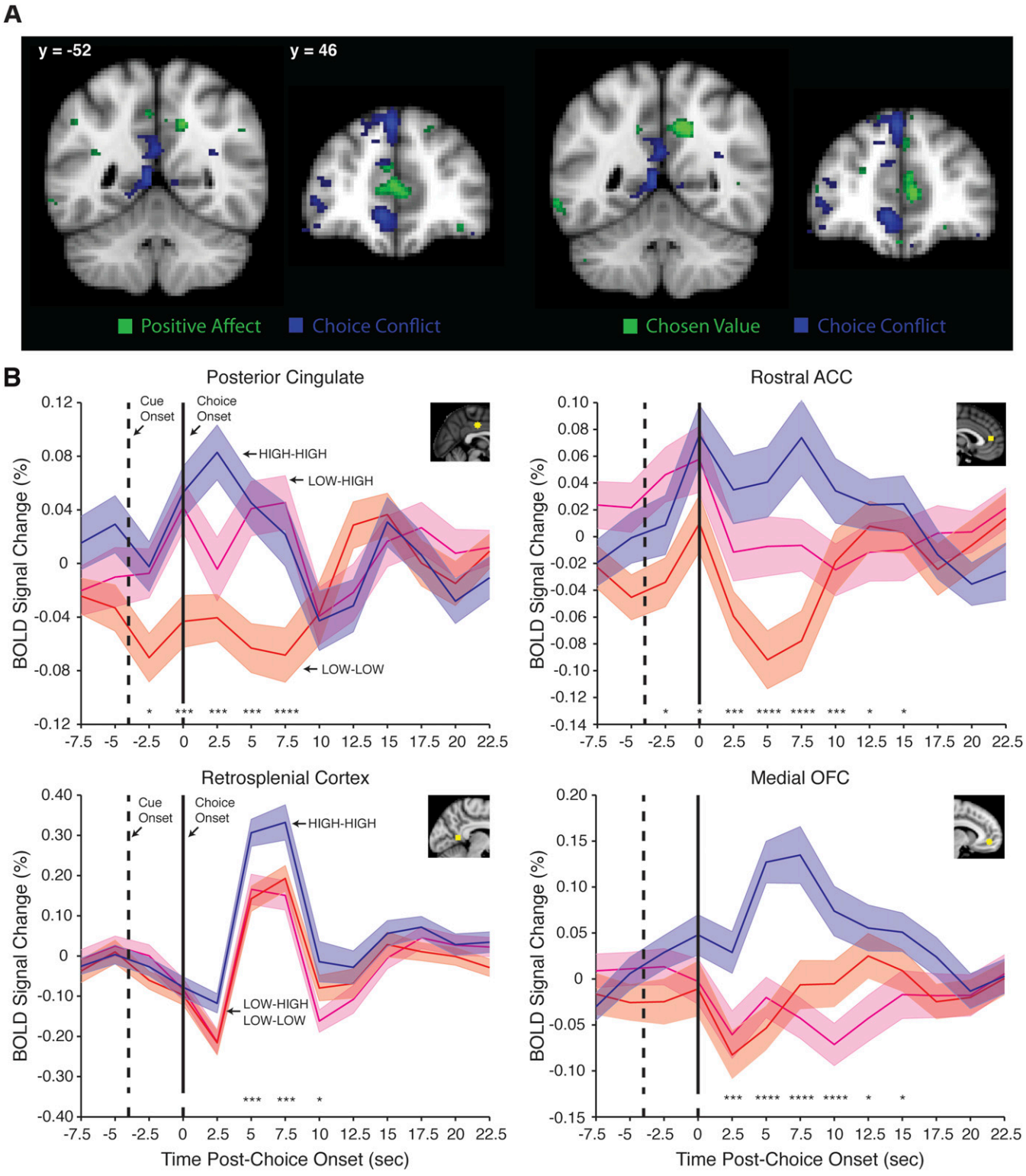

Fig. S6. BOLD activity in the rACC and PCC is associated with the highest available reward and responds to anticipatory cues before choice onset. (*A*) A whole-brain contrast for the value of the chosen item (green, *Right*) produces very similar patterns of activity as seen for positive affect (green, *Left*) (for both, study 1 is shown, but results are highly similar in study 2). Both of these analyses exclude low–low choices to minimize confounds between chosen and total value and to provide a more conservative comparison with the choice conflict contrast (blue). (*B*) Average BOLD time courses for the regions of the ventral mPFC and posterior midline that differentially track positive affect (rACC and PCC) and choice conflict (mOFC and RSC). To explore whether any of these regions were potentially sensitive to the anticipatory cues presented before each choice, we extracted time courses beginning 7.5 s before choice onset (continuing until 22.5 s post-choice onset, as with other analyses). PCC and, to a lesser degree, rACC exhibit patterns consistent with such anticipatory encoding. The dashed vertical line represents onset of anticipatory cue (0.75-s duration); the solid vertical lines represent onset of choice.

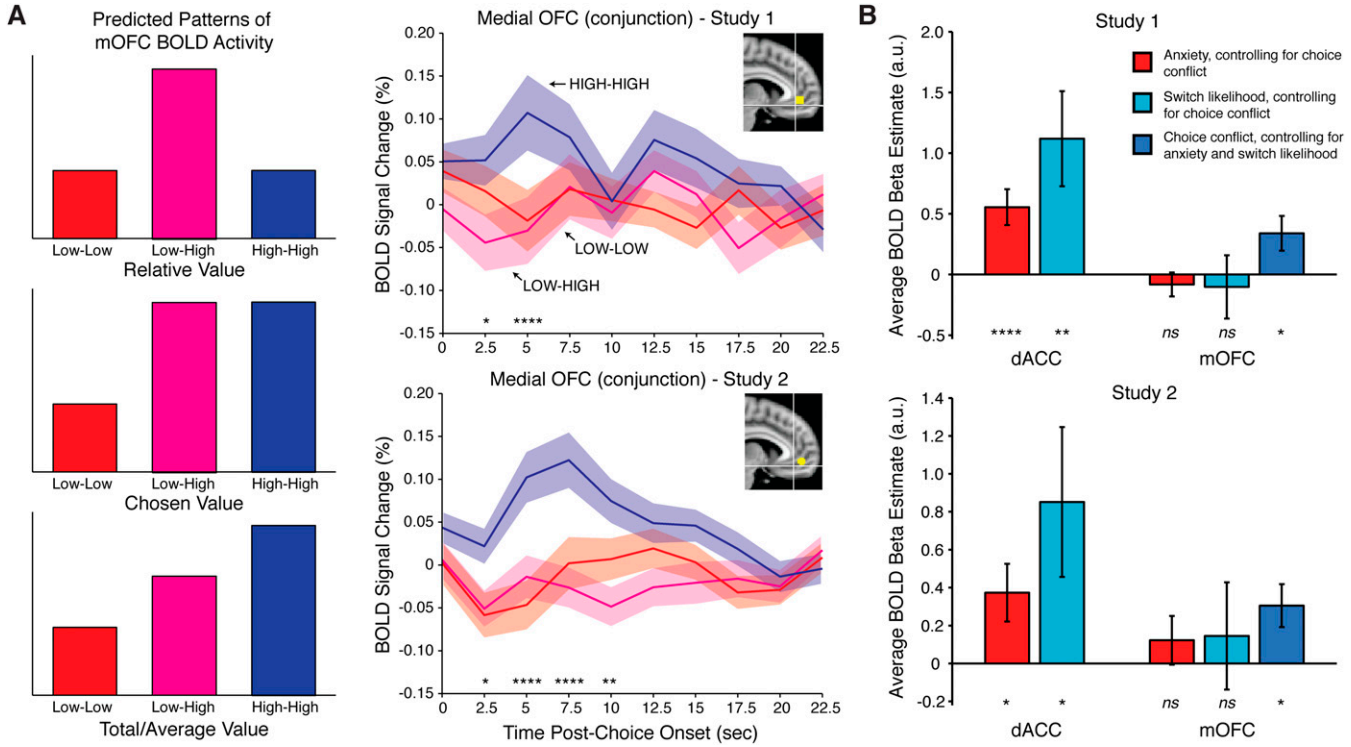

Fig. S7. The mOFC's relationship with choice conflict is not accounted for by subjective value alone and differs from that of the dACC. (*A*, *Left*) Prominent value-related accounts of mOFC (total value, relative value, chosen value) all make the prediction that low–high choices should activate this region more than low–low choices. As shown in Fig. S6*B*, this prediction failed to obtain for the mOFC and RSC ROIs identified by the choice conflict contrast (t_{41_mOFC} = 0.69, t_{41_RSC} = -0.53; two-tailed $P > 0.48$). The same was true for a post hoc analysis within the original study in which these ROIs were defined (study 1, t_{41_mOFC} = −0.13, t_{41_RSC} = −0.53; two-tailed $P > 0.59$). Overall value also failed to explain dACC's encoding of choice conflict (Fig. 4) (study 1, $t_{41} = -0.76$, $P = 0.45$; study 2, $t_{41} = 1.97$, $P = 0.06$). (*Right*) A final test confirmed that this difference failed to obtain even in the region of the mOFC most sensitive to total value (the only account that could fit our positive findings). Average BOLD time courses for each choice type were extracted from a region of the mOFC more active for high–high relative to the other two choice types. Time courses were extracted from mOFC ROIs identified by the opposite study, such that the ROI shown *Upper* is formed around the conjunction peak for high–high > low–high and high–high > low–low in study 2 (−2, 48, −6), and the ROI shown *Lower* is the same but for a conjunction peak in study 1 (−8, 44, −4). Low–high choices still did not yield greater BOLD activity than low–low. Crosshairs on both volume images indicate the peak left-hemisphere coordinates (−8, 38, −10) identified in a recent metaanalysis as a weighted average of vmPFC coordinates from choice value studies (17). See also *SI Discussion*. (*B*) Averaged beta estimates extracted from the mOFC show that, unlike the dACC, this region is not sensitive to anxiety or switch likelihood after controlling for choice conflict. The mOFC's sensitivity to choice conflict is in fact robust to controlling for both anxiety and switch likelihood. *$P < 0.05$, **$P < 0.01$, ****$P < 0.001$.

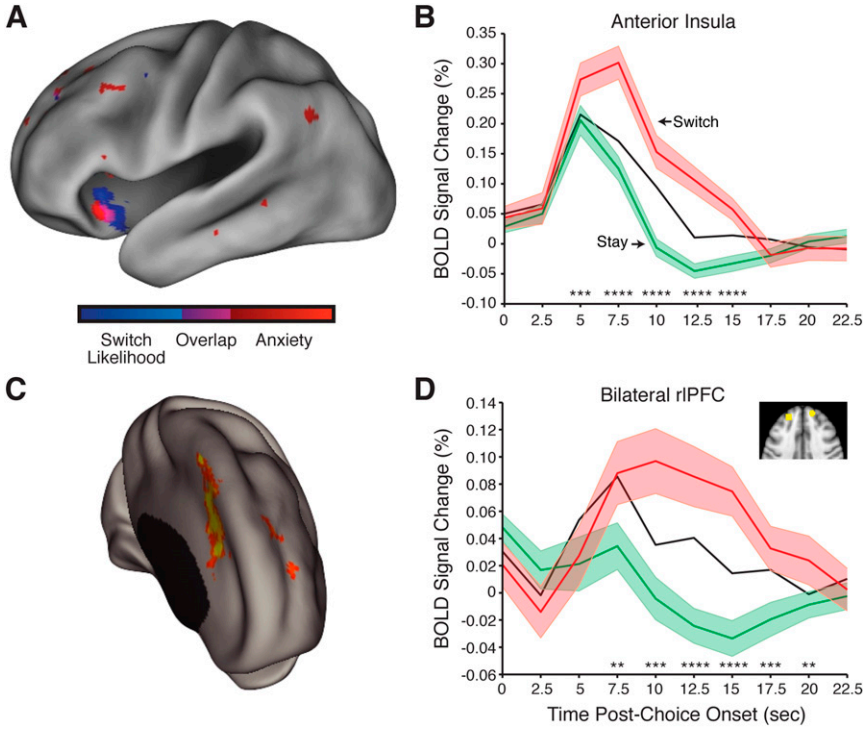

Fig. S8. The anterior insula and rostrolateral PFC are associated with choice reversal. (*A*) Whole-brain activations for anxiety (red) and choice reversal (blue; overlap in magenta), shown on the lateral surface (medial view shown in Fig. 4*C*). These activations were bilateral, but only the left hemisphere is shown. (*B*) Average BOLD time course for bilateral anterior insula ROI (L, −30, 18, −12; R, 30, 18, −16, combined) comparing choices where participants later decided to switch from versus stay with their previous choice (study 2). Toss-up trials (average shown in black) are excluded from analysis. This figure excludes participants without any toss-up trials and without at least five switch trials. Including participants without toss-ups, we find a significant difference for switch vs. stay trials at the choice peak ($t_{38} = 3.04$, $P < 0.005$). (*C*) Shifting event onsets for the choice reversal analysis in *A* (Fig. 4*C*) to the participants' responses rather than the appearance of the options reveals additional switch-related activations in the bilateral rlPFC. (*D*) Study 2 replicates switch-related effects found in the bilateral rlPFC (L, −22, 42, 40; R, 16, 48, 34, combined) and shows that these effects are only significant beginning 7.5 s after the onset of the choice options. *$P < 0.05$, **$P < 0.01$, ***$P < 0.005$, ****$P < 0.001$.