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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 highvalued 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

n 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. S1C 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 (mixedeffects 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),

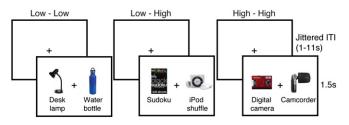


Fig. 1. Behavioral task performed in the scanner (study 1). Participants viewed pairs of products and pressed a button to indicate whether they preferred the item on the left or right side of the screen. Subjective values indicated in an earlier task were used to generate three kinds of choice pairs: 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.

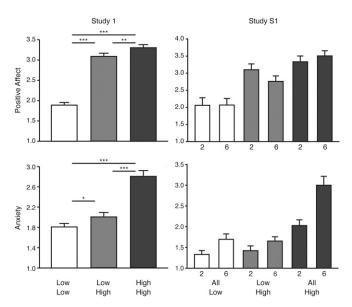


Fig. 2. Choices between similarly high-valued options generated the most positive affect and the most anxiety. Participants rated choices between all high-value options as significantly more positive (*Upper*) than choices between all low-value options and significantly more anxiety-inducing (*Lower*) 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.

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 $(F_{2,42} = 11.2, P_{1,21} = 11.2)$ P < 0.0005). The six-high choices were significantly more anxietyprovoking 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).

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

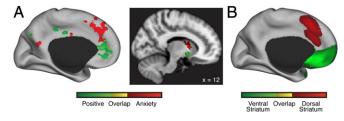


Fig. 3. Dissociable neural circuits simultaneously tracked positive and anxious feelings about a choice. (*A*) Whole-brain parametric analyses identifying regions where activity correlated with retrospective affective ratings (study 1). Activations in green correlated with how positive participants felt 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 $r \ge 0.10$ (*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. S1A). 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. S1B). 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. S1B) (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, $t_{41 \text{ dACC}} = 2.72, P < 0.005, t_{41 \text{ dmStr}} = 3.32, P < 0.001, t_{41 \text{ aIns}} = 3.68,$ P < 0.001; positive affect, $t_{41 \text{ rACC}} = 4.92$, P < 0.001, $t_{41 \text{ vStr}} = 7.78$, $P < 0.001, t_{41 \text{ PCC}} = 3.04, P < 0.005$; 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. 4A). This pattern was found even when participants knew in advance that either choice would yield similarly positive outcomes (Fig. 4B) ($t_{41} = 3.53$, 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. S1D 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.

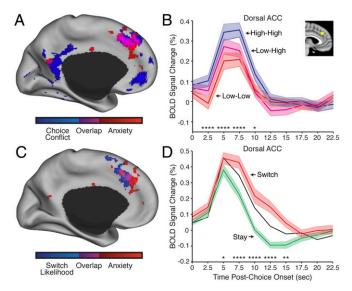


Fig. 4. Anxiety-related region of dorsal ACC tracks choice conflict and predicts postscan choice reversal. (A) Whole-brain contrast in study 1 for brain regions with greater activity during increased choice conflict, holding outcome value constant (high-high vs. low-high; blue), overlaid on parametric 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 decisionmaker 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. 2B). 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 in stitutional 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. S1C). 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. S1A).

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 wholebrain 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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- 1. Iyengar SS, Lepper MR (2000) When choice is demotivating: Can one desire too much of a good thing? J Pers Soc Psychol 79(6):995–1006.
- Anderson CJ (2003) The psychology of doing nothing: Forms of decision avoidance result from reason and emotion. *Psychol Bull* 129(1):139–167.
- Patall EA (2012) The motivational complexity of choosing: A review of theory and research. *The Oxford Handbook of Human Motivation*, ed Ryan RM (Oxford Univ Press, New York), pp 248–279.
- Dewberry C, Juanchich M, Narendran S (2013) The latent structure of decision styles. Pers Individ Dif 54(5):566–571.
- Luce MF (1998) Choosing to avoid: Coping with negatively emotion-laden consumer decisions. J Consum Res 24(4):409–433.
- 6. Schwartz B (2004) The Paradox of Choice: Why More is Less (Ecco, New York).
- Redelmeier DA, Shafir E (1995) Medical decision making in situations that offer multiple alternatives. JAMA 273(4):302–305.
- Botti S, Iyengar SS (2006) The dark side of choice: When choice impairs social welfare. J Public Policy Mark 25(1):24–38.
- 9. Schwartz B, et al. (2002) Maximizing versus satisficing: Happiness is a matter of choice. J Pers Soc Psychol 83(5):1178–1197.
- Lipowski ZJ (1970) The conflict of Buridan's ass or some dilemmas of affluence: The theory of attractive stimulus overload. Am J Psychiatry 127(3):273–279.
- Festinger L (1957) A Theory of Cognitive Dissonance (Stanford Univ Press, Stanford, CA).
 Rangel A, Hare T (2010) Neural computations associated with goal-directed choice.
- Curr Opin Neurobiol 20(2):262–270.
 Rushworth MFS, Behrens TEJ, Rudebeck PH, Walton ME (2007) Contrasting roles for cingulate and orbitofrontal cortex in decisions and social behaviour. *Trends Cogn Sci* 11(4):168–176.
- Bornstein AM, Daw ND (2011) Multiplicity of control in the basal ganglia: Computational roles of striatal subregions. *Curr Opin Neurobiol* 21(3):374–380.
- Balleine BW, O'Doherty JP (2010) Human and rodent homologies in action control: Corticostriatal determinants of goal-directed and habitual action. *Neuropsychopharmacology* 35(1):48–69.
- Rushworth MFS, Noonan MP, Boorman ED, Walton ME, Behrens TE (2011) Frontal cortex and reward-guided learning and decision-making. *Neuron* 70(6):1054–1069.
- Lebreton M, Jorge S, Michel V, Thirion B, Pessiglione M (2009) An automatic valuation system in the human brain: Evidence from functional neuroimaging. *Neuron* 64(3): 431–439.
- Goldstein BL, et al. (2012) Ventral striatum encodes past and predicted value independent of motor contingencies. J Neurosci 32(6):2027–2036.
- Levy DJ, Glimcher PW (2012) The root of all value: A neural common currency for choice. Curr Opin Neurobiol 22(6):1027–1038.
- Knutson B, Greer SM (2008) Anticipatory affect: Neural correlates and consequences for choice. *Philos Trans R Soc Lond B Biol Sci* 363(1511):3771–3786.
- 21. Shenhav A, Botvinick MM, Cohen JD (2013) The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron* 79(2):217–240.
- Shackman AJ, et al. (2011) The integration of negative affect, pain and cognitive control in the cingulate cortex. Nat Rev Neurosci 12(3):154–167.
- Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S (2004) The role of the medial frontal cortex in cognitive control. *Science* 306(5695):443–447.
- Amemori K, Graybiel AM (2012) Localized microstimulation of primate pregenual cingulate cortex induces negative decision-making. Nat Neurosci 15(5):776–785.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. *Psychol Rev* 108(3):624–652.
- Blair K, et al. (2006) Choosing the lesser of two evils, the better of two goods: Specifying the roles of ventromedial prefrontal cortex and dorsal anterior cingulate in object choice. J Neurosci 26(44):11379–11386.
- 27. FitzGerald THB, Seymour B, Dolan RJ (2009) The role of human orbitofrontal cortex in value comparison for incommensurable objects. J Neurosci 29(26):8388–8395.
- Kitayama S, Chua HF, Tompson S, Han S (2013) Neural mechanisms of dissonance: An fMRI investigation of choice justification. *Neuroimage* 69:206–212.
- Frank MJ, Woroch BS, Curran T (2005) Error-related negativity predicts reinforcement learning and conflict biases. *Neuron* 47(4):495–501.
- Kim HY, Shin Y, Han S (2014) The reconstruction of choice value in the brain: A look into the size of consideration sets and their affective consequences. J Cogn Neurosci 26(4):810–824.
- Chernev A, Hamilton R (2009) Assortment size and option attractiveness in consumer choice among retailers. J Mark Res 46(3):410–420.

- 32. Alchian AA (1968) Cost. International Encyclopedia of the Social Sciences (Macmillan, New York), Vol 3, pp 404–415.
- Kurzban R, Duckworth A, Kable JW, Myers J (2013) An opportunity cost model of subjective effort and task performance. *Behav Brain Sci* 36(6):661–679.
- Haber SN, Knutson B (2010) The reward circuit: Linking primate anatomy and human imaging. Neuropsychopharmacology 35(1):4–26.
- Choi EY, Yeo BTT, Buckner RL (2012) The organization of the human striatum estimated by intrinsic functional connectivity. J Neurophysiol 108(8):2242–2263.
- 36. Yeo BTT, et al. (2011) The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J Neurophysiol* 106(3):1125–1165.
- Behrens TEJ, Woolrich MW, Walton ME, Rushworth MFS (2007) Learning the value of information in an uncertain world. Nat Neurosci 10(9):1214–1221.
- Garrison J, Erdeniz B, Done J (2013) Prediction error in reinforcement learning: A meta-analysis of neuroimaging studies. *Neurosci Biobehav Rev* 37(7):1297–1310.
- 39. Hirsh JB, Mar RA, Peterson JB (2012) Psychological entropy: A framework for understanding uncertainty-related anxiety. *Psychol Rev* 119(2):304–320.
- Venkatraman V, Huettel SA (2012) Strategic control in decision-making under uncertainty. Eur J Neurosci 35(7):1075–1082.
- Kerns JG, et al. (2004) Anterior cingulate conflict monitoring and adjustments in control. Science 303(5660):1023–1026.
- Boorman ED, Behrens TEJ, Woolrich MW, Rushworth MFS (2009) How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action. *Neuron* 62(5):733–743.
- Hampton AN, Bossaerts P, O'Doherty JP (2006) The role of the ventromedial prefrontal cortex in abstract state-based inference during decision making in humans. J Neurosci 26(32):8360–8367.
- Yeung N, Botvinick MM, Cohen JD (2004) The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychol Rev* 111(4):931–959.
- Spunt RP, Rassin E, Epstein LM (2009) Aversive and avoidant indecisiveness: Roles for regret proneness, maximization, and BIS/BAS sensitivities. *Pers Individ Dif* 47(4): 256–261.
- Bechara A, Damasio AR (2005) The somatic marker hypothesis: A neural theory of economic decision. Games Econ Behav 52(2):336–372.
- Prévost C, Pessiglione M, Météreau E, Cléry-Melin ML, Dreher JC (2010) Separate valuation subsystems for delay and effort decision costs. J Neurosci 30(42):14080–14090.
 Gan JO, Walton ME, Phillips PEM (2010) Dissociable cost and benefit encoding of
- 40. Gan JC, Watch ME, Finings FEW (2016) Disociable cost and benefit encoding of future rewards by mesolimbic dopamine. Nat Neurosci 13(1):25–27.
- McGuire JT, Botvinick MM (2010) Prefrontal cortex, cognitive control, and the registration of decision costs. Proc Natl Acad Sci USA 107(17):7922–7926.
- Miller NE (1944) Experimental studies of conflict. Personality and the Behavior Disorders, ed Hunt JM (Ronald Press, New York), Vol 1, pp 431–465.
- Gray JA, McNaughton N (2000) The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-Hippocampal System (Oxford Univ Press, Oxford).
 Grinband J. et al. (2011) The dorsal medial frontal cortex is sensitive to time on task.
- not response conflict or error likelihood. *Neuroimage* 57(2):303–311. 53. Brown JW, Braver TS (2005) Learned predictions of error likelihood in the anterior
- c) Brown W, Braver 15 (2005) tearned predictions of error inkelmood in the anterior cingulate cortex. Science 307(5712):1118–1121.
- Becker SW, Ronen J, Sorter GH (1974) Opportunity costs: An experimental approach. J Account Res 12(2):317–329.
- 55. Niv Y, Daw ND, Joel D, Dayan P (2007) Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology (Berl)* 191(3):507–520.
- Okada EM, Hoch SJ (2004) Spending time versus spending money. J Consum Res 31(2): 313–323.
- Kahneman D, Knetsch JL, Thaler RH (1991) Anomalies: The endowment effect, loss aversion, and status quo bias. J Econ Perspect 5(1):193–206.
- Knutson B, et al. (2008) Neural antecedents of the endowment effect. *Neuron* 58(5): 814–822.
- 59. Knutson B, Katovich K, Suri G (2014) Inferring affect from fMRI data. *Trends Cogn Sci*, in press.
- Samanez-Larkin GR, et al. (2007) Anticipation of monetary gain but not loss in healthy older adults. Nat Neurosci 10(6):787–791.
- Robinson MD, Clore GL (2002) Belief and feeling: Evidence for an accessibility model of emotional self-report. Psychol Bull 128(6):934–960.
- Becker GM, DeGroot MH, Marschak J (1964) Measuring utility by a single-response sequential method. *Behav Sci* 9(3):226–232.

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