

The Inherent Reward of Choice

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Supplementary Materials

Supplementary Methods

Participants. Twenty-seven healthy right-handed individuals from the Rutgers University – Newark campus responded to posted advertisements and were recruited to participate in this study. Nine participants were excluded from analyses due to excessive motion ($n = 2$), scanner hardware malfunction ($n = 2$), or failure to comply with task requirements (e.g. failing to respond on a large proportion of trials – more than 3 SDs above the average number of missed trials; $n = 5$). Thus, the final sample included in the analysis consisted of eighteen participants. Participants gave informed consent according to the Rutgers University Institutional Review Board for the Protection of Human Subjects in Research and the Newark Campus Institutional Review Board of the University of Medicine and Dentistry of New Jersey.

fMRI Data Acquisition and Analyses.

A 3T Siemens Allegra head-only scanner and a Siemens standard head coil were used for data acquisition at Rutgers' University Heights Center for Advanced Imaging. Anatomical images were acquired using a T1-weighted protocol (256 x 256 matrix, 176 1 mm sagittal slices). Functional images were acquired using a single-shot gradient echo EPI sequence (TR = 2000 ms, TE = 25 ms, FOV = 192 cm, flip angle = 80° , bandwidth = 2604 Hz/px, echo spacing =

0.29 ms). Thirty-five contiguous oblique-axial slices (3 x 3 x 3 mm voxels) parallel to the AC-PC line were obtained. Analysis of imaging data was conducted using Brain Voyager software (version 1.9; Brain Innovation, Maastricht, The Netherlands). The data were initially corrected for motion (using a threshold of 2 mm or less), and slice scan time using sinc interpolation was applied. Further, spatial smoothing was performed using a three-dimensional Gaussian filter (8 mm FWHM), along with voxel-wise linear detrending and high-pass filtering of frequencies (three cycles per time course). Structural and functional data of each participant were then transformed to standard Talairach stereotaxic space (Talairach & Tournoux, 1988).

A random effects analysis was performed on the functional data using a general linear model, including the following conditions: (1) Choice cue, (2) No choice cue (3) Non-informative cue, (4) Predictive No-Choice cue, (5) Response Phase, (6) Monetary Outcome: Large reward (\$100), (7) Monetary Outcome: Small reward (\$50), and (8) Monetary Outcome: No reward (\$0). We focused on two main analyses: Analysis 1 was a region of interest (ROI) analysis, with a priori ROIs defined by coordinates reported in the literature as selective to the anticipation of monetary reward (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005). ROIs (eight 1mm³ voxels) were defined in the midbrain (X = 0, Y = -18, Z = -10), left ventral striatum (X = -9, Y = 10, Z = 0), right ventral striatum (X = 11, Y = 12, Z = 0), left orbitofrontal cortex (X = -1, Y = 46, Z = -11) and right orbitofrontal cortex (X = 4, Y = 53, Z = -10). Within each ROI, BOLD activity was averaged across all voxels to obtain a single parameter estimate (z-score) for

each cue type. These values were then compared across cue-types (regressors #1-4) using paired t-tests. Analysis 2 was a whole-brain analysis examining differences in anticipatory BOLD activity associated with the four cue types. A repeated measures ANOVA of cue type on anticipatory BOLD activity was thresholded at $p < 0.005$ and corrected for multiple comparisons using Monte-Carlo simulated cluster-size thresholding ($k=6$) to achieve an effective corrected threshold of $\alpha = 0.05$ (Forman et al., 1995; Goebel, Esposito, & Formisano, 2006), which establishes a reasonable balance between potential Type I and Type II errors (Lieberman & Cunningham, 2009).

Supplementary Results & Discussion

Main Effects of Cue Type in Reward Anticipation ROIs:

Parameter estimates (mean betas) were extracted from ROIs defined a priori in the midbrain, bilateral VS and OFC. Paired t-tests revealed that betas for the choice condition were significantly greater than betas for the no-choice condition in the midbrain and bilateral VS. Relative to the choice condition, betas for the experimental control conditions were not significantly different, with the exception of a significant difference between choice and predictive cues in the right VS. Supplementary Table 1 lists the betas for each experimental condition in each of the a priori ROIs.

One potential interpretation of the findings from Analysis 1 is that the anticipation of choice carries a value signal that may be important for learning and goal-directed behavior. While the human striatum has been linked with reward-related learning (e.g., Delgado, 2007; O'Doherty, 2004), activity in this

region in neuroimaging paradigms has also been associated with other reward-related processes, such as risk and uncertainty (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Kuhnen & Knutson, 2005). Thus, it is possible that anticipation of choice modulates activity in this region specifically due to perceived uncertainty or the predictability of an outcome. Because the choice condition is not statistically different from the control conditions, we cannot conclude that the effects observed in the VS are free from the influence of uncertainty and predictability. However, because the ROI analysis involves averaging over all voxels in an ROI, significant effects may be smoothed out. Thus, the findings of the whole-brain exploratory analysis are critical for understanding how the different conditions modulate activity in reward regions. The data in the whole-brain analysis show that activity is greater for the Choice condition relative to the control conditions in the bilateral striatum, suggesting that relative differences between Choice and No-choice in the ventral striatum are not entirely driven by differences in perceived uncertainty or predictability, but rather by variations in affective experience of perceived control elicited by the main experimental condition (Choice).

Linear Contrast of Choice vs. No-choice

We performed a simple linear contrast ($p < .005$, cluster threshold correction) comparing activity in response to cues predicting choice and no-choice (Choice > No-choice) to complement our whole-brain ANOVA findings. We observed greater activity for choice cues in the right striatum (ventral and

dorsal), left dorsal striatum, bilateral insula, medial PFC, right inferior frontal gyrus, and right dorsolateral PFC (see Supplementary Table 2). These regions overlap considerably with those identified by the whole-brain exploratory analysis of all cue types. This analysis confirms significant differences between choice and no-choice cue types in regions of the human reward circuitry.

Anticipation of Choice Opportunity in the Reward Network

In the main text of the manuscript, we focus our analysis on choice-related BOLD activity in a priori ROIs that were previously shown to be particularly active during the anticipation of monetary reward (Knutson et al., 2005). Additionally, we looked for main effects of cue type across the whole brain in a secondary exploratory analysis. Here, we address how the current findings are consistent or inconsistent with the existing literature.

Greater choice-related activity observed in the dorsal striatum may reflect the perceived contingency between the participants' choices and the resulting reward. The dorsal striatum has been shown to respond preferentially to the anticipation and delivery of rewards that are contingent on an individual's behavior, in both animals (Ito, Dalley, Howes, Robbins, & Everitt, 2000; Ito, Dalley, Robbins, & Everitt, 2002; Samejima, Ueda, Doya, & Kimura, 2005; Yin, Knowlton, & Balleine, 2006; Yin, Ostlund, Knowlton, & Balleine, 2005) and humans (Bjork & Hommer, 2007; Delgado, Miller, Inati, & Phelps, 2005; Elliott, Newman, Longe, & William Deakin, 2004; O'Doherty et al., 2004). Furthermore, because studies have found that this particular region in the head of the caudate

nucleus is more responsive to conditions of greater motivational incentive (Delgado, Stenger, & Fiez, 2004; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004), we might conclude that activity observed in the dorsal striatum in the current study reflects greater salience of the choice condition relative to the no-choice condition. Perception of control over an action and its consequences may further influence the motivational salience of rewards resulting from choice, since studies have demonstrated that rewards that are a consequence of personal choice, as opposed to forced-choice, produce greater activity in the striatum (Coricelli et al., 2005; Tricomi, Delgado, & Fiez, 2004).

Whereas some of these previous neuroimaging studies have focused on the outcome period following choice or the expectation of the outcome itself, the present study is unique because it examines the affective and motivational processes occurring when anticipating choice opportunity. Despite this critical difference, we still demonstrate greater choice-related activity in both the dorsal and ventral striatum. Because the dorsal striatum has been more associated with action-outcome contingencies, and the ventral striatum has been associated with both action-outcome and stimulus-outcome contingencies (O'Doherty et al., 2004), our findings suggest that anticipation of choice may involve reward processes related to both types of learning. Interestingly, a recent study suggests that more anterior regions of the caudate and ventromedial PFC code for action-outcome contingencies, whereas more posterior regions of the caudate and the inferior frontal gyrus (both observed in the current study), code for reward that is not contingent on actions (Liljeholm, Tricomi, O'Doherty, & Balleine, 2011).

Because we observe activity in a more posterior region of the caudate in the present study, this may suggest that anticipation of choice may carry a value signal in and of itself, which is not related to expectations about contingencies between actions and outcomes. Future research designed to tease apart these processes will be extremely valuable for characterizing the affective experience of choice and perceived control.

Although our whole-brain analysis revealed significant activity for choice relative to no-choice in some reward-related regions (e.g. striatum), other regions that are commonly reported in studies of reward processing, such as the orbitofrontal cortex (OFC), did not demonstrate main effects of cue type in the current study. Many previous neuroimaging studies have demonstrated that activity in the OFC responds to both primary (de Araujo, Kringelbach, Rolls, & McGlone, 2003; de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Plassmann, O'Doherty, & Rangel, 2007) and secondary reinforcers (Elliott et al., 2004; Galvan et al., 2006; Knutson, Fong, Bennett, Adams, & Hommer, 2003; O'Doherty, Critchley, Deichmann, & Dolan, 2003; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Tobler, O'Doherty, Dolan, & Schultz, 2007; Yacubian et al., 2006), and more specifically, studies have demonstrated greater activity in the OFC for rewards in the context of choice (e.g., Arana et al., 2003; O'Doherty et al., 2003).

In the present study, absence of main effects of choice in the OFC may be due to signal dropout in this area, since our fMRI acquisition is not optimized for ventral PFC regions that are highly susceptible to artifact. Alternately, we may

not observe differences in this specific ROI, due to variations in task. The current results may differ from earlier studies (e.g. O'Doherty et al 2003; Arana et al 2003) because the present study focuses on the anticipation of choice opportunity. For example, a study by O'Doherty and colleagues (2003) focused on separating BOLD responses *following* free-choice vs. forced-choices, which resulted in positive and negative outcomes. In that study, subjects learned that the outcomes associated with responses were different (i.e. one choice was good and one was bad). A critical difference in our study is that we focus on the anticipation of choice opportunity, where there is no actual difference in the outcome associated with the choice, suggesting that differences in affective response during anticipation may reflect values associated with the act of choosing, rather than the associated outcome. Furthermore, location of OFC activity in response to rewards varies considerably from study to study, and there is some debate about functional localization within the OFC, where some studies suggest that different regions may respond to different types of reinforcers (primary vs. secondary), and to rewards vs. punishments (Kringelbach & Rolls, 2004). Additionally, many studies have demonstrated that the OFC is not only important for processing expected value, but is also critical for updating stimulus-reward contingencies and consequential behavior. In fact, in the O'Doherty et al 2003 study, the authors report that there was greater activity in the medial OFC for free-choice trials only when subjects maintained the same response on subsequent trials (i.e. they did not update behavior based on the outcome). When participants switched their choices on the subsequent trial, greater activity

was observed in the insula and dorsal anterior cingulate cortex. These regions are very similar to those we observed in our whole-brain analyses and our simple linear contrast of Choice > No-Choice, and suggest that perhaps the anticipation of choice involves processes related to updating value information for modification of behavior

Predictive Cue Analysis

The Predictive No-Choice cue consisted of two different cue types: one indicated that computer would choose blue and the other indicated that the computer would choose yellow. On average, participants chose the blue key on 52% of choice trials. Immediately following the scanning session, we asked participants to rate the perceived difference between yellow and blue keys on a scale from 1-5 with the following anchors: 1 = yellow key is far better than the blue key; 2 = yellow key is slightly better than blue key; 3 = there is no difference between keys; 4 = blue key is slightly better than yellow key; and 5 = blue key is far better than yellow key.

Post-scan self-reports of key ratings revealed that participants generally perceived a slight difference between the keys. Two participants perceived no difference between keys, seven expressed a preference for the yellow key (mean rating = 1.6), and nine expressed a preference for the blue key (mean rating = 4.2). There were no actual differences in expected value for the keys for any of the participants.

These perceived differences may be the result of the illusion of control, where the mere presence of choice opportunity may enhance the perceived contingency between the choice and the outcome, when the outcome is desirable (Langer, 1975; Langer & Rodin, 1976). Also, because we know that simply choosing an option increases its subjective value (Brehm, 1956; Lieberman, Ochsner, Gilbert, & Schacter, 2001), individuals may have attributed greater value to keys simply because they liked to assert a preference through choice. Consistent with this theory, we found no differences in BOLD signals when probing the whole-brain for activity anticipating the preferred color vs. non-preferred color.

Based on participant's self-reports of preferences between blue and yellow keys, we characterized the Predictive cues as two separate regressors in a separate exploratory GLM: (1) Preferred Predictive and (2) nonpreferred Predictive. Contrasting BOLD activity for Preferred vs. Non-preferred Predictive Cues at a liberal threshold of $p < 0.005$ uncorrected, we observed no differences in any of the a priori ROIs, or more generally, in any regions that are commonly reported for the anticipation or delivery of reward. This provides support that anticipatory activity during the predictive cue in the main analysis was not coding for the expected value (real or perceived) of the outcome. This is important for interpreting the main effects of cue-type because it suggests that activity associated with the anticipation of choice is not likely reflecting anticipation of choosing a specific key that is associated additional reward.

Exploring the Role of Reward Learning

The Predictive Cue Analysis (described above) revealed that explicit key preference and associated expectations of reward prediction did not modulate activity in the striatum during the anticipation phase. These findings suggest that the affective valuation of the opportunity of choice is independent of predicted reward outcomes. An alternative explanation, however, may be that trial-by-trial fluctuations in experienced rewards may actually induce temporary changes in key preference (blue vs. yellow), which may in turn create perceived advantages for choice opportunity. Overall experienced reward did not significantly differ by trial type. The expected, or average value was \$50 for both choice and no-choice trials and for blue and yellow keys for all participants.

It is possible, however, that individuals experienced variations in rewards based on choice history and randomization of reward outcomes, which could differentially influence expectations about the value of the two keys. Regardless of the specific preference on a given trial, if participants perceive that one option is better than the other, then anticipating an opportunity to choose may involve expectation of greater reward than what would be expected in the no-choice condition. Though adaptive learning models have been very useful for explaining reward-related activity in the striatum, (e.g., Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; O'Doherty et al., 2004; O'Doherty, Hampton, & Kim, 2007; Schonberg, Daw, Joel, & O'Doherty, 2007; Wittmann, Daw, Seymour, & Dolan, 2008), modeling such trial-by-trial variations in experienced and expected rewards is beyond the scope of

the current design. While this hypothesis can be tested in future research, it may provide an explanation for why individuals find choice and control desirable in the real world.

Supplementary Text References

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Supplementary Table 1: Parameter Estimates from Reward ROIs

ROI	X, Y, Z	Betas			Predictable
		Choice	No-choice	No-Info	
midbrain	0, -18, -10	.020 (.016)	-.015 (.012)	.013 (.013)	.001 (.014)
right VS	11, 12, 0	.030 (.015)	-.014 (.011)	.024 (.011)	-.004 (.012)
left VS	-9, 10, 0	.013 (.016)	-.016 (.011)	.016 (.014)	-.007 (.016)
right OFC	4, 53, -10	-.008 (.013)	-.027 (.011)	-.009 (.015)	-.022 (.014)
left OFC	-1, 46, -11	-.023 (.015)	-.040(.011)	-.018 (.010)	-.015 (.013)

Average beta estimates (SEM) extracted from each a priori ROI in response to the cue (anticipation phase). Bold-faced entries reflect conditions that were significantly different from the Choice condition in a paired t-test. Talairach coordinates (X, Y, Z) for peak voxels in each region are reported. Abbreviations: VS = ventral striatum, MPFC = medial prefrontal cortex.

Supplementary Table 2: Choice > No-choice (Whole-brain analysis)

Region	X, Y, Z	Betas			Predictable
		Choice	No-choice	No-Info	
left putamen	-19, -2, 12	.038 (.015)	-.012 (.010)	.019 (.012)	.006 (.014)*
right VS	11, 4, -6	.025 (.014)	-.028 (.010)	.015 (.011)	-.011 (.012)
right caudate	14, 4, 6	.035 (.016)	-.025 (.012)	.013 (.015)	-.005 (.014)
left insula	-31, 19, 6	.037 (.017)	-.008 (.013)	.011 (.015)*	-.010 (.014)
right insula	26, 19, 0	.021 (.015)	-.020 (.012)	.003 (.012)	-.019 (.013)
right IFG	41, 16, 6	.033 (.016)	-.025 (.013)	-.002 (.015)	-.010 (.015)
right DLPFC	23, 43, 24	.049 (.015)	-.000 (.014)	.023 (.016)	.019 (.018)*
rACC	5, 25, 30	.062 (.017)	.012 (.018)	.050 (.018)	.016 (.016)
rdACC	2, 4, 48	.091 (.020)	.035 (.018)	.074 (.021)	.045 (.020)

Average beta estimates (SEM) extracted from ROIs identified by whole-brain linear contrast of Choice v. No-choice cue ($p < .005$, cluster corrected). Bold-faced entries reflect conditions that were significantly different ($p < .05$) from the Choice condition in a paired t-test, and asterisks indicate marginal significance ($p < .1$). Talairach coordinates (X, Y, Z) for peak voxels in each region are reported. Abbreviations: IFG (inferior frontal gyrus), DLPFC (dorsolateral prefrontal cortex), rACC (rostral anterior cingulate cortex), rdACC (rostral dorsal anterior cingulate cortex).