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Psychological Science 2011 22: 1310 originally published online 19 September 2011
DOI: 10.1177/0956797611417005

Research Article

Psychological Science
22(10) 1310–1318

DOI: 10.1177/0956797611417005
http://pss.sagepub.com

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Lauren A. Leotti and Mauricio R. Delgado
Rutgers University

Abstract

Research suggests that the exercise of control is desirable and adaptive, but the precise mechanisms underlying the affective value of control are not well understood. The study reported here characterized the affective experience of personal control by examining the neural substrates recruited when individuals anticipate the opportunity to make a choice—in other words, when they anticipate the means for exercising control. We used an experimental paradigm that probed the value of having a choice. Participants reported liking cues that predicted a future opportunity to make a choice more than cues that predicted no choice. The anticipation of choice itself was associated with increased activity in corticostriatal regions, particularly the ventral striatum, involved in affective and motivational processes. This study is the first direct examination of the affective value of having the opportunity to choose. These findings have important implications for understanding the role of perception of control, and choice itself, in self-regulatory processes.

Keywords

MRI, striatum, anticipation, choice, perceived control, reward

Received 1/14/11; Revision accepted 5/9/11

Perceiving and exercising personal control are highly adaptive, for the presence or absence of control can have a significant impact on the regulation of cognition, emotion, and even physical health (Bandura, Caprara, Barbaranelli, Gerbino, & Pastorelli, 2003; Ryan & Deci, 2006; Shapiro, Schwartz, & Astin, 1996). Individuals exercise control over their environment by making choices ranging from basic perceptual decisions to complex and emotionally salient decisions. Converging evidence suggests that choice is desirable (for a review, see Leotti, Iyengar, & Ochsner, 2010). For example, animals and humans demonstrate a preference for having a choice over not having a choice, even when the choice confers no additional reward (Bown, Read, & Summers, 2003; Suzuki, 1997, 1999). The fact that choice is desirable under such conditions suggests that choice itself has a positive affective component that increases the value of choice relative to nonchoice. However, this hypothesis has not been tested directly experimentally, and, as a result, the neural mechanisms underlying the affective value of both choice and control are not well understood.

The goal of the study reported here was to examine the affective experience of perceiving that one has control, as exercised through choice behavior. We used functional magnetic resonance imaging (fMRI) to identify the neural substrates recruited during the anticipation of a future choice opportunity. We expected that if choice is rewarding, then anticipating having a choice (relative to anticipating having no choice) would modulate activity in corticostriatal systems implicated in motivated behavior and reward processing (Delgado, 2007; Haber & Knutson, 2010; Montague & Berns, 2002; O'Doherty, 2004; Rangel, Camerer, & Montague, 2008; Robbins & Everitt, 1996).

Our hypothesis was motivated by findings from previous neuroimaging studies suggesting that the exercise of personal control may be particularly motivating and rewarding. For example, rewards that are instrumentally delivered activate reward-related circuitry to a greater extent than do rewards that are passively received (Arana et al., 2003; Bjork & Hommer, 2007; O'Doherty, Critchley, Deichmann, & Dolan, 2003; O'Doherty et al., 2004; Tricomi, Delgado, & Fiez, 2004; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). Similarly, simply choosing an item (as opposed to rejecting an item) increases its subjective rating and recruits reward-related circuitry, such as the striatum (Sharot, De Martino, & Dolan, 2009). Although such results help support the idea that control is an important component of the valuation process, these previous studies were not specifically designed to examine the affective value of the opportunity for choice, and thus do not separate the contributions of cognitive processes from the contributions of affective processes to decision making. The current study builds on and extends these prior findings to characterize the affective components of choice and perceived

Corresponding Author:
Mauricio R. Delgado, Department of Psychology, Rutgers University, Smith Hall, Room 340, 101 Warren St., Newark, NJ 07102
E-mail: delgado@psychology.rutgers.edu

control, and thus provides an important contribution to understanding why the perception and exercise of control is so adaptive in diverse spheres of psychosocial functioning.

We tested whether the mere anticipation of personal involvement through choice would recruit reward-related brain circuitry, particularly the striatum. This finding would suggest that choice is valuable in and of itself. In our study, participants either had the opportunity to choose between two keys (choice scenario), which could lead to a potential monetary gain, or had to accept a computer-selected key, which led to similar rewards (no-choice scenario). A symbolic cue signaled the type of each upcoming trial. We measured blood-oxygen-level-dependent (BOLD) activity in response to the cue during the anticipation of choice. Behavioral measures of the value of choice were obtained directly, through subjective ratings of the symbolic cues used in the choice task, and indirectly, through choice behavior on a choice-preference task performed outside the scanner. Because the choice and no-choice trial types were matched in the value of the expected monetary gain, we interpreted any differences in behavioral ratings and BOLD activity between these trial types as reflecting the affective valuation of choice.

Method

Participants

Eighteen healthy right-handed individuals from the Rutgers University, Newark, campus gave informed consent and were included in the final sample (10 females and 8 males; median age = 21 years; see the Participants section in the Supplemental Material available online).

Procedure

We used E-Prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA) to collect data and present stimuli.

Choice task. We used a simple choice paradigm to examine the affective experience of anticipating choice. On each trial, participants were presented with two keys (represented by two rectangles displayed on a computer screen). When participants pressed a key, they received feedback that they had gained $0, $50, or $100, with each outcome occurring on 33% of the trials regardless of the choice of key. Participants were not informed of these reward probabilities. On some trials, participants could freely choose between the keys (choice scenario), but on other trials, participants were forced to accept a computer-selected key (no-choice scenario). Participants were informed that their goal was to earn as many experimental dollars as possible and that these earnings would be translated into a monetary bonus at the end of the experiment. Because the two keys had the same average value, all subjects earned approximately the same number of experimental dollars, and this number was translated into a $5 bonus that was independent of specific choices.

Participants completed the choice task while in the fMRI scanner. The trial structure of this task is outlined in Figure 1a. At the start of each trial, one of four possible symbolic cues indicated the upcoming trial type (see the next paragraph). In all trials, the subject either had a choice of keys or had to accept the computer's choice of key. The cue was presented centrally for 2 s and was followed by a randomly jittered interstimulus interval (2–5 s) constituting the anticipation phase. In the following response phase (2 s), participants were presented with either a choice scenario, in which they indicated the location (left or right) of the key (yellow or blue) they wished to choose, or a no-choice scenario, in which they indicated the location of the one available key (blue or yellow) selected by the computer. Responses were recorded on each trial. In the immediately following outcome phase, the monetary outcome ($0, $50, or $100) was presented on-screen for 2 s. The reward outcome was followed by a randomly jittered intertrial interval (4–7 s). Participants experienced the same expected value for each trial type, so that experienced rewards and perceived success were controlled. The position of the blue and yellow keys (left vs. right) varied across trials to avoid any confounding effects of motor-response preparation during the anticipation phase.

There were four trial types represented by symbolic cues (e.g., circle, triangle). Each cue marked the beginning of a new

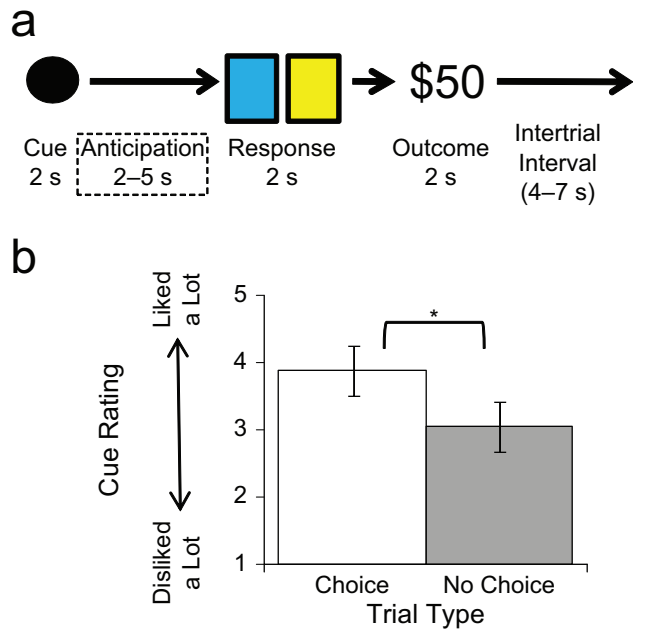

Fig. 1. Structure of an example trial (a) and participants' subjective behavioral ratings (b). A symbolic cue (e.g., a circle) informed participants about the upcoming trial type, before a brief anticipation phase. During the response phase (2 s), participants chose between a yellow key and a blue key (choice scenario) or responded to the location of the computer-selected key (no-choice scenario). Next, the monetary outcome ($0, $50, or $100) was displayed for 2 s. The graph shows participants' subjective liking ratings of the choice and no-choice cues. Error bars represent standard errors of the mean. The asterisk marks a significant difference ($p < .05$).

trial and indicated which one of four trial types would occur. Associations between cues and trial types were learned explicitly prior to the experimental trials. Choice cues signaled that participants would have the opportunity to choose between two colored keys. No-choice cues signaled that participants would be forced to accept the computer-selected key (one colored key was presented next to an unavailable gray key); no-choice cues did not indicate which key (yellow or blue) would be selected by the computer. These two trial types served as the main conditions of interest.

Two additional trial types served as control conditions. In the noninformative trial type, the cue provided no information about whether participants would have a choice (this cue was equally likely to be followed by a choice or a no-choice scenario). The purpose of this cue was to provide an expectation-free condition, which would elicit uncertainty (of choice availability) during the anticipation phase, that could be compared with anticipation of choice and anticipation of no choice. The other trial type was the predictive trial type, in which the cue signaled that participants would have no choice between keys and also indicated ahead of time which key the computer would select (the cue was the same color as the key selected, blue or yellow). This trial type provided an experimental control for potential anticipatory differences between the choice and no-choice trial types due to differences in the predictability of keys and their associated outcomes. The predictive cue provided information about the upcoming key selection, which would be important if participants developed preferences for one key over the other and if brain activity was therefore due to anticipation of the preferred key rather than anticipation of choice (see the Predictive Cue Analysis and Exploring the Role of Reward Learning sections in the Supplemental Material). Thirty trials of each type were presented, and trial order was randomized within four separate functional runs.

Immediately following the scanning session, participants were asked to rate how much they liked or disliked the choice and no-choice cues, using a scale from 1 (*disliked a lot*) to 5 (*liked a lot*). A rating of 3 indicated that the cue was neither liked nor disliked (neutral rating).

Choice-preference task. After completing the choice task, participants performed a choice-preference task outside the scanner ($n = 17$; 1 participant withdrew because of time constraints). The choice-preference task was based on an experimental design previously tested across species (Suzuki, 1997, 1999) and was included to provide an independent measure of choice desirability that was based on behavior rather than self-report.

On each trial, participants were presented with a white key (Path A) and a black key (Path B), and could select either key. Selection of the black key led to the presentation of another choice (striped key vs. dotted key), whereas selection of the white key always led to a single option (either a striped key or a dotted key, presented on either the left or the right). The likelihoods of the three possible levels of reward ($0, $1, or $5) were the same across the two paths (black vs. white key and striped vs. dotted key), and these values occurred randomly at 33% probability each.

Participants learned the associations of the keys with future choice and rewards instrumentally in an initial learning block of 100 trials. On each trial, participants chose between Path A and Path B, and then either made a choice (Path B) or responded to the location of the forced-choice option (Path A) before receiving feedback on the trial's outcome (monetary reward). In the next block, which consisted of 50 trials, participants were instructed to strategically choose the keys that they believed would lead to the most money. The timing of the trials, probabilities of the three reward values, and method of providing reward feedback were the same as in the first block. In this second block, we assessed preference for the path that led to a subsequent choice (Path B) over the path that led to no choice (Path A). If choice itself did not confer any value, then participants should have chosen the black key (Path B) 50% of the time. Alternatively, if choice was inherently desirable, then subjects should have chosen the black key significantly more often than the white key.

fMRI data acquisition and analyses

Imaging data were collected on a 3-T Siemens Allegra (Erlangen, Germany) head-only scanner at University Heights Center for Advanced Imaging, and analyses were performed using Brain Voyager software (Version 1.9; Brain Innovation, Maastricht, The Netherlands). We focused on two main analyses to identify regions of interest (ROIs; see fMRI Data Acquisition and Analyses in the Supplemental Material for additional details). First, we defined three a priori reward-related regions that have previously been shown to respond to the anticipation of reward (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005): the midbrain, bilateral ventral striatum (VS), and orbitofrontal cortex (OFC; see Fig. 2a). Second, we conducted a whole-brain analysis to identify all regions showing main effects of cue type (i.e., not limiting results to these a priori regions).

Results

Behavioral results

Participants demonstrated a preference for choice cues over no-choice cues. Specifically, they rated the choice cue ($M = 3.9$, $SD = 0.9$) significantly higher than the no-choice cue ($M = 3.1$, $SD = 1.1$), $t(17) = 2.14$, $p < .05$ (see Fig. 1b). Additionally, participants' ratings of the choice cue were significantly higher than the neutral score, $t(17) = 4.89$, $p = .0006$, whereas their ratings of the no-choice cue were not significantly different from the neutral score, $t(17) = 0.212$, $p = 0.83$. Thus, choice cues were liked more than no-choice cues.

During the response phase of the choice task, response times were collected. We compared response times following the choice and no-choice cues to determine if factors other

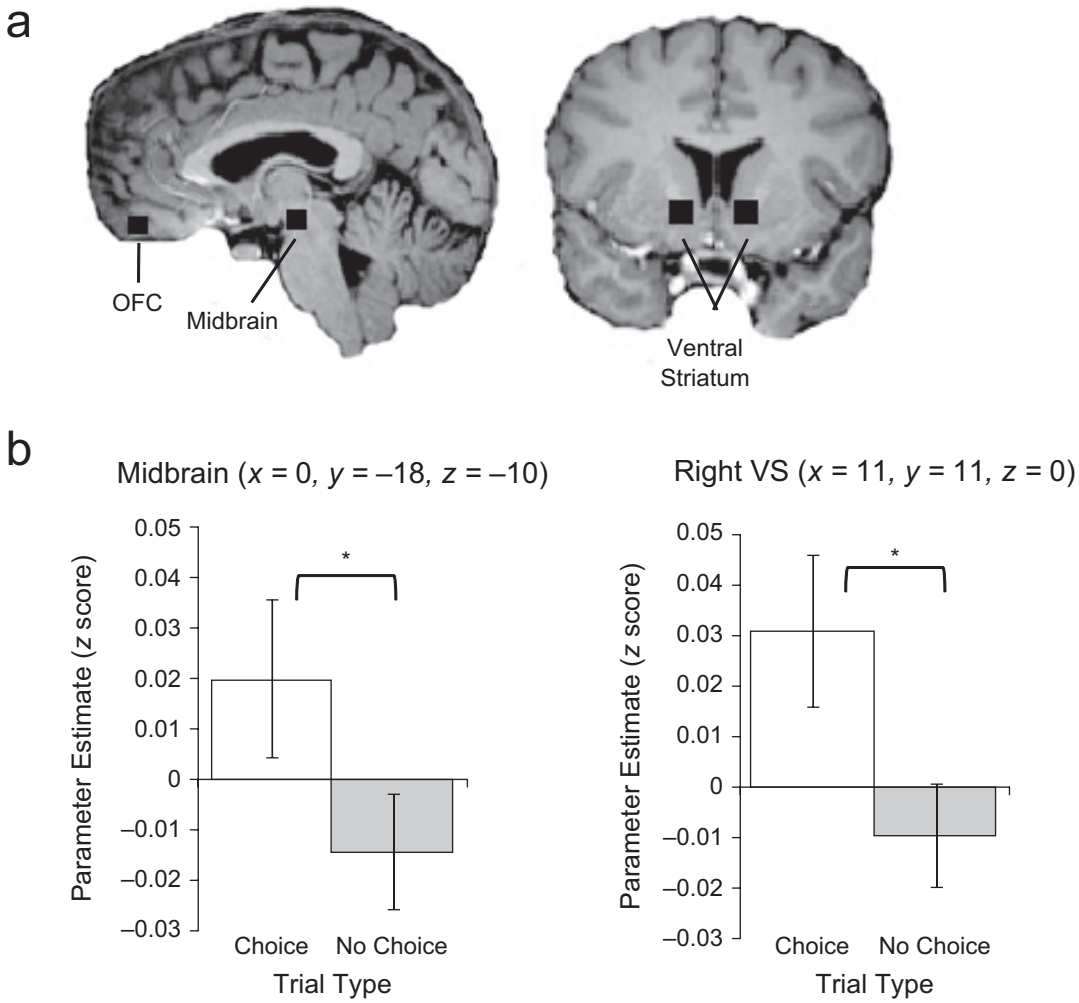

Fig. 2. Activity in reward regions when participants anticipated an upcoming choice. Three a priori regions of interest (a) involved in anticipation of reward magnitude (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005)—the bilateral ventral striatum (VS), orbitofrontal cortex (OFC), and midbrain—are indicated by black squares. The bar plots (b) show parameter estimates (mean beta weights) in the midbrain and the right VS when participants anticipated either a choice trial or a no-choice trial. Error bars represent standard errors of the mean. Asterisks indicate significant differences in activity between trial types ($p < .05$).

than choice (e.g., response preparation or attentional demands) differed between these trial types. There was no significant difference between response times following choice and no-choice cues ($p > .05$). These results suggest that any anticipatory differences in BOLD activity (i.e., those that occurred before key selection) may not reflect differences in factors such as response preparation or attentional demands, but rather likely reflect processes related to goal-directed behavior.

In the choice-preference task, participants selected an option that led to a future choice significantly more often than an option that led to no choice, even though the two options led to equivalent rewards. On average, participants chose the path that led to a subsequent choice 64% of the time, which was significantly different from 50% (chance), $t(16) = 3.98$, $p < .001$. Thus, the direct evidence from the subjective cue ratings and this indirect evidence of a preference for choice both support the notion that participants perceived the opportunity for choice as inherently valuable.

Neuroimaging results

ROI analysis. To conduct an unbiased exploration of the value associated with the anticipation of choice, we extracted parameter estimates (mean beta weights) for BOLD activity following each cue type from ROIs defined independently in a previous study about monetary reward anticipation (Knutson et al., 2005). Parameter estimates associated with the choice cue were significantly greater than those associated with the

no-choice cue in the midbrain, $t(17) = 3.2$, $p = .005$; left VS, $t(17) = 2.4$, $p = .03$; and right VS, $t(17) = 3.4$, $p = .004$ (Fig. 2b). In the bilateral OFC, BOLD activity was greater when participants anticipated choice rather than no choice, but this difference was not significant. There were no significant differences between parameter estimates extracted for the choice trials and those extracted for either of the control trial types (i.e., noninformative and predictive) in any of the ROIs, with the exception of the right VS, where activity in response to the choice cue was greater than activity in response to the predictive cue (see Supplementary Table 1 in the Supplemental Material for details).

Whole-brain analysis. We performed a one-way repeated measures analysis of variance of BOLD activity during the anticipation phase with cue type (choice, no choice, noninformative, or predictive) as a within-subjects factor. This analysis allowed us to explore main effects of cue type without limiting the search to putative reward regions while also including all experimental trial types.

Main effects of cue type were observed in regions that have been identified previously as being involved in affective and motivational processes, including the left and right striatum (with peaks in the caudate nucleus), dorsal anterior cingulate cortex (dACC), right inferior frontal cortex (IFC), and amygdala (Table 1, Fig. 3a). The results of this analysis were similar to those obtained from a simple linear contrast comparing BOLD activity directly between the choice and no-choice trial types (see Supplementary Table 2 in the Supplemental Material). As Figure 3b illustrates, we found that the choice cue recruited the right striatum more than the other cues did, with the noninformative and predictive cues eliciting intermediate levels of activity. Cue-related differences in activity in the ventral amygdala region (Fig. 3c) may reflect effects of perceived uncertainty (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Sarinopoulos et al., 2009; Whalen, 2007), given that this effect was driven primarily by greater activity following the ambiguous, noninformative cue than following the other cues. In the dACC (Fig. 3d), activity was greater for the cues predicting certain choice (choice cue) and possible choice (noninformative cue) relative to the cues predicting no choice (no-choice and predictive cues); this pattern may reflect the motivational salience of future choice opportunity when effortful decision making is anticipated (Rushworth, Walton, Kennerley, & Bannerman, 2004; Sanfey, Loewenstein, McClure, & Cohen, 2006).

Discussion

In summary, we obtained behavioral evidence that choice is desirable, and, furthermore, we found that anticipating an opportunity for choice was associated with increased activity in a network of brain regions thought to be involved in reward processing. Collectively, the findings suggest that simply having the opportunity to choose is inherently valuable in some situations.

These results provide empirical evidence supporting the hypothesis that the need for control—and the need for choice—is biologically motivated (Leotti et al., 2010). Choice is the means by which individuals exercise control over the environment, and the perception of having control seems to be critical for an individual's well-being (Bandura et al., 2003; Ryan & Deci, 2006; Shapiro et al., 1996). If individuals did not believe they could exercise control over their environments, they would have little motivation to thrive. If the need for control is biologically motivated, and choice is a vehicle for exercising control, then it would make sense for people to find the opportunity for choice rewarding and for anticipation of choice to engage affective and motivational brain circuitry that promotes behavior adaptive for survival. The study reported here demonstrates that brain circuitry involved in reward-related processes is, in fact, engaged by the anticipation of an opportunity for choice. Our findings are critical for understanding

Table 1. Main Effects of Cue Type During the Anticipation Phase of the Choice Task

	Talairach coordinates					
Region	*x*	*y*	*z*	BA	No. of voxels	$F(3, 51)$
Dorsal ACC (L)	−8	16	36	32	645	7.33
Dorsal ACC (R)	1	10	42	32	824	8.98
IFC/insula (R)	38	13	9	13	531	7.51
Striatum: caudate (L)	−13	1	6	—	486	7.14
Striatum: caudate (R)	14	7	3	—	736	6.40
Amygdala (R)	27	4	−21	—	345	8.46
Fusiform gyrus (R)	26	−41	−15	20	568	6.78
Cuneus (L)	−7	−74	27	18	3,678	9.94
Occipital cortex (R)	32	−89	3	18	1,896	8.86
Occipital cortex (L)	−28	−98	−3	18	3,307	11.75

Note: BA = Brodmann's area; ACC = anterior cingulate cortex; L = left side; R = right side; IFC = inferior frontal cortex.

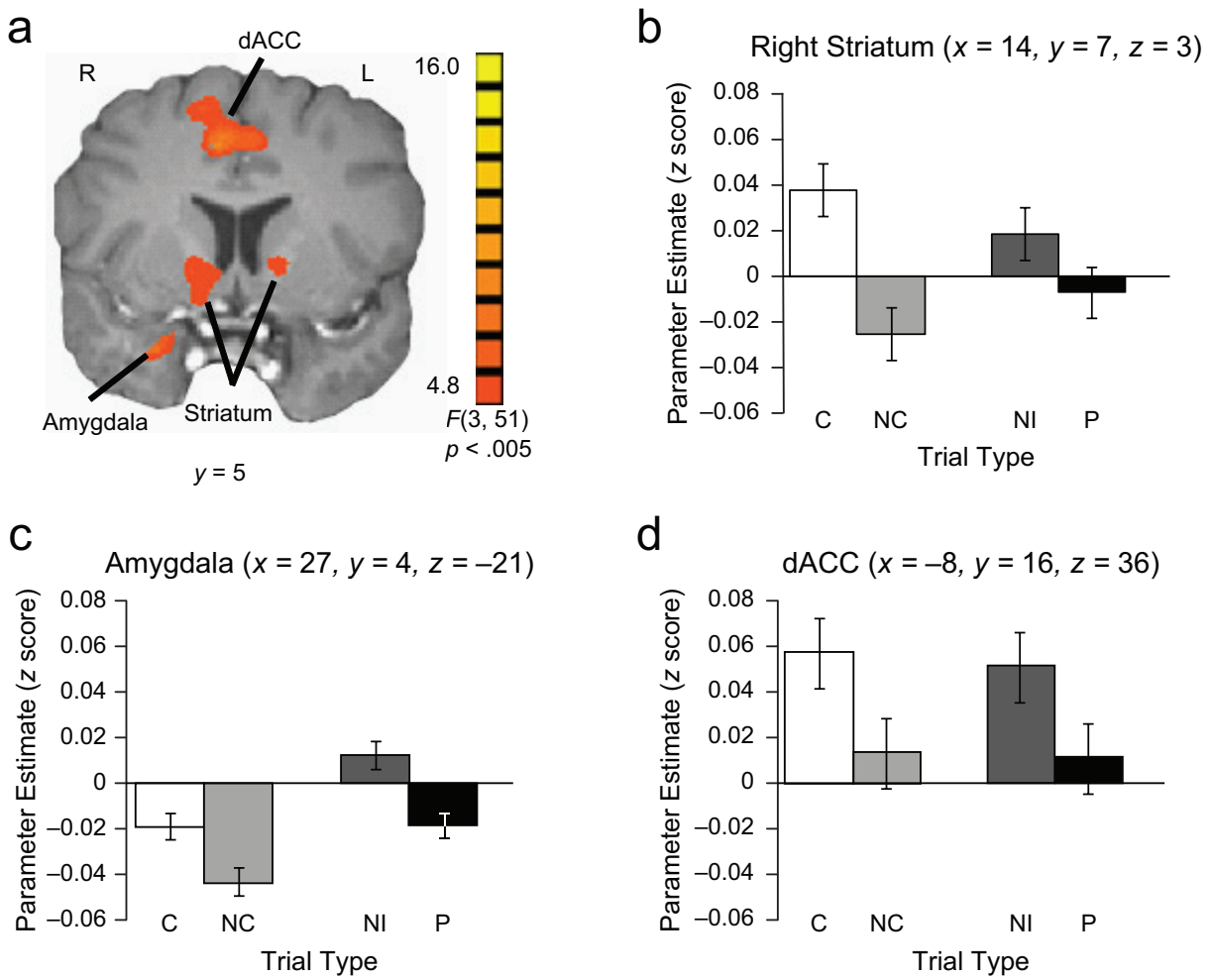

Fig. 3. Neural activity in response to the four cue types during the anticipation phase of the choice task. The brain image (a) shows regions where main effects of cue type were observed (R = right; L = left). The color coding indicates the results of the analysis of variance for each area. The bar graphs show the parameter estimates for the choice (C), no-choice (NC), noninformative (NI), and predictive (P) cues in the (b) right ventral striatum, (c) amygdala, and (d) dorsal anterior cingulate cortex (dACC). Error bars represent standard errors of the mean.

the neural substrates of control and the affective experience of choice, which may be important aspects of adaptive emotion regulation.

Our behavioral findings provide both direct (subjective ratings) and indirect (decision making) evidence that choice is preferred over nonchoice. These findings are consistent with previous studies demonstrating, through indirect measures, that choice is desirable for both animals and humans (Bown et al., 2003; Suzuki, 1997, 1999). Supporting the behavioral results, BOLD activity in reward-anticipation ROIs, including the VS and midbrain, was significantly greater following the choice cue than following the no-choice cue. Furthermore, in the whole-brain analysis, the anticipation of choice opportunity recruited corticostriatal circuitry previously linked to reward processing (Delgado, 2007; Knutson, Adams, Fong, & Hommer, 2001; Knutson et al., 2005; O'Doherty, 2004), a result suggesting that signals in this circuitry in response to choice (relative to signals in response to no choice) may reflect greater expectation or prediction of potential rewards. Because the actual rewards did not vary between the choice and no-choice cue types, differences observed between these cues may reflect differences in anticipated reward associated with the exercise of control through choice.

Choice-related activity was also observed in the dorsal striatum, a finding consistent with the literature demonstrating that this region is highly responsive to action-outcome contingencies (e.g., Bjork & Hommer, 2007; O'Doherty et al., 2004; Tricomi et al., 2004; see Supplementary Results & Discussion in the Supplemental Material for further discussion). Additionally, recruitment of the dACC, as well as the IFC, may have reflected adaptive updating of reward information, which is important for strategic control over behavior (Botvinick, Cohen, & Carter, 2004; Sanfey et al., 2006) and may be even more imperative when participants anticipate having control than when they anticipate not having control (O'Doherty et al., 2003). However, our exploratory analysis did not reveal

significant main effects of cue type in other reward regions, including the OFC, that have been shown to respond to reward under choice conditions in previous studies (Arana et al., 2003; O'Doherty et al., 2003). These discrepancies may be explained by differences in experimental paradigms, which may influence processes related to reward and decision making (see Anticipation of Choice Opportunity in the Reward Network in the Supplemental Material for additional discussion).

In the striatum bilaterally, we observed the greatest activity for the choice cue, the lowest activity for the no-choice cue, and intermediate activity for the noninformative and predictive cues. One interpretation of these results is that striatal activity reflects the value of each of these cues, with choice having the highest value and no choice having the lowest value. These levels of activity in the striatum may have resulted because choice is perceived as appetitive and representative of personal control. Alternatively, not having a choice may be perceived as aversive, given that BOLD signals in the human striatum have been shown to decrease when people experience a negative stimulus, such as a monetary loss (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Seymour, Daw, Dayan, Singer, & Dolan, 2007; Tom, Fox, Trepel, & Poldrack, 2007).

Merely having an opportunity to choose is known to elicit an increased perception of personal control (Langer, 1975; Langer & Rodin, 1976). As a result, the observed differences in cue-related brain activity may reflect the value associated with each of the cues, and this value may have been based on variations in perceived control or on reward associated with experiencing control. However, because both uncertainty and predictability may contribute to the perception of control (Thompson, 1999), we included control conditions to address these potential influences. Although they were somewhat limited, these control conditions nonetheless provided important information about responses to the uncertainty of choice (the noninformative trial type) and the predictability of outcomes (the predictive trial type).

Activity in the striatum increased with increasing probability of having a choice (choice > no information > no choice). This graded response is consistent with the probability of choice, which occurred on 100% of choice trials, 50% of noninformative trials, and 0% of no-choice trials. Increases in the perceived probability of choice may have led to concurrent increases in BOLD signals in the striatum for reasons similar to those underlying previous demonstrations of increased activity in this region as a function of the probability of reward (Knutson et al., 2005; Tobler, O'Doherty, Dolan, & Schultz, 2007; Yacubian et al., 2006).

In contrast, the predictive cue did not elicit a discernible change in striatal activity, which suggests that choice-related activity in this region was not driven by the predictability of the outcome. The predictive cue also allowed us to rule out the possibility that the activity related to anticipation of choice is influenced by anticipation of a specific choice (i.e., blue or yellow; see Predictive Cue Analysis in the Supplemental Material). Nonetheless, because the brain activity following the choice cues was not statistically different from the activity following the control cues for most of the reward ROIs (see Main Effects of Cue Type in Reward Anticipation ROIs in the Supplemental Material), we cannot conclude definitively that the affective experience of choice is free from the influence of uncertainty and predictability. Future research designed to specifically address the roles of uncertainty and predictability will be of paramount importance to the accurate characterization of the affective experience of choice and control.

Increased perception of control is only one possible reason why participants found choice rewarding. They may also have preferred choice because choice trials were more engaging (and less boring) than the other trial types. It is also possible that they perceived differences between the key options, even though there were no actual differences in expected value between the two keys for any of the participants, and there were no differences in whole-brain BOLD signals following the predictive cues when participants were anticipating their reported preferred color (see Predictive Cue Analysis in the Supplemental Material) relative to their nonpreferred color. One issue that merits exploration in future investigations is the idea that trial-by-trial fluctuations in experienced rewards may induce temporary changes in key preference by creating the perception that rewards will be higher for one key than for the other. Any of these possibilities may explain why choice opportunity was inherently valuable, and perhaps desirable, and why choice led to an increased response in reward-related regions, such as the VS (see Supplementary Results & Discussion in the Supplemental Material for additional analyses and discussion).

Although previous research has suggested that personal involvement in decision making may modulate activity in brain networks similar to those observed in the study reported here (Arana et al., 2003; Bjork & Hommer, 2007; O'Doherty et al., 2003, 2004; Sharot et al., 2009; Tricomi et al., 2004; Zink et al., 2004), this study is the first direct demonstration that simply anticipating choice recruits affective brain circuitry, and it suggests that having an opportunity to choose may be valuable in and of itself. Whereas most of the literature on decision making has focused on understanding the value of specific choices as they relate to specific consequences, we argue here that the opportunity to choose is inherently rewarding and is independent of outcome. Our findings specifically suggest that choice, or the opportunity for choice, is associated with a higher signal of positive value than what is observed during anticipation of potential reward in the absence of choice. Nonetheless, additional work is needed to determine how other reward-related processes, such as fluctuations in learning, may influence this signal. Characterization of the affective properties of choice, as choice was presented in this study, may provide the foundation for understanding how the presence or absence of choice can influence people's ability to self-regulate and contribute to maladaptive control-seeking behavior.

Acknowledgments

We are grateful to Michael Niznikiewicz for assistance and to Nathaniel Daw, Susan Ravizza, and Elizabeth Tricomi for discussion.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported by grants from the National Institute of Mental Health (MH-084041) and the National Institute on Drug Abuse (DA-027764 and F32-DA027308).

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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