Article

Separate Neural Mechanisms Underlie Choices and Strategic Preferences in Risky Decision Making

Vinod Venkatraman,[1,2] John W. Payne,[2,3] James R. Bettman,[2,3] Mary Frances Luce,[2,3] and Scott A. Huettel[1,2,*]
[1]Brain Imaging and Analysis Center, Duke University Medical Center, Box 3918, Durham, NC 27710, USA
[2]Center for Neuroeconomic Studies, Duke University, Box 90999, Durham, NC 27710, USA
[3]Fuqua School of Business, Duke University, 1 Towerview Drive, Durham, NC 27708, USA
*Correspondence: scott.huettel@duke.edu
DOI 10.1016/j.neuron.2009.04.007

SUMMARY

Adaptive decision making in real-world contexts often relies on strategic simplifications of decision problems. Yet, the neural mechanisms that shape these strategies and their implementation remain largely unknown. Using an economic decision-making task, we dissociate brain regions that predict specific choices from those predicting an individual's preferred strategy. Choices that maximized gains or minimized losses were predicted by functional magnetic resonance imaging activation in ventromedial prefrontal cortex or anterior insula, respectively. However, choices that followed a simplifying strategy (i.e., attending to overall probability of winning) were associated with activation in parietal and lateral prefrontal cortices. Dorsomedial prefrontal cortex, through differential functional connectivity with parietal and insular cortex, predicted individual variability in strategic preferences. Finally, we demonstrate that robust decision strategies follow from neural sensitivity to rewards. We conclude that decision making reflects more than compensatory interaction of choice-related regions; in addition, specific brain systems potentiate choices depending on strategies, traits, and context.

INTRODUCTION

The neuroscience of decision making under risk has focused on identifying brain systems that shape behavior toward or against particular choices (Hsu et al., 2005; Kuhnen and Knutson, 2005; Platt and Huettel, 2008). These studies typically involve compensatory paradigms that trade two decision variables against each other, as when individuals choose between a safer, lower-value option and a riskier, higher-value option (Coricelli et al., 2005; De Martino et al., 2006; Huettel, 2006; Tom et al., 2007). Activation in distinct regions reliably predicts the choices that are made: increased activation in the anterior insula follows risk-averse choices (Paulus et al., 2003; Preuschoff et al., 2008) and increased activation in the ventromedial prefrontal cortex (vmPFC) and striatum predicts risk-seeking choices (Kuhnen and Knutson, 2005; Tobler et al., 2007). In contrast, prefrontal

and parietal control regions support executive control processes associated with risky decisions, as well as the evaluation of risk and judgments about probability and value (Barraclough et al., 2004; Huettel et al., 2005; Paulus et al., 2001; Sanfey et al., 2003). These and other studies have led to a choice-centric neural conception of decision making: tradeoffs between decision variables, such as whether someone seeks to minimize potential losses or maximize potential gains, reflect similar tradeoffs between the activation of brain regions (Kuhnen and Knutson, 2005; Loewenstein et al., 2008; Sanfey et al., 2003). Accordingly, individual differences in decision making have been characterized neurometrically by estimating parameters associated with a single model of risky choice and identifying regions that correlate with individual differences in those parameters (De Martino et al., 2006; Huettel et al., 2006; Tom et al., 2007).

Yet, following a purely compensatory approach to decision making would require substantial computational resources, especially for complex decision problems that involve multiple decision variables. It has become increasingly apparent that people employ a variety of strategies to simplify the representations of decision problems and reduce computational demands (Camerer, 2003; Gigerenzer and Goldstein, 1996; Kahneman and Frederick, 2002; Payne et al., 1992, 1988; Tversky and Kahneman, 1974). For example, when faced with a complex decision scenario that could result in a range of positive or negative monetary outcomes, some individuals adopt a simplifying strategy that deemphasizes the relative magnitudes of the outcomes but maximizes the overall probability of winning. Other individuals emphasize the minimization of potential losses or the maximization of potential gains in ways consistent with more compensatory models of risky choice such as expected utility maximization (Payne, 2005). Adaptive decision making in real-world settings typically involves multiple strategies that may be adopted based on the context and computational demands of the task (Gigerenzer and Goldstein, 1996; Payne et al., 1993). As noted above, there has been considerable research on identifying brain systems that shape behavior toward or against particular choices (risky or safer gambles); however, much less is known about the neural mechanisms that underlie inter- and intraindividual variability in decision strategies. We sought to address this limitation in the present study by dissociating choice-related and strategy-related neural contributors to decision making.

We used an incentive-compatible decision-making task (Payne, 2005) that contained economic gambles with five rank-ordered
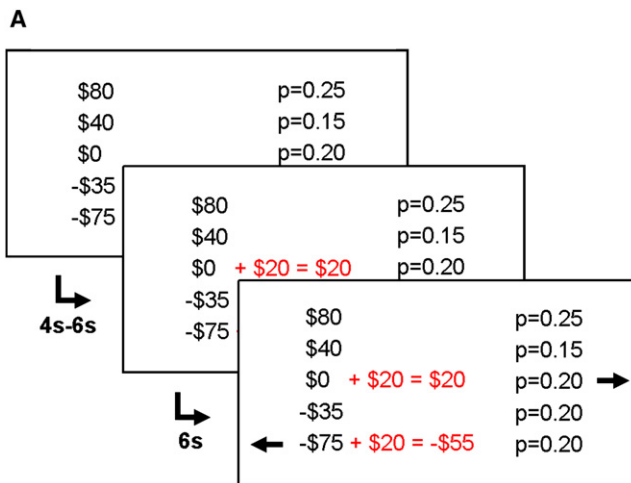
A

Figure 1. Experimental Task and Behavioral Results

(A) Subjects were first shown, for 4–6 s, a multiattribute mixed gamble consisting of five potential outcomes, each associated with a probability of occurrence. Then, two alternatives for improving the gambles were highlighted in red, whereupon subjects had 6 s to decide which improvement they preferred. Finally, after two arrows identified the buttons corresponding to the choices, subjects indicated their choice by pressing the corresponding button as soon as possible. Here, the addition of \$20 to the central, reference outcome would maximize the overall probability of winning (P_{max} choice), whereas the addition of \$20 to the extreme loss would reflect a L_{min} choice. The next trial appeared after a variable interval of 4, 6, or 8 s. In other trials, subjects could have a chance to add money to the extreme gain outcome, reflecting a G_{max} choice.

outcomes, ranging from large monetary losses to large monetary gains (Figure 1). There were three types of choices: gain maximizing (G_{max}), loss minimizing (L_{min}), or probability maximizing (P_{max}). Making a G_{max} choice increased the magnitude of the largest monetary gain (i.e., the most money that could be won), whereas making a L_{min} choice reduced the magnitude of the largest monetary loss (i.e., the most money that could be lost). The gambles were constructed so that these two choices (G_{max} and L_{min}) were generally consistent with a compensatory strategy (see Supplemental Experimental Procedures for a discussion of model predictions), such as following expected utility theory and/or rank-dependent expectation models like cumulative prospect theory (Birnbaum, 2008; Payne, 2005; Tversky and Kahneman, 1992). On the other hand, making a P_{max} choice increases the overall probability of winning money compared to losing money. Therefore, such choices would be consistent with a simplifying strategy (e.g., "maximize the chance of winning") that ignores reward magnitude. Finally, we characterized our subjects' strategic preferences according to their relative proportion of simplifying (P_{max}) versus compensatory (G_{max} and L_{min}) choices. Such a definition positions the two strategies as the end points of a continuum with a high value indicating an individual's preference for a simplifying strategy and a low value indicating a preference for a compensatory strategy. We emphasize that, as defined operationally here, strategies for decision making may be either explicit or implicit.

To distinguish neural mechanisms underlying choices from those underlying the strategies that generate those choices,

we collected several forms of behavioral and functional magnetic resonance imaging (fMRI) data. Consistent with many previous studies (De Martino et al., 2006; Sanfey et al., 2003), we characterized brain regions as choice related if the magnitude of their activation predicted a specific behavior (e.g., selecting the option providing the largest gain) throughout our subject sample. In contrast, we characterized brain regions as strategy related based on their association with individual difference measures; i.e., if the magnitude of their activation depended on whether or not an individual engages in their preferred strategy, regardless of which of the choices that entails. Moreover, strategy-related regions should exert a modulatory influence on choice-related regions. A strong candidate for a strategy-related region is the dorsomedial prefrontal cortex (dmPFC), which has been shown to play an important role in tasks involving decision conflict, as well as in making decisions that run counter to general behavioral tendencies (De Martino et al., 2006; Pochon et al., 2008). Moreover, this region exhibits distinct patterns of functional connectivity to affective and cognitive networks (Meriau et al., 2006), making it a candidate for shaping activation in those networks based on context and computational demands (Behrens et al., 2007; Kennerley et al., 2006).

Using large-sample behavioral experiments, we first demonstrate systematic individual variability in decision making, with a significant bias toward choices that maximize the overall probability of winning (i.e., toward a simplifying strategy). Then, using fMRI, we show that distinct neural systems underlie choices made on each trial and variability in strategic preferences across individuals. Finally, we also demonstrate a striking relation between neural sensitivity to monetary outcomes and individual differences in strategic preferences, indicating that robust decision strategies may follow from the neural response to rewards. These results demonstrate that decision making under uncertainty does not merely reflect competition between brain regions predicting distinct decision variables; in addition, the relation between neural activation and subsequent decisions is mediated by underlying strategic tendency.

RESULTS

We conducted two behavioral experiments ($n_1 = 128$ and $n_2 = 71$) and one fMRI experiment ($n = 23$), all involving the basic paradigm illustrated in Figure 1. Subjects were young adult volunteers from the Duke University community (see Supplemental Experimental Procedures for details on the experiments). Research was conducted under protocols approved by the Institutional Review Boards of Duke University and Duke University Medical Center.

Across both behavioral experiments (details available in Supplemental Experimental Procedures), we found a significant bias toward the P_{max} choices (Figure S1 available online), extending prior findings in the behavioral literature (Payne, 2005). In addition to demonstrating the robustness of the preferences toward the P_{max} choices, the second experiment also indicates that this bias can be reversed or accentuated by experimental manipulations. The findings from these studies are also consistent with P_{max} choice representing a simplifying strategy (see Supplemental Experimental Procedures). Finally, importantly
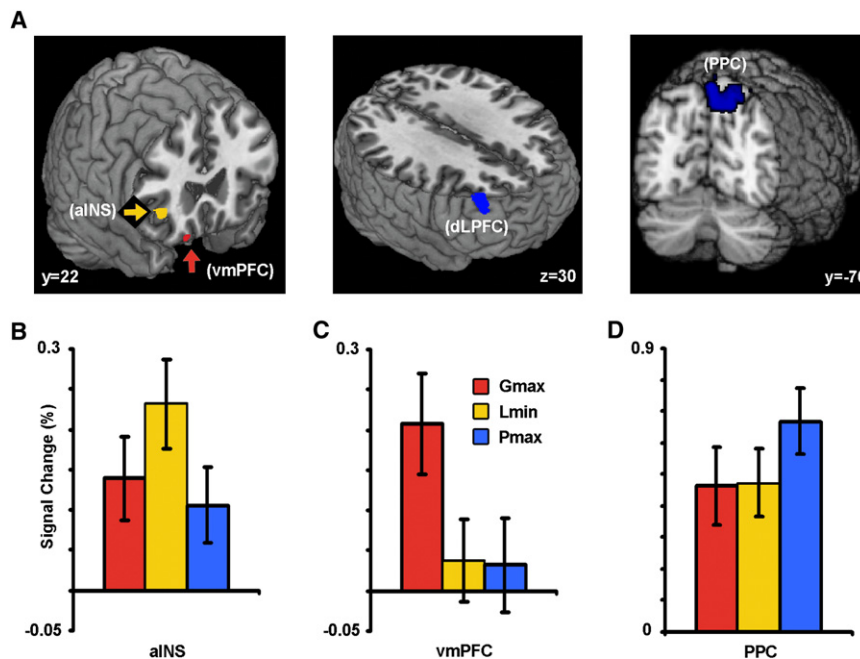
Figure 2. Distinct Sets of Brain Regions Predict Choices

(A) Increased activation in the right anterior insula (peak MNI space coordinates: x = 38, y = 28, z = 0) and in the vmPFC (x = 16, y = 21, z = −23) predicted L_{min} and G_{max} choices, respectively, while increased activation in the lateral prefrontal cortex (x = 44, y = 44, z = 27) and PPC (x = 20, y = −76, z = 57) predicted P_{max} choices. Activation maps show active clusters that surpassed a threshold of z > 2.3 with cluster-based Gaussian random field correction.

(B–D) Percent signal change in these three regions to each type of choice. Error bars represent ± 1 standard error of the mean for each column.

for the goals of our imaging studies, we also found substantial interindividual variability: some subjects nearly always preferred a simplifying strategy (choosing the P_{max} option in most trials); others nearly always preferred a compensatory strategy (choosing the G_{max} or L_{min} options in most trials), while still others switched strategies on different trials resulting in both intra- and intersubject variability in strategy (Figure S2).

Variability in Underlying Neural Mechanisms

We used high-field (4T) fMRI to evaluate the neural systems associated with strategic decision making under uncertainty. We adapted the basic design from our behavioral experiments to the fMRI setting. Subjects first made a series of choices without feedback. On each trial, subjects initially viewed the decision options and then learned the assignment of choices to responses, to eliminate any potential confounding effects of response selection (Pochon et al., 2008). Then, following the completion of all decision trials, we resolved a set of those trials for real monetary rewards. This allowed us to measure reward-related activation without altering subsequent decisions through learning.

Consistent with our two behavioral experiments, fMRI subjects made P_{max} choices on approximately 70% of the trials when the choices were matched for expected value. Moreover, the proportion of P_{max} choices was systematically modulated by the trade-off in expected value between the choices, indicating that subjects were not simply insensitive to expected value (Table S1). We evaluated intrasubject choice consistency using split-sample analysis. We split each subject's choices into samples from odd-numbered runs and from even-numbered runs. There was a strong correlation between the proportion of P_{max} choices in each sample (r = 0.61; p < 0.01), even without considering other factors like relative expected value. For comparison, we used a similar split-sample approach to estimate subject-specific

parameters for canonical expected utility and cumulative prospect theory models of decision making (see Supplemental Experimental Procedures). We found that model parameters estimated from one half of the experimental data did not significantly classify choices within the other runs (Figure S3). Finally, the proportion of P_{max} choices decreased with increasing self-reported tendency to maximize (r = −0.67, p < 0.001; Figure S4).

Neural Predictors of Choices

Our initial analyses identified brain regions whose activation was driven, across subjects and trials, by the selected choice. There was greater activation in anterior insular cortex (aINS) and vmPFC (Figure 2A) for the compensatory magnitude-sensitive choices (combined across G_{max} and L_{min}). These regions are typically associated with emotional function, particularly the affective evaluation of the outcome of a choice in decision-making tasks (Bechara et al., 2000; Dalgleish, 2004; Paulus et al., 2003; Sanfey et al., 2003). We subsequently performed a region of interest (ROI) analysis to explore specifically the differences in activation between G_{max} and L_{min}. Note that this analysis was restricted, a priori, to a subset of 15 subjects with a sufficient number of choices in each condition of interest. We found a clear double dissociation between aINS and vmPFC: G_{max} choices were associated with greater activation within vmPFC, whereas L_{min} choices were associated with increased activation in aINS (Figures 2B and 2C). Conversely, P_{max} choices resulted in increased activation in the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC; Figure 2A and Table S2), regions typically associated with executive function and decision making under risk and uncertainty (Bunge et al., 2002; Huettel et al., 2005, 2006; Paulus et al., 2001). These regions showed greater activation for P_{max} choices compared to both G_{max} and L_{min}, but no difference between G_{max} and L_{min} options (Figure 2D).

Neural Predictors of Strategic Variability across Individuals

We next investigated whether there were brain regions whose activation varied systematically with individual differences in strategic preferences. To do this, we entered each subject's
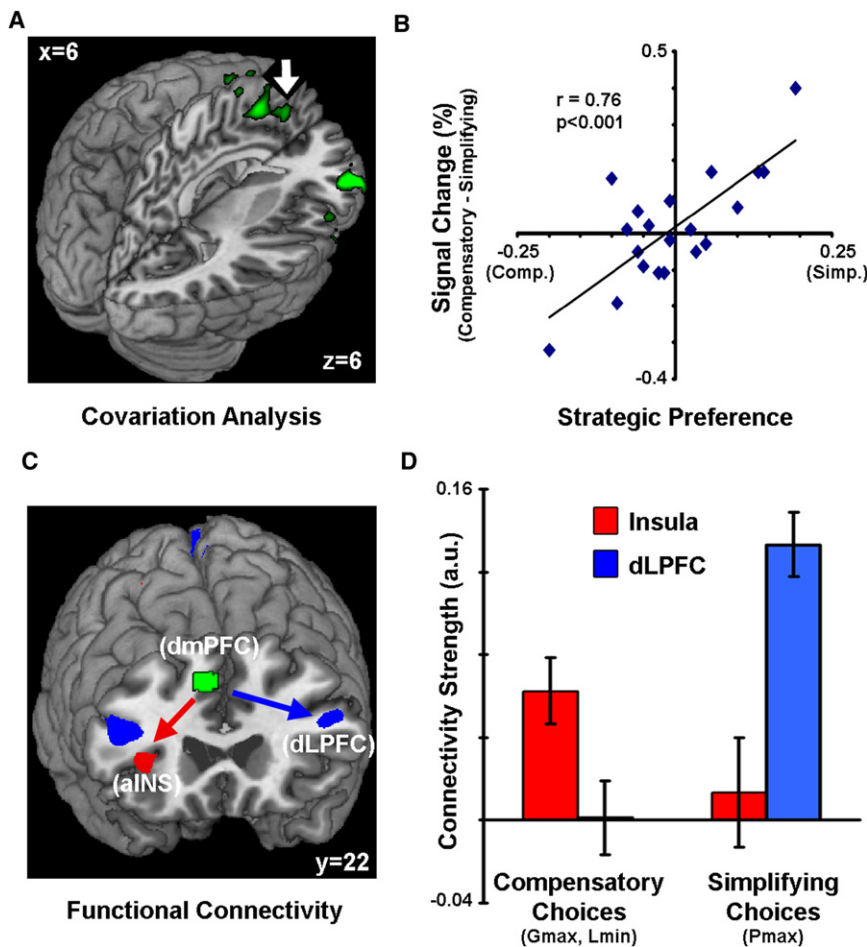
Figure 3. dmPFC Predicts Strategy Use during Decision Making

(A and B) Activation in dmPFC (x = 10, y = 22, z = 45; indicated with arrow) and the rIFG exhibited a significant decision-by-trait interaction, such that the difference in activation between compensatory and simplifying choices was significantly correlated with preference for simplifying strategy (mean-subtracted) across individuals.

(C and D) Functional connectivity of dmPFC varied as a function of strategy: there was increased connectivity with dlPFC (and PPC) for simplifying choices and increased connectivity with aINS (and amygdala) for compensatory choices. Error bars represent ± 1 standard error of the mean for each column.

strategic preference as a normalized regressor into the across-subjects fMRI analyses of the contrast between choices. Strategic variability predicted individual differences in activation in two clusters (Figures 3A and 3B): the dmPFC and the right inferior frontal gyrus (rIFG). Within these regions, there was no significant difference in activation between the choices. However, there was a significant interaction: activation increased when an individual with preference for the more compensatory strategy made a simplifying P_{max} choice and vice versa. We focus on the dmPFC in the rest of this manuscript, based on our prior hypothesis about the role of this region as well as the fact that only this region significantly predicted trial-by-trial choices (as discussed later).

We next evaluated whether dmPFC activation might shape activation in those regions that predicted specific choices (i.e., P_{max}: dlPFC and PPC; L_{min}: aINS; G_{max}: vmPFC), using seed-voxel-based whole-brain functional connectivity analyses. This would provide additional converging evidence for the role of this region in determining choice behavior, contingent on preferred strategies. We found a double dissociation in the functional connectivity of dmPFC depending on the choice made by the subject (Figures 3C and 3D). When subjects made P_{max} choices, connectivity with dmPFC increased in dlPFC and PPC, whereas when subjects made more magnitude-sensitive compensatory

choices, connectivity increased in the aINS (and amygdala, but not in vmPFC). Moreover, the relative strength of the connectivity between dmPFC and these regions was significantly associated with individual differences in strategy preferences across subjects (Figure S5). Finally, we also conducted additional analyses to rule out the possibility that dmPFC activation was related to response conflict, as has been found in several previous studies (Botvinick et al., 1999; Kerns et al., 2004; details can be found in Supplemental Experimental Procedures).

Thus, we provide a broad range of converging results, drawn from overall activation, functional connectivity, factor analysis of behavioral data (see Supplemental Experimental Procedures), association with individual differences in strategy, and trial-by-trial analysis (below), that together indicate that dmPFC supports strategic considerations during decision making by shaping behavior toward or against individual strategic preferences.

Integrating Choices and Strategies to Predict Behavior

We used the brain regions implicated above as choice related (aINS, vmPFC, dlPFC, and PPC) or strategy related (rIFG and dmPFC) to predict choices on individual trials. We extracted, for every trial for every subject, the activation amplitude in each of these ROIs, along with the decision made on that trial. We used a hierarchical logistic regression approach to evaluate which of these regions were significant and independent predictors of trial-to-trial decisions (Table 1).

We first entered into the model subjects' overall preference for the simplifying strategy (proportion of P_{max} choices). We found, unsurprisingly, that this was a highly significant predictor of trial-to-trial choices. Next, we used activation values from our brain ROIs, considering them both in isolation and with strategic preference already entered into the model. We found that activation in insular cortex was a significant predictor of magnitude-sensitive choices, while parietal activation was a significant

Table 1. Predicting Trial-by-Trial Choices from Trait and Neural Data

Model Variables	Coefficient (SE)	Wald (Significance)	Model Significance (χ^2)	Model Fit (Nagelkerke R^2)
Trait			76.09	0.069
Constant	−0.14 (0.05)	6.19 (0.13)		
Proportion of P_{max} choices	1.02 (.12)	70.79 (0.000)		
Brain			18.05	0.017
Constant	−0.21 (0.06)	13.10 (0.000)		
Right PPC	32.41 (8.43)	14.80 (0.000)		
Right anterior insula	−40.52 (13.28)	9.31 (0.002)		
Trait (+ Brain)			90.26	0.081
Constant	−0.22 (0.06)	13.38 (0.000)		
Proportion of P_{max} choices	1.00 (0.12)	67.23 (0.000)		
Right PPC	30.54 (8.62)	12.56 (0.000)		
Right anterior insula	−33.32 (13.69)	5.93 (.012)		
Trait + Brain + (Trait*Brain)			97.66	0.088
Constant	−0.23 (0.06)	13.78 (.000)		
Proportion of P_{max} choices	1.10 (0.13)	71.75 (.000)		
Right PPC	31.96 (8.70)	13.49 (.000)		
Right anterior insula	−33.00 (13.77)	5.74 (.017)		
dMPFC * strategic variability	−70.58 (26.28)	7.21 (.007)		

All χ^2 values were highly significant ($p < 10^{-4}$). We used stepwise logistic regression to evaluate the contributions of trait effects (i.e., overall proportion of choices) and brain effects (i.e., activation of a given region on a given trial) to the specific choices (coded as a binary variable of P_{max} choice) made by subjects. As expected, subjects' overall preference for simplifying strategy was a good predictor of P_{max} choices on individual trials. An independent logistic regression analysis revealed that two brain regions, the PPC and anterior insula, were significant positive and negative predictors of P_{max} choices and that these regions remained significant predictors even when the behavioral data were included in the model. Note that the dmPFC activation, when not weighted by strategy, did not significantly improve the model fit at any stage. However, when weighted by strategy, the resulting brain * strategy variable was a highly significant predictor of choices, even when the strategy itself was already included in the model. Regions not indicated in this table were not significant predictors of choice behavior.

predictor of P_{max} choices. Critically, activation in these brain regions improved the fit of the model even when the behavioral data had already been included. None of the other regions, including dmPFC, predicted either type of choice. Yet, when we weighted dmPFC activation with each subject's strategy preference, the resulting variable became a significant and robust predictor of behavior and overall model error was reduced (Table 1). Thus, dmPFC activation does not predict either type of choice, but instead predicts choices that are inconsistent with one's preferred decision strategy.

We emphasize that the brain-behavior relations reported here were highly significant even though the behavioral choice data across trials for each subject (an indicator of behavioral strategy) were already included in the logistic regression model. That is, we could use the fMRI activation evoked within key brain regions to improve our predictions of subjects' decisions on individual trials over what was predicted from behavioral data alone.

Neural Reward Sensitivity Predicts Individual Differences in Strategy

Finally, we evaluated whether an independent neural measure of reward sensitivity could predict the strategic preferences outlined in the previous sections. At the end of the scanning session, each subject passively viewed a subset of their improved gambles, which were each resolved to an actual monetary gain or loss. While subjects were anticipating the outcome of each gamble, there was increased activation in the ventral striatum (vSTR), a brain region commonly implicated in learning about positive and negative rewards (Schultz et al., 1997; Seymour et al., 2007; Yacubian et al., 2006). Then, when the gamble was resolved, vSTR activation increased to gains but decreased to losses (Figures 4A and 4B). Moreover, there were striking and significant correlations between strategic variability and vSTR activation: those individuals who showed the greatest vSTR increases to gains and decreases to losses both preferred the simplifying P_{max} strategy (Figure 4C) and scored low on a behavioral measure of maximizing (Figure S6). These results suggest that the use of a simplifying strategy that improves one's overall chances of winning (P_{max}) may result from increased neural sensitivity to reward outcomes.

DISCUSSION

When facing complex decision situations, many individuals engage in simplifying strategies, such as choosing based on the overall probability of a positive outcome, to reduce computational demands compared to compensatory strategies. Here, we demonstrated two neural predictors of strategic variability in decision making. First, during the decision process, the dmPFC shapes choices (in a manner depending on strategic tendency) through changes in functional connectivity with insular and prefrontal cortices. Second, independent neurometric responses
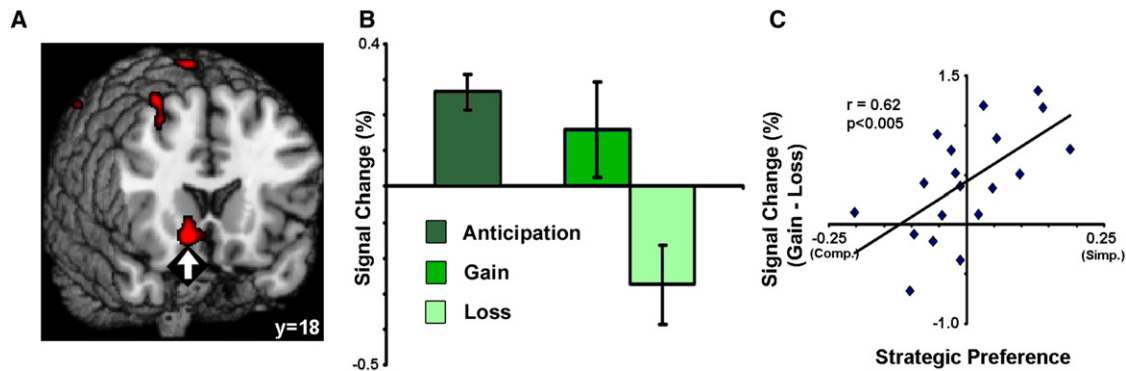
Figure 4. Ventral Striatal Sensitivity to Rewards Predicts Strategic Variability
At the end of the experiment, some gambles were resolved to monetary gains or losses.
(A and B) Activation in the vSTR (x = 14, y = 16, z = −10) increased when subjects were waiting for gambles to be resolved (anticipation) and, after resolution, increased to gains but decreased to losses. Error bars represent ± 1 standard error of the mean for each column.
(C) Notably, the difference between gain-related and loss-related activation in the vSTR correlated with variability in strategic preferences across subjects, with subjects who were most likely to prefer the P_{max} exhibiting the greatest neural sensitivity to rewards.

to rewards predicted strategic preferences: those individuals with the greatest striatal sensitivity to reward valence are most likely to use a simplifying strategy that emphasizes valence, but ignores magnitude. These results provide clear and converging evidence that the neural mechanisms of choice reflect more than competition between decision variables; they additionally involve strategic influences that vary across trials and individuals.

A large literature suggests that decisions between simple gambles can be predicted by compensatory models like expected utility and Cumulative Prospect Theory (Fennema and Wakker, 1997; Huettel et al., 2006; Preuschoff et al., 2008; Wu et al., 2004). Individual differences in sensitivity to the parameters within these models lead to distinct patterns of choices, even when the same model is applied to all individuals (Huettel et al., 2006; Tom et al., 2007). As decision problems become more complex, however, the assumption of a single canonical decision strategy becomes more and more problematic. As suggested by Tversky and Kahneman (1992) and Payne et al. (1993), people employ a variety of strategies to represent decision problems and evaluate options. Some of those strategies will be consistent with traditional models like expected utility maximization, whereas other strategies will be more heuristic or simplifying. Further, depending on the decision context, people shift among multiple strategies to maintain a balance between minimizing cognitive effort or maximizing decision accuracy, among other goals (Payne et al., 1993). Finally, strategy use to solve the same decision problem differs across individuals, perhaps reflecting trait differences such as a tendency toward satisficing versus maximizing. Our findings, from both behavioral and neuroimaging experiments, provide evidence in favor of intra- and intersubject variability in the use of strategies across participants. Importantly, we show that the parameters estimated using traditional economic models of risky choice were poor predictors of choices in our paradigm, providing possible evidence for differences in decision strategy within and across participants.

One influential conjecture in decision making is that people frequently use a variety of simplifying heuristics that reduce effort

associated with the decision process (Shah and Oppenheimer, 2008; Simon, 1957). P_{max} choices in the current task are consistent with such an effort-reduction framework, given that they were associated with faster response times in the behavioral experiments (note that we do not have accurate estimates of response times in the imaging experiment as we sought to explicitly separate the decision and response phases in our design) and that the proportion of P_{max} choices decreased adaptively with increasing cost in terms of expected value in all experiments. We suggest, therefore, that strategic preferences in the current task reflect tradeoffs, resolved differently by individual subjects and over trials, between one strategy that simplifies a complex decision problem by using a simple heuristic of maximizing the chances of winning (P_{max}) and another, more compensatory strategy that involves consideration of additional information as well as the emotions associated with extreme gains (G_{max}) or losses (L_{min}).

To the extent that the P_{max} choices reflect a more simplifying strategy, the pattern of activations seen in this study seems counterintuitive: the regions conventionally associated with automatic and affective processing (aINS and vmPFC) predicted magnitude-sensitive choices that were more consistent with traditional economic models such as expected utility maximization, whereas the regions conventionally associated with executive functions (dlPFC and PPC) predicted choices more consistent with a simplifying strategy. The lateral prefrontal cortex has been shown in previous studies to be active during probabilistic decision making (Heekeren et al., 2004, 2006) as well as sensitive to individual differences in the processing of probability (Tobler et al., 2008). Neurons within this region have also been shown to track reward probabilities (Kobayashi et al., 2002) and process reward and action in stochastic situations (Barraclough et al., 2004). Similarly, the parietal cortex also plays an important role in tracking outcome probabilities (Dorris and Glimcher, 2004; Huettel et al., 2005). Given that P_{max} choices are based on the overall probability of winning, activation in dlPFC and PPC could be associated with tracking subjective probabilities in these gambles.

Conversely, the G_{max} and L_{min} choices increase the chances of an aversive outcome, relative to a neutral aspiration level (Lopes and Oden, 1999). Supporting this interpretation, we found a clear double dissociation with activation in vmPFC predicting G_{max} choices and activation in aINS predicting L_{min} choices. The contributions of vmPFC to gain-seeking behavior (at the expense of potential losses) have been documented in both patient (Bechara et al., 2000) and neuroimaging studies (Tobler et al., 2007). Conversely, there has been substantial recent work demonstrating the importance of aINS for aversion to negative consequences, even to the point of making risk-averse mistakes in economic decisions (Kuhnen and Knutson, 2005; Paulus et al., 2003; Preuschoff et al., 2008; Rolls et al., 2008). Together, these findings suggest that the conventional notion that decisions reflect compensatory balancing of decision variables is an oversimplification. In addition, different brain regions bias how people approach decision problems, which may in turn lead to one form of behavior or another depending on the task context.

Furthermore, the balance between cognitive and affective brain regions did not, by itself, explain individual differences in strategy preferences. Activation in another region, dmPFC, predicted variability in strategic preferences across subjects. We note that the role of dmPFC in complex decision making remains relatively unknown. One very recent experiment found increased activation in this region when subjects faced greater decision-related conflict (Pochon et al., 2008), as dissociable from the more commonly reported response conflict (Botvinick et al., 2001). A similar region of dmPFC was implicated by De Martino et al. (2006), again when subjects made decisions counter to their general behavioral tendency (i.e., against typical framing effects). However, it is important to note that all subjects in their study exhibited a bias toward using the framing heuristic, while in the current study subjects varied in their relative preference for two different strategies. Therefore, a parsimonious explanation for the function of this region of dmPFC is that it supports aspects of decision making that are coded in relation to an underlying strategic tendency, not effects specific to framing. Further support for this hypothesis is provided by the differential functional connectivity of the dmPFC to dlPFC and anterior insula for simplifying and compensatory choices, respectively. These findings are consistent with the interpretation that activation differences of the dmPFC shape behavior by modulating choice-related brain regions, with the strength of this modulatory effect dependent on an individual's preferred strategy.

We additionally observed a striking relationship between neurometric sensitivity to reward and strategic biases across individuals. Our initial analyses found that activation of the vSTR increased when anticipating the outcome of a monetary gamble, increased further if that gamble was resolved to a gain, but decreased if that gamble was resolved to a loss. This pattern of results was consistent with numerous prior studies using human neuroimaging (Breiter et al., 2001; Delgado et al., 2000; Seymour et al., 2007) and primate electrophysiology (Schultz et al., 1997). However, we additionally observed the result that the magnitude of the vSTR response was a strong predictor of individual strategic preferences. Specifically, the sensitivity to gains and losses in the vSTR is greatest for individuals who prefer the P_{max} choices, consistent with their strategy of

maximizing their chances of winning. We emphasize that the gambles were not resolved until after all decisions were made, so this effect could not be attributed to learning from outcomes. Although our design does not allow determination of the direction of causation, these results suggest that an increased sensitivity to reward valence may lead to simple decision rules that overemphasize the probability of achieving a positive outcome.

Depending on the circumstances, organisms may adopt strategies that emphasize different forms of computation, whether to obtain additional information (Daw et al., 2006), to improve models of outcome utility (Montague and Berns, 2002), or to simplify a complex decision problem. Accordingly, the activation of a given brain system (e.g., dlPFC) may sometimes lead to behavior consistent with economic theories of rationality (Sanfey et al., 2003) and in other circumstances (such as the present experiment) predict a nonnormative choice consistent with a simplifying strategy. Our results demonstrate that decision making reflects an interaction among brain systems coding for different sorts of computations, with some regions (e.g., aINS and vmPFC) coding for specific behaviors and others (e.g., dmPFC) for preferred strategies.

EXPERIMENTAL PROCEDURES

Subjects

We conducted two behavioral experiments ($n_1 = 128$ and $n_2 = 71$) and one fMRI experiment (n = 23). All subjects were young adults who participated for monetary payment. All subjects gave written informed consent as part of protocols approved by the Institutional Review Boards of Duke University and Duke University Medical Center. Details of the procedures for the behavioral experiments can be found in the Supplemental Experimental Procedures.

Twenty-three healthy, neurologically normal young-adult volunteers (13 female; age range 18–31 years; mean age 24 years) participated in the fMRI session. No subject was repeated from the behavioral pilot session. All subjects acclimated to the fMRI environment using a mock MRI scanner and participated in two short practice runs consisting of six trials each, one inside and one outside of the fMRI scanner. Three subjects were excluded from some analyses involving strategy effects due to lack of variability in their response (two subjects always chose the P_{max} option while the third subject never chose the P_{max} option), leaving a total of 20 subjects in the complete analyses of the decision-making trials. One additional subject was excluded from the outcome-delivery trials due to a computer error in saving the timing associated with the trials.

At the outset of the experiment, subjects were provided detailed instructions about the payment procedures (see Supplemental Experimental Procedures for details). They were then given a sealed envelope that contained an endowment to offset potential losses; this envelope was sufficiently translucent that they could see that there was cash inside, even though the quantity could not be determined. Subjects were also told that there was no deception in the study and were given an opportunity to question the experimenter about any procedures before entering the scanner. All subjects expressed that they understood and believed in the procedures.

Experimental Stimuli

In the fMRI experiment, all subjects were presented with a total of 120 five-outcome mixed gambles in a completely randomized order. Each of the gambles comprised two positive outcomes (an extreme outcome of $65 to $80 and an intermediate outcome of $35 to $50), two negative outcomes (an extreme outcome of −$65 to −$85 and an intermediate outcome of −$35 to −$50), and a central, reference outcome. The reference outcome was $0 in half the trials and a negative value ranging from −$10 to −$25 in the remaining half of the trials. Probabilities of each of the five outcomes varied between 0.1 and 0.3 in units of 0.05 and always summed to 1 across the five outcomes. We

describe the similar stimuli and methods for the behavioral experiments in the Supplemental Experimental Procedures.

On each trial, subjects could choose between two options for adding money to one of the outcomes. Adding to the reference outcome increased the overall chance of winning money compared to losing money and hence was called the P_{max} choice. Alternatively, adding money to an extreme option either increased the magnitude of the best monetary outcome or decreased the magnitude of the worst monetary outcome and hence were referred to as G_{max} and L_{min} choices, respectively. The amount of money that subjects could add to the outcomes ranged between $10 and $25 and could differ between the two outcomes. For trials with negative reference values, one of the options for adding money always changed the reference option to $0. All outcome values used in this experiment were multiples of $5.

Expected value relations between the two choices were systematically manipulated by changing the amount and/or probabilities associated with each of the options (See Supplemental Experimental Procedures). Only trial types that placed the two choices in maximal conflict (72 gambles per subject) were included in the primary imaging analyses; other trials were included in the model as separate regressors, but not further analyzed. Note that the trials were counterbalanced for valence of the extreme outcome (i.e., gain or loss) and for valence of the reference outcome (i.e., neutral or loss).

Experimental Design

Each trial began with the display of a five-outcome gamble for 4 or 6 s (Figure 1). Subjects were instructed to examine each gamble as it was presented. Subsequently, subjects were given a choice between two ways of improving the gamble. The amount that could be added and the resulting modified outcome values were displayed in red for both choices, to minimize individual differences resulting from calculation or estimation biases. The modified gamble remained on the screen for 6 s, whereupon two arrows appeared to specify which button corresponded to which choice. The association of the buttons to choice was random. Subjects then pressed the button corresponding to their choice. Response times were coded as the time between the appearance of arrows and the button press response (note that this may not be a true representation of the actual decision times in this task). Subjects were instructed to arrive at their decision during the 6 s interval and to press the button corresponding to their choice as soon as the arrows appeared. The decision and response phases were explicitly separated to prevent the contamination of decision effects with response-preparation effects. During the intertrial interval of 4–8 s, a fixation cross was displayed on the screen. Notice that no feedback was provided at the end of each trial and hence there was no explicit learning during the decision phase of the task.

Subjects participated in six runs of this decision task, each containing 20 gambles and lasting approximately 6 min. Before those runs, subjects had the opportunity to practice the experimental task (without reward) in two six-gamble blocks, one presented outside the MRI scanner and the other presented within the MRI scanner but prior to collection of the fMRI data. All stimuli were created using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for MATLAB (Mathworks, Inc.) and were presented to the subjects via MR-compatible LCD goggles. Subjects responded with the index fingers of each hand via a MR-compatible response box.

After completion of the decision phase, there was a final 6 min run in which 40 of the improved gambles were resolved to an actual monetary gain or loss. These gambles were selected randomly from the gambles presented during the decision phase and were presented in modified form based on that subject's choices. On each trial, subjects passively viewed one of these improved gambles on the screen for 2 s (anticipation phase), during which time random numbers flashed rapidly at the bottom of the screen before stopping at a particular value. A text message corresponding to the amount won or lost was then displayed for 1 s, followed by an intertrial fixation period of 3–7 s before the onset of the next trial.

Imaging Methods

We acquired fMRI data on a 4T GE scanner using an inverse-spiral pulse sequence (Glover and Law, 2001; Guo and Song, 2003) with the following parameters: TR = 2000 ms; TE = 30 ms; 34 axial slices parallel to the AC-PC plane, with voxel size of 3.75 × 3.75 × 3.8 mm. High-resolution 3D full-brain SPGR anatomical images were acquired and used for normalizing and coregistering individual subjects' data.

Analysis was carried out using FMRI Expert Analysis Tool (version 5.63), which is part of FMRIB's Software Library (www.fmrib.ox.ac.uk/fsl) package (Smith et al., 2004). The following pre-statistics processing steps were applied: motion correction using MCFLIRT, slice-timing correction, removal of non-brain voxels using BET, spatial smoothing with a Gaussian kernel of FWHM 8 mm, and high-pass temporal filtering. Registration to high-resolution and standard images was carried out using FLIRT. All statistical images presented were thresholded using clusters determined by $z > 2.3$ and a whole-brain corrected cluster significance threshold of $p < 0.05$.

We used separate first-level regression models to analyze decision effects and outcome effects. The decision model comprised two regressors modeling the magnitude-sensitive compensatory choices (G_{max} and L_{min} were combined for additional power) and simplifying P_{max} choices in the conflict conditions, one regressor modeling the responses in the remaining conditions, one regressor for the initial presentation of the gamble, and one regressor to model the subject responses. (An additional post-hoc analysis on a subset of 15 subjects separated the magnitude-sensitive choices according to whether they were G_{max} or L_{min}.) Analysis for the outcome phase consisted of three regressors: one to model the anticipation phase (as subjects were waiting for the corresponding outcome to be revealed), one for positive outcomes (gain), and one for negative outcomes (loss). All regressors were generated by convolving impulses at the onsets of events of interest with a double-gamma hemodynamic response function. Second-level analysis for condition and decision effects within each subject was carried out using a fixed-effects model across runs. Random-effects across-subjects analyses were carried out using FLAME (stage 1 only). When evaluating the effects of behavioral traits (transformed into z scores) on brain function, we included our subjects' trait measures as additional covariates in the third-level analysis.

Logistic Regression Models of Trial-by-Trial Choices

For obtaining the parameter estimates from individual trials for trial-by-trial prediction analysis, we used data that were corrected for motion and differences in slice scan timing but were not smoothed. The data were also transformed into standard space on which the individual ROIs were defined. We used seven different ROIs for this analysis: the right anterior insula and vmPFC, which show greater activation for L_{min} and G_{max} choices respectively; the right PPC, the right precuneus, and right dlPFC, which show greater activation for P_{max} choices; and finally the dmPFC and rIFG, which track strategic variability across subjects. All ROIs were defined functionally based on the third-level activation maps. Activation amplitude was defined as the mean signal change (in percent) over the 6 s time interval from 4 s to 10 s after the onset of decision phase (i.e., when subjects are shown the two alternative choices). This time window was chosen to encompass the maximal signal change of the fMRI hemodynamic response. A summary measure was obtained for each ROI by averaging over all constituent voxels.

We then performed a hierarchical logistic regression using SPSS to predict the choices made by subjects on each individual trial based on strategic preference (proportion of P_{max} choices), brain activation, and interactions between trait and activation. The complete model included a total of 1440 trials (72 trials for each of 20 subjects). Parameters were entered into the model in a stepwise manner, starting with just the behavioral trait measure, then brain activations from the seven ROIs, and finally an interaction term consisting of activation in dmPFC multiplied by strategic tendency. All parameters that significantly improved the model at each stage are summarized in Table 1. The results were consistent regardless of whether forward selection or backward elimination was used in the hierarchical regression.

Functional-Connectivity Analyses

We used a modified version of the decision model described above to perform task-related connectivity analysis. A seed region was defined using activation in the dmPFC that covaried with the strategic variability across subjects (Figure 3). For each run for each subject, we then extracted the time series from this region. A box-car vector was then defined for each condition of interest, with the "on" period defined from 4 s to 10 s after the onset of decision phase for each trial in that condition. These box-car vectors were

then multiplied with the extracted time series to form the connectivity regressors. This allowed us to examine brain connectivity as a function of strategy, specific to the decision phase. These regressors were then used as covariates in a separate GLM analysis, which included the original variables of interest, from the decision model described above (Cohen et al., 2005). Group activation maps were then obtained in the same way as the traditional regression analysis. A positive activation for the connectivity regressors indicates that the region correlates more positively with the seed region during the experimental condition of interest.

SUPPLEMENTAL DATA

Supplemental Data include Supplemental Experimental Procedures, two tables, and eight figures and can be found with this article online at http://www.cell.com/neuron/supplemental/S0896-6273(09)00288-8.

REFERENCES

Barraclough, D.J., Conroy, M.L., and Lee, D. (2004). Prefrontal cortex and decision making in a mixed-strategy game. Nat. Neurosci. 7, 404–410.

Bechara, A., Tranel, D., and Damasio, H. (2000). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. Brain 123, 2189–2202.

Behrens, T.E., Woolrich, M.W., Walton, M.E., and Rushworth, M.F. (2007). Learning the value of information in an uncertain world. Nat. Neurosci. 10, 1214–1221.

Birnbaum, M.H. (2008). New paradoxes of risky decision making. Psychol. Rev. 115, 463–501.

Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., and Cohen, J.D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402, 179–181.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., and Cohen, J.D. (2001). Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Brainard, D.H. (1997). The psychophysics toolbox. Spat. Vis. 10, 433–436.

Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., and Shizgal, P. (2001). Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron 30, 619–639.

Bunge, S.A., Hazeltine, E., Scanlon, M.D., Rosen, A.C., and Gabrieli, J.D. (2002). Dissociable contributions of prefrontal and parietal cortices to response selection. Neuroimage 17, 1562–1571.

Camerer, C.F. (2003). Behavioural studies of strategic thinking in games. Trends Cogn. Sci. 7, 225–231.

Cohen, M.X., Heller, A.S., and Ranganath, C. (2005). Functional connectivity with anterior cingulate and orbitofrontal cortices during decision-making. Brain Res. Cogn. Brain Res. 23, 61–70.

Coricelli, G., Critchley, H.D., Joffily, M., O'Doherty, J.P., Sirigu, A., and Dolan, R.J. (2005). Regret and its avoidance: a neuroimaging study of choice behavior. Nat. Neurosci. 8, 1255–1262.

Dalgleish, T. (2004). The emotional brain. Nat. Rev. Neurosci. 5, 583–589.

Daw, N.D., O'Doherty, J.P., Dayan, P., Seymour, B., and Dolan, R.J. (2006). Cortical substrates for exploratory decisions in humans. Nature 441, 876–879.

De Martino, B., Kumaran, D., Seymour, B., and Dolan, R.J. (2006). Frames, biases, and rational decision-making in the human brain. Science 313, 684–687.

Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, D.C., and Fiez, J.A. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. J. Neurophysiol. 84, 3072–3077.

Dorris, M.C., and Glimcher, P.W. (2004). Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. Neuron 44, 365–378.

Fennema, H., and Wakker, P. (1997). Original and cumulative prospect theory: a discussion of empirical differences. J. Behav. Decis. Making 10, 53–64.

Gigerenzer, G., and Goldstein, D.G. (1996). Reasoning the fast and frugal way: models of bounded rationality. Psychol. Rev. 103, 650–669.

Glover, G.H., and Law, C.S. (2001). Spiral-in/out BOLD fMRI for increased SNR and reduced susceptibility artifacts. Magn. Reson. Med. 46, 515–522.

Guo, H., and Song, A.W. (2003). Spiral-in-and-out functional image acquisition with embedded z-shimming for susceptibility signal recovery. J. Magn. Reson. Imaging 18, 389–395.

Heekeren, H.R., Marrett, S., Bandettini, P.A., and Ungerleider, L.G. (2004). A general mechanism for perceptual decision-making in the human brain. Nature 431, 859–862.

Heekeren, H.R., Marrett, S., Ruff, D.A., Bandettini, P.A., and Ungerleider, L.G. (2006). Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. Proc. Natl. Acad. Sci. USA 103, 10023–10028.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., and Camerer, C.F. (2005). Neural systems responding to degrees of uncertainty in human decision-making. Science 310, 1680–1683.

Huettel, S.A. (2006). Behavioral, but not reward, risk modulates activation of prefrontal, parietal, and insular cortices. Cogn. Affect. Behav. Neurosci. 6, 141–151.

Huettel, S.A., Song, A.W., and McCarthy, G. (2005). Decisions under uncertainty: probabilistic context influences activity of prefrontal and parietal cortices. J. Neurosci. 25, 3304–3311.

Huettel, S.A., Stowe, C.J., Gordon, E.M., Warner, B.T., and Platt, M.L. (2006). Neural signatures of economic preferences for risk and ambiguity. Neuron 49, 765–775.

Kahneman, D., and Frederick, S. (2002). Representativeness revisited: attribute substitution in intuitive judgement. In Hurestics and Biases: The Psychology of Intuitive Thought, T. Gilovich, D. Griffin, and D. Kahneman, eds. (New York: Cambridge University Press), pp. 49–81.

Kennerley, S.W., Walton, M.E., Behrens, T.E., Buckley, M.J., and Rushworth, M.F. (2006). Optimal decision making and the anterior cingulate cortex. Nat. Neurosci. 9, 940–947.

Kerns, J.G., Cohen, J.D., MacDonald, A.W., 3rd, Cho, R.Y., Stenger, V.A., and Carter, C.S. (2004). Anterior cingulate conflict monitoring and adjustments in control. Science 303, 1023–1026.

Kobayashi, S., Lauwereyns, J., Koizumi, M., Sakagami, M., and Hikosaka, O. (2002). Influence of reward expectation on visuospatial processing in macaque lateral prefrontal cortex. J. Neurophysiol. 87, 1488–1498.

Kuhnen, C.M., and Knutson, B. (2005). The neural basis of financial risk taking. Neuron 47, 763–770.

Lopes, L.L., and Oden, G.C. (1999). The role of aspiration level in risky choice: a comparison of cumulative prospect theory and SP/A theory. J. Math. Psychol. 43, 286–313.

Loewenstein, G., Rick, S., and Cohen, J.D. (2008). Neuroeconomics. Annu. Rev. Psychol. *59*, 647–672.

Meriau, K., Wartenburger, I., Kazzer, P., Prehn, K., Lammers, C.H., van der Meer, E., Villringer, A., and Heekeren, H.R. (2006). A neural network reflecting individual differences in cognitive processing of emotions during perceptual decision making. Neuroimage *33*, 1016–1027.

Montague, P.R., and Berns, G.S. (2002). Neural economics and the biological substrates of valuation. Neuron *36*, 265–284.

Paulus, M.P., Hozack, N., Zauscher, B., McDowell, J.E., Frank, L., Brown, G.G., and Braff, D.L. (2001). Prefrontal, parietal, and temporal cortex networks underlie decision-making in the presence of uncertainty. Neuroimage *13*, 91–100.

Paulus, M.P., Rogalsky, C., Simmons, A., Feinstein, J.S., and Stein, M.B. (2003). Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. Neuroimage *19*, 1439–1448.

Payne, J.W. (2005). It is whether you win or lose: the importance of the overall probabilities of winning or losing in risky choice. J. Risk Uncertain. *30*, 5–19.

Payne, J.W., Bettman, J.R., and Johnson, E.J. (1988). Adaptive strategy selection in decision making. J. Exp. Psychol. Learn. Mem. Cogn. *14*, 534–552.

Payne, J.W., Bettman, J.R., Coupey, E., and Johnson, E.J. (1992). A constructive process view of decision-making—multiple strategies in judgment and choice. Acta Psychol. (Amst.) *80*, 107–141.

Payne, J.W., Bettman, J.R., and Johnson, E.J. (1993). The Adaptive Decision Maker (Cambridge, UK: Cambridge University Press).

Pelli, D.G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vis. *10*, 437–442.

Platt, M.L., and Huettel, S.A. (2008). Risky business: the neuroeconomics of decision making under uncertainty. Nat. Neurosci. *11*, 398–403.

Pochon, J.B., Riis, J., Sanfey, A.G., Nystrom, L.E., and Cohen, J.D. (2008). Functional imaging of decision conflict. J. Neurosci. *28*, 3468–3473.

Preuschoff, K., Quartz, S.R., and Bossaerts, P. (2008). Human insula activation reflects risk prediction errors as well as risk. J. Neurosci. *28*, 2745–2752.

Rolls, E.T., McCabe, C., and Redoute, J. (2008). Expected value, reward outcome, and temporal difference error representations in a probabilistic decision task. Cereb. Cortex *18*, 652–663.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., and Cohen, J.D. (2003). The neural basis of economic decision-making in the Ultimatum Game. Science *300*, 1755–1758.

Schultz, W., Dayan, P., and Montague, P.R. (1997). A neural substrate of prediction and reward. Science *275*, 1593–1599.

Seymour, B., Daw, N., Dayan, P., Singer, T., and Dolan, R. (2007). Differential encoding of losses and gains in the human striatum. J. Neurosci. *27*, 4826–4831.

Shah, A.K., and Oppenheimer, D.M. (2008). Heuristics made easy: an effort-reduction framework. Psychol. Bull. *134*, 207–222.

Simon, H.A. (1957). Models of Man: Social and Rational (New York: Wiley).

Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E.J., Johansen-Berg, H., Bannister, P.R., De Luca, M., Drobnjak, I., Flitney, D.E., et al. (2004). Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage *23*, S208–S219.

Tobler, P.N., O'Doherty, J.P., Dolan, R.J., and Schultz, W. (2007). Reward value coding distinct from risk attitude-related uncertainty coding in human reward systems. J. Neurophysiol. *97*, 1621–1632.

Tobler, P.N., Christopoulos, G.I., O'Doherty, J.P., Dolan, R.J., and Schultz, W. (2008). Neuronal distortions of reward probability without choice. J. Neurosci. *28*, 11703–11711.

Tom, S.M., Fox, C.R., Trepel, C., and Poldrack, R.A. (2007). The neural basis of loss aversion in decision-making under risk. Science *315*, 515–518.

Tversky, A., and Kahneman, D. (1974). Judgment under uncertainty: heuristics and biases. Science *185*, 1124–1131.

Tversky, A., and Kahneman, D. (1992). Advances in prospect theory: cumulative representation of uncertainty. J. Risk Uncertain. *5*, 297–323.

Wu, G., Zhang, J., and Gonzalez, R. (2004). Decision under risk. In Handbook of Judgment and Decision Making, D. Koehler and N. Harvey, eds. (Oxford, UK: Blackwell Publishing).

Yacubian, J., Glascher, J., Schroeder, K., Sommer, T., Braus, D.F., and Buchel, C. (2006). Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain. J. Neurosci. *26*, 9530–9537.