Strategic Variability in Risky Choice: Mechanisms and Implications for Neuroanatomy

of Cognitive Control

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor of Philosophy in the Department of
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ABSTRACT

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Abstract

We make a variety of decisions throughout our lives. Some decisions involve outcomes whose values can be readily compared, especially when those outcomes are simple, immediate, and familiar. Other decisions involve imperfect knowledge about their potential consequences: Should I accept the job offer I have now or wait for a possible better offer in the future? Understanding the choice process when consequences are uncertain – often called the study of decision making under risk – has been the focus of research in behavioral economics, cognitive psychology, and now neuroscience. Hallmark of human decision making is the ability to use multiple strategies in representing and evaluating complex decision problems, and to flexibly adapt these strategies to contextual changes in the environment. Yet, little is known about the mechanisms underlying this flexible use of strategies, both across individuals as well as decision contexts.

In a series of risky choice experiments, individuals demonstrate systematic bias towards choices that maximize the overall probability of winning (or not losing) contrary to the predictions of most economic models of risky choice. More importantly, there is substantial variability in choice preferences as a function of decision context as well as individual's current state and traits. Analysis of information processing using eye tracking reveals that this variability is associated with systematic differences in information acquisition, consistent with the adaptive use of multiple strategies in decision making.

Findings obtained using functional magnetic resonance imaging (fMRI) show that distinct neural mechanisms are associated with choices and variability in strategic preferences. Choices that maximize gains are associated with increased activation in ventromedial prefrontal cortex while choices that minimize losses are predicted by activation in anterior insula. However, choices that follow a simplifying strategy (i.e., attending only to the overall probability of winning) are associated with activation in parietal and lateral prefrontal cortices. Dorsomedial prefrontal cortex, through its differential functional connectivity with parietal and insular cortex, predicts individual variability in strategic preference. There is also a striking relationship between neural sensitivity to monetary outcomes in the ventral striatum and individual's strategic preferences, indicating that robust decision strategies may follow from the neural response to rewards. Finally, 24 hours of total sleep deprivation (SD) evokes a strategy shift during risky decision making such that the same individual moves from defending against losses to seeking increased gains.

Though substantial recent research points to the role of the dorsomedial prefrontal cortex (dmPFC) in the flexible control of behavior, nearly all such evidence comes from paradigms involving executive function or response selection, not complex decision making. However, empirical evidence from two independent experiments suggest that the dmPFC contributes to *strategic* control in complex decision making: it signals changes in how a decision problem is represented, and thus shapes computational processing elsewhere in the brain based on the current strategy. FMRI experiment using multiple

tasks that evoke distinct forms of control demands – response, decision and strategy – provides new insight into the functional organization of dmPFC. Specifically, there is evidence for three spatially distinct regions within the dmPFC: a posterior region associated with control demands evoked by multiple incompatible responses, a middle region associated with control demands evoked by the relative desirability of decision options, and an anterior region that predicts control demands related to deviations from an individual's preferred decision-making strategy.

Such a functional topography in dmPFC is consistent with a similar hierarchical organization of the dorsolateral prefrontal cortex (dlPFC), where progressively anterior regions guide increasingly abstract choices. Evidence obtained using resting-state fMRI demonstrates a posterior-to-anterior connectivity gradient between dmPFC and dlPFC, with posterior dmPFC maximally connected to posterior dlPFC and anterior dmPFC maximally connected to anterior dlPFC. This parallel topographic pattern replicates across three independent datasets collected on different scanners, within individual participants, and through both point-to-point and voxelwise analyses.

Based on these findings, I propose a hypothetical model of cognitive control that is primarily characterized by hierarchical interactions – whose level depends on current environmental demands – between functional subdivisions of medial and lateral PFC.

Dedication

This thesis is dedicated to my wife, Dhivya Chandrasekaran, who has been a constant source of inspiration and a pillar of support. She has always stood by me and supported my quest to complete my Doctorate in Philosophy wholeheartedly. In the process, she has made numerous sacrifices of her own, without which this dissertation would not be possible. Dhivya, thank you for everything and it means a lot to me. You are very special and I love you.

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1 Decision Making: Models and Strategies

We make thousands of decisions each day, from simple choices about where to look in the environment to social judgments about strangers. In making these decisions, we synthesize a variety of information quickly and devise strategies to navigate the challenges and make appropriate decisions. It is becoming increasingly evident that people construct preferences when required instead of having stable, well-defined beliefs that generalize across all contexts (Payne, 1976, 1982; Payne et al., 1992b). Additionally, different individuals vary in their decision preferences even when faced with exactly the same task demands (Epstein et al., 1996a; Weber et al., 2002). Therefore, a thorough understanding of decision strategies requires the need to focus on the processes underlying the decision, rather than just the final outcome. Simon argued that a theory of human decision rationality "must be as concerned with procedural rationality – the ways in which decisions are made – as with substantive rationality – the content of those decisions" (Simon, 1981). The traditional focus in economics, on the other hand, has been on what decisions are made rather than how they are made. There is also much research in psychology that makes no pretense of describing the actual decision processes used by people; for example see (Luce et al., 2000). Models describing the relationships between the inputs and outputs of a decision are proposed without claiming to be anything other than "as-if" models. That is, the mechanisms of judgment and choice are treated as a "black box". In contrast, one could focus on the processes of judgment and choice (the how of decisions) and the use of various methods to trace processing beyond the insights provided by more traditional input-output analyses. In recent years, there has

been an increasing concern with the processes of decision due to increasing awareness that judgments and choices are highly sensitive to seemingly minor changes in tasks and contexts (Weber and Johnson, 2009).

1.1 Multi-attribute Decision Making

Real-world decision making often involves choosing between multiple **alternatives** that differ along multiple **attributes**. For instance, buying a house would involve trade-off between several attributes: price, safety, size and distance to work; houses that are safe and close to work might tend to be small and more expensive compared to ones that involve a daily commute of several miles in heavy traffic to work. There are a variety of strategies available to a decision maker for integrating information about each of the attributes before deciding on the best alternative. How then do we go about this information acquisition process and what is the role of context and emotions in shaping decisions? Answering these questions requires insight into the decision process and mechanisms underlying decision making and not merely studying the final outputs.

Research on multi-attribute decision making can be broadly classified into paradigms that look at **preferences** between alternatives, and paradigms that make **inferences** about the best alternative. While preference paradigms are typically focused on deciding between alternatives that vary qualitatively on several attributes such as choosing between apartment to rent or job candidates (Payne et al., 1992b; Payne et al., 1993), the inference paradigms focus more on inferences between alternatives based on cue validities whose accuracy can be assessed, such as which soccer team would perform better or which city is bigger (Gigerenzer and Goldstein, 1996; Gigerenzer et al., 1999).

Therefore, there is a lack of an objective accuracy measure in the preference paradigms, and the gold standard against which the performance of a strategy is compared is a compensatory weighted additive model. On the other hand, the inference paradigms pit all the strategies against each other by comparing them to external real-world criteria. Feedback and learning play a crucial role in the prediction paradigms with the validities of the cues being updated based on feedback from the previous decision (Gigerenzer et al., 1999). The main focus of the dissertation is on decision preferences and not inferences.

1.1.1 Process Tracing Methods

In one of the first experiments looking at decision process, participants acquired information about the various attributes for each of the alternatives in the decision task (Payne, 1976). The information was hidden in cards placed inside sealed envelopes that we then pinned to an information board. By examining the pattern of information acquisition, one could obtain a better understanding of the underlying decision process and strategies. Several techniques have been used since for information monitoring including verbal protocol analyses, MOUSELAB and more sophisticated eye tracking methods (Russo and Dosher, 1983).

A popular method for understanding decision processes involves verbal protocols, which encourages participants to “think aloud” and reveal their thought process when making decisions (Payne, 1976). An advantage of verbal protocol analysis as a process-tracing method is that it can provide information on meta-cognitive processing. For example, verbal protocols provide some evidence that people adapt their processing in a

top-down fashion. The following two excerpts from verbal protocols of two decision makers illustrate this point: 1) “Well, with these many apartments (six) to choose from, I’m not going to work through all the characteristics. Start eliminating them as soon as possible” (Payne, 1976). 2) “With just two (gambles) to choose from, I’m going to go after all the information, it won’t be that much trouble” (Payne and Braunstein, 1978). Researchers have since used verbal protocols to study environmental valuation judgments and to understand juror and jury judgments in civil cases involving punitive damages among others (Schkade and Payne, 1994; Hastie et al., 1999). One strength of the verbal protocol method is its ease of use in more natural (field) type settings. On the other hand, it is important to note that verbal protocol methods can be difficult to use. They are labor intensive, require considerable transcription and coding effort, and involve difficult, and sometimes controversial, analysis.

Perhaps the most commonly used information acquisition technique in the literature is MOUSELAB, a Java based computer software that presents a matrix of rectangular boxes on the screen. Each box can be opened by moving a mouse pointer to reveal information (Payne et al., 1993). The information in that box remains exposed as long as the pointer is held on the box, after which it closes. The responses and timings are recorded and available to the experimenter for further detailed analysis. One of the common criticisms of mouselab is that the information acquisition process is unnatural as participants have to move the mouse over a particular box to acquire information. Yet, it has been a tremendously useful and popular tool for understanding decision process over the past few decades.

Another process-tracing method that should find greater use in more applied decision research is eye-tracking. Eye tracking has been used as a tool to investigate decision processes for the past few decades (Russo and Rosen, 1975; Lohse and Johnson, 1996; Rayner, 1998). Process methods like verbal protocols and Mouselab may interact with decision behavior and hinder participants from relying on automatic processing due to the unnatural nature of information presentation and acquisition, i.e. pressing mouse to sequentially acquire information (Glockner and Herbold, 2011). Eye tracking on the other hand has the advantage of providing more natural environment for studying decision processes, thereby not hindering automatic processing when required. One can also obtain a measure of pupil dilation using eye tracking which in turn provides information about emotional and cognitive processing (Siegle et al., 2003a; Siegle et al., 2003b).

There is no "perfect" process-tracing method for decision research with each having its own pros and cons. Therefore, one approach to this problem is to match the method to the type of problem being investigated. For instance, tools like Mouselab, Active Information Search, and the collection of verbal protocols may be best suited for decision problems that represent more serial processing. On the other hand, tools like eye-tracking together with response times and skin conductance may be useful in dissociating between decisions that are based on intuition and heuristic processing against those based on more deliberative processing (System 1 vs. System 2). Another approach that has long been advocated is to combine methods. For instance, one converging evidence using the same paradigm across more than one process-tracing technique to make inferences (Payne et al., 1978; Payne and Venkatraman, 2011).

1.2 Strategies in Multi-attribute Decision Making

The term "strategy" has different meanings in different fields and contexts. Within game theory it usually refers to a particular choice option available to a player (Camerer, 2003b). In an outcome-oriented definition in decision making, a decision strategy can be defined as the average preference across trials for a particular decision outcome (Venkatraman et al., 2009b). In a more process-oriented approach, strategy refers to the sequence and content of information that people acquire and process to reach a decision (Cope and Murphy, 1981; Payne et al., 1993). I contend that these definitions are related (increased preference for a particular choice across trials will be a result of systematic differences in information acquisition process). Hence, these two decision-making definitions of strategy will be used interchangeably through the course of this dissertation.

In the context of multi-attribute decision making, information acquisition and processing strategies can be broadly classified into compensatory and non-compensatory strategies.

1.2.1 Compensatory Decision Making

Decisions that involve explicit trade-off between competing alternatives are referred to as compensatory decisions since alternatives that are deficient in certain attributes are compensated by their superiority on other attributes. The most popular among compensatory decision making strategies is the weighted additive (WADD) strategy. According to this strategy, the utility of a multi-attribute option is the weighted sum of subjective utilities of its components. Therefore, a WADD process would

typically involve examining each alternative on each of the attributes, determining the subjective value of each of the attributes and multiplying it with the relative importance of that attribute, and finally summing across all the attributes to obtain an overall value for that alternative. The final step involves comparing the value across all alternatives and the one with the highest value gets selected.

The WADD strategy is hence characterized by extensive alternative-based processing of information as well as explicit trade-offs in dealing with conflicts, making it an appropriate choice for normative decision strategy. The WADD model also has several parallels with the expected utility model of risky choices discussed later (Payne et al., 1988).

Another commonly used compensatory decision strategy is the equal weight (EQW) strategy, which is a simplification of the WADD in the sense that all attributes are considered to be of equal importance (Payne et al., 1988). As a result, the net value of each alternative is obtained by merely summing the individual subjective values of each of the attributes for that alternative.

1.2.2 Heuristics and Non-Compensatory Decision Making

Limitations in human cognitive capacities suggest that people cannot process all the available information in a particular situation or even if they could, there would be a large overhead in terms of cognitive costs. This necessitates selective processing of information. A heuristic is a decision strategy in which only a subset of relevant information is processed prior to making a decision. Heuristic strategies are usually non-compensatory in the sense that they do not involve explicit trade-offs between attributes.

Heuristics, by their very nature, are fast and frugal due to the limited information processing.

Herbert Simon, in 1955, introduced the notion of ***Satisficing*** (SAT) where people choose an alternative, that though not optimal, is good enough (Simon, 1955). Therefore, alternatives are considered sequentially in the order they occur in the choice set. The subjective values for each attribute of that alternative is then compared against a pre-determined cutoff value and the first alternative for which all attributes pass the cutoff value is selected as winner. The satisficing strategy is selective across alternatives and non-compensatory. The extent of processing depends largely on the cutoff values, which in some instances can be adaptive based on the values of the first few alternatives examined.

The simplest form of heuristic for multi-attribute decisions is the ***Lexicographic*** (LEX) strategy, which involves identifying the most important attribute and selecting the alternative with the highest value on that attribute (Payne et al., 1988). If multiple alternatives are tied on the most important attribute, then their value on the next most important attribute is considered to break the tie. A LEX strategy, therefore, is selective across attributes, involves limited information processing and is clearly non-compensatory.

Elimination by Aspects (EBA) is a combination of the LEX and SAT strategies. First, the attributes are ranked in the order of importance, similar to LEX and each is associated with a cutoff rating (Tversky, 1972). Then, the alternatives are compared on the most important attributes and the alternatives which fail to reach a minimum cutoff

level for that attribute are eliminated. This process is repeated with the second most important attribute and the remaining alternatives, until only one alterative remains. Thus, EBA focuses on attributes as a means of processing information.

There are several other heuristics that can be used for multi-attribute decision making like majority of conforming dimensions (MCD), least important minimum (LIM) heuristic, least variance (LVA) heuristic, multi attribute utility (MAU) model and so on (see (Riedl et al., 2008) for details). Therefore, decision makers have access to a "toolbox" of strategies (both compensatory and non-compensatory) available at their disposal, which can then be used in an adaptive manner depending on decision context and individual variability as discussed below.

1.3 Contextual Effects on Multi-attribute Decision Making

The contingent nature of decision behavior has been one of the most important findings of behavioral decision research. It has also become clear that not only do people change what they decide based on task and context variations but also they change how they decide. Thus, to understand what judgments and choices will be made in various decision environments we must have an understanding of task demands, an understanding of the processes of judgment and choice, and an understanding of how task demands and psychological processes interact. Again, in the words of Simon, "Human rational behavior is shaped by a scissors whose two blades are the structure of task environments and the computational capabilities of the actor" (Simon, 1990). Recent research in decision making has sought to extend Simon's insight to include all of the psychological processes of the decision maker.

A related point is that decision researchers increasingly believe that preferences for and beliefs about objects or events of any complexity are often constructed – not merely revealed – in the generation of a response to a judgment or choice task (Payne et al., 1992a; Slovic, 1995; Lichtenstein and Slovic, 2006). That is, people are seen as constructing preferences and beliefs on the spot when needed, instead of having known, well-defined, and stable preferences or beliefs that are retrieved from memory. Further, preferences and beliefs are not generated by some invariant algorithm such as Bayesian updating or expected utility calculations when memory is insufficient, but instead are generated by the contingent use of a variety of different decision heuristics or simplification mechanisms. Understanding when, and why, a task variable elicits a particular process for constructing a solution to a decision problem will be facilitated by data that reflect more than just the end product of the processing.

More specifically, a constructed response to a decision problem will often involve the highly selective use of information in judgment and choice processes. Simon has argued that attention is the scarce cognitive resource in decision making (Simon, 1978). Consequently, understanding what drives selective attention in decision making is one of the most critical tasks for a researcher. Many of the process-tracing methods discussed above are very useful in identifying the selective use of information during decision making. In particular, methods that trace information acquisition behavior such as Mouselab, eye fixations, and active information search are well suited to studies of attention and decision making.

Factors that influence decision strategy can be classified as: (i) task variables (like complexity of the problem, timing constraints, response mode) that are related to the general characteristics of the decision problem, (ii) and context variables (like inter-attribute correlation and presence or absence of dominated alternatives) that reflect the particular values of the alternatives (Bettman et al., 1993). ***Task difficulty*** represents the best example of contingent strategy use: people typically switch from the usage of a compensatory strategy for simple two or three alternative decision problems to more non-compensatory and heuristic based strategies for complex decision tasks (Payne, 1976). These findings similarly extend to task environments involving time pressure (Payne et al., 1996) and additional cognitive load (Drolet and Luce, 2004).

Even something as subtle and independent as variations in information display could lead to changes in decision strategies. Individuals tend to acquire information in a fashion that is consistent with the format of display (Bettman and Kakkar, 1977). Consistent with the cost/benefit framework, any information display that involves storage of information or transformation and additional processing will be discounted or ignored from the decision process.

Another robust effect of context in decision literature refers to the **attraction effect**. Here, the addition of a new dominated alternative increases the preference for the original alternative that dominates it. The introduction of the "decoy" makes the original alternative more attractive. A possible explanation for this effect is that the introduction of a decoy reduces the negative emotion typically associated with the original impoverished trade-off choice set (Hedgcock and Rao, 2008). Framing effect is similar to

attraction effect, where the manner in which the decision problem is framed or instructions are presented can lead to changes in decision strategies (Tversky and Kahneman, 1981, 1986).

Inter-attribute correlation is another factor that affects decision strategies. Unlike the general characteristics of the decision problem, inter-attribute correlation refers to the conflict that arises due to the correlation between different attributes based on their values for each given alternative. A greater negative correlation between attributes implies a greater conflict in the decision process. Bettman and colleagues show that decision contexts with increased negative correlation between attributes lead to an alternative-based extensive processing of information in an effort to confront the conflict (Bettman et al., 1993).

1.4 Individual Differences in Strategy Use

It is obvious that individuals differ in what judgments or choices they will make when faced by the same task demands. For example, some people save more for retirement, some less. Some people put more of their savings into bonds while others put more of their savings into stocks. How should such individual differences in decisions be modeled? A common view underlying many studies of individual differences is captured by Birnbaum's argument that the principle "that every individual is represented by the same model in which different people can have different parameters in that model" (p. 497) should be retained for risky decisions until researchers have a clear reason to abandon it (Birnbaum, 2008a). Nonetheless, it is becoming increasingly clear that individuals differ in how judgments or choices are made (processes) as well as in the

content of their decisions, e.g., amount of risk-taking. Understanding individual differences in both behavior and processes is an ongoing challenge in decision research, and will be facilitated by considering the interaction of tasks and processes. For instance, Bishara and colleagues argued that understanding how two complex tasks designed to measure the same individual trait, e.g., risk-taking, may relate across individuals depends on examining the component processes involved in performing those tasks (Bishara et al., 2009). Individual-difference analysis is also a key means through which neuroscience methods can aid in the study of choice behavior. There is a clear need to go beyond the traditional focus on individual differences in the content of decisions to a better understanding of individual differences in the processes of decisions.

One popular area of research that has played an important role in decision sciences literature is risky choice involving monetary gambles (Slovic and Lichtenstein, 1968; Payne and Braunstein, 1978; Kahneman and Tversky, 1979). Risky choice studies are popular because they are easy to administer in laboratory settings, can be made incentive-compatible to reveal true preferences and yet share similarities to real-world decisions due to its probabilistic nature.

1.5 Risky Choice as a Prototype for Studying Decision Making

Most decisions involve situations with imperfect knowledge about the associated outcomes, a notion termed as uncertainty in decision making. One specific aspect of uncertainty that has been extensively studied by researchers is risk, where the decision maker has some knowledge about the distribution of outcomes (Wu et al., 2007; Platt and Huettel, 2008). Risky choice research involving monetary gambles has played an

important role in decision sciences literature (Slovic and Lichtenstein, 1968; Kahneman and Tversky, 1979; Payne et al., 1992a). Following Blaise Pascal's formulation of the notion of expected value through his famous wager argument in the 17th century, several economists have proposed normative and descriptive models to explain risky choice behavior. Some of these models are reviewed in this section.

1.5.1 Compensatory Models of Risky Choice

Expected Utility

At the heart of risky choice models is the expected utility model, first proposed by Daniel Bernaulli in 1738, which is still a popular and dominant theory for explaining how people choose between two choices under uncertainty (Bernoulli, 1738). According to this normative model, people evaluate options based on their desirability or "utility" of each of the outcomes weighted by the probability of the event occurring and choose the option with the greatest value of this product. The utility function in itself is logarithmic (rather than linear) and concave: a small increase in money should mean more to a poor man than a millionaire. In the mid twentieth century, Von Neumann and Morgenstern axiomatized the expected utility theory by providing a set of conditions that were necessary and sufficient for expected utility (von Neumann and Morgenstern, 1944). One such axiom is the Independence Axiom that was subsequently revised by Samuelson in 1952 (Samuelson, 1952). According to this axiom, if you prefer gamble A to gamble B, then you should prefer the mixture of A and some other gamble C (in some probabilistic proportion) to the mixture of B and C in the same proportion.

Expected Utility theory assumes that the utility of a particular outcome is not simply based on that outcome, but on the integration of that outcome with all wealth accumulated till that point. Several anomalies have been associated with the predictions of EU theory. The most common known examples is the Allais paradox, which demonstrate clear violations of the independence axiom (Wu et al., 2004). The utility function in EU models also cannot explain both gambling and purchasing of insurance, simultaneous phenomenon demonstrated by most people in everyday life (Wu et al., 2004).

Prospect Theory

Prospect theory consists of two components: a value function and probability weighting function (Kahneman and Tversky, 1979).. The value function is concave over gains and convex for losses with the slope being steeper in the loss domain, a feature termed as loss aversion. It is important to highlight that the value function in prospect theory is defined over relative changes in wealth rather than absolute wealth levels, unlike the utility function in expected utility that is defined over finite wealth states. The probability weighting function captures how different probability levels contribute to the gamble. Specifically, prospect theory proposes that people tend to overweight smaller probabilities and underweight medium and larger probabilities.

Prospect theory, therefore, suggests that people are risk seeking for gains involving small probabilities and risk averse for medium to large probabilities. In the loss domain, people are risk averse for small probabilities and risk seeking for medium to large probabilities. This dichotomy can explain gambling and insurance purchasing

behavior, both of which are associated with overweighting of lower probabilities. However, prospect theory suffers from possible violations of stochastic dominance. A gamble of the form (p, x; q, x-ε) could exceed (p+q, x) even though the later stochastically dominates the first gamble, due to the shape of the weighting curves in prospect theory. Prospect theory was also designed mainly for two-outcome gambles and could not be readily extended to gambles with multiple outcomes. This forced researchers to look for alternatives to prospect theory in the form of rank-dependent utility models (Tversky and Kahneman, 1992).

Cumulative Prospect Theory

Many important risky decisions involve multi-outcome and mixed gambles, consisting of both gains and losses, a key area that is not well addressed using Prospect Theory. Also the evaluation of mixed gambles is more than just the sum of evaluation of the individual gain and loss components. To address some of these concerns as well as the violations of stochastic dominance, Tversky and Kahnemann proposed the Cumulative Prospect theory (CPT), a rank-dependent utility model. While using the same basic framework of the prospect theory, CPT involves application of a separate rank-dependent transformation to the probabilities of the gain and loss portions of a gamble (Tversky and Kahneman, 1992). Therefore, CPT can be applied to gambles that involved an arbitrary number of outcomes unlike prospect theory, which was restricted to only two non-zero outcomes. Several researchers have since focused on parameterizing the weighting functions (Gonzalez and Wu, 1999). However, several new experiments have shown violations of CPT in risky choice (Payne, 2005; Birnbaum, 2007, 2008b).

Transfer of Attention Model

The Transfer of Attention (TAX) model represents the utility of a gamble as a weighted average of the utilities of the consequences (or outcomes). The key idea is that branches (multiple outcomes) compete for attention (Birnbaum and Bahra, 2007). In the simplest scenario, the attention (weight) allocated to each branch will be directly proportional to their probabilities, with the more probable outcomes getting more weight. The model allows for transfer of attention from branch to branch according to the ranks and consequences of the branches. Therefore, if a participant is risk-averse, branches leading to lower valued outcomes can get enhanced weighting at the expense of attention to the higher valued outcomes. The net sum of weight transfers is zero; that is, weight is neither created nor destroyed but only transferred between branches (Birnbaum, 2008a).

1.5.2 Non-compensatory Models of Risky Choice: Priority Heuristic

The Priority Heuristic is a framework adapted from the fast and frugal heuristics framework for inferences (introduced in detail in the next section) to explain people's preferences in risky choice (Brandstatter et al., 2006). The priority heuristic consists of (i) **a priority rule** that involves going through several reasons (minimum gain, probability of minimum gain, maximum gain) in order; (ii) **a stopping rule** that stops examination if the minimum gain differs by 1/10 (or more) of the maximum gain or if the probabilities differ by 1/10 (or more); and (iii) **a decision rule** that involves choosing the gamble with the more attractive gain (or probability). The same rules can also be extended to the loss domain for gambles involving gambles (Brandstatter et al., 2006).

The proponents of the priority heuristic demonstrate its effectiveness in outperforming CPT and TAX models. They argue that the complicated mathematics behind the alternative CPT and TAX models makes them unlikely candidates for explaining risky behavior. However, more recent analysis suggest that the priority heuristics may not explain certain classes of data involving multi-outcome gambles and shows systematic violations of stochastic dominance and distribution independence using priority heuristic (Birnbaum, 2008b).

1.6 Risky Choice: Single or Multiple Strategies?

As introduced above, decision making differs across contexts and across individuals. Different individuals will often respond differently to the same problem. The same individual will respond differently to what appear to be subtle changes in problem descriptions and environment. An ongoing debate in decision research is how to account for these individual and contextual differences. One perspective argues for a single decision strategy, with the observed differences in behavior explained in terms of differences in parameter values. An alternative perspective is the multiple strategy view which argues that individuals have access to a set of heuristic strategies that will be used contingently as a function of problem type, individual's prior experience, and individual differences in capabilities and tendencies.

Over the years, theoretical perspectives have changed on this issue. Initially, models like expected utility for risky choice, weighted additive models for multi-attribute decision making, and Bayesian models for subjective probability judgments, all supported the single strategy perspective. In these compensatory models, differences in

choices across individuals and decision contexts are often explained by differences in the parameter values associated with the corresponding model. Birnbaum (2008a) argues strongly that every individual should be represented by the same expectation model in which both individual differences and context differences across different problems types are all explained by differences in parameters within that model. More recently, Newell has argued for a more general purpose compensatory evidence accumulation process where people are seen as acquiring information sequentially, forming updated valuations of options based on the information, and then responding (making a decision) once a threshold of evidence has been reached (Newell et al., 2004; Newell, 2005). The key source of individual and problem differences is in the thresholds, and therefore the amount of information acquired before a decision is reached.

The other general perspective on differences across individuals and problems is captured by the adaptive toolbox metaphor (Payne et al., 1993; Gigerenzer and Goldstein, 1996). Under this view, it is believed that people have a large adaptive toolbox of strategies available to them and they adaptively draw upon these heuristics depending on context, individual differences and task structure (Payne et al., 1988; Gigerenzer and Goldstein, 1996). Therefore, a large part of variability in decision making can be explained by adaptive use of these heuristics, consistent with use of multiple strategies.

There is still considerable debate between the single and multiple strategy approaches among judgment and decision-making researchers (Payne et al., 1992b; Newell et al., 2004; Birnbaum, 2008a; Glockner and Betsch, 2010; Glockner et al., 2010; Marewski, 2010). In the next chapter, I will address this debate and demonstrate the use

of multiple strategies in decision making using converging experimental data from choice proportions, eye tracking, response times and fMRI.

1.6.1 Demonstrating the use of Multiple Strategies in Risky Choice

When an individual solves a decision problem, how can one demonstrate that multiple strategies are used in the process? One approach is to examine the outcomes of the decision episode. However, differences in outcomes are neither necessary nor sufficient. For example, different parameter values for a constant strategy could lead to different choices. Similarly, different strategies could lead to the same decision for many problems. A different approach is to focus on response times. Response times, however, are only suggestive but not definitive regarding strategy differences. Different people might use the same strategy but exhibit faster (slower) response times based on the degree of confidence required or verification needed (see Montgomery (1983) for a model of choice based on cycling through decision structuring) or simply differences in the execution of a strategy (Lemaire, 2010).

Measuring information acquisition behavior using tools like Mouselab and eye tracking has become a popular approach to investigating strategy differences in decision making (Russo and Dosher, 1983; Payne et al., 1988). Yet, this approach is still only suggestive and not definitive. One problem is that information acquisition often involves two, and perhaps three, distinct phases. First, people essentially read or scan a problem to get a sense of what the problem is all about. Second, people acquire information (often in a selective fashion) as part of the evaluation of the information, a phase that is generally seen as most relevant for strategy use (Johnson et al., 2008). Finally, there can also be a

verification phase, where information related to the tentatively selected option is re-examined.

Recently, the nascent field of neuroeconomics (studying the neural bases of decision preferences) has provided tremendous promise for advancing our understanding of decision making (Glimcher, 2003; Platt and Huettel, 2008). Neuroscience can help illuminate the neural mechanisms underlying decision preferences, particularly with respect to individual variability in decision preferences (Venkatraman et al., 2011). By carefully evaluating the underlying neural mechanisms, one can make inferences about whether different choices arise from the use of same or different strategies. Additionally, neuroscience can also provide insights into strategy selection and help answer the metacognitive question of how people decide to decide. However, it is still a correlative method with the activated regions being associated with and not necessarily essential for the task. This often necessitates the need for additional follow-up behavioral experiments to validate the findings (Huettel and Payne, 2009).

In summary, there is no one perfect method for detecting the use of multiple strategies. Instead, there is a need for integrating evidence from multiple methodologies to develop a complete understanding of decision strategies and individual variability. In the next few chapters, I will present evidence in favor of a multiple strategy view of decision making under risk using a multi-outcome risky choice task where participants had the option to improve a mixed gamble by adding value to one of the outcomes. I will use risky choice as it is one area of research where the evidence in favor of the single strategy approach is strongest. Using data integrated across multiple experiments

involving behavioral, neuroimaging and eye tracking methods, I will argue that there is sufficient data to abandon the assumption of a single underlying calculus or strategy for risky choice and replace it with the assumption of multiple strategies that are used contingent upon the decision context and individual differences.

1.7 Summary

Several decades of research in the field of behavioral decision making and economics have advanced our understanding about how people make decisions under uncertainty. These studies also highlight the adaptive nature of these decisions. However, they leave unanswered the question about the mechanisms that underlie these behavioral phenomena. Understanding mechanisms provide a better understanding of how judgments and choices are made. This is particularly true when the approach to improving decisions is one of nudging people towards better judgments and choices (Thaler and Sunstein, 2008). The central idea is that by knowing how people think we can design choice environments that make it easier for people to choose what is best for themselves, their families, and their society, without restricting freedom of choice. Weber and Johnson (2009) make the similar argument that knowledge about the psychological processes provides entry points for interventions designed to help people overcome judgments or choices considered undesirable. Psychological process explanations of decision behaviors are likely to be of increasing interest to policy makers and business leaders. Therefore, the next few chapters are focused on experiments that seek to elucidate the mechanisms underlying variability in decision making using multiple methodologies like choice data, response times, eye tracking and neuroscience.

2 Contextual and Individual Variability in Risky Choice

Most studies of risky choice use simple gambles of the form ($x, p; 0, 1 – p), where one receives $x with probability p or $0 with probability 1-p (for reasons of experimental control and simplicity, Luce (2010) refers to such gambles as "unitary" gambles). Yet, more complex gambles with multiple gain and loss outcomes are needed to simulate real-world decision scenarios (Lopes, 1995; Lopes and Oden, 1999). Complex mixed gambles with more than two outcomes also inform researchers about underlying models and strategies that guide behavior. The focus of this chapter is on a series of behavioral and eye-tracking experiments that use a complex multi-attribute multiple-alternative value allocation task. The findings from these experiments demonstrate systematic variability in preferences across individuals and across what appear to be subtle changes in problem descriptions and environments (decision context).

2.1 Value Allocation Task

In the original version of this task (Payne, 2005), participants were presented with a five-outcome mixed gamble of the form $G = [x_1, p_1; x_2, p_2; x_3, p_3; x_4, p_4; x_5, p_5]$, where p_i indicates the probability of monetary outcome x_i. The outcomes were rank-ordered $x_1 > x_2 > x_3 > x_4 > x_5$, where at least two outcomes were strict gains ($x_1 > x_2 > \$0$) and two were strict losses ($x_5 < x_4 < \$0$). The value of the middle, referent outcome (x_3) varied across trials, but is typically $0 or slightly negative**.** Participants then chose to improve the base gamble by adding (allocating) a fixed amount of money (δ) to either one of the extreme outcomes (x_1 or x_5), or the middle outcome (x_3).

Many of the models introduced in the earlier chapter make specific predictions to the value allocation problem above (see section on consistency with economic models below). For instance, the classic, compensatory, expected utility (EU) model predicts that people would generally choose to add value to the lowest ranked (in terms of preference) outcome, assuming that people are generally risk averse (i.e., a concave utility function). CPT predicts that greater weight will be placed on both the extreme worst (x_5) and best outcomes (x_1) that could occur, with the greater focus on the worse outcome, if the worst outcome is a loss and the best outcome is a gain due to loss aversion. The transfer of attention exchange (TAX) model makes a similar prediction as EU if the individual is risk averse and the gambles have at least one gain outcome (Birnbaum and Bahra, 2007). The order of attention is assumed to be reversed for strictly negative outcome gambles. Even the non-compensatory priority heuristic predicts that people will select the option that is better in terms of the extreme loss outcome. If there is no difference on loss outcomes and probabilities, then people will select the option that is better on extreme gain outcome (Brandstatter et al., 2006).

Yet, by adding amount to the intermediate ranked outcome, one can maximize the overall probability of winning (Pmax)[1]. In the original study, more than 2/3 of the participants preferred this option (Payne, 2005). The Pmax heuristic represents a clear computational simplification for multi-outcome risky choice problems that can be construed as responding to the "gist" (gain vs. loss) of an outcome value as compared to

[1] The overall probability of winning (not losing) is defined across all outcomes and is not the probability of a single outcome.

aspiration or target level (Simon, 1955; Payne et al., 1980; Lopes and Oden, 1999; Shah and Oppenheimer, 2008). This heuristic also ignores payoff magnitude information.

2.2 Variability in Preference for Probability-maximizing Heuristic

In two experiments, we modified the value allocation paradigm to explore, in greater detail, individual differences in the bias toward maximizing the probability of winning compared to losing (i.e., a *probability-maximizing strategy*). To match the procedure of Payne (2005), participants chose among two of the above ways to improve five-outcome mixed gambles, but those gambles were not resolved and participant compensation was unrelated to their decisions.

2.2.1 E1: Individuals Demonstrate Bias towards Pmax Option

One hundred twenty eight young adults participated in this behavioral experiment conducted at the Fuqua School of Business. All participants were compensated for their participation in this study, and their payout was fixed ($8) and not related to their choices. All participants provided informed consent as a part of a protocol approved by the Institutional Review Board of Duke University.

Participants were presented with eight five-outcome mixed gambles on a computer using the Psychophysics Toolbox program in MATLAB. Cognitive load was also manipulated between participants by asking them to memorize 3 or 7-letter pseudo-words for each trial. For all analyses, data was collapsed across both the load conditions since we did not find any effect of load. First, each participant was presented with a risky gamble and asked to rate its attractiveness. Subsequently, they were given two choices for modifying the gamble, one of which always involved adding a fixed amount to the

reference to change the overall probability of winning or losing (Pmax option) and another which involved adding the same amount to either the extreme loss or gain outcome (Vmax option). Participants were shown both versions of the modified gamble on the screen beside each other and were asked to choose one of the options. There was no time constraint for making the choice. In four gambles, the probabilities of the two outcomes were matched (equal expected value) while for the remaining four gambles, the probability associated with Pmax choice was less than the probability of the Vmax choice by 5 or 10% (unequal expected value).

Results: As hypothesized, there were significant biases towards Pmax choice (choice proportion = 0.69) when expected value was matched. Even when choosing the Pmax option required sacrificing expected value (i.e., when the alternative option resulted in a bigger increase in value and/or probability), individuals preferred the Pmax option in 59% of the trials. We also observed substantial inter-individual variability: some individuals nearly always preferred the Pmax option; others nearly always preferred the alternative Vmax option while still others switch based on both individual traits and decision variables **(Figure 2-1)**. Finally, the Pmax choices were also associated with faster response times **(Figure 2-2)**.

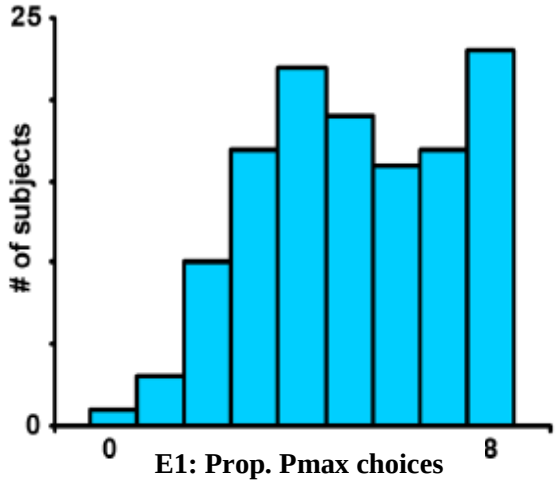

Figure 2-1: Individuals demonstrated variability in bias towards Pmax choices.

2.2.2 E2: Pmax Bias is Modulated by Decision Context

The second behavioral experiment (E2) manipulated the basic paradigm in three ways – to maintain, eliminate, or exaggerate the probability-maximizing choice – to rule out potential confounding factors and establish that these effects were indeed driven by the need to maximize the overall probability of winning. Seventy one young adults participated in a second behavioral experiment conducted at the Fuqua School of Business. Compensation for participants was similar to the previous experiment. All participants provided informed consent as a part of a protocol approved by the Institutional Review Board of Duke University.

Participants were presented with eight five-outcome mixed gambles similar to the first experiment on a computer. Four of these gambles were matched for expected value and the other four were not. Additionally, participants were also presented with eight gambles where adding value to the middle option did not involve a change in overall

probability. In these Pmax-unavailable trials, we made one very subtle change to the experimental design: we added or subtracted a small amount from the central choice option (e.g., adding value to an option that was already $5 and not $0; or adding money to an option that changes it from -$20 to -$5). Thus, there were no options in the gamble whose selection would change the overall probability of success.

Finally, participants were presented with four additional trials where adding values to the *extreme* loss or gain outcomes changed the overall probability of the gamble. In these Pmax-exaggerated trials, we altered the basic gambles so that one of options, if selected, would translate a certain loss gamble to an uncertain loss gamble (by modifying an all loss-outcome gamble to a gamble with one gain outcome) or translate an uncertain gain gamble to a certain gain gamble (by modifying a gamble with one loss outcome to an all gain-outcome gamble). These gambles were created by selecting two basic gambles from the set of four equal expected value core problems above and transposing them by adding or subtracting a constant value from all outcomes. For e.g., the core gamble: [60, 0.2; 45, 0.2; -20, 0.2; -40, 0.2; -80, 0.2] was transposed it to the new gamble: [130, 0.2; 115, 0.2; 50, 0.2; 30, 0.2; -10, 0.2] and participants were given a choice between adding $30 to the -$10 option (making it a certain win gamble) or to the $50 reference option (which would correspond to the Pmax option in the untranslated version).

Results: In the control trials, which replicate the design of the first behavioral experiment, participants still showed a systematic bias (65%) towards the Pmax choices.

Again, the preference for Pmax response reduced slightly (58%, but was still the majority response) when it was associated with lower expected value.

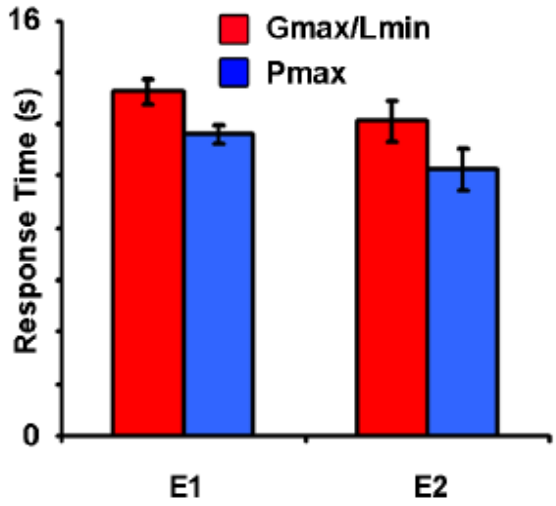

Figure 2-2: Participants were faster for overall probability maximizing choices

In the critical Pmax-*unavailable* trials, we found a significant shift in the pattern of participants' choices: participants now chose the option nearest to $0 only 39% of the time. This result provides confirmation that many participants do preferentially select the choice that improves the overall probability of winning when it is available, but readily switch to magnitude-sensitive choices otherwise. Moreover, these results also indicate that the choices of participants for these mixed gambles cannot be explained solely by parameters within standard descriptive economic models, because the addition of $5 to one option of a complex, large-magnitude gamble should have negligible effects upon the predictions of those models. Finally, in the Pmax-*exaggerated* trials, participants overwhelmingly preferred the probability-maximizing option (83%). Thus, our behavioral data not only demonstrate the robustness of the preferences toward the Pmax

choices, but more importantly that this bias can be reversed or accentuated by experimental manipulations.

Consistent with our first behavioral experiment, we also found substantial inter-individual variability in this participant population. Again, P_{max} choices were associated with faster response times **(Figure 2-2)**. To identify potential individual trait correlates of this strategic variability, we collected psychometric data that included tendency toward satisficing (Schwartz et al., 2002) and emotional sadness (Fordyce, 1988). Across our participant sample, increased maximizing trait responses predicted a decreased bias toward probability-maximizing choices (r = -0.26; $p < 0.05$). In other words, satisficers preferred the probability-maximizing choices more than maximizers, consistent with these choices representing a simplifying strategy. Similarly, an increase in the sadness trait measure also predicted a decreased bias towards probability maximizing (r = -0.29; $p < 0.05$). Sadness has also been typically associated with reduced certainty, increased elaboration and reduced heuristic processing (Schwarz et al., 1991; Bodenhausen et al., 1994).

2.2.3 Pmax Choices are Consistent with a Simplifying Strategy

Across both experiments, we find four lines of evidence that support the view that Pmax choices represent an effort-reduction simplifying strategy. First, Pmax choices were significantly faster in terms or response times, as would be expected of a less effortful strategy. Second, individual differences in the preference for Pmax were significantly and negatively correlated with a trait measure of maximizing in E2, consistent with effort-reduction. Third, individual variability in proportion of Pmax

choices also significantly and negatively correlated with a trait measure of sadness in E2, consistent with sadness being associated with reduced heuristic processing (Schwarz et al., 1991; Bodenhausen et al., 1994). Finally, the proportion of Pmax choices decreased with increasing cost in terms of expected value. Together, these findings are consistent with Pmax representing a simplifying strategy. Additionally, as discussed below in the comparison of choice models, these choices were also inconsistent with compensatory models like expected utility and cumulative prospect theory.

In summary, we show a consistent strong bias towards probability-maximizing choices across two independent experiments. Within participants, we demonstrate that this bias is indeed related to the overall probability of winning and that it can be attenuated or exaggerated by subtle manipulations in decision context. Across participants, we show that differences in decision strategies can be explained by individual variability in trait measures like satisficing. Taken together, these strategy-trait relationships suggest that the robust individual differences in these risky choice paradigms (and, presumably, other settings) may reflect measurable cognitive or affective differences across individuals. This bias towards probability-maximizing choices is also consistent with a recent dual-criterion model for risky choice (Diecidue and van de Ven, 2008), in which an overall probability criterion can be traded off against other decision variables.

2.3 Evaluations of Consistency with Economic Models

Given the overall bias towards the probability-maximizing strategy in the previous experiments, we next sought to explicitly evaluate whether choices associated

with this response strategy were consistent with traditional economic models such as Expected Utility (EU) maximization and Cumulative Prospect theory (CPT). For this test, we used data from 72 trials of the value allocation task, collected during an fMRI study with 23 participants (the neural data and details about the gambles are discussed in greater detail in the next chapter). Unlike the two behavioral experiments, the fMRI experiment used an incentive-compatible payment method such that participants were provided an initial unknown but fixed endowment and were later paid for a subset of their improved gambles, selected randomly. Despite the large number of trials and incentive-compatible nature, we still found a strong bias for Pmax option with participants choosing this option in about 70% of the trials when expected value was balanced.

Our model comparisons used both standard and free parameters for the EU and CPT models. All gambles used in this study were of the form $G = [x_1,p_1; x_2,p_2; x_3,p_3; x_4,p_4; x_5,p_5]$. The **expected utility** (**EU**) of each gamble is given by:

$$EU = \sum_{i=1}^{5} u(x_i)\, p_i, \text{ where } u(x_i) = \begin{Bmatrix} x_i^{\beta}, x_i \geq 0 \\ -|x_i|^{1+(1-\beta)}, x_i < 0 \end{Bmatrix}.$$

The **cumulative prospect theory** (**CPT**) predictions were obtained using:

$$CPT = \sum_{i=1}^{5} v(x_i)c(i) \text{ where } v(x_i) = \begin{Bmatrix} x_i^{\beta}, x_i \geq 0 \\ -\lambda |x_i|^{\beta}, x_i < 0 \end{Bmatrix},$$

$$c(i) = \left\{ \begin{array}{l} w^+(p_i), i = 1 \\ w^+\left(\sum_{j=1}^{i} p_j\right) - w^+\left(\sum_{j=1}^{i-1} p_j\right),\ i = 2,..,k\ (gains) \\ w^-\left(\sum_{j=i}^{5} p_j\right) - w^-\left(\sum_{j=1+1}^{5} p_j\right),\ i = k+1,..,4\ (losses) \\ w^-(p_i), i = 5 \end{array} \right\},$$

$$w^+(p) = \frac{p^{\gamma^+}}{[p^{\gamma^+} + (1-p)^{\gamma^+}]^{1/\gamma^+}} \text{ and } w^-(p) = \frac{p^{\gamma^-}}{[p^{\gamma^-} + (1-p)^{\gamma^-}]^{1/\gamma^-}}$$

For the first level of model comparisons, we used parameters drawn from the prior literature. The EU model used a concave utility function with $\beta = 0.88$. For the CPT model, we used parameter values of $\gamma^+ = 0.61$, $\gamma^- = 0.69$ and $\lambda = 2.25$ (Tversky and Kahneman, 1992; Tversky and Fox, 1995). Despite these standard parameters, neither model was a good predictor of participants' aggregate choices. As one example, consider a trial on which a participant chooses whether to add a fixed amount of money either to a large negative outcome (e.g., -$75) or to a middle outcome of $0, each of which is equally likely to occur. Both EU and CPT models predict that participants should always add the money to the large negative outcome (i.e., minimizing the worst loss). However, participants showed an opposite effect, adding money to the middle outcome 68% of the time (i.e., typically making a probability-maximizing choice). This and other observations indicated that participants' behavior in these experiments was inconsistent with standard model predictions.

To account for potential individual differences in model parameter values, we performed a robustness check using a split-sample analysis. We used one half of the choices of each participant to estimate model parameters: for EU, β; and for CPT, β and γ, keeping λ fixed at 2.25. We also simplified the equation for CPT in our estimation by assuming $\gamma^{+} = \gamma^{-}$. We then assessed the performance of the EU and CPT models by estimating the reliability of the fitted model in predicting the other half of that participant's data. We found that parameters estimated from one half of the sample showed poor reliability in predicting choices in the complementary sample (EU: Cronbach α=0.37; CPT: α=0.39). However, the proportion of probability-maximizing choices was much more reliable across the two samples (α=0.78), indicating that participants remained highly consistent in their strategy preference across the experiment **(Figure 2-3)**.

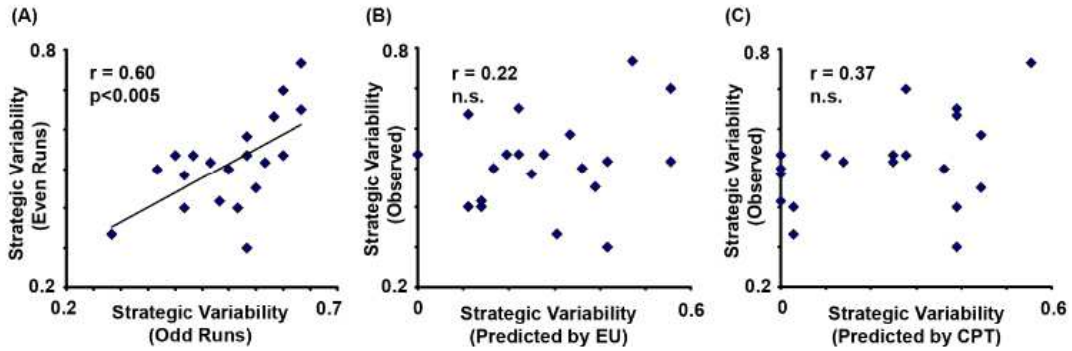

Figure 2-3: Robustness of various models in predicting choices across trials

We stress that these results should not be interpreted to imply that the probability-maximizing strategy provides a new, better, and general model of risky choice behavior.

On the contrary, this particular simplifying strategy only applies to a subset of decision problems – those that involve comparisons between similar gambles that differ in their overall probability of winning – and cannot be used for choice problems that involve only gains or only losses, or that involve constant probability of winning. In such cases, people may use other heuristic strategies such as the Priority heuristic (Brandstatter et al., 2006) that focuses more on the outcomes of the gambles. We do suggest that, under certain contexts, most individuals adopt heuristic decision strategies not encapsulated in standard models (but see Birnbaum, 2008a).

2.4 E3: Eye-tracking Evidence for Multiple Strategies[†]

As discussed in Chapter 1, eye tracking provides a more natural environment for studying decision processes, thereby not hindering automatic processing when required. Fixation durations obtained using eye tracking provide additional insights into underlying cognitive processes: shorter fixations are typically associated with implicit and automatic processing while longer fixations are associated with deeper processing (Glockner and Herbold, 2011). One can also obtain a measure of pupil dilation using eye tracking which in turn provides information about emotional and cognitive processing (Siegle et al., 2003a; Siegle et al., 2003b). For these reasons, we chose to use eye tracking as the primary process tool to understand decision strategies.

In this study, we focused primarily on the following eye-tracking variables: number of data acquisitions (a fixation longer than 60mecs on the same cell was

[†] The contents of this chapter are part of a working paper "Venkatraman V, Payne JW and Huettel SA. Contextual and individual variability in risky choice: eye-tracking evidence for multiple strategies."

considered a data acquisition), duration of time spent on each of the decision variables, and the sequence of information acquisition for each trial. To account for differences in response times across trials and individuals, we normalized the amount of time spent on each of the cells by the response time for that trial. Therefore, our normalized gaze duration measure represents the proportion of time participant spent on a particular cell, relative to the others within a trial.

Participants and Procedures

A total of thirty six young adults participated in this study. We obtained eye gaze information as participants made a series of choices on value allocation problems of the kind introduced above. All stimuli were created using the Psychophysics toolbox in Matlab and were presented to the participant sitting in front of a Tobii 1750 eyetracker system. We used a dual computer set up where stimulus was presented using Matlab running on one computer while eye gaze information was collected using Tobii's Clearview software running on an independent computer. Time stamp information stored in both programs was then used to synchronize the stimulus presentation with the eye gaze information for subsequent data analysis. Participants used a standard computer keyboard to indicate their responses. We positioned the participants' fingers on the appropriate keys at the beginning of the experiment to minimize eye movements to the key board on every trial. Each experimental session lasted an hour and participants were compensated $10 in exchange for their participation. All participants gave written informed consent as part of the experimental protocol approved by the Institutional Review Board of Duke University.

In the first part of the experiment, participants were presented with a total of thirty-two three-outcome gambles. Each gamble typically consisted of one large gain outcome, one large loss outcome and a third intermediate outcome that was either a small gain, $0 or a small loss. Each outcome was associated with its own probability ranging from 0.15 to 0.4 across trials. On each trial, participants first rated each gamble on a scale of 1 to 5, with 1 corresponding to “least preferred” and 5 corresponding to “most preferred”. Participants could take as long as they needed to rate the gamble. After rating the gamble, participants were presented with a fixed amount of money that they could add to any one of the three outcomes to improve the gamble. In other words, on each trial, participants could choose to increase the magnitude of the highest gain (gain-maximizing, Gmax), decrease the magnitude of the worst loss (loss-minimizing, Lmin) or improve the overall probability of winning money compared to losing money (probability-of-winning maximizing, Pmax).

During the decision phase, the resulting three modified gambles were displayed in the form of a 4x4 grid matrix, where the first row corresponded to the probabilities and the remaining three rows correspond to the three modified gambles, labeled G1, G2 and G3 **(Figure 2-4)**. For each trial, the mapping of these labels to Gmax, Pmax and Lmin choices was performed in a pseudo-random manner. However, the three outcomes were always presented in a rank-ordered manner with the first column representing gains and last column representing losses. Participants indicated their response by pressing the keys corresponding to their preferred choice. There were no time constraints for indicating their choice, and no feedback was provided at the end of each trial.

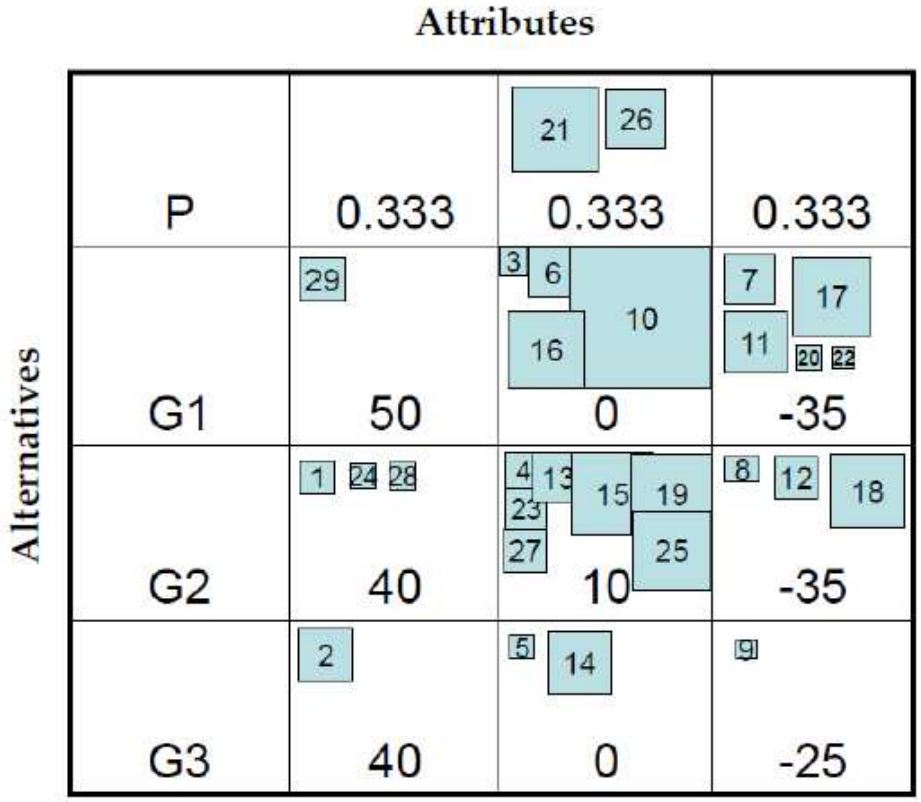

Figure 2-4: Schematic of stimuli and sample of eye-gaze movements (box numbers represent sequence and size represents normalized gaze duration).

Experimental Stimuli

The first two trials were kept constant across all participants. These problems were essentially practice trials that allowed the participants to familiarize with the decision environment and were excluded from all subsequent analyses. The remaining thirty trials were randomized across participants. These trials fell into the following five categories:

- Twelve gambles, where all three outcomes were associated with the same probability (Equal expected value).

- Six gambles, where probabilities differed across the different outcomes, leading to differences in expected value (Unequal EV). The intermediate outcome was always associated with a lower EV, compared to the other two alternatives.
- Eight Pmax-unavailable gambles, where the adding money to the intermediate option did not change the overall probability of winning. Four of these trials had equal probabilities across all attributes, whereas the remaining four had unequal probabilities.
- Four Pmax-exaggerated trials, which were obtained by first translating the initial gamble by adding or subtracting a fixed amount to each of the outcomes. Since there were very few of these trials for full analysis, they are not discussed further here.

Since the natural reading order is from left-to-right, we randomized the format in which gambles were presented between participants. For one half of the participants, stimuli were presented in a horizontal format where rows (alternatives) represent the gambles and columns (attributes) the probabilities. For the other half, stimuli were presented in a vertical format where gambles were represented along columns and probabilities along the rows. Finally, to prevent fatigue-related effects towards the end of the experiments, participants were provided with an option to take a break after completing half of the trials.

Analysis

We had two primary objectives in this study. First, we sought to evaluate the performance of several popular models of risky choice like CPT and PH in predicting choice preferences and process measures in the value allocation task. Second, we sought to dissociate between the use of single or multiple strategies in risky choice.

For each eye-tracking variable, we ran individual GLM analyses for each of our variables of interest. On each trial, participants were presented with a 4x4 matrix of information. We restrict most of our analyses to the three unique cells (cell C_{win} which contains the highest gain outcome, C_{inter} which contains the highest intermediate outcome and C_{loss} which contains the lowest loss). Therefore, we analyzed the effect of OPtype (Pmax-available and Pmax-unavailable), EVtype (equal probabilities and unequal probabilities), Choice (Gmax, Pmax, Lmin), Strategy Type (Pmax-Preferring or non Pmax-Preferring participants), Presentation format (Horizontal, Vertical) and their interactions on the following factors: Response times, normalized duration on the three unique cells (C_{win}, C_{inter}, C_{loss}), total number of acquisitions and Payne Index (which measures the pattern of transitions).

Hypothesis

Choice Hypothesis

H1a (CPT, PH): Across all trials, participants should show a greater preference for alternatives that improve the extreme gain or extreme loss outcomes. There should be no difference in preferences between Pmax-available and Pmax-unavailable trials.

H1b (Pmax-heuristic): Participants will show a greater preference for Pmax alternative for trials where the option is available. But their preference should shift to other alternatives in the Pmax-unavailable trials.

Response Time Hypothesis

H2a (PH): Since the number of reasons to be considered does not change across trials (there is always an option in our stimuli that is significantly better on the worst loss outcome), the response times should be similar across all trials.

H2b (CPT): Since participants are employing the same computations in all cases, the response times should be same across all trials.

H2c (Pmax): Participants should be faster in the Pmax-available trials since they can easily apply the heuristic compared to Pmax-unavailable trials. Decisions should also be faster in the Equal EV trials compared to Unequal EV due to reduced conflict between multiple strategies. Finally, participants should be faster when choosing the Pmax alternative relative to other choices, consistent with a heuristic strategy.

Information Processing Hypothesis

H3a (PH): The total amount of information inspected should be similar across all trial types for the same reasons discussed under response times. Within each trial, the fixations are biased towards the loss attributes.

H3b (CPT): The total amount of information inspected should be similar across all trial types and the fixations should be distributed across all cells.

H3c (Pmax): The amount of information inspected changes as a function of trial types. Participants process more information in the Pmax-unavailable trials.

Participants process more information for the equal EV trials, particularly relying more on probability information in these trials. Finally, the total proportion of time spent on each cell will be correlated with the final choices.

Sequence of Processing

H4a (PH): Information processing is mainly attribute-based. Participants use a reasoning rule and choose the gamble that is better in terms of that rule. Processing does not vary as a function of trial types.

H4b (CPT): Information processing is mainly alternative-based. Since participants are trying to estimate weighted additive information about each gamble, transitions are mostly within alternatives. Processing does not vary as a function of trial types.

H4c (Pmax): Information processing is mainly alternative-based. Participants are trying to determine the probabilities of all the good and bad outcomes before choosing the alternative with the best chance of good outcomes. For Pmax-unavailable trials, since this rule does not distinguish between the gambles, additional information is acquired using other strategies.

Single vs. Multiple Strategy

H5a (Single): Under the single strategy view, participants should acquire all problems in a similar manner and choose based on computational differences. Therefore, we should see no significant differences in eye tracking measures when participants shift from preference for one alternative to another across trials.

H5b (Multiple): There would be a significant cost associated with shifting away from a preferred strategy across trials. Such a cost will be present in terms of response times and amount of information acquisition.

Pattern Changes across Time

H6a (PH): Participants will start with an initial screening and continue with a more thorough inspection of information.

H6b (CPT): Participants will make decisions based on a thorough inspection of all information provided in a systematic manner.

H6c (Pmax): Participants will make decisions based on an initial screening of key cells followed by increased processing of additional information as a function of problem type. Therefore we should see a shift from short to long fixations across the course of each trial.

Results

Choice Data and Response Times

Table 2-1: Choice proportions varied as a function of experimental conditions.

Condition Type	Pmax_Available		Pmax_Unavailable	
	Equal EV	Unequal EV	Equal EV	Unequal EV
Proportion of Pmax Choices	0.69	0.52	0.41	0.36
Proportion of Lmin Choices	0.23	0.36	0.44	0.44

We found a significant effect of EVtype ($\chi^2 = 12.97$, $p<0.001$) and OPtype ($\chi^2 = 47.65$, $p<0.001$) on choice proportions as well as an EVtype x OPtype interaction ($\chi^2 = 7.81$, $p=0.02$). For the Pmax-available trials, the bias for Pmax choices was greater in the Equal EV trials, but was still the preferred choice even in the Unequal EV trials **(Table 2-1)**. Therefore, like previous experiments, participants preferred the Pmax option, even when it involved sacrificing expected value. There was no significant effect of presentation format on choice preferences. Importantly, the preference to add value to the intermediate outcome was not present in the Pmax-unavailable trials, suggesting that participants were willing to switch to a different strategy based on decision context. In fact, we found a inverted-U shaped preference for the middle outcome as a function of the change in valence, with smallest preference when there is no change in valence and greatest preference for a complete change in valence from a loss to a gain **(Figure 2-5)**. These findings are inconsistent with predictions of CPT and PH, leading us to reject hypothesis H1a in favor of H1b.

We also found significant variability in preference for the Pmax-heuristic across individuals with some participants always preferring to use this heuristic and others almost never **(Figure 2-6)**. To investigate the effects of individual differences further, we split our participants into two groups based on the proportion of Pmax choices in the Pmax-available trials. Participants who preferred the Pmax choices in more than 2/3rd of the trials were classified as Pmax-preferring and the rest as non Pmax-preferring strategy type. Next, we sought to explore the interaction between individual variability (Strategy type) and problem type (EVtype and OPtype) on preference for Pmax-heuristic.

Specifically, under the multiple strategy view, the Pmax-preferring individuals should be more sensitive to OPtype and less sensitive to EVtype. Similarly, the non Pmax-preferring individuals should be more sensitive to EVtype and less sensitive to OPtype. Consistent with these predictions, we found a significant Strategy Type (individual difference) x OPtype (problem type) x EVtype (problem type) interaction **(Table 2-2).**

Table 2-2: Proportion of Pmax choices varied as a function of both individual variability and problem type.

	Pmax_Available		Pmax_Unavailable	
	Equal EV	Unequal EV	Equal EV	Unequal EV
Pmax-Preferring	0.96	0.83	0.56	0.63
Non Pmax-Preferring	0.52	0.31	0.39	0.24

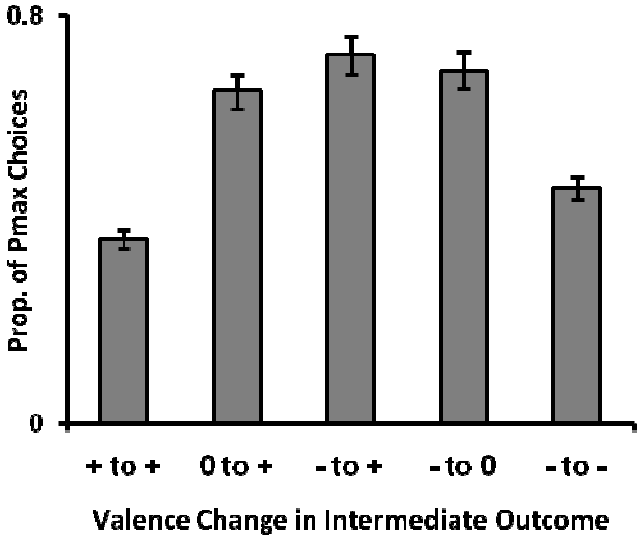

Figure 2-5: Preference for the Pmax-heuristic was modulated by valence changes.

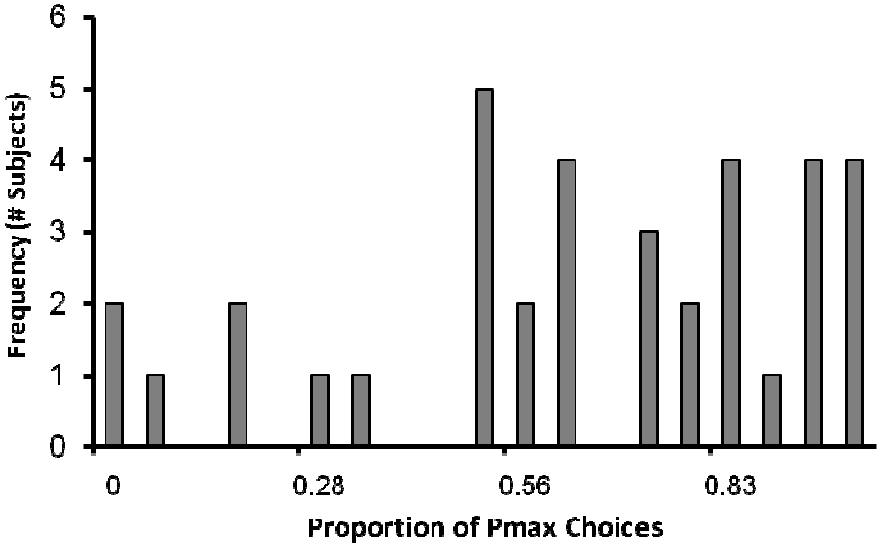

Figure 2-6: Variability in preference for Pmax choices across individuals.

Response Times

The analysis of choice proportions showed evidence for differences in strategy use differences as a function of problem type and individual differences. In terms of response times, we found a main effect of EVtype ($F=6.32$, $p = 0.01$) and OPtype ($F=4.40$, $p = 0.03$). As expected, participants were slower for unequal EV compared to equal EV trials and slower for Pmax-unavailable trials relative to Pmax-available trials **(Figure 2-7)**. Interestingly, we also observed a main effect of Choice on response times ($F=3.06$, $p < 0.05$). Overall, participants were slowest for Pmax relative to Lmin and Gmax choices. There was also a significant OPtype x Choice interaction ($F = 2.93$, $p < 0.05$) with participants being significantly faster for Pmax choices only in the Pmax-available trials **(Figure 2-7)**. Together, these findings are again consistent with hypothesis H2c and inconsistent with hypotheses H2a and H2b.

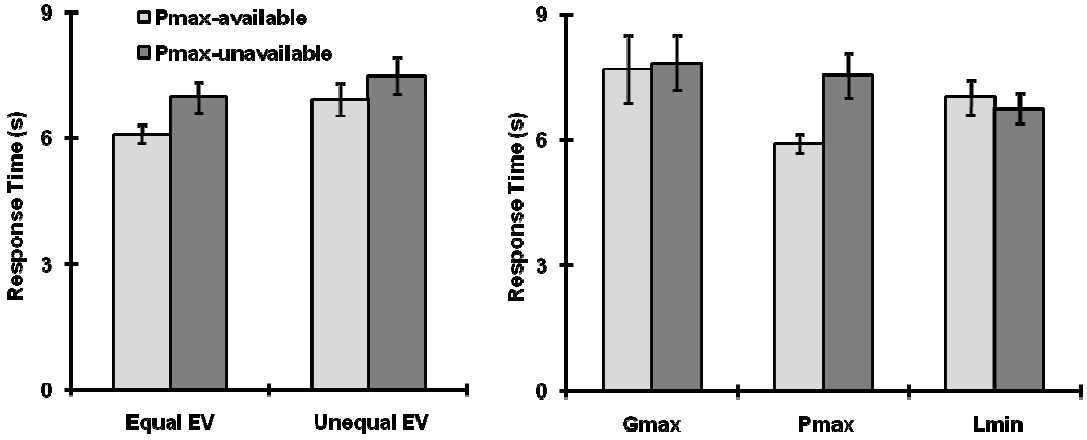

Figure 2-7: Response times showed a significant effect of EVtype, OPtype, Choice and a significant OPtype x Choice interaction.

Measuring Information Acquisitions

Number of Acquisitions: We found a main effect of OPtype on information acquisition: individuals acquired lesser information for the Pmax-available trials compared to Pmax-unavailable, rejecting both hypotheses H3a and H3b **(Table 2-3)**. Pmax choices were also associated with lesser number of acquisitions, particularly for the Pmax-available trials though the interaction was not statistically significant. We did not find any significant interactions of this effect with EVtype.

Table 2-3: Average number of acquisitions varied as a function of choice and OPtype

Choice	**Gmax**	**Pmax**	**Lmin**
# Acquisitions (Pmax-available)	18.13	14.81	16.45
# Acquisitions (Pmax-unavailable)	17.95	18.03	16.71

Normalized Duration: Overall, valid fixations accounted for about 80% of the response times within a given trial. In terms of normalized durations, we found that participants spent very little time processing the probabilities during the decision-making phase, relative to the values (less than 5% of total trial time). This is because the probabilities are introduced in the first stage and do not change subsequently. Yet, there was a significant main effect of EVtype on the gaze duration of probability values, with participants acquiring more information about probabilities in the unequal EV trials relative to equal EV trials.

We also found that choices on each trial were predicted by the magnitude of gaze duration for each of the corresponding unique attributes. In other words, Gmax choices were associated with increased processing of the cell that had the greatest gain value, Lmin choices with the cell that had the lowest loss value and Pmax with the intermediate cell that was different in valence from the other two **(Figure 2-8)**. Not surprisingly, there was in general greater amount of time spent on the intermediate attributes, which could be a function of the fact that these were always in the middle and hence participants had to pass through this column when moving from gains to losses. These findings are inconsistent with PH hypothesis H3a (which states that the loss attributes receive the greatest amount of processing) as well as CPT hypothesis H3b (which states that processing is distributed equally across all cells).

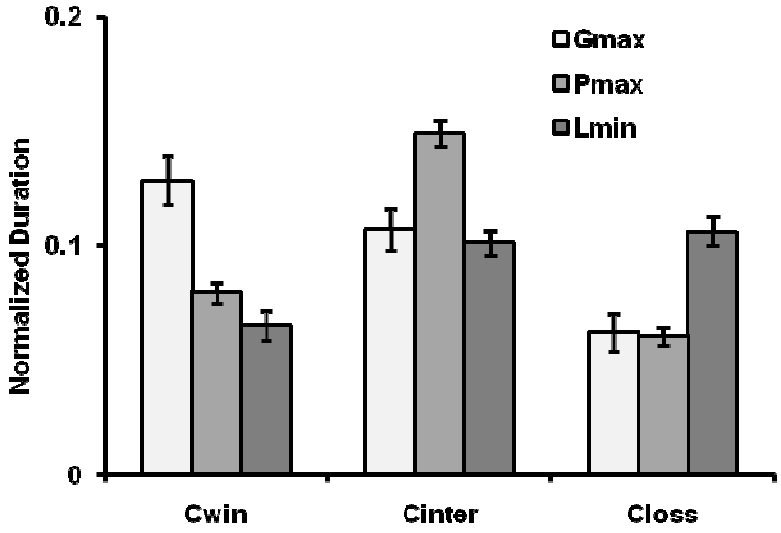

Figure 2-8: Normalized Gaze durations indicated a significant bias in processing for cells that had the most unique information for the final choice.

Sequence of Acquisitions (Payne Index): One of the primary advantages of using eye tracking is that it provides access to the sequence (path) in which information is acquired, in addition to magnitude of processing. We simplified the sequence of acquisitions by estimating the Payne Index, which is defined as the normalized difference between the numbers of alternative- and attribute-based information acquisitions for the nine-payoff cells. A positive value for this index indicates more alternative-based processing and a negative value indicates more attribute-based processing. We found a main effect of OPtype ($F = 6.03$, $p=0.01$) and Choice ($F = 10.99$, $p<0.001$) on the Payne Index. We found that participants make relatively more alternative-based transitions for Pmax-available than Pmax-unavailable trials, as well as when selecting the Pmax option relative to the other choices **(Table 2-4)**. More importantly, we found that an overall estimate of the Payne Index for each participant was significantly correlated with the proportion of

Pmax choices made by that participant (r^2=0.43, p<0.05, **Figure 2-9**). Importantly, this correlation was true only for the Pmax-available trials and not for the Pmax-unavailable trials (r^2=0.3, n.s.). These results suggest that Pmax choices represent some form of a counting strategy, where participants are estimating the probabilities of good relative to bad outcomes in Pmax-available trials. However when such a strategy does not distinguish between the choices, as in the Pmax-unavailable trials, participants shift to other strategies to decide on an alternative.

Table 2-4: Significant effect of OPtype and Choice on Payne Index

Choice	Gmax	Pmax	Lmin
Payne Index (Pmax-available)	0.05	0.22	0.04
Payne Index (Pmax-unavailable)	0.11	0.10	0.05

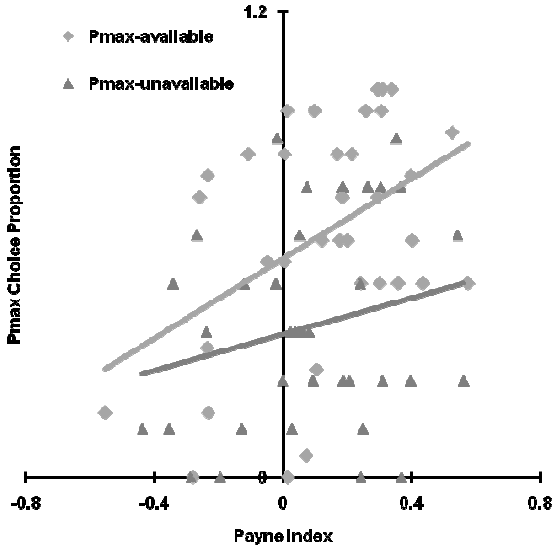

Figure 2-9: Payne Index was significantly correlated with the proportion of Pmax choices across individuals only for the Pmax-available trials.

Due to a strong bias in everyday reading order (left to right), one explanation for the increased alternative-based processing is a bias due to natural reading order. However, to address this concern, we randomized the presentation of gambles between participants with half the participants receiving alternatives along rows and other half along columns. When we analyzed these groups separately, we did find a main effect of presentation format ($F = 83.7$, $o < 0.001$) with participants in the alternatives-along-rows (horizontal) group making more alternative-based transitions **(Table 2-5)**. However, this effect did not interact significantly with choices ($F = 2.1$, n.s.). In other words, independent of presentation format, the Pmax choices were associated with more alternative-based processing than the other choices.

Table 2-5: The presentation format did not interact with Choices.

Pmax-available trials	Gmax	Pmax	Lmin
Payne Index: Horizontal	0.21	0.32	0.20
Payne Index: Vertical	-0.13	0.12	-0.13

Combining choice and information acquisition measures

We performed a stepwise trial-by-trial logistic regression analysis using PROC LOGISTIC in SAS to see if the eye tracking variables improved the prediction of choices on each trial. For this analysis, we tried to predict whether or not the participant made a Pmax choice on a given trial. We assessed the effect of decision context variables like EVtype and OPtype, as well as eye tracking variables like normalized durations of the

three unique cells (C_{win}, C_{inter} and C_{loss}) and the Payne Index on trial-by-trial choices. We found, not surprisingly, that OPtype and EVtype were significant predictors of choice (R^2 = 0.09). When we then introduced the normalized durations into the model, these variables lead to a significant improvement in the model (R^2 = 0.15). Importantly, the relative duration of time spent on the unique intermediate cell (C_{inter}) was a significant predictor of Pmax choices and the unique loss attribute cell (C_{loss}) was a significant negative predictor of Pmax choices. The unique gain cell (C_{win}) did not predict choice, presumably due to the smaller proportion of Gmax choices overall. Finally, when we introduced the Payne Index, the overall model fit improved further (R^2 = 0.18) with the Payne Index also significantly predicting choices. (Note that the results were the same when Payne Index was introduced before the normalized durations.) All results are summarized in **Table 2-6**.

It could be argued that the results above are confounded by correlated data arising from repeated trials within a participant. This prevents the observations from being truly independent, leading to invalid statistical inferences. To address this concern, we repeated the same analysis using PROC GENMOD in SAS which allows for repeated-measures, but not in a stepwise manner. Using this procedure, we still found that all variables that we significant earlier were still significant, validating our findings from before.

Table 2-6: Results from stepwise logistic regression of trial-by-trial choice preferences.

	Parameter Estimate	Wald Chi-square	P-value
Participant	-0.008	1.64	0.2
EVtype	-0.25	12.03	0.0005
OPtype	-0.46	36.27	<0.0001
Duration (C_{win})	-1.58	3.06	0.144
Duration (C_{inter})	2.44	13.43	0.0002
Duration (C_{loss})	-3.29	17.25	<0.0001
Payne Index	0.71	18.05	<0.0001

Strategy Type

Here, we sought to explore how differences in strategic preferences across individuals related to process measures obtained from eye tracking. We found a significant Choice x Strategy type interaction on response times ($F = 5.39$, $p=0.02$), number of acquisitions ($F = 6.18$, $p=0.01$), as well as the Payne Index ($F = 17.83$, $p<0.001$, **Table 2-7**). Particularly, the Pmax-preferring participants took longer, and acquired more information when making a non Pmax choice **(Figure 2-10)**. Similarly, the non Pmax-preferring participants took longer, and acquired more information when making Pmax choices. The non Pmax-preferring participants were also more alternative-based when switching to a Pmax choice. Taken together, these findings are inconsistent with the single strategy hypothesis H5a and instead argue for a multiple strategy

viewpoint hypothesis H5b. We also found similar evidence in our neuroscience study using a similar paradigm, with increased activation in the dorsomedial prefrontal cortex region of the brain when individuals switched away from their preferred strategy (Venkatraman et al., 2009b). We will return to the implications of these findings for strategy selection in the later chapters when talking about neural data.

Table 2-7: Significant Choice x Strategy Type interaction on response times, number of acquisitions and Payne Index

All Trials	**Pmax-preferring**		**Non Pmax-preferring**	
	Pmax	**Non Pmax**	**Pmax**	**Non Pmax**
Number of acquisitions	15.1	20.87	16.39	15.11
Response Times (s)	5.97	8.29	6.83	6.42
Payne Index	0.17	0.20	0.23	-0.01

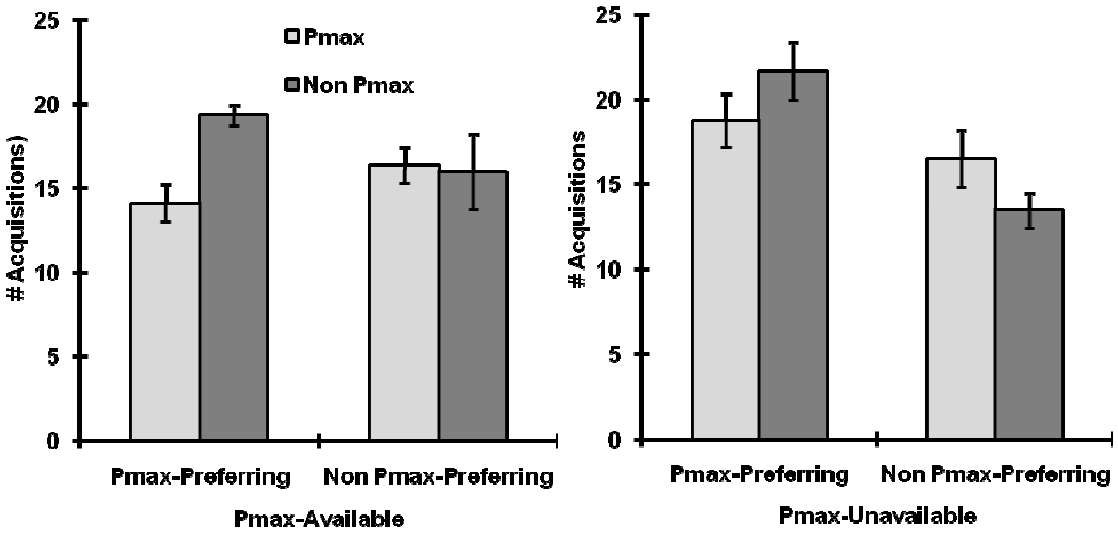

Figure 2-10: Individuals demonstrated a greater cost for moving away from a preferred strategy on a particular trial.

Acquisition Patterns across Time within and across trials

To explore how eye-tracking variables change as a function of time within each trial, we divided each trial into four phases based on the total number of fixations for that trial. We restricted our analyses to Pmax-available trials only. One conjecture is that participants employ a more exploratory strategy at the beginning of the trial and a more accumulative or analytic strategy towards the end. As expected, we found that the dwell times increased during the course of the trial, consistent with hypotheses H6a and H6c and inconsistent with CPT hypothesis H6b. In other words, the average duration of each fixation was greater during the later part of each trial, consistent with a shift from exploratory information gathering phase (shorter duration) to an information processing and analysis phase. Both the priority heuristic and Pmax-heuristic predict such a pattern of information acquisition. We also observed that participants shifted towards more alternative-based processing later in the trial **(Table 2-8)**, again consistent with the overall probability focused strategy. Note however that this later result is inconsistent with PH hypothesis H6a, which suggests that individuals should still process information based on attributes.

Table 2-8: Dwell times indicated a shift from exploratory to deliberative processing

Bin	Q1	Q2	Q3	Q4
Dwell Time (msec)	279	293	304	371
Payne Index	0.03	0.14	0.21	0.30

2.5 E4: Replication of Eye-tracking Results

A total of fifteen young adults participated in this study. Most experimental procedures were similar to experiment 3 (E3). The key change from the first experiment was that the columns were no longer rank-ordered. Instead, the locations of gain, loss and intermediate outcomes were randomized across trials in addition to randomizing the alternatives. Therefore, there were a total of pre-determined nine orders in which the three three-outcome gambles were presented to each participant across trials. This explicitly avoids the attentional bias to the intermediate outcomes by virtue of them always being in the middle column. The number of problems in each category was also slightly varied (ten equal EV Pmax-available trials, 12 unequal EV Pmax-unavailable trials, 4 Equal Pmax-unavailable trials and 4 unequal EV Pmax-unavailable trials).

We were primarily interested in investigating the effect of complete randomization on the amount of processing for each of the three unique cells. Specifically for this replication, we hypothesized that there will no longer be a bias on the intermediate cells for trials where participants were not making the Pmax choices. We also sought to replicate the effects of trial-by-trial logistic regression analyses, to confirm that eye-tracking variables do indeed improve the overall model prediction.

Results

Behavior in this experiment was consistent with previous findings with individuals showing a strong bias for Pmax choices (53% overall; 67% for equal EV and 40% for unequal) in the Pmax-available trials, followed by Gmax (24%) and Lmin (23%). We found a stronger preference for Gmax choices in this experiment relative to

E3. Like E3, we found that choices on each trial were correlated with the magnitude of gaze duration for each of the corresponding unique attributes. In other words, Gmax choices were associated with increased processing of the cell that had the greatest gain value, Lmin choices with the cell that had the lowest loss value and Pmax with the intermediate cell that was different in valence from the other two **(Figure 2-11)**. However, as hypothesized, there was no longer a greater bias for the intermediate outcome.

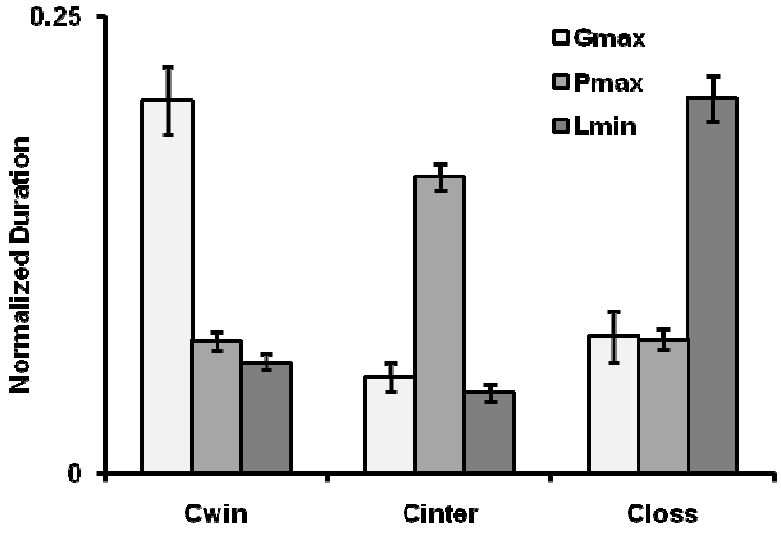

Figure 2-11: Normalized gaze durations indicated a significant bias in processing for cells associated with the final choice.

We also performed a stepwise trial-by-trial logistic regression analysis, similar to E1. We sought to predict whether or not the participant made a Pmax choice on a given trial. We assessed the effect of decision context variables like EVtype and OPtype, as well as eye-tracking variables like normalized durations of the three unique cells (C_{win}, C_{inter} and C_{loss}) and the Payne Index on trial-by-trial choices, controlling for repeated-

measures across participants. Consistent with E1, we found that OPtype and EVtype were significant predictors of choice ($R^2 = 0.13$). When we then introduced the normalized durations into the model, these variables lead to a significant improvement in the model ($R^2 = 0.37$). Importantly, duration of processing on C_{inter} was a significant predictor of Pmax choices, while duration on cells C_{win} and C_{loss} were significant negative predictors of Pmax choices. Note that the unique gain cell C_{win} was also a significant predictor in this experiment unlike E1, possibly due to an increase in Gmax choices in this group of individuals. Finally, when we introduced the Payne Index, the overall model fit improved further ($R^2 = 0.39$) with the Payne Index also significantly predicting choices. (Note that the results were the same when Payne Index was introduced before the normalized durations.) All results are summarized in **Table 2-9**.

Table 2-9: Result summary from stepwise logistic regression for E4

	Parameter Estimate	**Wald Chi-square**	**P-value**
Participant	0.02	6.02	0.01
EVtype	-0.58	26.09	<0.0001
OPtype	-0.27	4.61	0.03
Duration (C_{win})	-3.06	10.18	0.001
Duration (C_{inter})	7.04	32.01	<0.0001
Duration (C_{loss})	-2.55	8.50	0.003
Payne Index	0.75	10.29	0.001

2.6 General Discussion

Using choice proportions, response times and process measures obtained using eye tracking, we demonstrate that individuals shift between multiple strategies as a function of decision context and individual variability. We also showed that the process information obtained using eye tracking helped significantly improve choice predictions on a trial-by-trial level, over and above what was predicted by simple problem characteristics. These results also replicated in a second independent experiment. We reconcile these results with earlier findings from neuroscience and discuss the implications of these findings for models of risky choice and strategy selection below.

Validity of Risky Choice Models in Value Allocation Task

The bulk of experimental work on decision making under risk has been concerned with the relative descriptive fit of a single model of strategy for decision making like the classic expected utility maximization model along with measurement of individual difference parameters like the degree of risk aversion. A common view underlying many studies of individual differences is captured by Birnbaum's argument that the principle "that every individual is represented by the same model in which different people can have different parameters in that model" (p. 497) should be retained for risky decisions until researchers have a clear reason to abandon it (Birnbaum, 2008a).

Several models have been proposed for risky choice, including the compensatory ones like EU, CPT and TAX and non-compensatory ones like PH. Yet, there is still considerable controversy over the suitability of any of these models in explaining process measures in risky choice. For instance, Glockner and Betsch (2008) demonstrate using

information-search paradigms that choices in their study support weighted compensatory models like CPT, and are largely inconsistent with predictions of PH. In contrast, Birnbaum and colleagues demonstrate choices that violate both PH and CPT (Birnbaum, 2008b) and argue in favor of TAX. Similarly, Payne (2005) demonstrates systematic violations of the predictions of CPT and EU using multi-outcome mixed gambles. Even in instances where choices are consistent with compensatory strategies like CPT, process data corroborates the assumption that people may not apply them by deliberately calculating weighted sums (Glockner and Herbold, 2011).

Choice data using the value allocation task in our studies was largely inconsistent with the predictions of EU, CPT and PH. Neither of these models predicts the large amount of emphasis paid to the intermediate outcome in the Pmax-available trials. Similarly, all these models should be unaffected by the subtle changes made to the intermediate outcomes in the Pmax-unavailable trials. Yet, our data indicates a huge bias towards Pmax choices in Pmax-available trials that is not present in the Pmax-unavailable trials. We also demonstrate variability across individuals in the extent of the bias. Though the variability across individuals could be accounted for by parameter changes to the models, the shift between Pmax-available and Pmax-unavailable trials cannot. Our process data, including response times and information search measures, corroborate our choice data about the validity of these models in this particular task.

Therefore, the validity of any descriptive model of decision behavior may depend on the class of problems to which it is applied; and different models may be more or less successful only in certain scenarios (Loomes, 2010). We go further and argue that these

different models represent different strategies available to people and they adaptively select between these and other heuristic strategies based on appropriate interactions between task context and individual traits. One again, we emphasize that the Pmax-heuristic cannot be viewed as a general process model for risky choice, but rather just one of the processing strategies that might be used to solve a complex risky choice problem.

Comparison to Single Strategy based on Parallel Constraint Satisfaction (PCS) Models

Another class of compensatory models that has been discussed extensively in recent times is a network-mode based PCS model. We discuss these models separately because of recent eye-tracking evidence for compensatory strategies based on automatic processing that is consistent with these models (Glockner and Herbold, 2011). In their study, Glockner and Herbold made explicit hypotheses about eye-tracking data that would be consistent with PCS models. We used data from E1 to validate those hypotheses. Glockner and Herbold argued that:

H1b: Choices should follow a compensatory integration of subjective utilities

H4c: In the entire decision process, information search is mainly based on screening

H6d: Fixations are concentrated on the outcomes of the favored gambles and on the most attractive outcomes.

Our behavioral data provide evidence against hypothesis H1b. Under any compensatory integration strategy, a small difference in the magnitude of intermediate outcomes between Pmax-available and Pmax-unavailable trials should not lead to changes in choice preferences. Similarly, increasing dwell times (fixation durations) during the course of the trial indicates that screening is not the main basis of information

search, rejecting hypothesis H4c. Our data though are consistent with hypothesis H6d, with fixations being concentrated on the unique outcomes for alternatives that were subsequently selected. Yet, the inability to validate the other two hypotheses suggests that the PCS model cannot always explain decision processes in the value allocation task here. These data therefore argue against their push for a single strategy view for decision preferences and instead support the use of multiple strategies in risky choice.

Clarifying the neural mechanisms that support such strategies will be the focus of the next chapter. Specifically, we sought to elucidate the mechanisms underlying different choice preferences and strategic variability across individuals using fMRI. Consistent with the multiple strategy perspective, we were also interested in identifying brain region(s) that play a key role in facilitating strategy switching, as a function of task and individual variability.

3 Neural Correlates of Choice and Strategic Variability in Risky Choice[†]

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 PFC 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 (Paulus et al., 2001; Sanfey et al., 2003b; Barraclough et al., 2004; Huettel et al., 2005a). 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 (Sanfey et al., 2003b; Kuhnen and

[†] The contents of this chapter have been published as "Venkatraman V, Payne JW, Bettman JR, Luce MF, Huettel SA (2009) Separate neural mechanisms underlie choices and strategic preferences in risky decision making. Neuron 62:593-602."

Knutson, 2005; Loewenstein et al., 2008). 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 (Tversky and Kahneman, 1974; Payne et al., 1988; Payne et al., 1992b; Gigerenzer and Goldstein, 1996; Kahneman and Frederick, 2002; Camerer, 2003b). 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 de-emphasizes 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 each may be adopted based on the context and computational demands of the task (Payne et al., 1993; Gigerenzer and Goldstein, 1996). 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 intra-individual 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.

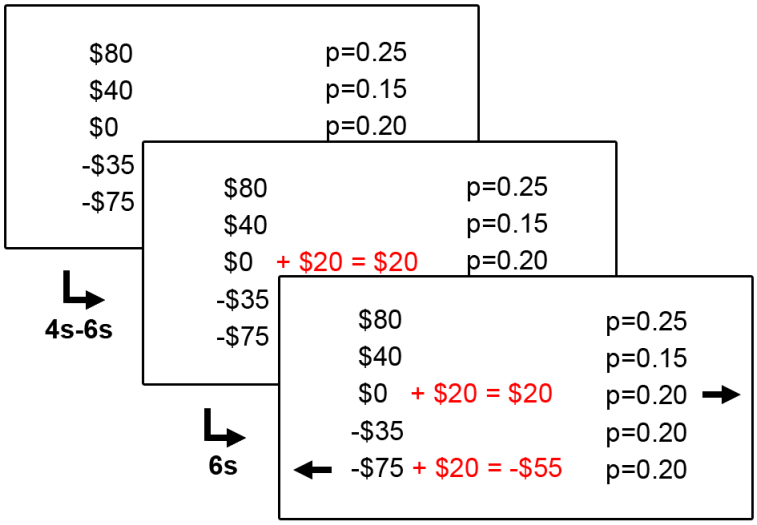

Figure 3-1: Schematic of the fMRI value allocation task.

We used an incentive-compatible value allocation task similar to the one introduced in earlier chapter that contained economic gambles with five rank-ordered outcomes, ranging from large monetary losses to large monetary gains (**Figure 3-1**). There were three types of choices: gain-maximizing, loss-minimizing or probability-maximizing. Making a gain-maximizing (Gmax) choice increased the magnitude of the largest monetary gain (i.e., the most money that could be won), whereas making a loss-minimizing (Lmin) choice reduced the magnitude of the largest monetary loss (i.e., the most money that could be lost). The gambles in this study were constructed so that these two choices (Gmax and Lmin) were generally consistent with a compensatory strategy, such as following expected utility and/or rank-dependent expectation models like

cumulative prospect theory (Tversky and Kahneman, 1992; Payne, 2005; Birnbaum, 2008a). On the other hand, making a probability-maximizing (Pmax) 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 participants' strategic preferences according to their relative proportion of simplifying (Pmax) versus compensatory (Gmax and Lmin) 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 (Sanfey et al., 2003b; De Martino et al., 2006), we characterized brain regions as choice-related if the magnitude of their activation predicted a specific behavior (e.g., select the option providing the largest gain) throughout our participant 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 two strategies 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, 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 (Kennerley et al., 2006; Behrens et al., 2007).

3.1 Experimental Methods

Twenty-three healthy, neurologically normal young-adult volunteers (13 female; age range: 18-31y; mean age: 24y) participated in the fMRI session. All participants gave written informed consent as part of protocols approved by the Institutional Review Boards of Duke University and Duke University Medical Center. All participants 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 participants were excluded from some analyses involving strategy effects due to lack of variability in their response (two participants always chose the Pmax option while the third participant never chose the Pmax option), leaving a total of 20 participants in the complete analyses of the decision-making trials. One additional participant 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, participants were provided detailed instructions about the payment procedures. 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. Participants 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 participants expressed that they understood and believed in the procedures.

Experimental Stimuli. All participants 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; an intermediate outcome of $35 to $50), two negative outcomes (an extreme outcome of -$65 to -$85; 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 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.

On each trial, participants 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 *probability-maximizing* (Pmax) 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 gain-maximizing (Gmax) and loss-minimizing (Lmin) choices respectively. The amount of money that participants 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. Only trial types that placed the two choices in maximal conflict (72 gambles per participant) 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 6s (**Figure 3-1**). Participants were instructed to examine each gamble as it was presented. Subsequently, participants 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 6s, whereupon two arrows appeared to specify which button corresponded to which choice. The association of the buttons to choice was random. Participants 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). Participants were instructed to arrive at their decision during the 6s 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 inter-trial interval of 4-8 seconds, 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.

Participants participated in six runs of this decision task, each containing 20 gambles and lasting approximately 6 minutes. Before those runs, participants 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 participants via MR-compatible LCD goggles. Participants responded with the index fingers of each hand via a MR-compatible response box.

Following completion of the decision phase, there was a final 6-minute 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 participant's choices. On each trial, participants passively viewed one of these improved gambles on the screen for 2s (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 1s, followed by an inter-trial fixation period of 3-7s 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 parameters: TR = 2000ms; TE = 30ms; 34 axial slices parallel to the AC-PC plane, with voxel size of 3.75*3.75*3.8mm. High resolution 3D full-brain SPGR anatomical images were acquired and used for normalizing and co-registering individual participants' data.

Analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.63, part of FSL (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 8mm, 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 (Gmax and Lmin were combined for additional power) and simplifying Pmax 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 participant responses. (An additional post-hoc analysis on a subset of fifteen participants separated the magnitude-sensitive choices according to whether they were gain-maximizing or loss-minimizing.) Analysis for the outcome phase consisted of three regressors: one to model the anticipation phase (as

participants 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 participant was carried out using a fixed-effects model across runs. Random-effects across-participants analyses were carried out using FLAME (stage 1 only). When evaluating the effects of behavioral traits (transformed into z-scores) upon brain function, we included our participants' trait measures as additional covariates in the third-level analysis.

Logistic Regression Models of Trial-to-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 regions-of-interest (ROI) were defined. We used seven different ROIs for this analysis: the right anterior insula and ventromedial prefrontal cortex, which show greater activation for Lmin and Gmax choices respectively; the right posterior parietal cortex, the right precuneus, and right dorsolateral prefrontal cortex, which show greater activation for Pmax choices; and finally the dorsomedial prefrontal cortex and right inferior frontal gyrus, which track strategic variability across participants. 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 6s time-interval from 4s to 10s after the onset of decision phase (i.e., when participants 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 participants on each individual trial based on strategic preference (proportion of Pmax choices), brain activation, and interactions between trait and activation. The complete model included a total of 1440 trials (72 trials for each of 20 participants). 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.

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 participants. For each run for each participant, 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 4s-10s after the onset of the 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 indicate that the region correlates more positively with the seed region during the experimental condition of interest.

3.2 Results

Consistent with our two behavioral experiments, participants made Pmax choices on approximately 70% of the trials when the choices were matched for expected value. Moreover, the proportion of Pmax choices was systematically modulated by the tradeoff in expected value between the choices, indicating that participants were not simply insensitive to expected value (**Appendix Table A-1**). Finally, the proportion of Pmax choices decreased with increasing self-reported tendency to maximize (r = -0.67, p < 0.001).

Neural Predictors of Choices. Our initial analyses identified brain regions whose activation was driven, across participants and trials, by the selected choice. There was greater activation in anterior insular cortex (aINS) and ventromedial prefrontal cortex (vmPFC; **Figure 3-2A**) for the compensatory magnitude-sensitive choices (combined across Gmax and Lmin). 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., 2000b; Paulus et al., 2003; Sanfey et al., 2003a; Dalgleish, 2004). We subsequently performed a region of interest analysis to explore specifically the differences in activation between Gmax and Lmin. Note that this analysis was restricted, *a priori*, to a subset of fifteen participants with a sufficient number of choices in each condition of interest. We found a clear double dissociation between aINS and vmPFC:

Gmax choices were predicted by greater activation within vmPFC while Lmin choices were predicted by increased activation in aINS (**Figure 3-2B,C**). Conversely, Pmax choices were associated with increased activation in the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC; **Figure 3-2A, Appendix Table A-2**), regions typically associated with executive function and decision making under risk and uncertainty (Paulus et al., 2001; Bunge et al., 2002; Huettel et al., 2005b; Huettel et al., 2006). These regions showed greater activation for Pmax choices compared to both Gmax and Lmin, but no difference between Gmax and Lmin options (**Figure 3-2D**).

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 participant's strategic preference as a normalized regressor into the across-participants fMRI analyses of the contrast between choices. Strategic variability predicted individual differences in activation in two clusters (**Figure 3-3**): the dorsomedial prefrontal cortex (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 Pmax 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).

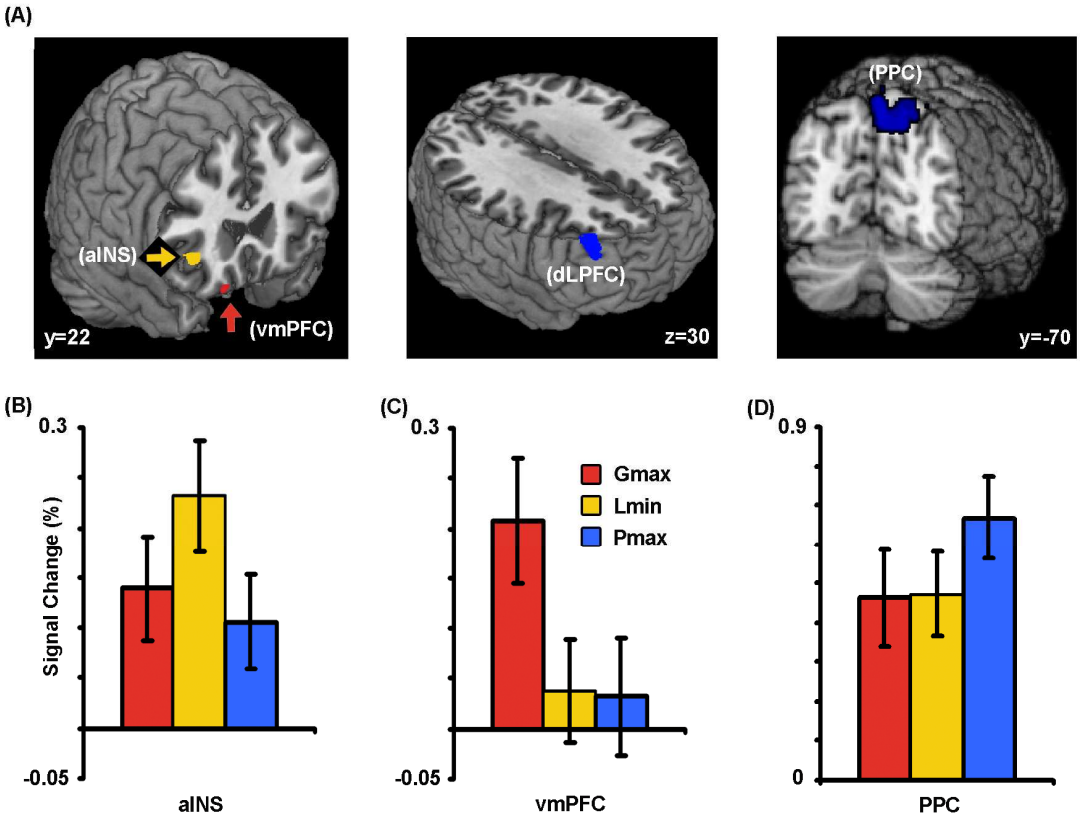

Figure 3-2: Distinct sets of brain regions predicted choices.

We next evaluated whether dmPFC activation might shape activation in those regions that predicted specific choices (i.e., Pmax: dlPFC and PPC; Lmin: aINS and Gmax: 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 upon the choice made by the participant (**Figure 3-4**). When participants made Pmax choices, connectivity with dmPFC increased in dlPFC and PPC, whereas when participants 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 participants (**Appendix Figure A-1**). Finally, we also conducted additional analysis 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).

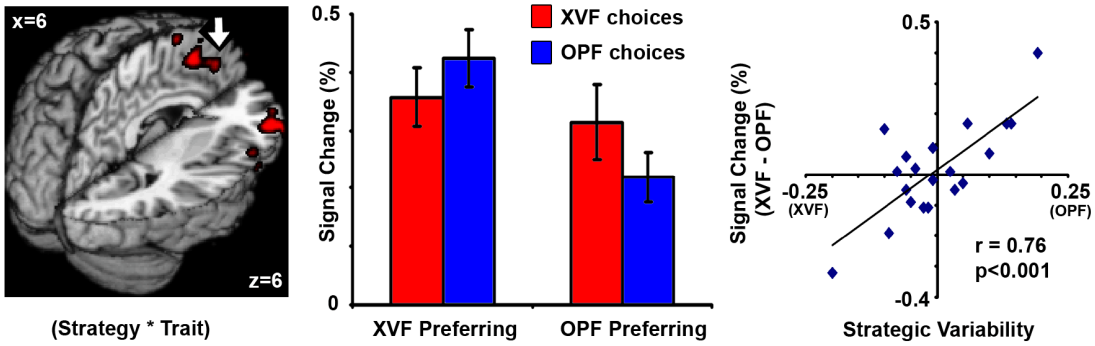

Figure 3-3: Dorsomedial prefrontal cortex predicted strategy use during decision making.

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

Integrating Choices and Strategies to Predict Behavior. We used the brain regions implicated above as choice-related (aINS, vmPFC, dlPFC, PPC) or strategy-related (rIFG, dmPFC) to predict choices on individual trials. We extracted, for every trial for

every participant, the activation amplitude in each of these regions of interest, 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 3-1**).

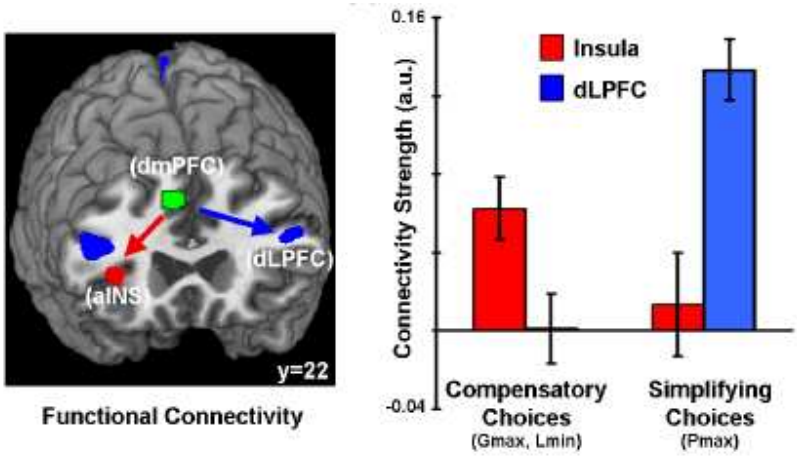

Figure 3-4: DmPFC showed differential functional connectivity with choice-related regions.

We first entered into the model participants' overall preference for the simplifying strategy (proportion of Pmax choices). We found, unsurprisingly, that this was a highly significant predictor of trial-to-trial choices. Next, we used activation values from our brain regions of interest, 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 predictor of Pmax 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 participant's strategy preference, the resulting

variable became a significant and robust predictor of behavior, and overall model error was reduced (**Table 3-1**). Thus, dmPFC activation does not predict either type of choice, but instead predicts choices that are inconsistent with one's preferred decision strategy.

Table 3-1: Results from logistic regression predicted trial-by-trial Pmax choices.

Model Variables	Coefficient (S.E.)	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 Pmax choices	1.02 (.12)	70.79 (.000)		
Brain			**18.05**	**0.017**
Constant	-0.21 (0.06)	13.10 (.000)		
Right Posterior Parietal Cortex	32.41 (8.43)	14.80 (.000)		
Right Anterior Insula	-40.52 (13.28)	9.31 (.002)		
Trait (+ Brain)			**90.26**	**0.081**
Constant	-0.22 (0.06)	13.38 (.000)		
Proportion of Pmax choices	1.00 (0.12)	67.23 (.000)		
Right Posterior Parietal Cortex	30.54 (8.62)	12.56 (.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 Pmax choices	1.10 (0.13)	71.75 (.000)		
Right Posterior Parietal Cortex	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 emphasize that the brain-behavior relations reported here were highly significant even though the behavioral choice data across trials for each participant (a behavioral strategy indictor) 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 participants' 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 participant passively viewed a subset of their improved gambles, which were each resolved to an actual monetary gain or loss. While participants 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; Yacubian et al., 2006; Seymour et al., 2007). Then, when the gamble was resolved, vSTR activation increased to gains but decreased to losses (**Figure 3-5**). 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 Pmax strategy (**Figure 3-5**) and scored low on a behavioral measure of maximizing reward magnitudes **(Appendix Figure A-2)**. These results suggest that the use of a simplifying strategy that

improves one's overall chances of winning (Pmax) may result from increased neural sensitivity to reward outcomes.

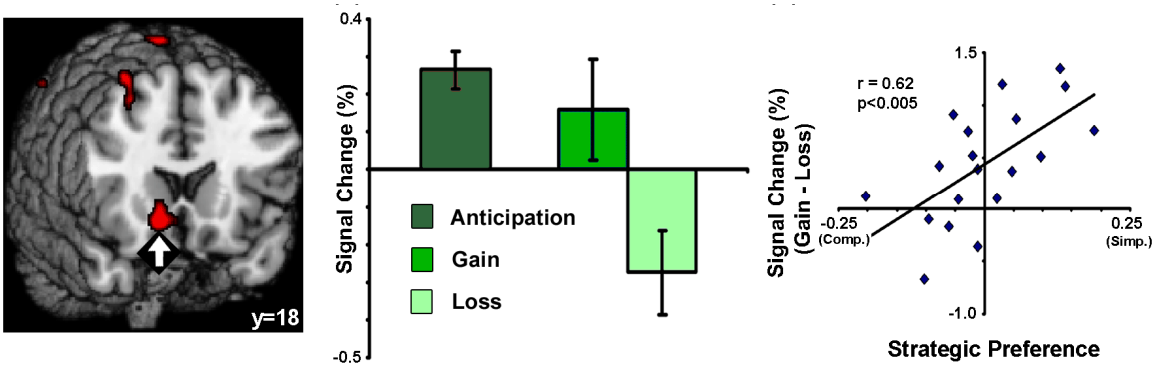

Figure 3-5: Ventral striatal sensitivity to rewards predicted strategic variability.

3.3 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 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; Wu et al., 2007; Preuschoff et al., 2008). 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 such trait differences as a tendency towards satisficing versus maximizing. Our findings, involving a complex risky choice task, across both behavioral and neuroimaging experiments, provide evidence in favor of intra- and inter-participant 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 (Simon, 1957; Shah and Oppenheimer, 2008). Pmax 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 Pmax choices decreased adaptively with increasing cost in terms of expected value in all experiments. We suggest, therefore, that strategic preferences in the current task reflects tradeoffs – resolved differently by individual participants and over trials – between one strategy that simplifies a complex decision problem by using a simple heuristic of maximizing the chances of winning (Pmax) and another, more compensatory strategy that involves consideration of additional information as well as the emotions associated with extreme gains (Gmax) or losses (Lmin).

To the extent that the Pmax 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; Heekeren et al., 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., 2005a). Given that Pmax 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 Gmax and Lmin 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 Gmax choices and activation in aINS predicting Lmin choices. The contributions of vmPFC to gain-seeking behavior (at the expense of potential losses) have been documented in both patient (Bechara et al., 2000a) 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 (Paulus et al., 2003; Kuhnen and Knutson, 2005; 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 participants. 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 participants 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 and colleagues (De Martino et al., 2006), again when participants made decisions counter to their general behavioral tendency (i.e., against typical framing effects). However, it is important to note that all participants in their study exhibited a bias toward using the framing heuristic, while in the current study, participants 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 aINS for simplifying and compensatory choices respectively. These findings are consistent with interpretation that dmPFC shapes 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 (Delgado et al., 2000; Breiter et al., 2001; Seymour et al., 2007) and primate electrophysiology (Schultz et al., 1997). However, we additionally observed the novel 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 Pmax 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 we cannot be certain about 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.

Our results demonstrate that decision making reflects an interaction among brain systems coding for different sorts of computations, with some regions (e.g., aINS, vmPFC) coding for specific behaviors and others (e.g., dmPFC) for preferred strategies. Depending upon the circumstances and state, 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. Sleep deprivation is one such state that has received a lot of interest in recent years, particularly in the realm of decision making. In a follow-up study presented in next chapter, we sought to understand how 24 hours of total sleep deprivation biases economic decision making within the same individual.

4 State Effects on Risky Choice: Sleep Deprivation Biases the Underlying Neural Mechanisms[†]

Many persons living in developed societies sleep inadequately (Institute of Medicine, 2006; Centres for Disease Control, 2009), believing that sustained wakefulness has no untoward effects. Several functional neuroimaging studies have revealed how short-term sleep deprivation (SD) can negatively affect attention (Chee et al., 2008; Tomasi et al., 2009), working memory (Chee and Choo, 2004; Habeck et al., 2004; Mu et al., 2005) and learning (Drummond et al., 2005; Sterpenich et al., 2009). Yet, it remains unclear whether and how SD shapes the very preferences that guide decision-making, independently of these more general effects on cognition.

Behavioral studies suggest that SD-generated impairments in cognition lead to deficits in the overall quality of decision-making (Harrison and Horne, 1999; Linde et al., 1999). More recent studies that involve making decisions under uncertainty have found that sleep-deprived persons tend towards riskier options (Harrison and Horne, 2000; Killgore et al., 2006; McKenna et al., 2007), mirroring the behavior of patients with medial frontal damage (Bechara et al., 2000a). In the sole functional neuroimaging study on risky decision-making with feedback, 24 hours of SD resulted in increased nucleus accumbens activation for anticipated monetary gains, and attenuated insula activation for experienced monetary losses (Venkatraman et al., 2007).

[†] The contents of this chapter have been published as "Venkatraman V, Huettel SA, Chuah YM, Payne JW, Chee MW (2011) Sleep deprivation biases the mechanisms underlying economic decision making, Journal of Neuroscience, 31(10):3712-8."

Here, we sought to study SD-induced changes in risk preferences by using a novel, incentive-compatible, decision-making task (Payne, 2005; Venkatraman et al., 2009b) where participants evaluated a series of complex mixed gambles, each consisting of probabilistic outcomes that spanned monetary losses and gains (**Figure 4-1A).** Volunteers were given an opportunity to improve each gamble by adding money to *one* of the outcomes in one of three ways: increasing the magnitude of the highest gain (Gmax), decreasing the magnitude of the worst loss (Lmin), or by improving the overall probability of winning (Pmax) by adding money to a central reference outcome (Venkatraman et al., 2009b) (**Figure 4-1B**).

To assess changes in risk *preference* in the absence of learning, participants first made their decisions without feedback. Then, to ascertain changes in *response* to reward (or loss), a subset of gambles was resolved for real monetary rewards or losses at the end of the experiment **(Figure 4-1C)**. Separating the decision and outcome phases could be important as sleep deprivation might interact with task context to influence neural responses and behavior. For example, the propensity to take higher risks in a gambling task was found to be modulated by decision frames (McKenna et al., 2007) and task differences may contribute to lowered (Killgore et al., 2008) or increased (Killgore et al., 2006; Venkatraman et al., 2007) risky decisions.

Finally, we evaluated the extent to which sleep deprivation jointly alters sustained attention along with risky decision-making. Although SD may have reproducibly different effects on subjective measures of fatigue, vigilance and other cognitive functions (Van Dongen et al., 2004), decision-making has not been evaluated together

with other cognitive functions in the same experiment. Existing countermeasures against SD have only been shown to consistently benefit vigilant attention (Wesensten et al., 2005; Killgore et al., 2007). If decision-making were to be affected independent of effects on vigilance, prevailing beliefs concerning the generalized utility of existing countermeasures would merit reappraisal.

4.1 Experimental Methods

Twenty-nine healthy young adults (mean age 22.34 years, stdev. 1.23 years, 15 males) participated in this neuroimaging study. All participants provided informed consent, and the study was approved by the Singapore General Hospital Institutional Review Board.

Participants visited the lab three times over 2 weeks. On the first visit, participants provided informed consent and practiced the in-scanner task. At the end of this session, participants were instructed to maintain regular sleeping hours throughout the study duration, verified using wrist actigraphy (Philips Respironics, USA). Participants returned to the lab weekly for two fMRI sessions: a rested-wakefulness (RW) session and a sleep-deprivation (SD) session (order counterbalanced).

Scans at RW took place at 8:00 AM. For the SD session, participants were monitored in the laboratory from 6:00 PM onwards, and scanning took place at 6:00 AM the next day. They were allowed to engage in non-strenuous activities such as reading, watching videos and conversing.

Prior to each scan, participants confirmed that they had not smoked or consumed any medications, stimulants, alcohol or caffeine for at least 24 hours prior to the scan. For

10 minutes every hour from 7:00 PM until 5:00 AM, participants completed the Psychomotor Vigilance Task (Dinges et al., 1997; Doran et al., 2001), an extensively used test of sustained attention.

Within each scanning session, participants performed three different tasks. First, they completed six runs of a risky decision-making task, each run comprising 20 gambles and lasting 6 minutes. Following these decision runs, they completed one run of a Counting Stroop task (data not discussed here). Finally, to evaluate neural sensitivity to rewards, participants watched passively while a subset of modified gambles from the decision runs was resolved to gains and losses during a single outcome run, lasting 7 minutes.

Stimuli were created using the Psychophysics Toolbox for MATLAB (Mathworks, Inc.). At the beginning of the experiment, participants were briefed on the incentive-compatible payment procedure and were told that the study did not involve deception. Two outcomes (one from each session, RW and SD) were randomly selected and scaled for bonus payment (see **Appendix B**). All participants acknowledged their understanding and acceptance of these procedures.

Experimental Tasks and Stimuli. In the risky decision-making task, participants evaluated a series of 120 five-outcome gambles, each of which posed choices that ranged from large monetary losses to large monetary gains **(Figure 4-1A)**. These gambles were identical to the ones used in the fMRI study introduced in Chapter 3.

Each trial began with the display of a five-outcome gamble for 4 or 6 s. Participants were instructed to examine each gamble as it was presented. In the **gain-**

focus (GF) trials, participants could make one of two possible choices: a gain-maximizing (Gmax) choice that involved increasing the magnitude of the highest gain, and a probability-maximizing (Pmax) choice that improved the overall probability of winning money compared to losing money. Conversely, in the **loss-focus (LF) trials**, participants decided between a loss-minimizing (Lmin) choice that involved decreasing the magnitude of the worst loss, and the Pmax choice **(Figure 4-1B)**. The relative change in expected value associated with the two choices was varied across trials.

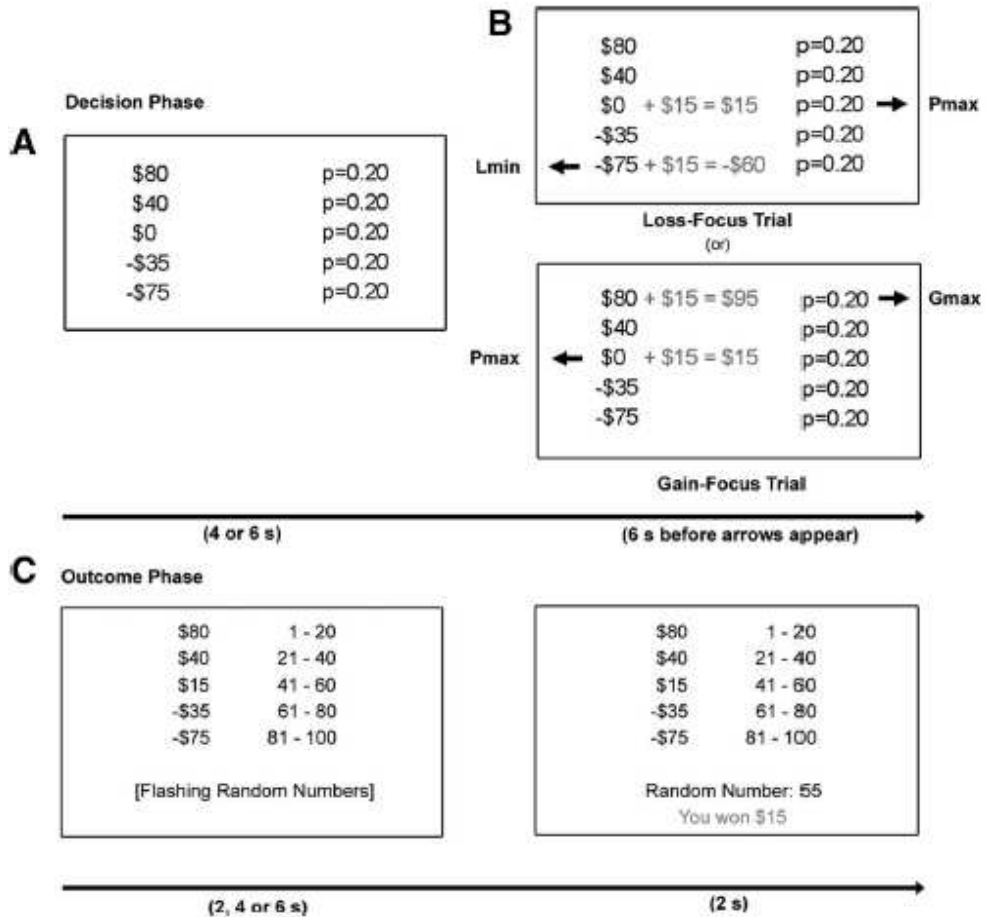

Figure 4-1: Schematic of (A) Experimental Stimuli, (B) Trial types and (C) Outcome phase.

The amount that participants could add to the outcomes ranged between $10 and $25 and could differ between the two outcomes. All outcome values used in this experiment were multiples of $5. Expected values of the two choices were systematically manipulated by changing the amount and/or probabilities associated with each of the options. The amount that could be added and the resulting modified outcome values were displayed in red for both choices, to minimize individual differences that could arise from calculation or estimation biases.

Participants viewed the two options without any response cues for 6 s, whereupon arrows appeared on the screen to indicate which button corresponded to each option. They were instructed to respond as quickly as possible when the arrows appeared. The next trial appeared after a variable inter-trial interval of 4, 6, or 8 s. No feedback was given after each trial, thus precluding any SD-related changes in trial-to-trial learning from influencing behavior.

In the final run, 40 of the gambles from the decision phase were randomly selected and resolved to an actual monetary gain or loss. These gambles were presented in modified form based on the participants' earlier decisions (**Figure 4-1C**). On each trial, participants passively viewed a gamble on the screen for 2-6 s (anticipation phase) while random numbers flashed at the bottom of the screen before stopping at a particular value. The amount won or lost was displayed for 2 s, followed by an inter-trial fixation period of 2, 4 or 6 s before the onset of the next trial.

Participants viewed the stimuli using MR-compatible LCD visual goggles (Resonance Technologies, California) and responded using a button box held in their right hand.

Imaging Procedure. MR imaging was performed using a 3T Siemens Tim Trio system (Siemens, Erlangen). For all runs, a single-shot, gradient-echo EPI sequence was used (TR 2000 ms, TE 30 ms, flip angle 90°, FOV 192 X 192 mm, Matrix 64 X 64). Parallel imaging (GRAPPA) was enabled. 180 volumes were collected in each decision run and 220 in the outcome run. Thirty-six oblique axial slices (3 mm thick with 0.3 mm interslice gap) approximately parallel to the intercommisural plane were acquired. High-resolution coplanar T1 anatomical images were also obtained. For the purpose of image display on Talairach space, 3D high-resolution anatomical reference images were acquired using a T1-weighted MPRAGE sequence.

Data Analysis. The proportions of Gmax or Lmin decisions, relative to Pmax decisions, were computed for the gain-focus and loss-focus trials respectively. Effects of condition, state and their interaction were investigated using a 2 by 2 repeated-measures ANOVA with factors of choice (Gmax, Lmin) and state (RW, SD).

Imaging analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.63, part of the FSL (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 8mm, and high-pass

temporal filtering. Registration to high resolution and standard images was carried out using FLIRT.

Analysis of the decision phase focused on two regressors for each state that modeled the two types of decision trials: gain-focus and loss-focus. We included additional predictors that modeled the initial presentation of the wager as well as the response period (scaled by reaction time). Data from multiple runs collected for each participant were used to generate participant-specific contrast maps using fixed-effects analysis.

Analysis of the outcome phase involved the use of three regressors in each state to model the anticipation phase (as participants were waiting for the corresponding outcome to be revealed), non-negative outcomes (gain and zero gain), and negative outcomes (loss).

Each of the three regressors was generated by convolving the impulse at the onset of events of interest with a double-gamma function. Higher level across-participants statistical maps were generated using FSL's linear analysis of mixed effects (FLAME stage 1 only) tool, using a cluster threshold of $z > 2.3$ and a whole-brain corrected cluster significance threshold of $p < 0.05$. We used two-sample paired t-tests at the higher level FLAME analysis for estimating state effects. Regions of interest (ROI) were functionally defined based on the thresholded statistical maps. The parameter estimates from these ROIs were then correlated with the behavioral measures.

4.2 Results

4.2.1 Behavioral Findings

A 2 (choice: Gmax, Lmin) by 2 (state: RW, SD) repeated-measures ANOVA showed no main effects of state or choice, but a significant state-by-choice interaction ($F(1, 28) = 8.71$, $p < 0.01$). Sleep-deprived participants exhibited an increased tendency to seek gain, as evidenced by an increased proportion of Gmax vs. Pmax choices in gain-focus trials ($t(28) = 2.18$, $p < 0.05$), together with a lower proportion of Lmin vs. Pmax choices in loss-focus trials **(**$t(28) = 2.05$, $p < 0.05$, **Appendix Figure B-1)**. SD also resulted in increased response times during the response phase of the decision-making task ($t(28) = 5.61$, $p < 0.001$). Importantly, participants remained sensitive to the expected-value relationship between the two choices in both states, indicating that SD led to a change in preferences, not a simple increase in decision variability (**Appendix Figure B-2**).

SD also resulted in reduced psychomotor vigilance, a measure of sustained attention, as indexed by increased average response times ($t(28) = 2.7$, $p < 0.05$) and lapses ($t(28) = 3.42$, $p < 0.01$) in the Psychomotor Vigilance Task. Critically, this decline in sustained attention did not correlate with changes in economic preference.

We next estimated a risk parameter (alpha) and loss-aversion parameter (lambda) for each participant in each state. Participants were more risk-seeking following SD ($\alpha_{RW} = 0.95$, $\alpha_{SD} = 1.10$, $t(28) = 2.16$, $p<0.05$), consistent with an increased tendency to chase large gains. Importantly, this parameter was positively correlated with proportion of Gmax choices ($r_{RW} = 0.6$, $r_{SD} = 0.46$) and negatively correlated with proportion of Lmin

choices in both states (r_{RW} = -0.62, r_{SD} = -0.58). There was no significant difference in the loss-aversion parameters across state. Thus, we emphasize that these effects of SD can be considered either as changes in decision parameters or as an overall shift in choice bias (without recourse to any specific model). We note that previous studies using similar multi-attribute risky choice task suggest that using standard decision parameters to predict behavior leads to specific errors; e.g., not accounting for the high proportion of Pmax choices (Payne, 2005; Venkatraman et al., 2009b). Thus, we hereafter use proportions of choices as covariates in subsequent analyses, while noting that these specific effects may be consistent with an overall increase in a risk-seeking parameter.

4.2.2 Neuroimaging Findings: Decision Phase

Across both states, consistent with prior studies of risky decision making (Huettel et al., 2006; Platt and Huettel, 2008; Rangel et al., 2008), we observed task-related increases in bilateral intraparietal sulcus, dorsolateral prefrontal cortex (dlPFC), anterior insula (aINS) and dorsomedial prefrontal cortex (dmPFC) activation **(Appendix Table B-1)**.

After a night of normal sleep, higher activity in the right aINS for loss-focus trials correlated with increased preference for the Lmin option ($r = 0.43$, $p < 0.05$), while increased activity (in this case, reduced deactivation) in the ventromedial prefrontal cortex (vmPFC) for gain-focus trials correlated with an increased proportion of Gmax choices **(**$r = 0.43$, $p < 0.05$, **Appendix Figure B-3).** These findings concur with previous studies associating aINS activation with loss-averse behavior (Paulus et al., 2003; Kuhnen and Knutson, 2005; Venkatraman et al., 2009b) and vmPFC activation with gain-

seeking behavior (Bechara et al., 2000b; Tobler et al., 2007; Venkatraman et al., 2009b). Additionally, we also observed that activation in the vmPFC for gain-focus trials following normal sleep correlated positively with risk parameter α_{RW} ($r = 0.45$, $p < 0.001$) suggesting that our choice-based interpretations would be largely consistent even when using a parametric approach.

Sleep deprivation resulted in reduced activation of bilateral intraparietal sulci, and increased activation in vmPFC **(Figure 4-2A, B)** and right thalamus **(Appendix Table B-2)**. SD-related reduction of task-related parietal cortex activation has been extensively reported (Bell-McGinty et al., 2004; Chee and Chuah, 2007; Chee et al., 2008; Tomasi et al., 2009) and is not discussed further in this manuscript.

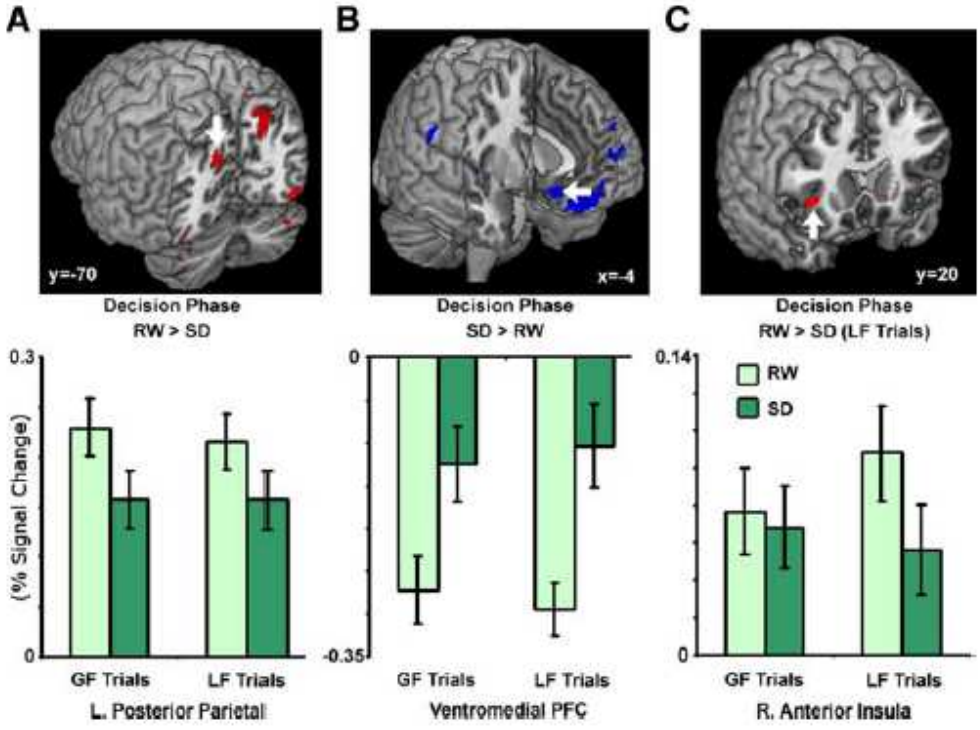

Figure 4-2: Sleep deprivation biased neural systems underlying decision making.

In addition to the main effects described above, sleep deprivation led to reduced activation in the right anterior insula **(Figure 4-2C)** and dorsomedial prefrontal cortex (dmPFC) during loss-focus trials **(Appendix Table B-2)**. Notably, these SD-induced changes in activation correlated with SD-induced changes in behavior. A reduced propensity to make Lmin choices when sleep deprived correlated with reduced right anterior insula activation during these trials ($r = 0.38$, $p < 0.05$ **Figure 4-3A**). There was also a significant negative correlation between state-related changes in the proportion of Lmin choices and changes in vmPFC activation ($r = 0.46$, $p < 0.01$, **Figure 4-3B**), driven possibly by the increased focus on the higher ranked Pmax choices during these trials following SD. The SD-related decrease in activation in the right anterior insula for loss-focus trials correlated positively, across participants, with an increase in activation in the vmPFC for the gain-focus trials ($r = -0.44$, $p < 0.01$, **Figure 4-3C)**. SD did not affect dorsolateral prefrontal cortex (dlPFC) activation, even at an uncorrected threshold of $p < 0.005$.

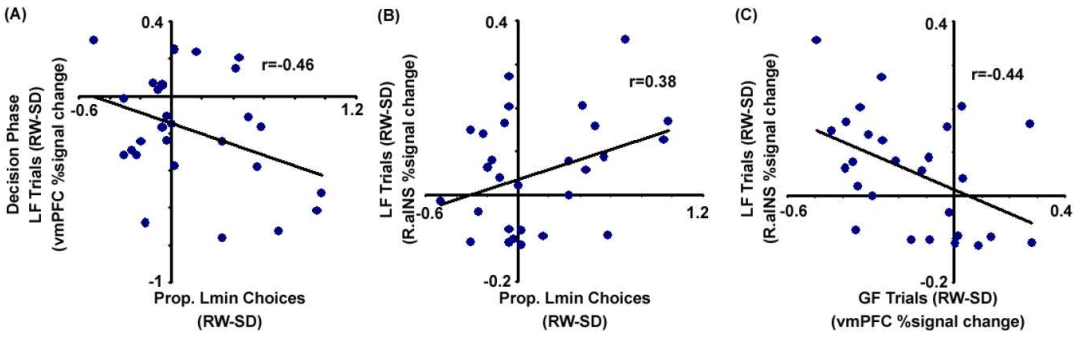

Figure 4-3: Changes in magnitude of activation predicted shifts in preferences following sleep deprivation

4.2.3 Neuroimaging Findings: Outcome Phase

After making a series of decisions about risky gambles, each participant passively viewed a subset of those gambles being resolved to an actual monetary gain or loss. Activity in the ventral striatum (vStr) and ventromedial prefrontal cortex (vmPFC) increased for gains relative to losses across both sessions, consistent with the association of these regions with reward processing (Breiter et al., 2001; Knutson et al., 2003; Seymour et al., 2007). No region showed significantly greater activation for losses over gains in either session.

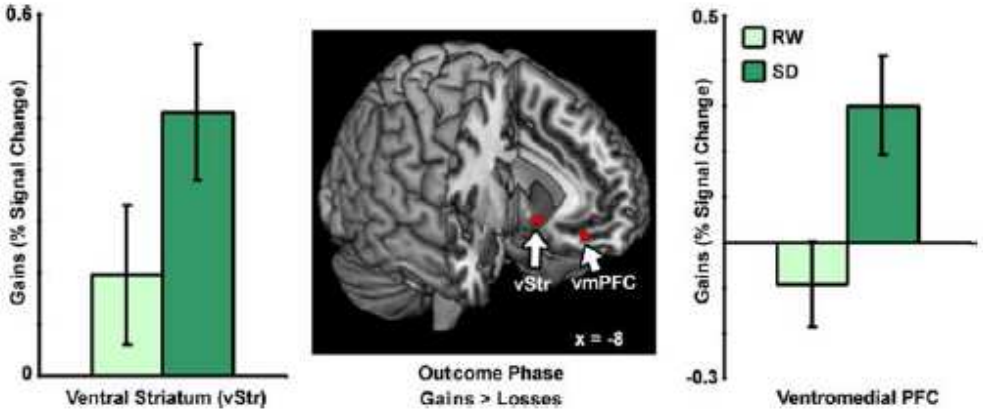

Figure 4-4: Sleep deprivation increased neural sensitivity to gain outcomes

Following SD, there was a significant increase in gain-related activity in the vStr and vmPFC compared to after a normal night of sleep (**Figure 4-4)**. Conversely, SD was associated with marked attenuation of loss-related activation within the left anterior insula (**Figure 4-5)**. Changes in anterior insula activation occurred at the identical location to where sleep-deprived persons showed attenuated responses to losses in an earlier study (Venkatraman et al., 2007). Finally, the decrease in activation of the left

anterior insula for losses correlated with the increase in activation in ventral striatum for gains ($r = -0.45$, $p < 0.05$).

Notably, there were no significant correlations between state-induced changes in the decision and outcome phases in any region of interest, suggesting that SD affects the processes underlying these two phases differently across individuals.

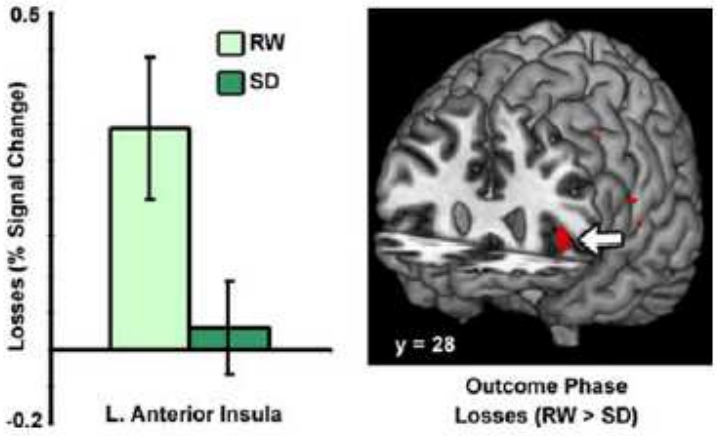

Figure 4-5: Sleep deprivation diminished neural sensitivity to loss outcomes

4.3 Discussion

Using a risky decision-making task, we showed that sleep deprivation shifted most persons' bias from avoiding loss to pursuing gain. This behavioral change accompanied congruent alterations of activation in brain regions associated with reward anticipation and emotional processing. Additionally, we observed altered neural sensitivity to received gains and losses that were directionally similar to but uncorrelated with altered activation associated with decision making. Finally, the magnitude of SD-

induced shifts in risky decision-making strategies was not correlated with SD-induced reductions in psychomotor vigilance.

Sleep deprivation favors the pursuit of gain

The current study is the first to link SD-induced changes in economic behavior with changes in brain activation. A previous study found that SD altered activation in reward-related regions in the absence of any significant differences in choice preferences (Venkatraman et al., 2007). Since that study only contrasted gambles with positive outcomes to mixed gambles involving both positive and negative outcomes, the SD-related alteration of risk preferences could have been masked by the tendency to maximize the overall probability of winning (Payne, 2005; Venkatraman et al., 2009b). The present study exclusively used mixed gambles and separated decision and outcome phases, facilitating the identification of state-related alterations in economic preferences.

While well-rested participants sought to minimize the effect of the worst loss, SD caused the same individuals to be less concerned about losses and to shift to a strategy that improved the magnitude of the best gain. In the absence of explicit feedback, this behavioral change suggests an unfounded rise in expectation for gain as reflected in a systematic bias in economic preferences following sleep deprivation.

Sleep deprivation altered vmPFC responses in both decision and outcome phases of the present study. The vmPFC has been shown to be instrumental in computing value as well as in supporting processes related to learning from reward and punishment (Rolls et al., 1994; Bechara et al., 2000b; Rangel et al., 2008). One explanation for the effects of SD on vmPFC activation is that SD could hamper the integration of feedback when

making decisions, consistent with the role of this region in learning. However, this seems unlikely, given that there was no explicit feedback at the end of each trial, and given the relative preservation of dlPFC engagement during SD.

A more likely alternative is that SD influences valuation. Though several studies associate vmPFC activation with the implicit overall value of the gamble (Tom et al., 2007; Levy et al., 2010), participants in this task may frequently be making decisions without computing an integrative value signal that incorporates all aspects of the gamble. Instead, there may be systematic biases in the attention paid to different aspects of the gamble like gains and losses. In this context, we argue that elevated vmPFC activation is predictive of biases placed on the higher-ranked outcomes (Venkatraman et al., 2009b). Our findings here fit well with this latter viewpoint, since the SD-related change in vmPFC activation during decision-making also correlated with an increased focus on the highest gains. Further, during loss-focus trials, an increase in vmPFC activation following SD correlated with a decreased preference for the Lmin choices, suggesting a reduced focus on the lower-ranked Lmin options in favor of higher-ranked Pmax choices within these trials. Together, these findings suggest that SD-induced increases in vmPFC activation might underlie the bias towards selecting higher-ranked outcomes when one is sleep-deprived.

Sleep deprivation reduces the minimization of loss

SD led to decreased activation in the right anterior insula and dmPFC during decisions that involved loss-focus trials. Activation in these regions has been widely observed in studies involving emotional awareness, particularly those relating to negative

affect (Dalgleish, 2004; Craig, 2009; van Veen et al., 2009). Consistent with these observations, we found that activation in anterior insula was positively correlated with Lmin choices in well-rested participants. SD lowered right anterior insula activation, and this correlated with a decrease in preference for the Lmin choices.

A natural alternative hypothesis is that SD introduces noise into the decision process, given that under SD participants were equally likely to make Lmin or Pmax choices on loss-focus trials. However, several aspects of the data make such an explanation unlikely: (i) Under SD, the proportion of Gmax choices *increased* and was significantly greater than chance ($\chi^2 = 16$, $p < 0.001$), (ii) participants showed significant variability in choice preferences; yet the proportion of Lmin choices varied systematically between states across participants ($r=0.36$, $p<0.06$), (iii) preferences following sleep deprivation remained sensitive to the expected-value relationship between the two choices, and (iv) activation levels in dorsolateral prefrontal cortex (associated with cognitive control and executive function) did not vary as a function of sleep deprivation. Thus, changes in preferences provide a more parsimonious explanation for the observed results.

Considered together, SD appears to create an optimism bias; for example, participants behave as if positive consequences are more likely (or more valuable) and as if negative consequences are less likely (or less harmful). In support of this general interpretation, we found that the SD-related decrease in anterior insula activation associated with loss-focus trials correlated with SD-related increases in vmPFC activation during gain-focus trials. As activation in these regions are typically associated with

salience of negative and positive outcomes respectively (Kuhnen and Knutson, 2005; Preuschoff et al., 2008; Venkatraman et al., 2009b), it appears that SD biases valuation by bringing about an increased attentional bias towards higher-ranked positive outcomes while concurrently reducing concern for losses.

Effects of SD: Choices or Parameters?

In this study, we identified brain systems whose activation correlated with different choices or with choice tendencies. An alternative yet popular approach in decision neuroscience involves estimating parameters using decision theoretic models like prospect theory and identifying brain functions that track changes in that parameter across individuals. However, in several studies using a similar multi-outcome risky choice task (but without a state manipulation), participants' show a strong bias towards Pmax choices, which is often inconsistent with traditional economic models like expected utility theory and prospect theory. Instead, individuals appear to adopt an aspiration level that emphasizes selected aspects of the decision problems that in turn bias choices (Payne, 2005; Venkatraman et al., 2009b; Venkatraman et al., 2011).

Since sleep deprivation did not lead to changes in the proportion of Pmax choices, the results in the current experiment are agnostic to model-based and model-free methods. Not surprisingly, analyzing choices using a parametric approach indicates that SD still changes risk but not loss-aversion parameter. Moreover, SD-induced changes in choices were highly correlated with SD-induced changes in the risk parameter across participants. Thus, SD alters underlying decision preferences, whether expressed in increased tendency for gain-seeking choices or in a change in parameter of models of

risk. One conjecture is that SD modulates these preferences by changing the relative emphasis paid to different aspects of the complex problem presented; specifically increasing the biases towards gains relative to losses. This would be consistent with prior work showing that framing a risky decision as a gain or as a loss leads to different patterns of choice following SD (McKenna et al., 2007).

SD independently amplifies optimism bias during the outcome phase

When a subset of gambles was resolved to gains or losses at the end of the experiment, sleep-deprived participants showed increased activation of ventral striatum and vmPFC following gain outcomes and decreased activation in anterior insula when gambles were resolved to losses. The attenuated anterior insula activation for losses mirrors previous findings concerning neural responses at the outcome phase (Venkatraman et al., 2007). Notably, in the present experiment, the effects of SD on decision and outcome phases of the task were not correlated.

In a real-world parallel, sleep-deprived gamblers and traders, already saddled with an optimism bias during decision-making, could further compound gain-seeking, high-risk behavior by being disproportionately incentivized toward reward-seeking while concurrently being desensitized to ongoing losses. More positively, because SD has dissociable effects on decision-making and response to outcomes, some sleep-deprived persons may transcend the state-induced optimism bias and respond more appropriately to losses as they occur.

Potential mechanisms underlying SD-related optimism bias

Risky choice often involves weighting potential gains against potential losses. Our findings suggest that SD might bias value computations by increasing the emphasis on the gain outcomes, relative to losses (Kuhnen and Knutson, 2005; Liu et al., 2007). Strikingly, the shifts in economic preferences were independent of the effects of SD on vigilance, suggesting that SD's influence on behavior could vary according to cognitive domain (Van Dongen et al., 2004). This is particularly relevant in light of increasing number of persons seeking to maintain performance when sleep-deprived by taking stimulants. Stimulants may improve vigilance but their influence on other aspects of cognition, such as decision-making, is less clear (Gottselig et al., 2006; Killgore et al., 2007; Huck et al., 2008; Killgore et al., 2008). Our findings that SD shapes decision preferences independent of its effects on vigilance suggest that the traditional countermeasures may be ineffective in ameliorating the decision biases engendered by limited sleep.

Future experiments should consider potential cross-sectional heterogeneity in the effects of SD upon preferences as inter-individual variation in the effect of sleep deprivation on attention has been shown to be trait like (Van Dongen et al., 2004). The behavior-imaging correlates of such variation has also been shown in several imaging studies (Mu et al., 2005; Lim et al., 2007; Chuah and Chee, 2008; Chee and Tan, 2010). Here, on top of significant main effects of SD, closer inspection also reveals substantial variability in its effects on individuals' choices as well as brain activation (**Figure 4-3**).

While there was an overall increase in preference for Gmax choices following SD, there was a subset of participants who were biased in the other direction.

We conjecture that changes in dopamine neurotransmission following SD may affect decision making in that state. In a recent study, healthy sleep-deprived persons showed elevations in dopamine levels in the striatum and thalamus, thought to contribute to maintaining wakefulness, albeit in a somewhat maladaptive way given the concurrent decline in visual attention as volunteers engaged in task performance (Volkow et al., 2008; Volkow et al., 2009). As L-Dopa administered to healthy young adults can transiently elevate subjective ratings of pleasantness (Sharot et al., 2009), we speculate that the optimism bias observed in SD could be a byproduct of attempts to sustain wakefulness by elevating dopamine levels. The varying extent to which this is successful in a given individual might then account for the dissociation between vigilance and shift in risk preference.

5 Strategic Control in Decision Making: Implications for Neuroanatomy of Cognitive Control[†]

In the previous three chapters, the mechanisms underlying variability in risky choice were elucidated using a complex multi-outcome value allocation task across multiple methodologies and states. Across all these experiments, choice patterns varied as a function of problem type, individual variability and state (sleep deprivation) in a manner that is inconsistent with predictions of most canonical economic models. The variability in preferences was also associated with systematic changes in the pattern of information acquisition and processing, and could be predicted by activation in dorsomedial prefrontal cortex. Together, these findings are consistent with a multiple strategy perspective in decision making. It is important to reiterate here that the Pmax-heuristic is not a comprehensive model for explaining all decision making under risk. Instead, it is another tool in the toolbox of strategies that are applicable to a certain class of problems. Individuals consider it when it is available and readily switch to other ones, including compensatory strategies consistent with EU and CPT in other situations. The threshold at which the shifts occur varies as a function of individual variability and traits, and is indexed by activation in control-related brain regions like the dmPFC.

The multiple strategy perspective for risky choice has been much less common till date in part due to the fact that risky choice studies have often used very simple stimuli where subtle changes in decision strategies are more difficult to detect. For example,

[†] The contents of this chapter are part of a working paper "Venkatraman, V and Huettel, SA. Strategic control in decision making under uncertainty."

most experimental studies have used gambles (lotteries or prospects) that have only a few positive (or zero) monetary amounts to be won. Generally there are no more than two non-zero outcomes that are possible and the number of alternatives to be considered at any one time is limited to two (a paired comparison choice problem) or one (a valuation problem where one rates or assigns a monetary value to a single gamble at a time). Surprisingly, very few studies exist that involve gambles with a mix of gain and loss outcomes (Wu & Markle, 2008). There are also very few studies that have investigated gambles with multiple outcomes or choices between more than two gambles at any one time (Lopes, 1995; Lopes & Oden, 1999).

The use of simple gamble stimuli plays into the hands of single strategy models as preferences in these trials are often explained by constructs (parameters) like risk aversion and loss aversion across individuals (Tom, Fox, Trepel, & Poldrack, 2007). Yet, these results often do not generalize to more complex gambles with multiple gain and loss outcomes, which are needed to simulate real-world choice scenarios. The complex gambles also often encourage the use of multiple strategies that vary across individuals and task contexts.

Results from studies presented earlier demonstrate that individuals shift strategies as a function of both problem type as well as individual variability. Individuals with a strong preference for Pmax heuristic were more sensitive to aspects of the problem that are related to whether or not this strategy is available; while people who were more focused on magnitudes and probabilities were more sensitive to changes in expected value. The variability in choice preferences was also associated with systematic

differences in response times and patterns of information acquisition. These findings are consistent with the use of multiple strategies, with the appropriate strategy selected contingent on contextual factors.

Multiple Strategy Perspective: The Issue of Strategy Selection

One common criticism of the multi-strategy approach is that the strategy toolbox essentially represents a flexible storage device, where one can simply launch another new heuristic to account for decision processes not accountable by the existing set of tools in the box (Glockner, et al., 2010). The problem is further exacerbated by the lack of well-constrained conditions for strategy selection, which makes the flexible toolbox approach an anything-goes model (Glockner, et al., 2010). However, other researchers have developed a number of approaches that detail how people select between different heuristics (Marewski, 2010; Payne, et al., 1988; Rieskamp & Otto, 2006). For instance, cognitive models of strategy selection argue that strategy selection occurs through a simple cost/benefit analysis (Payne, et al., 1988). In other words, an adaptive decision maker often evaluates costs (effort and computational resources) and benefits (outcomes, potential regret, ease of justification) before selecting and applying a strategy. Like other aspects of decision making, strategic preferences can vary both as a function of the decision context (like complexity of the problem and timing constraints) and the decision maker. Alternatively, strategy selection may represent a learned response that is based on past experiences with different strategies (Rieskamp, 2008; Rieskamp & Otto, 2006), such that the decision-maker merely chooses the most efficient strategy for each situation based on prior experience (e.g., reward history).

Using fMRI, we sought to find converging evidence for brain regions that are associated with strategy selection (Venkatraman, et al., 2009). A region that is associated with strategy selection should (i) show greater activation during trials where individuals shift from one strategy to another, and (ii) should be able to control activation in brain regions that are associated with implementing the selected strategy on any given trial. The dorsomedial PFC (dmPFC) fulfilled both these conditions. Activation in dmPFC increased when participants switched away from their preferred strategy on a particular trial (i.e., greater activation when people with a strong preference for Pmax heuristic in general made non-Pmax choices, and vice versa). Additional analysis revealed differential choice-related functional connectivity (correlation) of dmPFC to dlPFC and anterior insula, regions that were associated with the different types of choices above. Together, these findings support the interpretation that control signals from dmPFC modulate the activation of choice-related brain regions, with the strength and directionality of this influence dependent on an individual's preferred strategy.

These findings, though correlative, are consistent with findings from eye-tracking, where we find that the Pmax-preferring individuals are more sensitive to whether the Pmax option is available in a given trial while the non Pmax-preferring individuals are not. Similarly, the Pmax-preferring individuals also take longer and acquire more information when making non Pmax choices and vice versa. This increased processing may be associated with increased level of executive control that is necessary for switching strategies, as a function of problem type and individual traits. As would be expected in the case of strategy shifts, we also show differences in the Payne Index with

the non Pmax-preferring individuals shifting from an attribute-based information acquisition approach to a more alternative-based approach. In other words, same individuals shift their pattern and magnitude of information acquisition across trials due to changes in decision context. And different individuals demonstrate differences in information acquisition patterns when making the same choice (e.g., Pmax-preferring participants make more alternative-based processing for Lmin choices than non Pmax-preferring participants). Activation in the dmPFC may facilitate these strategy shifts as a function of decision context and individual variability.

Our neural results are consistent with the growing consensus that dmPFC reflects a mechanism for identifying and responding adaptively to changes in the environment. Notably, complex aspects of behavior, like full consideration of decision problems, require a wide range of processes of executive control. Therefore, one conjecture is that the dmPFC plays an important role in complex decision making: it signals changes in how a decision problem is represented, and thus shapes computational processing elsewhere in the brain based on the current decision strategy.

The rest of this chapter is focused on reviewing existing literature related to the neural correlates of cognitive control. Specifically, there is considerable evidence in favor of an important role for both dorsolateral and dorsomedial prefrontal cortex in exerting executive control. Yet, these do not incorporate strategic control of the form discussed in our previous experiments. The focus here, and in the remaining experiments presented in the subsequent chapters, is on developing a neuroanatomical model for cognitive control that also integrates aspects of strategic control involved in complex decision making.

5.1 Cognitive Control

The term *cognitive control* broadly describes the ability to shape behavior in an adaptive manner, as a function of current goals and constraints. Different theoretical models and definitions have emphasized different aspects of control: (i) the ability of the human cognitive system to configure itself for the performance of specific tasks (Botvinick et al., 2001); (ii) the ability to coordinate thoughts or actions in relation with internal goals (Koechlin et al., 2003); (iii) a system that can acquire and implement the 'rules of the game' needed to achieve a given goal in a given situation (Miller and Cohen, 2001) or (iv) a system that supports flexible behavior by selecting actions that are consistent with our goals and appropriate for our environment (Badre, 2008). Consolidating across these definitions, one can argue that three properties are fundamental to any system associated with cognitive control: it must be *selective*, it must engage in *optimization*, and it must be *hierarchical*.

- Selection: Cognitive control involves selection of actions that are consistent with present goals and context (Badre, 2008). This selection can occur at several levels ranging from simple response selection to complex strategy selection and task switching. An effective control system is therefore one that facilitates processing in volatile environments, as well as supports multitasking in the pursuit of multiple goals simultaneously.
- Optimization: A cognitive control system should have the ability to monitor and compare actual performance with internal goals and standards and use this information to optimally and adaptively organize behavior. Therefore, such a

system should detect errors and unfavorable outcomes and use this error-related feedback to guide subsequent performance adjustments.

- Hierarchy: Similar to an organization hierarchy that consists of superiors, subordinates and well-defined lines of communication, a hierarchical control system is one that operates at multiple levels with each level controlled by a higher level and exerting control on representations in lower levels. For example, the lowest level of control could be associated with sensory processing and selection of motor actions while the highest level of control might involve multi-tasking and selecting between several concurrent actions. Information within this hierarchy typically flows in a top-down manner.

5.2 Role of Lateral PFC in Cognitive Control

Historically, the lateral prefrontal cortex has been associated with subserving cognitive control or the flexible control of behavior (Miller, 2000; Koechlin et al., 2003; Ridderinkhof et al., 2004b; Badre, 2008; Egner, 2009). The frontal neurons assimilate and process contextual information, and bias subsequent selection of appropriate action pathways in other brain regions. These functions become particularly important when inputs are ambiguous; involve uncertainty or when one has to choose flexibly between multiple responses depending on task context. The prefrontal cortex can facilitate these functions due to its strong connections to other sensory regions in the brain (Barbas and Pandya, 1989; Petrides, 2005), its capacity for actively maintaining task and goal-related representations and its ability to learn and update these representations over time (Miller and Cohen, 2001).

Several recent lines of research also suggest a strong hierarchical organization within the lateral prefrontal cortex, with the more rostral regions involved in contextual control and more caudal regions associated with sensory control (Koechlin et al., 2003; Badre, 2008). For example, the cascade model proposed by Koechlin and colleagues argues for a hierarchy of executive processes from premotor to more anterior prefrontal regions that control behavior according to the stimuli (sensory control), current environmental constraints (contextual control) and the temporal episode (branching control) in which the stimulus occurs respectively (Koechlin et al., 2003). Along similar lines, Badre and colleagues posit that the rostral-caudal hierarchy can be better understood in terms of levels of abstractions in representations of rules for action selection (Badre and D'Esposito, 2007). Yet another proposal argues for a rostral-caudal hierarchy in the prefrontal cortex based on relational complexities (Christoff and Gabrieli, 2000; Christoff et al., 2001). Although these models differ in the details of their hypotheses about specific regions, what is common to all of them is a posterior-to-anterior gradient characterized by increasing complexity.

In summary, most of the postulated functions for the lateral PFC involve the implementation of cognitive control. However, when there is a need to monitor and detect changes in the environment, the lateral PFC still relies on feedback inputs from other brain systems, most notably the dorsomedial PFC. For this reason, the dmPFC has also been consistently associated with an active role in cognitive control, particularly in terms of performance monitoring as well as in shaping behavior in a flexible manner based on context, goals and motivation.

5.3 Role of Dorsomedial PFC in Cognitive Control

The interest in dorsomedial prefrontal cortex arise from several lines of research that implicate this region with functions that are integral to cognitive control like error monitoring (Carter et al., 1998; Brown and Braver, 2005b), conflict monitoring (Botvinick et al., 1999; Barch et al., 2000; Kerns et al., 2004), reward processing and outcome evaluation (Hadland et al., 2003; Rogers et al., 2004), reinforcement learning (Kim et al., 2006) and decision making under risk and uncertainty (Hadland et al., 2003; Rushworth et al., 2004; Kennerley et al., 2006). More importantly, the dmPFC satisfies all three characteristics of a control system: selection, optimization and hierarchy as discussed in detail below.

Selection: DmPFC exerts control preferentially in volatile environments

The dorsomedial prefrontal cortex has been associated with the detection of conflict in tasks that require overriding of prepotent responses as well as selection among a set of mutually incompatible response processes (Carter et al., 1998; Botvinick, 1999). The detected conflict signal then triggers strategic adjustments in cognitive control which serve to prevent conflict in subsequent performance. Many such studies have used variants of the Stroop paradigm (MacLeod, 1992), which requires individuals to inhibit a fast, prepotent response (e.g., color word reading) and instead engage in a slower, less common process (e.g., naming an ink color). Under such task conditions, a very large number of studies have reported activation in dmPFC (Bush et al., 1998; Derrfuss et al., 2005), as reviewed by (Bush et al., 2000). Similar findings have also been observed with other tasks that involve response incompatibilities like the flanker task (Bugg, 2008),

Simon task (Kerns, 2006) and go/no-go paradigms (Kawashima et al., 1996; Tsujimoto et al., 1997).

Given that conflict can occur at various levels, a key question that arises then is whether the involvement of dmPFC is specific to conflicts at the level of response selection or whether it extends to other types of conflict. While vast majority of initial studies suggest a specificity for response-related conflict especially given the strong connectivity of this region to motor structures including premotor cortex, more recent studies posit a more broader functional role for dmPFC in detecting conflict at other levels including stimulus evaluations and task representation (Botvinick et al., 2004). Several other studies have also found increased activation in the dmPFC for complex decisions, though these could have been confounded with activation related to response preparation (Paulus et al., 2002; Walton et al., 2003; Rushworth et al., 2004; Zysset et al., 2006; Botvinick and Rosen, 2008; Pochon et al., 2008).

Pochon and colleagues explicitly investigated whether the conflict monitoring role extended to complex decisions that involve the integration of higher-order beliefs and preferences. In their study, male participants chose the more attractive of two female faces. The similarity of the two faces was modulated such that some trials invoked higher decision conflict while others evoked lower-levels of decision conflict. Activity in the dmPFC was greater for trials involving higher decision conflict. Importantly, this increased activation was found even for trials where participants did not have to respond, suggesting that it was specific to decision conflict and not due to selecting between multiple motor responses (Pochon et al., 2008).

Activation in the dmPFC has also been associated with conflict arising from subjective decision preferences, particularly when choices run counter to general behavioral tendencies or strategies. We define the conflict arising in these instances as strategy-related control demands. For instance, in a study involving the framing task, all participants exhibited a strong tendency towards the framing heuristic, driven by increased activation in the emotional amygdala system. Participants also showed increased activation in the dmPFC for choices that were inconsistent with framing effects. The authors argued that increased activation in dmPFC in this study represents a conflict between the generally preferred emotional heuristic response and a more rational analytical choice (De Martino et al., 2006). In other words, increased activation in this region helps control the automatic activation of the emotional system and hence leads to more rational choices. Here, all participants exhibited the same bias towards using the framing heuristic. However, it is becoming increasingly evident from the studies presented in the earlier chapters that individuals use a variety of strategies in representing and solving complex decision problems (Payne et al., 1988; Gigerenzer et al., 1999; Venkatraman et al., 2009b). Importantly, people switch between these strategies in an adaptive manner as a function of decision context and individual traits (Payne et al., 1993) and dmPFC may play an important role in exerting strategic control.

For instance, in the fMRI study using risky choice paradigm in Chapter 3, we found that activation in dmPFC predicted whether an individual adaptively made a choice that was inconsistent with their overall preferred strategy. In other words, activation in this region was greater when people who normally prefer the simplifying strategy made a

compensatory choice and vice versa (Venkatraman et al., 2009b). Since our experimental design explicitly separated the decision and response components, one could rule out the alternative explanation of activation being related to response selection **(see Appendix A)**. Therefore, a parsimonious explanation for dmPFC function could be that it supports aspects of decision making that are coded in relation to an underlying strategic tendency. We validated this hypothesis further in an independent experiment using a different decision making task, as discussed in the next chapter.

Optimization: DmPFC regulates other brain regions

As introduced above, one of the key aspects of a control system is the ability to monitor and evaluate the performance of various systems and make appropriate adjustments as necessary. The dorsomedial prefrontal cortex performs such a function in cognitive control, as supported by evidence from neuropsychological studies where lesions to the anterior cingulate cortex lead to deficiencies in the ability to exert cognitive control (Ochsner et al., 2001; Swick and Jovanovic, 2002).

The dmPFC has been shown to play an important role in the continuous assessment of ongoing actions and their corresponding outcomes. Of particular interest is the postulated role of the dmPFC in commission of errors, demonstrated both using the transient potential known as the error-related negativity (ERN) in EEG (Gehring et al., 1995) as well as fMRI (Kiehl et al., 2000; Menon et al., 2001). Subsequent studies also demonstrate an increase in dmPFC activity when actions specifically lead to errors (Ullsperger and von Cramon, 2003).

A slightly different perspective argues for a more general error-likelihood estimation function within the dmPFC, of which conflict monitoring and error detection are special cases (Brown and Braver, 2005a). Brown and Braver demonstrate, using integrated computational neural modeling and neuroimaging experiments, that activation in dmPFC might predict error likelihood in a given context, even when these trials have no error or response conflict. According to this model, activation in dmPFC to a given task condition will be proportional to the perceived likelihood of an error in that condition, even before any external feedback is provided. The authors further speculate that this signal may be dopaminergic in nature and hence could play an important role in reinforcement learning and recruitment of cognitive control (Brown and Braver, 2005a).

Another proposal for the role of dmPFC in cognitive control is that it plays a more general role in representing and updating action values (Behrens et al., 2007). For instance, non-human primates could no longer use the most recent outcome to guide choice following lesions to the anterior cingulate sulcus (Kennerley et al., 2006). In a recent study, Behrens and colleagues demonstrate that humans have the ability to assess volatility in an optimal manner and adjust decision making accordingly. More importantly, this volatility is reflected by fMRI activation in the dmPFC when each trial outcome is observed. When a new piece of information becomes available, activity in this region increases proportional to its salience for predicting future events (Behrens et al., 2007). Since prediction error signals are often associated with dopaminergic regions and ventral striatum, the authors speculate that the projection from dmPFC to ventral striatum might allow the volatility-based learning rate to modulate the influence of current

prediction error on the next value estimate. This model could also explain the increased activation in this region during task switching, as the environment is highly volatile in these situations and hence outcomes are especially informative.

Any region that plays an optimizing role for cognitive control should also detect the need for greater control and subsequently signal this need for reactive adjustments to other regions of the brain. As discussed above, the lateral PFC has been postulated to play an important role in implementing cognitive control. Consistent with this notion, Kerns and colleagues hypothesized that increased activation in dmPFC should lead to greater implementation of cognitive control in the subsequent trial, as manifest in increased lateral PFC activation (Kerns et al., 2004). They found that when incongruent trials were associated with strong activity in the dmPFC, relatively low interference was observed in the next trial. More importantly, they demonstrated that the magnitude of activation change in the dmPFC for the current trial predicted subsequent change in dorsolateral PFC activation on the next trial, suggesting that dmPFC may engage executive control regions based on task demands (Kerns et al., 2004).

In our study involving risky choice discussed in Chapter 3, we showed that the dmPFC demonstrates differential task-specific functional connectivity with choice-related brain regions. Specifically, we found increased functional connectivity between dmPFC and dorsolateral PFC only for simplifying choices and increased functional connectivity between dmPFC and anterior insula for compensatory choices. Though these effects were correlative, we hypothesize that dmPFC shapes decision-making at a strategic level by switching between appropriate brain systems as a function of decision

context and individual traits. Such strategic considerations are unlikely to be limited to economic contexts; they are likely to extend to emotional and social contexts. For instance, evidence across primate lesion and neuroimaging studies suggest a spatial topography within dmPFC such that distinct subregions support volatility associated with social and non-social contexts, and that those subregions have distinct functional connectivity to regions in ventral PFC (Rushworth et al., 2007; Rudebeck et al., 2008).

In another recent study, Kouheiner and colleagues argue that the activation in the medial prefrontal cortex for errors, conflict situations, rewards and penalties across several studies represents its role in monitoring motivationally salient events (Kouneiher et al., 2009). Further, they argue that the motivational processes in the medial prefrontal cortex energize a cascade of top-down control processes in the lateral prefrontal cortex, along the lines demonstrated by Kerns and colleagues. Importantly, they also argue that motivational processes in the dmPFC operate according to the rewarding values of the actions rather than demands of cognitive control (Kouneiher et al., 2009). We return to the connectivity between medial and lateral prefrontal cortex and its role in cognitive control in Chapter 7.

Hierarchical: DmPFC exerts control in a topographic manner

The findings from several studies involving the dmPFC argue for a functional specialization within this region. An early form of specialization divided the dmPFC into a dorsal aspect involved in cognitive control and an anterior aspect associated with emotional processing (Bush et al., 2000; Bush et al., 2002).

Kouheiner and colleagues found an anterior-to-posterior organization of motivational processes in the dmPFC (Kouneiher et al., 2009). The posterior regions, specifically the pre-SMA, showed transient responses to immediate contextual incentives signaling the rewards and penalties at stake in immediate action. Similarly, the middle regions, particularly the dorsal anterior cingulate cortex, showed sustained activations that were associated with the rewards and penalties at stake in the ongoing behavioral episode, regardless of immediate contextual incentives (Kouneiher et al., 2009). Overall, these findings indicate that the dmPFC implements, from the posterior to the anterior regions, two levels of motivation processes, namely contextual and episodic motivation.

Along similar lines, Beckmann and colleagues used magnetic resonance diffusion tractography to delineate probabilistically the anatomical connectivity of the cingulate cortex to other brain regions (Beckmann et al., 2009). The authors first identified nine distinct subregions within the cingulate cortex based on its probabilistic connectivity profiles with the rest of the brain. Specifically, the authors found three distinct subregions within the dmPFC based on differential probabilistic connectivity to lateral PFC, premotor and precentral cortices respectively, strongly suggesting functional specialization within the region.

Based on the anatomical connectivity profiles (Beckmann et al., 2009), one hypothesis is that the posterior regions would be more involved in response-related control while the anterior regions would be associated with more decision-related control. In the first of two experiments, we sought to explicitly test this functional organization using two tasks in the same participants that evoke different levels of control, namely

response, decision and strategy related control. In the second experiment, we used resting-state data to test whether the topography in the dmPFC might even extend to the connectivity with corresponding regions in the lateral PFC. Based on the findings across these two experiments, which are discussed in detail in the next two chapters, a novel hypothetical model for cognitive control is proposed that is based on hierarchical interactions between the medial and lateral prefrontal cortex as a function of varying control demands.

6 Evidence of Topography in Dorsomedial Prefrontal Cortex[†]

As introduced in the previous chapter, many neuroscience studies have implicated the medial prefrontal cortex in a variety of cognitive functions like conflict monitoring (Botvinick et al., 2001; Pochon et al., 2008), error detection (Carter et al., 1998), outcome evaluation (Bush et al., 2002; Gehring and Willoughby, 2002), reinforcement learning (Kennerley et al., 2006), decision-making under risk and uncertainty (Rushworth et al., 2005; Behrens et al., 2008), emotions (Etkin et al., 2006) and social interactions (Amodio and Frith, 2006; Behrens et al., 2008; Behrens et al., 2009). Meta-analyses have suggested that these functions are supported by brain regions along the anterior cingulate sulcus and extending dorsally, hereafter collectively referred to as dorsomedial prefrontal cortex (dmPFC) (Ridderinkhof et al., 2004a; Beckmann et al., 2009).

There are important reasons to posit that functional specialization exists within the dmPFC. First, there exists long-standing evidence for topographic organization within the medial prefrontal cortex, considered more generally. As one related example, research on executive function has investigated the anterior cingulate cortex (ACC), which typically denotes a swath of medial prefrontal cortex that is broader and more ventral to dmPFC (e.g., including more rostral areas but not regions around the paracingulate gyrus). Reviews have divided ACC into a dorsal aspect associated with cognitive control and an anterior aspect associated with emotional function (Bush et al., 2000). Second,

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there is evidence that regions within dmPFC differ in their patterns of anatomical connectivity with other brain regions (Beckmann et al., 2009). Third, recent converging evidence from primate lesion studies and functional neuroimaging data indicates a dissociation between contributions of the anterior cingulate sulcus and the anterior cingulate gyrus to non-social and social behavior, respectively (Behrens et al., 2008). Finally, there is strong evidence for a topographic organization within the *lateral* prefrontal cortex (Koechlin et al., 2000; Christoff et al., 2003; Koechlin et al., 2003). Given the postulated role of dmPFC in shaping activation in lateral PFC (Kerns et al., 2004; Meriau et al., 2006), a similar pattern of functional specialization may exist within the dmPFC.

Here, we evaluated whether dmPFC evinces a functional topography associated with the form of task-related cognitive control. We hypothesize that posterior regions of dmPFC, which show greater connectivity to motor and pre-motor regions, would be associated with response-related control while more anterior regions, which show greater connectivity to dorsolateral prefrontal cortex, would predict control demands related to complex decision-making. Moreover, based on initial suggestions that dmPFC is also recruited when individuals make choices that run counter to general behavioural tendencies or strategies (Paulus et al., 2002; De Martino et al., 2006; Hampton and O'Doherty J, 2007; Venkatraman et al., 2009b), we also hypothesize that this strategy-related control would evoke activation in the most anterior aspect of dmPFC. Such a result would parallel the demonstrated topographic pattern in lateral PFC.

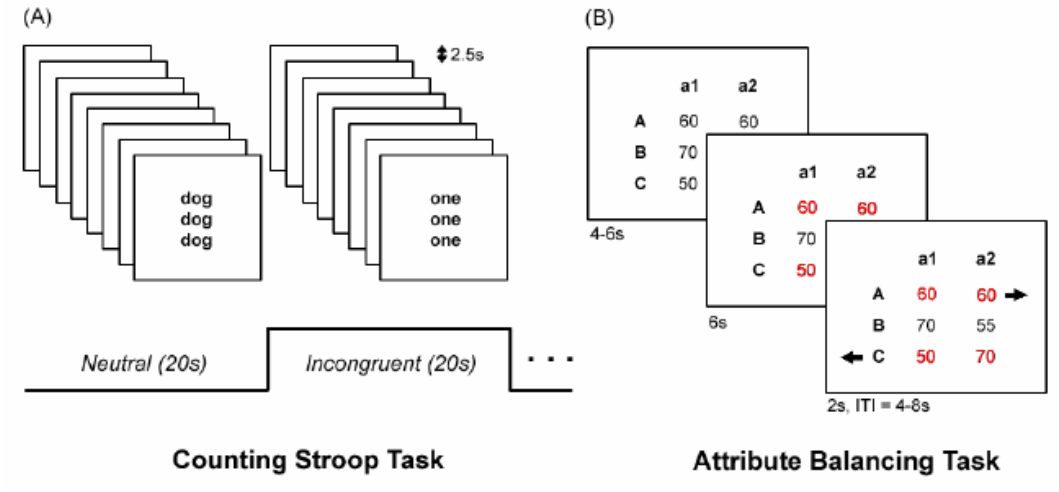


Figure 6-1: Schematic of Experimental Tasks

We tested these hypotheses in an fMRI study that evoked these three distinct forms of control demands – response, decision, and strategy – within the same participants and with distinct behavioral covariates. To evoke response-related control demands, we used a counting Stroop task **(Figure 6-1A)**, using the participant-by-participant response-incongruency effect as a measure of response-related control **(Figure 6-2A)**. For decision and strategic control demands, we used an attribute-balancing task **(Figure 6-1B)** where participants had to decide between two stocks based on their attribute ratings: the balanced stock had equal ratings on both attributes, while the extreme stock had a high rating on one attribute but lower rating on other. Participants showed a strong bias for the balancing strategy (choosing the balanced option), consistent with previous studies (Chernev, 2004, 2005). On each trial, the decision-related control demand was characterized by the difference in relative desirability of the two options **(Figure 6-2B)**. Strategic control demands were characterized according to the degree of bias toward the balancing strategy within each individual **(Figure 6-2C)**. Should these

three forms of control evoke activation in distinct regions of dmPFC, and moreover if that activation scales with different behavioral covariates, there would be strong evidence in support of a functional topography within dmPFC.

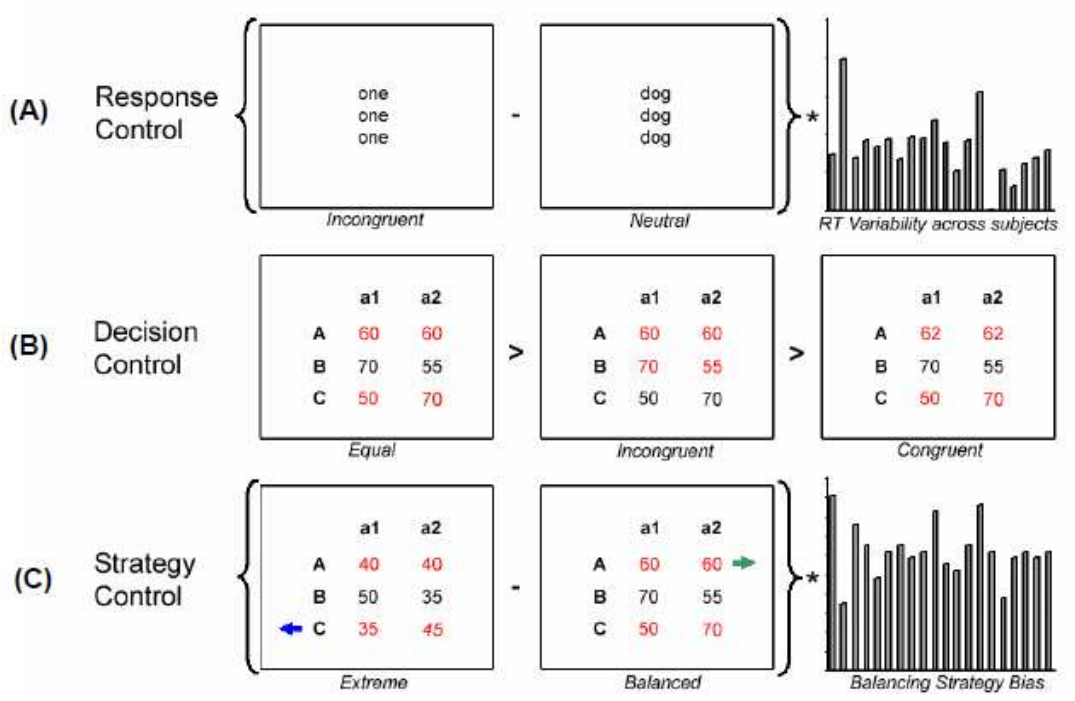


Figure 6-2: Definition of response-, decision- and strategy-related control.

6.1 Methods

Twenty-three young adults (7 males, mean age = 21.9) participated in this study. All participants acclimated to the scanning 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 MRI scanner. Three participants were excluded prior to data analysis – two due to excessive motion and one for poor behavioral performance – leaving a total of 20 participants in the final analyses. We used an incentive-compatible design in which participants received monetary compensation both for participation and for their

performance in the experiment (see **Appendix C** for details). All participants gave written informed consent as part of protocols approved by the Institutional Review Boards of Duke University and Duke University Medical Center.

Stimuli and Experimental Conditions. Response-related control demands were evoked using a counting Stroop task (Bush et al., 1998). We employed a block design for this task. In the *Neutral* condition, participants were presented with multiple repetitions of animal words (e.g. dog, cat) and asked to count the number of times the word was presented. In the *Incongruent* condition, they were presented with multiple repetitions of number words (one, two, three or four) and asked to count the number of times the word was presented. However, the number of repetitions was always incongruent with the number word itself (for e.g., "two" presented four times). Each word was repeated between 1-4 times and participants responded by pressing the corresponding button on a 4-button response box. We calculated, for each participant, the magnitude of the Stroop incongruency effect as a measure of response-control demands.

Decision-related and strategy-related control demands were evoked using an attribute-balancing task where all participants were presented with a total of 90 sets of three real stocks, each rated on two attributes that provided real metrics of stock performance **(Figure 6-1B)**. To minimize the influence of participants' prior knowledge or financial biases, the identity of the stocks and the nature of the attributes were concealed from the participants until after the experiment. On each trial, the three stocks were labeled as "A", "B", and "C", and the two attributes were labeled as "a1" and "a2"

and shown as percentile rankings. The participants' task was to predict the better-performing stock based only on these attributes.

All choice trials involved one stock that had balanced values for both attributes, one stock that had a good rating on attribute *a1* but a poorer rating on attribute *a2,* and a third stock in which this pattern was reversed with slightly varying attribute ratings (see **Appendix C** for more details). In each trial, participants had to choose between a *balanced* stock and an *extreme* stock that was randomly selected from the other two alternatives for that trial. Choosing the balanced stock was consistent with the simple attribute-balancing heuristic identified in previous studies using similar paradigms (Chernev, 2004, 2005).

In addition, we randomly interspersed six catch trials, where the extreme alternative had higher ratings than the balanced option for both attributes and thus was the more desirable option. These trials thus served to ensure that participants followed instructions and attended to the task. One participant who performed contrary to expectations in the catch trials was excluded from further analysis.

We manipulated the decision-related control demands across trials by varying the expected-value relationship (defined as the sum of two attributes for each stock) between the balanced and extreme choices **(Figure 6-2B)**. In 36 trials (*Congruent condition*), the balanced stock had a higher expected value compared to the alternative option. In another 36 trials (*Incongruent condition*), the balanced stock had a lower expected value compared to the alternative option. In the remaining 18 choice trials (*Equal condition*), the expected value for the balanced stock was equal to the expected value of the

alternative option. Decision-related control demands were minimal (i.e., where decisions were easiest) in the *congruent* condition, followed by the *incongruent* condition, and were maximal in the *equal* condition (i.e., where both choices have similar expected value).

Finally, we defined strategy-related control demands according to the degree to which a given choice (i.e., balanced or extreme, on each trial) deviates from the individual's empirical strategy preferences (i.e., the proportion of balanced choices across all trials). That is, strategic control demands are maximal when a participant who has a strong bias toward one type of choice makes the opposite choice, but minimal when participants make choices consistent with the strong bias **(Figure 6-2C)**. To obtain a measure of activation evoked by strategy-related control, we introduced each participant's strategic tendency into the analyses as a between-participants covariate.

Experimental Design and Task Timing. Participants first participated in four runs of the attribute-balancing decision task, each containing 24 gambles and lasting approximately 6 minutes. Each trial began with the display of all three stocks for 4 or 6s. Participants were instructed previously to examine the stocks as presented. Subsequently, two of the three stocks were highlighted in red (one involving balanced attributes and other extreme attributes). Participants were instructed to choose between one of these two stocks and incentivized with a monetary bonus for picking the better performing stock. They had 6s to make their choice, whereupon two arrows appeared specifying which button corresponded to which choice. The association of the buttons to choice was random. Participants were instructed to arrive at their decision during the 6s interval and

to press the button corresponding to their choice as soon as the arrows appeared. Response times were defined as the interval between the appearance of arrows and the button-press response. The decision and response phases were explicitly separated to prevent the contamination of decision effects with response-preparation effects. During the inter-trial interval of 4-8 seconds, 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.

After four runs of the decision task, all participants completed one run of the Counting Stroop task. To maximize power for the contrast between Neutral and Incongruent trials, our design alternated between blocks of 6 trials of each type (3s between trial onsets, 18s blocks, 17 blocks/run), without any fixation or non-task blocks. A final 6-minute run, whose data are not discussed in this manuscript, resolved a subset of the trials from the decision phase to actual stock labels and attributes. The winning stock was then identified based on data we collected on the real performance of these stocks (see **Appendix C**), and participants received a monetary bonus based on the performance of their selected stock on two randomly chosen trials.

Before the fMRI data collection, participants had the opportunity to practice the experimental task (without reward) in two six-trial 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 for MATLAB (Brainard, 1997; Pelli, 1997) and were presented to the participants via MR-compatible

LCD goggles. Participants responded with the index fingers of each hand via a MR-compatible response box.

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

Analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.63, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) package (Smith et al., 2004). The following pre-statistics processing steps were applied: artifact removal using MELODIC and in-house scripts, motion correction using MCFLIRT, slice-timing correction, removal of non-brain voxels using BET, spatial smoothing with a Gaussian kernel of FWHM 8mm, and high-pass temporal filtering. Registration to high resolution and standard images was carried out using FLIRT. All statistical images were thresholded using clusters determined by $z > 2.3$ and a whole-brain-corrected cluster significance threshold of $p < 0.05$. The same analysis procedures and thresholding were used for analyses involving a between-participants covariate. The MRIcron package was used for visualizing brain images (Rorden et al., 2007).

GLM Analysis. For the response-related control analysis, we used one regressor to model activation in the incongruent blocks of the Stroop task (i.e., treating the neutral blocks as baseline). We introduced the response-time difference between Incongruent and Neutral trials as a covariate in the across-participants analysis to determine the focus of

activation. The decision-related control analysis used six total regressors to model activation in the attribute-balancing task: three task regressors for the three conditions (congruent, incongruent and equal), one regressor for the initial presentation of the stocks, one regressor for catch trials, and one regressor for the response period (scaled by response time). We defined active voxels using a conjunction analysis of [equal > incongruent] and [incongruent > congruent]. The model used for the strategy-related control analysis contained five total regressors: two regressors modeling the *balanced* and *extreme* choices of participants in conditions that cause the greatest decision conflict, one regressor modeling the responses in the remaining conditions, one regressor for the initial presentation of the stocks, and one regressor to model the participant responses. We introduced each participant's relative bias towards the balancing strategy (*z*-transformed proportion of balancing choices) as a covariate in the contrast between the balanced and extreme choice regressors.

Event-related 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 choice effects within each participant was carried out using a fixed-effects model across runs. Random-effects across-participants analyses were carried out using FLAME Stage 1.

6.2 Results

For the Stroop task, participants were significantly more accurate in the Neutral compared to the Incongruent condition [$t(19)=2.46$, $p<0.05$]. Similarly, participants also took significantly longer in the Incongruent condition compared to the Neutral condition

[$t(19)=3.88$, $p<0.001$]. Taken together, these findings are consistent with increased demands for response-related control in the Incongruent condition.

For the attribute-balancing task, participants showed a significant bias toward the balanced alternative, preferring it in 58% of the trials. Within the equal condition, they preferred the balanced alternative in 65% of the trials [$t(19) = 3.9$, $p<0.005$]. Despite this overall bias, participants' choices were still sensitive to changes in expected value. Consistent with our predictions for decision-related control demands, we found that participants' response times were slowest for the equal trials, intermediate for incongruent trials, and fastest for congruent trials **(Appendix Table C-1)**. Finally, participants also showed substantial individual variability in their choice preferences, providing a foundation for our analyses of strategic control **(Appendix Figure C-1)**.

6.2.1 Response-related Control

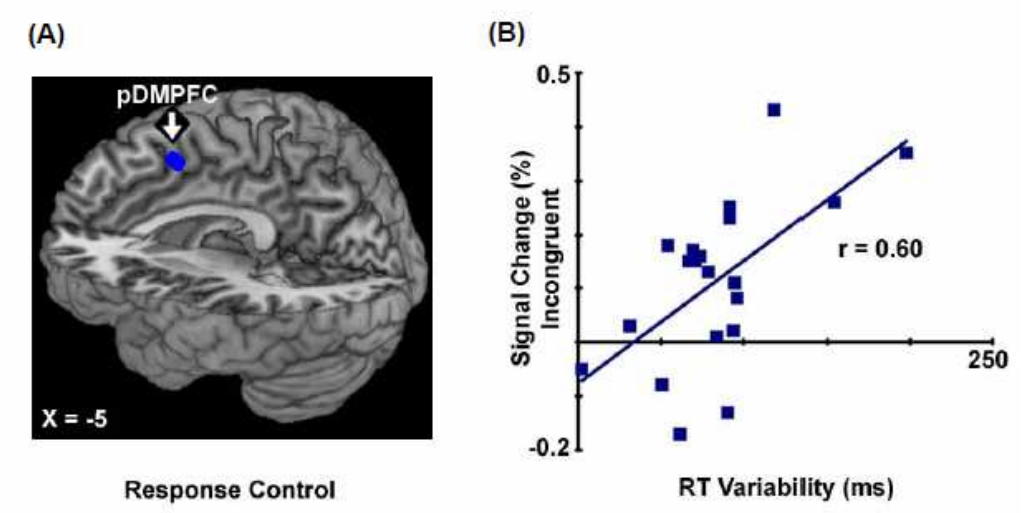


Figure 6-3: Posterior dmPFC activation predicted response-related control demands

We found increased activation in the dorsomedial PFC, dorsolateral PFC and parietal cortex for the Incongruent condition in the Stroop task **(Appendix Table C-2, Appendix Figure C-2)**. When we used the difference in response time between Incongruent and Neutral conditions as a covariate, we found that activation in left dorsolateral prefrontal cortex and a posterior region of the dmPFC (pDMPFC) increased linearly with increasing response conflict **(Figure 6-3)**. The pDMPFC activation cluster was localized to the posterior part of the cingulate sulcus (BA 32). Activation within this cluster also correlated with an independent trait measure of motor impulsiveness (Patton et al., 1995) across participants (r=0.49, p<0.05, **Appendix Figure C-3**).

6.2.2 Decision-related Control

We next sought to identify brain regions whose activation was driven by the decision phase (when participants deliberated between the two stock options) in the attribute-balancing task. We performed a conjunction analysis to identify regions showing significant effects for each of the two individual decision-related contrasts: equal > incongruent and incongruent > congruent. We found increased activation in right dorsolateral prefrontal cortex, right inferior parietal lobule, and a region of dmPFC anterior to that observed for response-related control **(Appendix Figure C-4, Appendix Table C-3)**. The dmPFC activation cluster for this contrast was also along the cingulate sulcus (BA32), anterior to the cluster for response-related control, and we refer to it as mDMPFC. Within this region, activation increased in a stepwise manner for our three levels of decision-related control **(Figure 6-4)**. Notably, these effects cannot be attributed

to response conflict, given that they are time-locked to the decision phase that occurs before response mappings had been indicated to the participant.

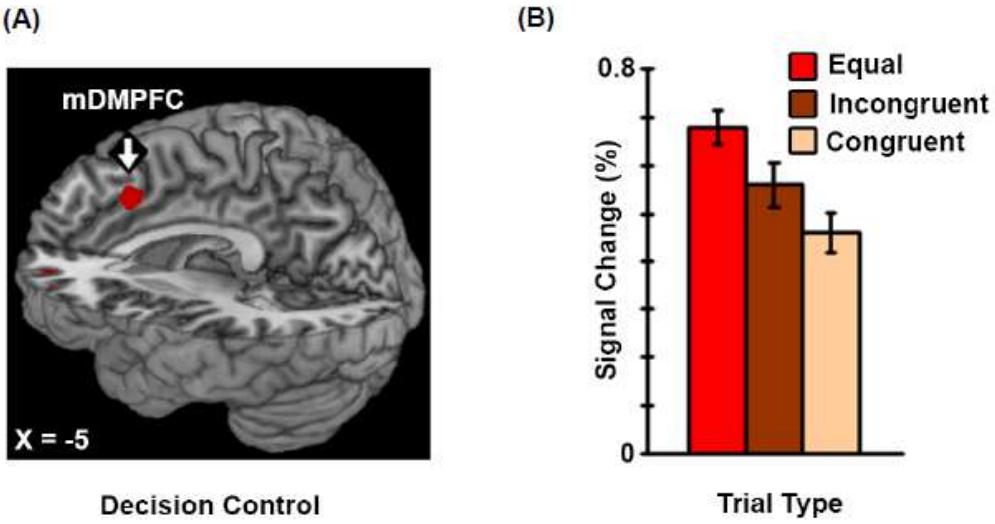


Figure 6-4: Activation in middle dmPFC predicted decision-related control demands

6.2.3 Strategy-related Control

Next, we sought to identify regions that indexed strategic control demands across participants, using individuals' preference for the balancing strategy as a covariate in our between-participant analysis. Analysis of the main-effect of choice is presented in Appendix C; see **Appendix Figure C-4**). We found that individual differences in strategic preferences across participants predicted the relative activation evoked by balanced and extreme choices in only one region: anterior dorsomedial prefrontal cortex (aDMPFC; **Figure 6-5**), along the paracingulate region (BA 9). People who expressed a greater preference for the balanced option exhibited a greater increase in dmPFC activation for the extreme option compared to the balanced option, and vice versa. The

difference in activation also correlated with an independent trait measure of need for cognition (Epstein et al., 1996b), which measures the relative cognitive effort associated with decision making (r=0.60, p<0.005, **Appendix Figure C-5**).

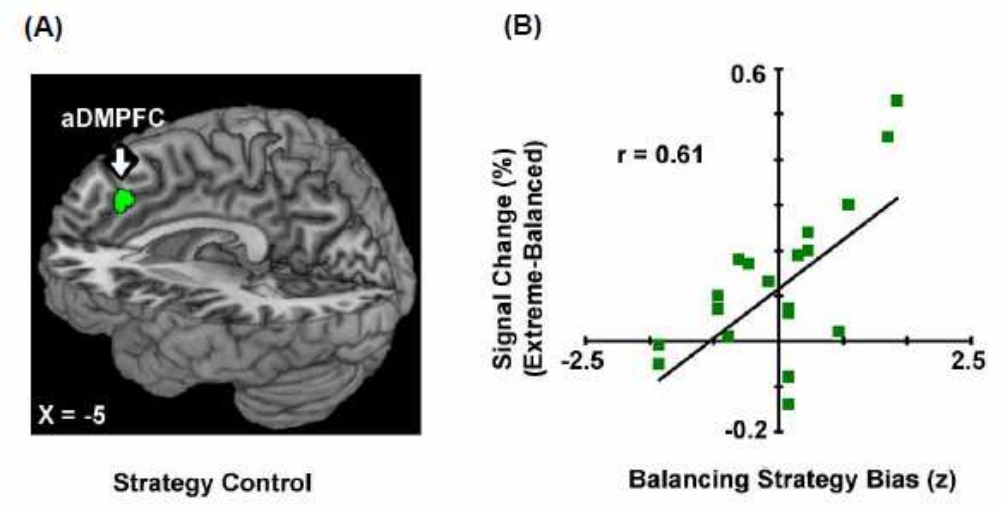


Figure 6-5: Activation in anterior dmPFC predicted strategy-related control demands

To verify that the clusters implicated in strategy- and decision-related control were functionally distinct, we conducted a *post hoc* ROI analysis within the aDMPFC and mDMPFC regions. We found that aDMPFC did not show a linear relationship with increasing decision conflict, nor did mDMPFC show a significant correlation with strategic variability across participants **(Appendix Figure C-6)**. Thus, we conclude that these regions made distinct functional contributions to performance of our experimental tasks.

6.2.4 Evidence for a Functional Topography in Dorsomedial PFC

The results presented above provide strong evidence for a functional topography within the dmPFC: the most anterior cluster tracked strategy-related control, a middle

cluster predicted decision-related control, and a more posterior cluster tracked response-related control (**Figure 6-6**). To ascertain the consistency of these results with the prior literature, we conducted a meta-analysis of 53 studies that reported dmPFC activation in tasks involving decision making and/or cognitive control. We classified each study as involving either decision-related or response-related control, based on task properties, and included every reported coordinate of medial frontal cortex activation in an Activation Likelihood Estimation (ALE) analysis (see **Appendix C**). We exclude strategy-related control in this meta-analysis due to lack of prior work in this area (but see De Martino et al., 2006; Venkatraman et al., 2009b).

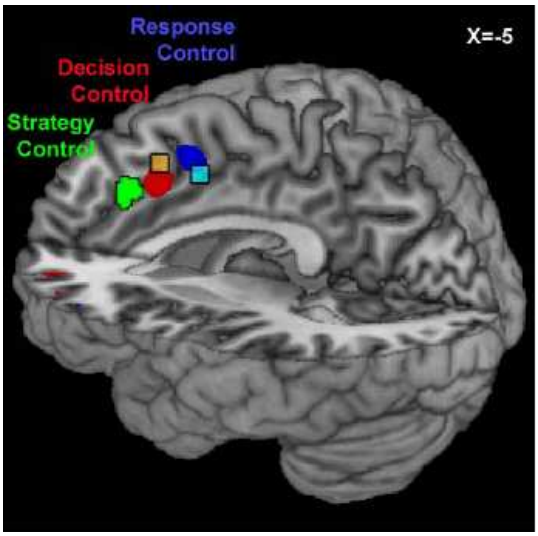


Figure 6-6: Summary of a functional topography in the dmPFC based on varying control demands

Our meta-analysis revealed a strong spatial dissociation within dmPFC between activations related to decisions and to responses, with more anterior regions being involved in decision-making and more posterior regions with response-related cognitive control **(Appendix Figure C-7)**. The centroids of maximum likelihood overlapped with

the observed activations for decision-related and response-related control demands in our study (**Figure 6-6**, solid squares), and both are posterior to the focus for strategy-related control in aDMPFC.

6.3 Discussion

We used tasks that evoked three distinct forms of control demands – response, decision, and strategy – and found strong evidence for a posterior to anterior topography within the dmPFC. Three distinct foci of activation were identified based on separate behavioral measures using data from the same individuals. These results both provide new insight into the functional organization of dmPFC and suggest a reconciliation of recent controversies about that region's role in complex decision-making and cognitive control.

Control demands play an important role in adaptive decision-making, particularly since decision preferences are strongly influenced by context (Simonson and Tversky, 1992; Tversky and Simonson, 1993). For example, people avoid decision options that seem extreme, whether compared to their alternatives or whether having attributes with highly disparate values (Chernev, 2004, 2005). Options that are balanced (e.g., their scores on various attributes are more equal) thus frequently serve as a desirable compromise relative to options containing attributes with high dispersion. We introduced a similar biasing context in the current study, which used an abstract market environment with anonymized options to control for participants' differential prior exposure to stocks. This task allowed us to manipulate the degree of decision-related and strategy-related

control independently, the former by varying the relative desirability of the choices and the latter by measuring individual variability in strategic bias.

Several aspects of our experimental design allow us to conclude that these distinct forms of control were represented in distinct regions within dmPFC. First, we explicitly separated the decision phase from the response phase so that activations related to decision control cannot be attributed to confounding effects from response selection or motor preparation (Pochon et al., 2008). Second, participants received no immediate feedback about their decisions when choosing between different stocks; instead, feedback was provided in a separate, later run. This allowed us to rule out effects of outcome history when characterizing our participants' decision preferences, while also precluding alternative explanations for the observed dmPFC activation like error detection, reinforcement learning, and signaling reward prediction errors (Kiehl et al., 2000; Kerns et al., 2004; Kennerley et al., 2006; Kim et al., 2006). We do not claim that dmPFC plays no role in these functions, but note that they did not contribute to the activations observed in this experiment. Third, we used an independent counting Stroop task to elucidate neural mechanisms of response-related control. Fourth, all analyses were conducted within the same set of participants, as critical for making clear spatial comparisons. And, finally, our distinct forms of control demands were each associated with a unique and independent behavioral covariate.

Several studies have found increased activation in the dmPFC associated with complex decision making (Paulus et al., 2002; Walton et al., 2003; Rushworth et al., 2004; Zysset et al., 2006; Botvinick and Rosen, 2008; Pochon et al., 2008), though these

findings could be confounded by activation related to response preparation (Pochon et al., 2008). A more recent study using a perceptual decision-making task sought to explore the role of dmPFC in decision conflict, defined as the difficulty arising from choosing between two equally likely choices, while accounting for response-related activation (Pochon et al., 2008). They demonstrated greater dmPFC activation for decisions involving alternatives that were equally attractive, even in the absence of an explicit response (e.g., precluding an explanation in terms of response-related control). Activation within this region also varied with subjective ratings of decision difficulty. While Pochon and colleagues did not include additional conditions to allow testing of topographic organization, the manipulation of decision conflict in that study led to activation in regions of the dmPFC similar to those associated with decision-related control in our current study.

Moreover, there are initial suggestions that dmPFC is also recruited when individuals make choices that run counter to general behavioural tendencies or strategies (Paulus et al., 2002; De Martino et al., 2006; Hampton and O'Doherty J, 2007), although these have heretofore been discussed in terms of decision preferences. Studies involving complex decision making have often focused on identifying brain systems that shape behaviour towards or against particular choices. Yet, it is becoming increasingly apparent that people employ a variety of strategies to simplify the representations of decision problems and reduce computational demands (Tversky and Kahneman, 1974; Payne et al., 1988; Payne et al., 1992b; Gigerenzer and Goldstein, 1996). In this study, we show that activation in a similar region of the dmPFC predicts variability in strategy-related

control across participants. Specifically, individuals with greater bias for the balancing strategy exhibited a greater increase in activation for the extreme choices compared to the balanced choices, and vice versa. Strikingly, the cluster within dmPFC associated with strategy-related control was anterior to and functionally distinct from the clusters associated with decision-related control and response-related control. Therefore, a parsimonious explanation for the role of dmPFC in complex decision making is that distinct functional clusters might be associated with distinct aspects of decision making, including strategy preferences and response preparation.

One potential conjecture for functional specialization within the dmPFC is related to differences in connectivity of these clusters to other regions in the brain. A commonly held framework, one advanced in different guises by different theorists, suggests that lateral prefrontal cortex contains a topographic organization along its posterior to anterior axis (Koechlin et al., 2000; Koechlin et al., 2003). More posterior regions, those immediately adjacent to premotor cortex, are associated with setting up general rules for behavior. Conversely, more anterior regions support the instantiation of rules for behavior based on the current context. Findings from functional neuroimaging studies argue for further divisions within anterior prefrontal cortex, such that regions around the frontal pole support relational integration, or the combination of disparate information into a single judgment (Christoff et al., 2001). We speculate that the different regions of dmPFC differ in their lateral prefrontal targets.

Initial evidence for such a functional organization stems from a recent study that demonstrates choice-specific changes in the functional connectivity of the dmPFC with

other regions involved in decision-making (Venkatraman et al., 2009b). Similarly, Beckmann and colleagues used magnetic resonance diffusion tractography to delineate probabilistic anatomical connectivity of the cingulate cortex to other brain regions (Beckmann et al., 2009). The authors found that the lateral prefrontal cortex exhibited the highest probability of anatomical connectivity with a cluster that corresponds spatially to the region that predicts decision-related control in our study, while the premotor and precentral cortices showed highest probability of connection with a cluster that predicted response-related control in the present study. Under this perspective, the current results point to a generalized role for the dmPFC in cognitive control, but specific computational roles for its subregions depending upon the task demands and current context.

Elucidating the functional connectivity of the different clusters in the dmPFC with corresponding lateral prefrontal cortex may hold the key to fully understanding its role in decision-making. In a follow-up study discussed in the next chapter, we sought to explore this connectivity using resting-state fMRI data from three independent datasets across different scanners.

7 A Parallel Functional Topography between Medial and Lateral Prefrontal Cortex[†]

A hallmark of the cerebral cortex is its topographic organization. Topographies have been long-recognized within sensory and motor systems, whose spatial and somatotopic maps were elucidated in early animal and subsequent human research (Udin and Fawcett, 1988; Reep et al., 1996; Swindale, 1996; Kaas, 1997; Schneider et al., 2004; Silver and Kastner, 2009). Other cortical regions, however, have less obvious large-scale structure. While early conceptions of the prefrontal cortex (PFC) were shaped by the lack of clear functional deficits associated with specific lesions (Ferrier, 1886; Lashley, 1929, 1950; Tizard, 1959), recent theoretical models have argued that all of PFC conjointly supports the adaptive control of behavior (Fuster et al., 2000; Miller and Cohen, 2001).

Within the last decade, functional neuroimaging has generated models of dlPFC that contain a topographic organization (Christoff and Gabrieli, 2000; Koechlin et al., 2000; Koechlin et al., 2003; Christoff and Keramatian, 2007; Koechlin and Summerfield, 2007; Badre and D'Esposito, 2009). Although the specific mapping of regions to functions differs across models, all share some familial properties: posterior dlPFC controls relatively simple mappings of stimuli to actions, anterior dlPFC shapes complex conditional relationships among behavioral rules, and information flows between regions in a largely hierarchical fashion from anterior to posterior regions.

[†] The contents of this chapter have been published as "Venkatraman V, Taren AA, Huettel SA (In press). A parallel functional topography between medial and lateral prefrontal cortex: Evidence and implications for Cognitive Control, J. Neurosci".

Considerably less is known about the organization of dorsomedial PFC (dmPFC). It contributes to a welter of cognitive processes, including monitoring performance, selecting actions based on goals, anticipating rewards, and signaling errors and adverse outcomes (Bush et al., 2000; Ridderinkhof et al., 2004a; Ridderinkhof et al., 2004b). One popular view is that this functional diversity parallels apparent structural heterogeneity, with the above processes considered to be intercalated throughout this region (Ridderinkhof et al., 2004b). Yet, recent evidence from neuroimaging studies suggests that dmPFC has functional, and potentially topographic, subdivisions. Direct comparison of three distinct types of cognitive control demands – response-related, decision-related, and strategy-related – revealed a posterior-to-anterior gradient reflecting the transition from simple to higher-order rules for control (Venkatraman et al., 2009a). Moreover, recent structural analyses indicate that subdivisions of cingulate cortex have distinct white-matter connectivity profiles (Beckmann et al., 2009), particularly with respect to the lateral PFC.

We hypothesized that the dlPFC and dmPFC share a common topographic pattern of functional connectivity, consistent both with the known anatomical connections between these regions (Petrides and Pandya, 1999; Petrides, 2005) and their putative joint contributions to cognitive control (Ridderinkhof et al., 2004a; Egner, 2009; Kouneiher et al., 2009). Here, we mapped functional connectivity within prefrontal cortex using resting-state fMRI (Fransson, 2005; Damoiseaux et al., 2006; De Luca et al., 2006; Margulies et al., 2007), drawing data from a large primary dataset and from two independent replications collected on different scanners. Our results demonstrated a clear

posterior-to-anterior gradient in connectivity: posterior dmPFC regions were maximally connected to posterior dlPFC regions, whereas anterior dmPFC regions were maximally connected to anterior dlPFC regions. This parallel topography supports an integrative and hierarchical view of PFC, such that its medial and lateral aspects jointly contribute to the adaptive control of behavior.

7.1 Methods

Participants and Data Collection: Primary Dataset. Sixty-four young adults (32 female, mean age = 24, range 18-43) participated in the primary experiment. All participants received monetary compensation for their participation in the study. Twelve participants were excluded before data analysis due to excessive motion (>2 mm), leaving a total of 52 participants (26 female) in the final analyses. All participants gave written informed consent as part of protocols approved by the Institutional Review Board of Duke University Medical Center.

We report data from a 6-minute resting-state scan, which was obtained at the end of a 90-minute experimental session. During this scan, participants were instructed to keep their eyes open, to focus on the fixation cross that was presented in the center of the screen, to remain alert, and to refrain from directing their thoughts toward anything specific.

Data were acquired on a 4T GE scanner using an inverse-spiral pulse sequence (Guo and Song, 2003) with the following parameters: TR = 2000 ms; TE = 27 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 individual participants' data.

Participants and Data Collection: Replication Datasets. We replicated all analyses in resting-state data from two additional datasets collected on different scanners, with different pulse sequences, and with different groups of participants. Twenty-two young adults (11 female, mean age = 23, range 19-32) participated in Replication 1. Fifteen young adults (5 female, mean age = 22, range 20-24) participated in Replication 2. All participants gave written informed consent as part of protocols approved by the Institutional Review Boards of Duke University Medical Center or of the Duke-NUS Graduate Medical School, Singapore.

Replication 1 data were acquired on a 3T GE scanner using a SENSE spiral pulse sequence with the following parameters: TR = 2000 ms; TE = 27 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 individual participants' data. Replication 2 data were acquired on a 3T Siemens scanner using an inverse spiral pulse sequence 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 T1-weighted MPRAGE anatomical images were acquired and used for normalizing individual participants' data.

Data Analyses. We used FEAT (FMRI Expert Analysis Tool) Version 5.92, part of FSL (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl) package (Smith et al., 2004). Preprocessing consisted of 1) motion correction using MCFLIRT (Motion

Correction using fMRIB's Linear Registration Tool), 2) slice timing correction, 3) removal of non-brain voxels using BET (Brain Extraction Tool), 4) spatial smoothing using a Gaussian kernel with full-width at half maximum 6mm, and 5) high pass temporal filtering (cutoff = 100s). Normalization to MNI standard space was carried out using FLIRT.

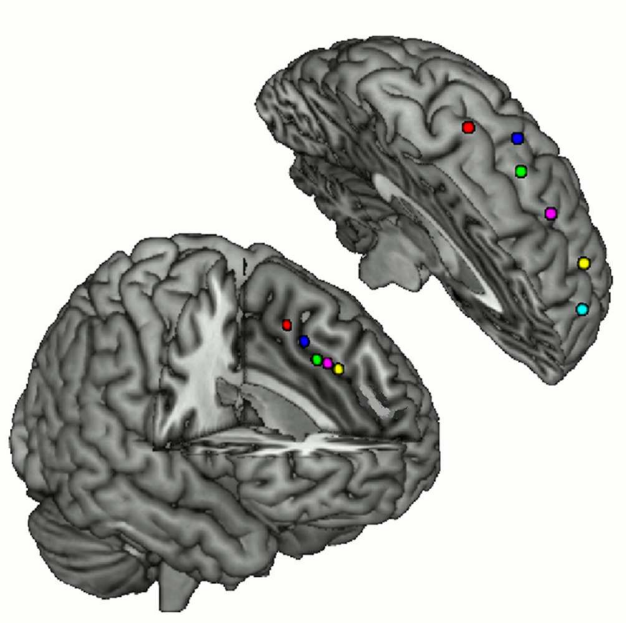


Figure 7-1: Selected seed regions in the medial and lateral PFC

Functional Connectivity: Selection of Seed Regions. We identified 5 seed regions in the dmPFC, hereafter described using the nomenclature DM1 through DM5 (i.e., posterior to anterior). The peak coordinates of these seeds were taken from previous work indicating distinct foci for response-, decision-, and strategy-related control (Venkatraman et al., 2009a), which became DM1, DM3, and DM5, respectively. The remaining two seeds, DM2 and DM4, were defined by linear interpolation between the above pairs of neighboring coordinates **(Figure 7-1, Table 7-1)**.

Table 7-1: MNI coordinates for dmPFC and dlPFC seed regions

	MNI			Functional Contrast	Source
	X	y	z		
DM1	-4	10	50	Response conflict	(Venkatraman et al., 2009a)
DM2	-4	16	45	-	Interpolated (DM1 and DM3)
DM3	-6	23	39	Decision conflict	(Venkatraman et al., 2009a)
DM4	-4	30	37	-	Interpolated (DM3 and DM5)
DM5	-6	35	34	Strategy conflict	(Venkatraman et al., 2009a)
DL1	-32	-11	60	Stimulus effect	(Koechlin et al., 2003)
DL2	-51	-2	39	-	Interpolated (DL1 and DL3)
DL3	-44	7	22	Context effect	(Koechlin et al., 2003)
DL4	-46	22	14	-	Interpolated (DL3 and DL5)
DL5	-42	45	7	Episode effect	(Koechlin et al., 2003)
DL6	-30	56	-2	Branching effect	(Koechlin et al., 1999)

We also identified 6 seed regions in the dlPFC, hereafter labeled as DL1 through DL6 (i.e., posterior to anterior). We identified three of the seed regions' peak coordinates based on prior work delineating a dlPFC topography based on stimulus, context and integrative demands (Koechlin et al., 2003); these became seeds DL1, DL3, and DL5 (Table 1). The intermediate seeds DL2 and DL4 were defined by linear interpolation between neighboring coordinates and coordinates for DL6 were determined based on prior work associating activation in the anterior prefrontal cortex with cognitive branching (Koechlin et al., 1999). Each seed consisted of 33 2mm x 2mm x 2mm voxels (defined using a sphere of radius 2 voxels around the peak coordinate described in Table

1). Time-series signal for all subsequent analyses was obtained by averaging data across all voxels within each seed.

Functional Connectivity: Data Analysis. To map the pattern of functional connectivity between medial and lateral PFC, we began with a dmPFC mask that included the anterior cingulate gyrus and the medial superior frontal gyrus. Following normalization of each participant's data to the standard MNI space, we extracted the time-series from each dmPFC voxel and measured the functional connectivity with each of the six dlPFC seed regions. This provided a voxel-by-voxel map, for each participant, of the correlation between each point in dmPFC with each of the seed regions in the dlPFC. The corresponding analysis was also performed to obtain a voxel-by-voxel map of the correlation between each point in dlPFC with each of the seed regions in the dmPFC. We used a dlPFC mask, extracted the time-series from each dlPFC voxel, and measured the functional connectivity with each of the five dmPFC seed regions.

The above analysis provides a visual representation of topography in dlPFC based on the seeds in dmPFC, and vice versa. To next evaluate the parallel connectivity between hierarchical regions in the dmPFC and dlPFC, we extracted the preprocessed mean time-series from each of the five dmPFC seed regions and six dlPFC seed regions defined above for every participant. We demeaned all dmPFC and dlPFC time series by subtracting the mean whole-brain time series (extracted from a whole-brain mask for every participant). To obtain a measure of point-to-point connectivity, we computed Pearson correlations between the five dmPFC time series and each of the six dlPFC time series, which were then combined across all participants (significance tests: Pearson

product-moment correlation coefficient, $p < 0.05$, two-tailed). All analyses were repeated independently for the left and right hemispheres.

Functional Connectivity: Specificity Analysis. For each dmPFC seed, we calculated the standard deviation of the correlation values to each of the six dlPFC seeds. A lower standard deviation would indicate broad, similar connectivity of voxels within that seed to different regions in the dlPFC, while a higher standard deviation would indicate greater specificity such that connectivity strength varies across seeds. To statistically test the presence of an anterior-posterior gradient in specificity, we ran an ANOVA of the standard deviation values for each of the five different dmPFC seeds across participants, followed by *post hoc* tests of specific seed pairs.

Regression Analyses. Each dlPFC/dmPFC correlation for each participant was entered as an observation (i.e., 30 pairwise correlations per participant) into an OLS regression analysis (JMP Version 7; SAS Institute Inc., Cary, NC). Each dlPFC/dmPFC correlation was served as a dependent variable, and explanatory variables included dmPFC region (normalized posterior to anterior as -1 to 1), dlPFC region (-1 to 1), a dmPFC*dlPFC interaction term, and a categorical variable coding for the data set from which each observation originated (primary, Replication 1, or Replication 2). Using spatial locations as predictors allowed us to answer the question of whether interaction between spatial locations predicts dmPFC-dlPFC correlation (i.e. our measure of connectivity). This analysis was run using the aggregate observations from all three data sets, and was replicated using only the primary data set.

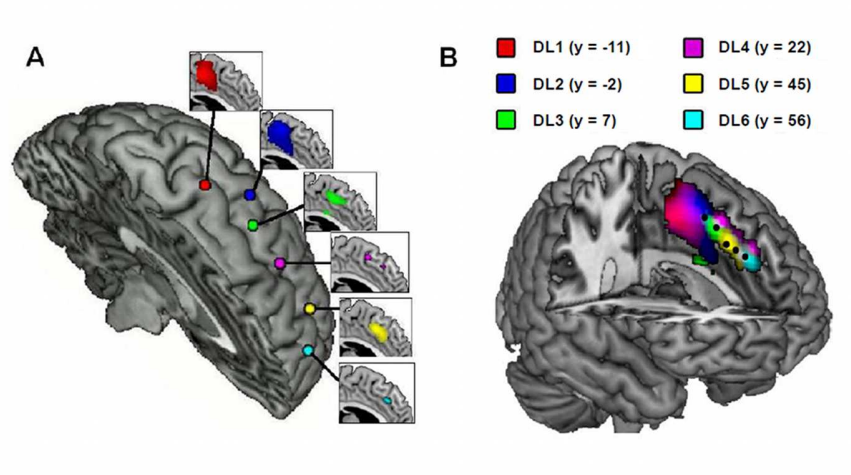


Figure 7-2: The dmPFC exhibited a topographically organized connectivity pattern with dlPFC

7.2 Results

We measured the unique, non-directional functional connectivity between locations within dmPFC and dlPFC using two independent methods, each controlling for the common fMRI signal covariation between the regions as a whole. First, we examined the connectivity between each of the six dlPFC seed regions and every voxel in dmPFC, defined anatomically. The results demonstrate a posterior-to-anterior gradient in connectivity, with posterior dlPFC having maximal connectivity to posterior dmPFC and anterior dlPFC having maximal connectivity to anterior dmPFC **(Figure 7-2)**. The corresponding analysis of connectivity between each of the five dmPFC seed regions and every voxel in dlPFC produces a similar gradient. Second, we examined point-to-point connectivity between the pre-selected seed regions in dlPFC and dmPFC. We found a similar topographic pattern when focusing on just the connectivity between seed regions, independently for both the left **(Figure 7-3A, Table 7-2)** and right hemispheres **(Figure**

7-3B, Table 2). This topography was replicated in two additional data sets collected on different scanners, with different participants, and using different imaging parameters.

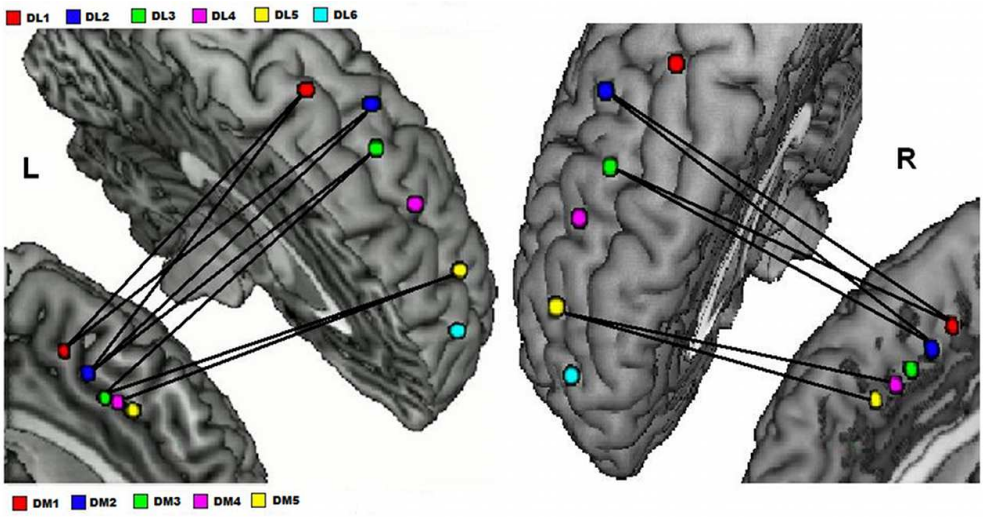


Figure 7-3: Pairwise connectivity between dmPFC and dlPFC functional regions.

We next evaluated the spatial pattern of functional connectivity using a regression analysis. Point-to-point connectivity values, for all pairs of dmPFC and dlPFC regions and for all participants, were included as dependent variables in the model. Predictor variables were dmPFC spatial location (i.e., 5 levels), dlPFC spatial location (i.e., 6 levels), and their interaction. Note that this analysis controls for any overall effects of increased connectivity in either posterior or anterior regions; of primary interest would be a significant interaction, such that connectivity is maximal between regions matched spatially. We found that the dmPFC*dlPFC interaction term was highly significant in both the left and right hemispheres (all *p*s $< 10^{-10}$; **Table 7-3**). This effect held both for the primary data set (when considered alone) and for the combination of all three data

sets, when including data set as an additional categorical predictor variable (all *p*s < 10^{-10} in similar analyses to those of Table 7-3).

Table 7-2: Pairwise correlations between each dmPFC and dlPFC seed region for each hemisphere.

Primary Dataset										
	Left Hemisphere					**Right Hemisphere**				
	DM1	**DM2**	**DM3**	**DM4**	**DM5**	**DM1**	**DM2**	**DM3**	**DM4**	**DM5**
DL1	0.45	0.24	0.19	0.10	0.08	0.26	0.19	0.11	0.04	-0.00
DL2	0.34	0.31	0.26	0.15	0.13	0.47	0.39	0.20	0.18	0.12
DL3	0.24	0.37	0.32	0.25	0.21	0.30	0.29	0.15	0.18	0.15
DL4	0.11	0.25	0.21	0.24	0.25	0.17	0.12	0.14	0.17	0.16
DL5	0.04	0.26	0.30	0.28	0.24	0.17	0.21	0.20	0.28	0.28
DL6	0.02	0.05	0.07	0.16	0.17	-0.04	-0.01	0.12	0.17	0.22

Finally, we evaluated whether these findings held for individual participants. We determined, for each participant and each dmPFC seed, the seed in dlPFC to which there was maximal functional connectivity. This provides a conservative measure of point-to-point connectivity, in that it collapses the entire distribution of connectivity values to a single maximum. As hypothesized, these maxima clustered along the diagonal, consistent with a parallel topography at the individual level in both hemispheres (left hemisphere is shown in **Figure 7-4**). A similar pattern was seen in our two replications.

Table 7-3: Summary of regression analysis using data pooled from all experiments.

	Left Hemisphere		Right Hemisphere	
	β	***p***	**β**	***P***
Intercept	0.21	$<10^{-20}$	0.18	$<10^{-20}$
dmPFC	-0.02	0.01	-0.04	$<10^{-7}$
dlPFC	-0.02	0.01	0.01	<0.04
dmPFC*dlPFC	0.18	$<10^{-20}$	0.19	$<10^{-20}$

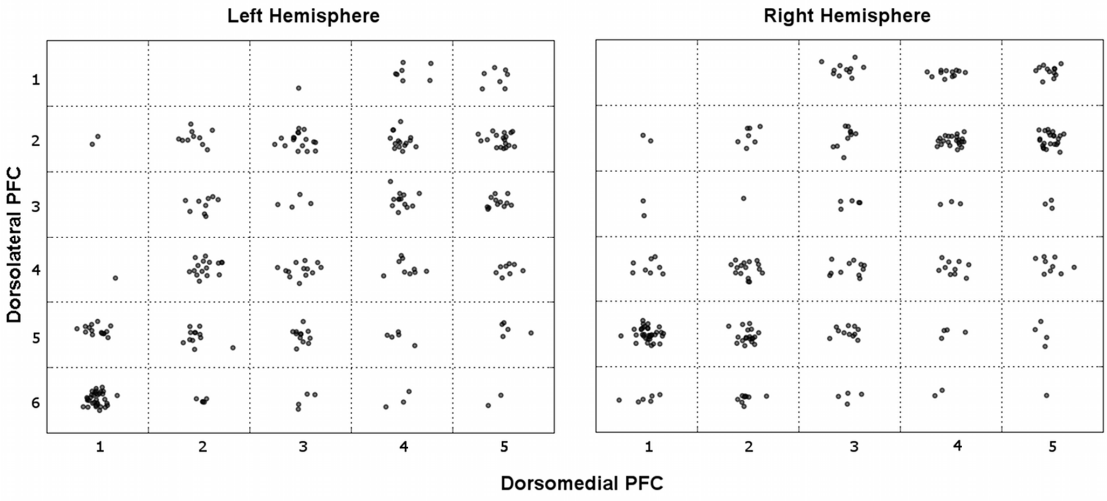


Figure 7-4: Individual participants' maximally correlated dmPFC-dlPFC pairs reveal parallel topography

We additionally observed that the specificity of the functional connectivity decreased when moving along the posterior-to-anterior gradient (cf. **Figure 7-4**) within the dmPFC. We computed the standard deviation of connectivity values from each dmPFC seed to the set of the six dlPFC seeds. There was a significant decrease from

posterior to anterior dmPFC seeds ($F(4,255) = 2.77$, $p = 0.02$). Voxels in posterior dmPFC exhibited greater specificity (mean = 0.23) in connectivity to dlPFC seeds than did voxels in anterior dmPFC (mean = 0.18, $t(51) = 3.20$, $p = 0.002$).

7.3 Discussion

Several lines of empirical evidence have suggested a hierarchical rostral-to-caudal organization within the dlPFC, with neurons in the more rostral regions processing more abstract goals and neurons in the more posterior regions processing more concrete information related to corresponding motor actions (Fuster et al., 2000; Fuster, 2001, 2004; Koechlin and Summerfield, 2007). More recent evidence also suggests a similar anterior-to-posterior topography within the dmPFC, with the more anterior regions being associated with more complex and abstract levels of cognitive control (Venkatraman et al., 2009b; Venkatraman et al., 2009a). Given the strong anatomical evidence for reciprocal connections between these regions based on studies in non-human primates (Bates and Goldman-Rakic, 1993; Petrides and Pandya, 1999), a natural hypothesis is that monitoring-related activity in dmPFC engages regulatory processes in the dlPFC that shape behavior (Botvinick et al., 2001; Kerns et al., 2004; Botvinick, 2008). Yet, despite the striking similarity in their hierarchical organization, it has been unclear whether a similar gradient also exists in the functional connectivity between these regions.

In one recent study, Kouneiher and colleagues demonstrate that the medial prefrontal cortex regulates processing resources in the lateral PFC according to motivational incentives. Specifically, there is increased effective connectivity between posterior dmPFC (pre-SMA) and posterior dlPFC for contextual incentives and increased

connectivity between middle dmPFC and mid-dlPFC for episodic incentives. However, there was no increased connectivity during control conditions that lacked such incentives. Therefore, the authors argue for a posterior-to-anterior hierarchical system of executive processes in the medial and lateral PFC with the functional interactions between them conveying motivational incentives rather than simple control demands (Kouneiher et al., 2009).

In the current study, we used spontaneous fluctuations in BOLD activity to characterize further the functional connectivity between the medial and lateral prefrontal regions in the absence of task-associated cognitive processes. This task-free approach using resting-state data relies on correlations among low-frequency BOLD changes to identify regions that function in tandem. Using such an approach, we demonstrated a posterior-to-anterior gradient in connectivity between the medial and lateral prefrontal regions, with posterior dlPFC having maximal connectivity to posterior dmPFC and anterior dlPFC to anterior dmPFC. This pattern replicated in three independent datasets collected using three different MR scanners and was evident even in individual participants.

This pattern of resting-state functional connectivity is consistent with prior mappings of structural connectivity between these regions in both non-human primates (Petrides and Pandya, 1999) and humans (Beckmann et al., 2009). Petrides and Pandya used florescent tracers placed in selected areas of the dorsolateral frontal cortex of monkeys to study their connectivity to the rest of the brain (Petrides and Pandya, 1999). They found that injections placed in posterior dlPFC (similar to DL1 in our study)

revealed labeled neurons in posterior dmPFC regions of the SMA, pre-SMA, and cingulate sulcus (similar to DM1 in our study). On the other hand, injections placed in mid-dlPFC (corresponding roughly to DL3 seed in our study) revealed labeled cells in a more anterior part of cingulate cortex (here, roughly DM3). Similar connection patterns in the medial regions were also observed for injections placed in rostrolateral dlPFC (corresponding to DL6 seed in our study). These findings suggest strong intrinsic structural connectivity between lateral and medial prefrontal regions in the macaque cortex.

In another study involving magnetic resonance tractography-based parcellation of the human cingulate cortex (Beckmann et al., 2009), the dorsolateral prefrontal regions (consistent with seeds DL3 and DL4 in our study) showed greatest connectivity with anterior cingulate sulcus (similar to DM4 in our study), while the premotor regions (overlapping with our seeds DL1 and DL2) showed greatest connectivity with the pre-SMA and more posterior regions within the cingulate (overlapping with seeds DM1 and DM2). Therefore, these studies provide independent evidence across different modalities about the robustness of the functional connections between these regions. Though these methods are largely agnostic about the directionality of these interactions, the findings of Kouneiher and colleagues suggests that the medial frontal regions may regulate the cognitive control resources in the lateral regions according to motivational incentives (Kouneiher et al., 2009). Therefore, we speculate that dmPFC exerts a regulatory or modulatory influence on dlPFC (Wood and Grafman, 2003; Egner, 2009; Kouneiher et al., 2009).

8 Conclusions

8.1 Neuroeconomics: From Variables to Strategies

Neuroeconomic research will, for the foreseeable future, continue to be focused on identifying neural mechanisms that underlie decision variables and the operators that process those variables. While elucidating the many factors that contribute to even simple decisions is important, findings across a series of risky choices experiments across different modalities presented earlier suggest that identifying the factors that shape how people differentially represent decision problems, both across contexts and across individuals, will become an increasingly critical topic.

Such an increased focus on strategic variability would have several salutary consequences. First, it would provide an avenue by which neuroscience data could be extended to modeling in economics (and other social sciences). A common criticism of neuroeconomics, at least among economic theorists, is that neuroscience data is simply irrelevant for core models in economics. Where such theories cannot be derived from first principles, it is argued, they can be identified based on expressed behavior without recourse to internal neural mechanisms. This criticism, which we have labeled the "behavioral sufficiency" argument, can be countered on several grounds (Clithero et al., 2008). Most relevant for the current topic, economic models of behavior are disconnected from the substantial psychological and neuroscientific literature on individual differences. Because of this disconnect, a model may well describe behavior of young adults making decisions in a relaxed setting, but nevertheless have little predictive validity when applied to older adults making decisions under time pressure. To the extent that neuroscience can

illuminate the mechanisms underlying individual choice biases and strategic preferences, it may become critical for creating robust and flexible models of real-world decision behavior.

Second, there will be substantial value in moving descriptions of decision mechanisms – within neuroeconomics, cognitive psychology, behavioral economics, and even the lay public – away from the oft-claimed interaction between competing decision systems. Clearly, there has been substantial process in mapping specific decision variables to specific brain regions. Yet, considering decisions to reflect the simple interactions between sets of these regions would be, much like hydraulic theories of personality, an unnecessary and misleading oversimplification. No one region, nor any set of regions, can be unambiguously claimed to implement a rational decision-making process. Instead, specific brain regions contribute to particular computations, which may or may not be consistent with models for rational behavior. Some such regions may even exert context-dependent influences, like that shown for dmPFC in the final experiment, making it impossible to categorize them within a two-systems framework (Frank et al., 2009).

Third and finally, results also indicate that an important direction for neuroeconomics will be to strengthen its connections to the broader cognitive neuroscience literature. For example, findings presented here are consistent with the growing consensus that dmPFC reflects a mechanism for identifying and responding adaptively to changes in the environment. Notably, complex aspects of behavior, like full consideration of decision problems, require a wide range of processes of executive

control. By adopting simplifying rules for behavior, and only changing those rules when environmental conditions change, the brain can operate with a much-reduced metabolic demand. The dmPFC plays such a role in complex decision making, signaling changes in how a decision problem is represented and thus shaping computational processing elsewhere in the brain based on the current decision strategy. Such strategic considerations are unlikely to limited to abstract economic decisions; they are also likely to be critical for interpersonal interactions in social contexts (Camerer, 2003a) and other social behaviors (Behrens et al., 2008; Behrens et al., 2009).

This role of dmPFC in *strategic* control during complex decision making can be integrated into a broader role for this region in cognitive control. In other words, there is now evidence both for generalized contributions of the dmPFC to cognitive control, and for specific computational roles for its subregions depending upon the task demands and context. Specifically, there is a hierarchical functional organization within this region, such that the posterior dmPFC supports response-related control, middle dmPFC supports decision-related control and the anterior dmPFC supports more abstract strategic control. Strikingly, such a hierarchical role extends also to the connections between the functional nodes in the medial and lateral prefrontal cortex, leading to a new neuroanatomical model of cognitive control.

8.2 A Hierarchical Model for Cognitive Control

Based on findings across several studies discussed in this dissertation, it is evident different regions of dmPFC and dlPFC interact to guide the adaptive control of behavior according to the computational demands of the task **(Figure 8-1)**. The proposed model

extends the hierarchical organization postulated for dlPFC to include a parallel organization in dmPFC, whose subregions shape processing in their lateral counterparts. That is, the anterior dmPFC regulates activity in the anterior dlPFC when the control demands are associated with high levels of abstraction (e.g., implementing strategic planning in a decision-making task), while the posterior dmPFC works in concert with posterior dlPFC and premotor cortices when the control demands are limited to choosing between two competing responses.

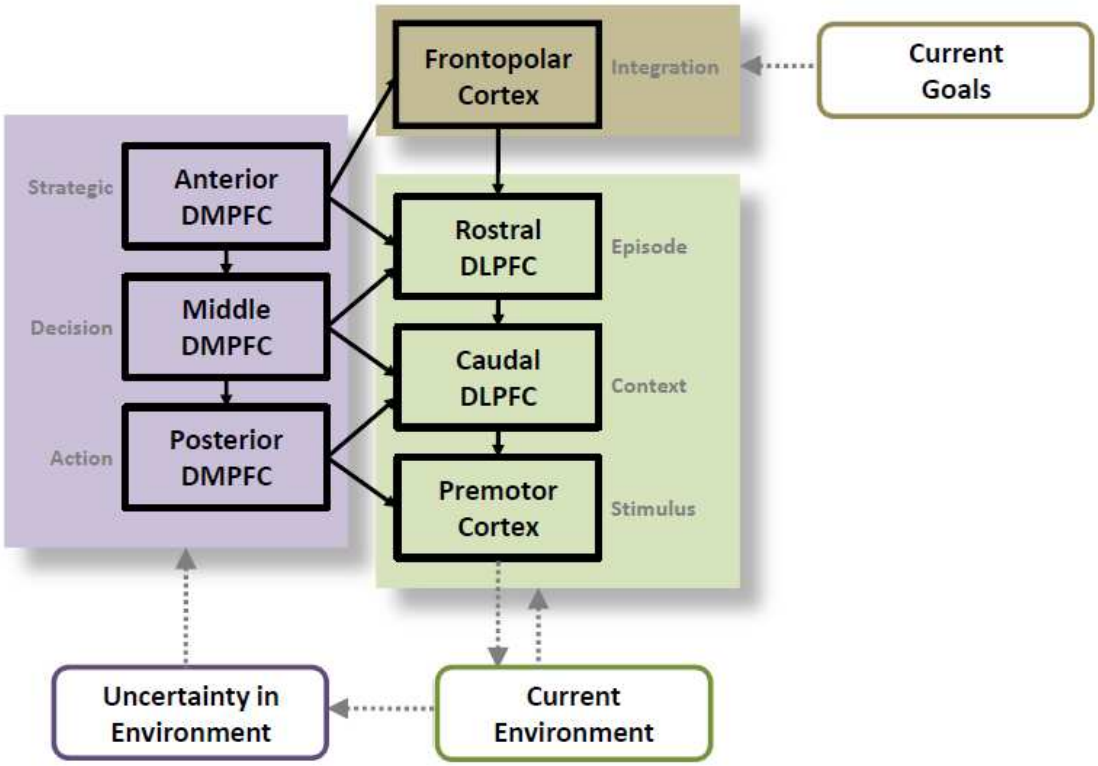


Figure 8-1: A hypothetical hierarchical model for cognitive control

While the emphasis here is primarily on potential medial-to-lateral effects, bidirectional influences are likely: dmPFC activity may be biased by dlPFC inputs,

consistent with the former's role in monitoring reward-value of action sets according to outcomes (Daw et al., 2006; Kennerley et al., 2006). Moreover, whether these regions interact in a hierarchical fashion remains a provocative question. Anterior regions of dlPFC influence processing in posterior regions of dlPFC in a task-dependent manner (Koechlin et al., 2003; Kouneiher et al., 2009), and damage to more anterior portions of prefrontal cortex leads to deficits on a wider array of tasks, including abstract processing (Badre and D'Esposito, 2009). The finding that the more anterior regions in the dmPFC demonstrate more diffuse projections to the lateral PFC, relative to the posterior regions, provides converging evidence toward a hierarchical perspective.

The new framework proposed here provides empirical evidence for a longstanding conjecture: that the PFC contributes to the temporal integration of behavior by simultaneously maintaining context and goal-related information at several levels (Fuster, 2001, 2004). Fuster argued that automatic behaviors only require integration at lower levels – sensory areas in the posterior perceptual hierarchy and motor areas in the frontal executive hierarchy – while more complex behaviors require integration at higher levels of perceptual and executive hierarchies. This influential conjecture has recently gained significant supporting evidence in the lateral PFC (Koechlin and Summerfield, 2007; Badre et al., 2009). We show that this topography extends to the functional interactions between the medial and lateral PFC. Such a functional gradient in connectivity could reflect a dynamic mechanism for identifying and responding adaptively to contextual changes in behavior.

Appendix A: Supplementary Material for Chapter 3

Stimuli: Trial Types

There were a total of five different types of conditions: (i) the value (amount added to the option) and probability were higher for the reference outcome (Ref_EV^{+}), (ii) the value and probability were the same for both reference and extreme outcomes (Ref_$EV^{=}$), (iii) the value was the same but the probability of the reference outcome was lower (Ref_P^{-}), (iv) the probability was the same but value added to the reference outcome was lower (Ref_V^{-}) and (v) both the probability and the value were lower for the reference option (Ref_EV^{-}). The proportion of Pmax choices was systematically modulated by the tradeoff in expected value of the two types of choices, indicating that participants were not simply insensitive to expected value (**Table A-1**). As seen from the table, the greatest conflict existed when the expected values were equal or close (when only one of value or probability was lower). Therefore, only these trials were included for analyzing the neural correlates of decisions.

Participant Payments

Participants were informed at the beginning of the fMRI session that a portion of their earnings would depend on their choices. Specifically, they would gain or lose money based on the outcomes of two randomly selected gambles (plus a fixed $40 participation payment). They were told that the outcome of each trial would be multiplied by an unknown, but fixed percentage, and that they could lose some or all of a monetary

endowment that was given to them at the start of the experiment. To ensure that choices were incentive-compatible, we gave each participant (before they entered the scanner) a sealed envelope containing both a cash endowment and a message indicating the payment multiplier. The values of the endowment and multiplier were both unknown to the participants. For all participants, the endowment was set at $20 and the multiplier was set at 10%. The final total payoffs ranged from $46 to $76 (mean = $61, s.d. = $8.66).

Behavioral Trait Measures.

At the end of the scanning session, participants completed a series of questionnaires. These included:

1. A Maximization Scale that consists of 13 questions aimed at distinguishing people based on those who try to get the best out of a situation from those who settle for something good enough(Schwartz et al., 2002),
2. Barratt's Impulsiveness Scale (BIS) that consists of 30 questions categorized into cognitive, planning and motor subscales(Patton et al., 1995),
3. A cognition-intuition questionnaire, where the two subscales are faith-in-intuition that leads to more heuristic experiential processing and need-for-cognition that leads to more analytic rational processing(Epstein et al., 1996a),
4. A decision-making styles inventory (DMSI) with sub-scales as rational, intuitive, avoidant, dependent and spontaneous(Scott and Bruce, 1995) and
5. A second decision styles inventory (WN_DMSI) with the sub-scales as analytical, intuitive and regret(Nygren and White, 2002).

Factor Analysis.

Individual participant responses from all subscales of these five questionnaires, along with the behavioral measure of choice tendency from the fMRI experiment, were then subjected to a factor analysis using SPSS. We used principal components analysis to extract the factors and performed varimax rotation of the resulting loading matrices to facilitate interpretation. The extraction criterion was set to an eigenvalue of one or greater.

The behavioral data loaded onto four factors which together accounted for approximately 75% of the total variance; these can be broadly labeled as impulsiveness, magnitude-focus, intuitiveness, and regretfulness in decreasing order of explained variance. The rotated factor matrix for each of the four factors is summarized in **Table A-3**. Loading values with absolute value of 0.5 and greater are shown in the table. We then calculated scores for each factor for each participant, which were then used as covariates in the third-level fMRI analyses to evaluate the robustness and specificity of our findings to strategic variability.

We included participants' scores on each of these factors as across-participants regressors in our third-level analysis looking at differences between magnitude-sensitive compensatory and simplifying Pmax choices. We found that the difference in activation between the two choices within the dmPFC was significantly negatively correlated with the magnitude-focus factor (the preference for simplifying strategy loaded negatively on this factor) but not with any other factor, replicating the interaction effect in Fig 3 in the main text of the manuscript (**Figure A-3**).

Dorsomedial Prefrontal Cortex: Strategy or Response Conflict?

We conducted two additional analysis 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). First, we evaluated whether there was any correlation, across participants, between response time and dmPFC activation, as would be expected in the case of response conflict. No such correlations were found, whether considering each strategy independently or their interaction (**Figure A-4**). Second, participants who selected were indifferent to compensatory and simplifying strategies (hence having maximal response conflict as they choose both options equally often) exhibited low dmPFC activation that was equal for both choices, a finding that is inconsistent with a response-conflict explanation **(Figure A-5)**.

Supplementary Tables

Appendix Table A-1: Proportion of Pmax choices and response times across trial types.

	Proportion of Pmax Choices (%)		**Response Time (s)**	
	Mean	**S.E**	**Mean**	**S.E.**
Ref_EV^{+}	90.58	2.63	0.883	0.068
Ref_EV$^{=}$	69.38	5.18	0.994	0.083
Ref_V^{-}	45.65	5.45	1.091	0.118
Ref_P^{-}	33.70	5.47	1.031	0.117
Ref_EV^{-}	29.17	5.45	0.992	0.088

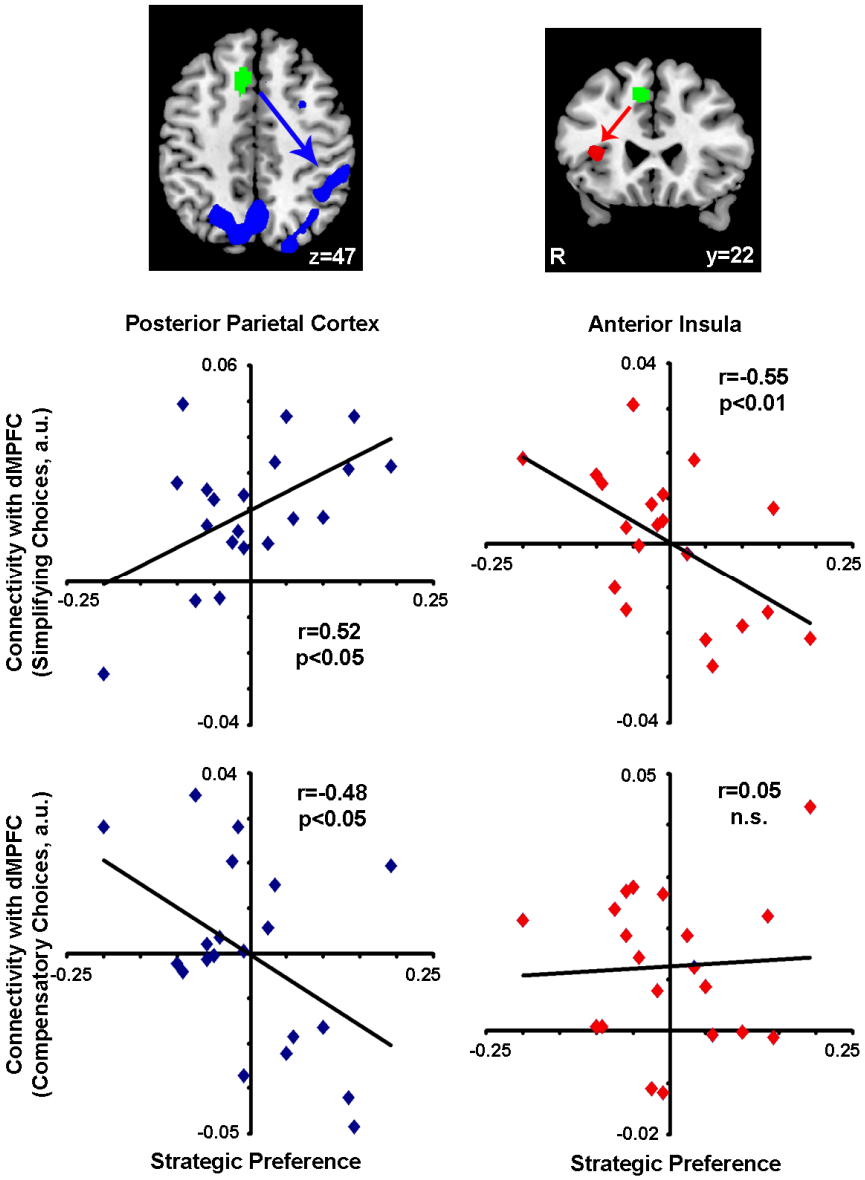
Appendix Table A-2: Peak coordinates of regions that were significantly activated in contrasts of interest.

	MNI Coordinates			Brodmann Area	z-value
	x	y	z		
Compensatory > Simplifying					
Right anterior Insula	38	28	0	13	3.42
Right ventromedial PFC	16	21	-23	11	2.74
Simplifying > Compensatory					
Right Posterior Parietal Cortex	20	-76	57	40	3.40
Precuneus	3	-72	57	7	2.79
Right dorsolateral Prefrontal Cortex	44	44	27	46	2.99
(Compensatory - Simplifying) * Strategy Preference					
Right Inferior Frontal Gyrus	47	42	8	46	3.64
Right dorsolateral Prefrontal Cortex	42	25	22	44	3.14
Dorsomedial Prefrontal Cortex	10	22	45	32	2.99
	10	42	29	32	2.77

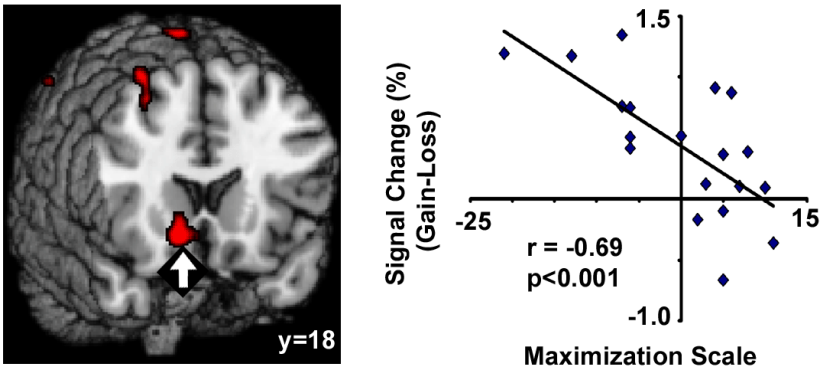
Appendix Table A-3: Behavioral data from questionnaires loaded onto four main factors

	Factor 1	Factor 2	Factor 3	Factor 4
Inferred Factor Label	**Impulsiveness**	**Magnitude-focus**	**Intuitiveness**	**Regretfulness**
BIS				
Nonplanning	0.76	-	-	-
Cognitive	-	0.67	-	-
Motor	0.87	-	-	-
WN-DMSI				
Analytical	-0.78	-	-	-
Intuitive	-	-	0.90	-
Regret-based	-	-	-	0.56
DMSI				
Spontaneity	0.86	-	-	-
Avoidant	-	0.75	-	-
Dependent	-	0.51	-	0.55
Intuitive	-	-	0.91	-
Rational	-0.80	-	-	-
Cognitive-Intuitive				
Need for Cognition	-	-	-	-0.88
Faith in Intuition	-	-	0.76	-
Maximizing Scale	-	0.78	-	-
Pmax Preference	-	-0.71	-	-

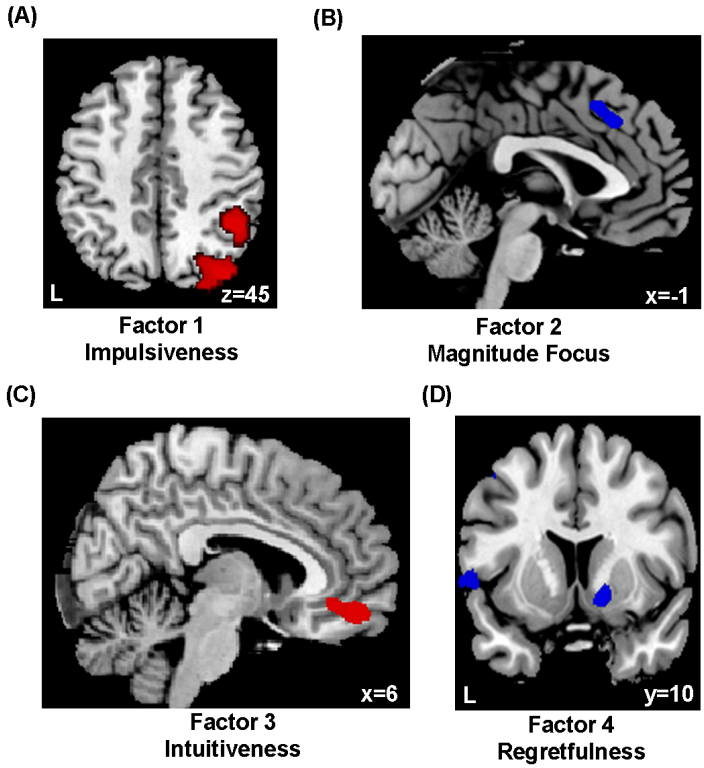
Supplementary Figures



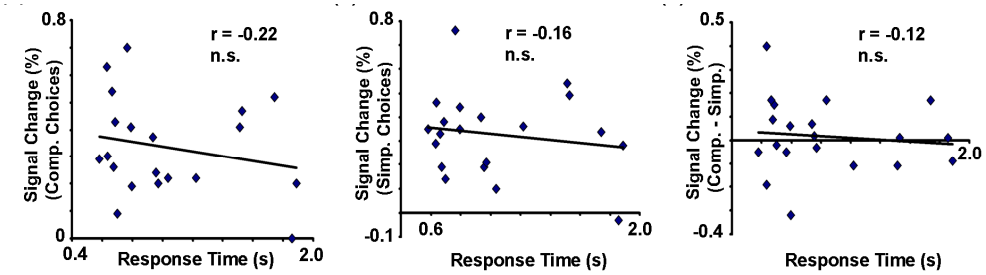
Appendix Figure A-1: Differences in dmPFC connectivity strength predict participant choices



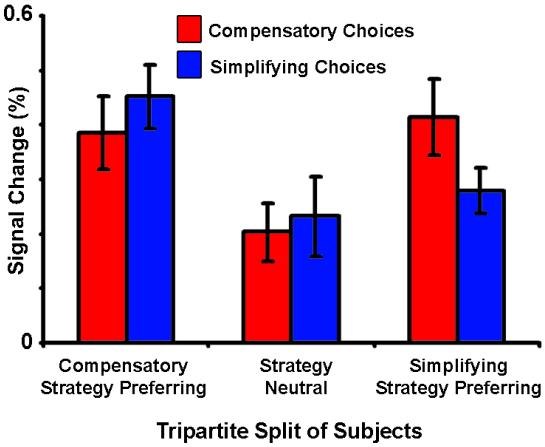
Appendix Figure A-2: Activation in ventral striatum is correlated with maximization trait measure.



Appendix Figure A-3: Areas of activation associated with specific decision factors from Table A-3.



Appendix Figure A-4: Activation in dmPFC is not correlated with response times.



Appendix Figure A-5: Activation in dmPFC is related to strategic control and not response conflict.

Appendix B: Supplementary Material for Chapter 4

Experimental Procedure

Scanning took place at approximately 9:00 AM for the RW session. Prior to the scan, compliance to a regular sleep schedule was verified by inspecting the volunteer's sleep diary and wrist actigraph (Actiwatch, Philips Respironics). Participants also completed a 10-minute psychomotor vigilance task (PVT). For the SD session, participants came to the laboratory at no later than 7:00 PM on the test night after staying awake the whole day. An inspection of their sleep habits was conducted as described for the RW session. Participants were monitored throughout the night and were allowed to engage only in non-strenuous activities such as reading, working on a computer and conversing. Every hour, from 8:00 PM to 5:00 AM, participants completed the 10-minute PVT task and the Karolinska Sleepiness Scale (KSS). Scanning took place at approximately 6:30 AM, close to, or at, the cognitive performance nadir for most persons.

The scanning times were chosen as they represent the start times of a regular workday and the low-point of cognitive performance after a night of sleep deprivation (Doran et al., 2001; Graw et al., 2004). However, we note that this schedule does not align the RW and SD sessions to the same circadian phase and does not allow a decomposition of the effects of sleep deprivation into 'circadian' and 'homeostatic' components. We acknowledge that small circadian phase differences may modulate, but not overcome, large sleep homeostatic effects.

Stimuli: Trial Types

There were a total of five different types of conditions: (a) lower expected value (due to lower amount added as well as lower probability) for Gmax/Lmin choices, (b) equal expected value for both choices, (c) greater expected value for Gmax/Lmin choices due to greater probability of this outcome, (d) greater expected value for Gmax/Lmin due to greater amount being added to this outcome and (e) greater expected value for Gmax/Lmin due to both greater probability and higher amount being added to this outcome. The proportion of choices were systematically modulated by the tradeoff in expected value of the two types of choices, indicating that participants were not simply insensitive to expected value in both states (**Figure B-2**). Conditions (a) and (e) acted as control conditions, with expected values heavily skewed towards one of the choices. The greatest conflict in choice preference existed when the expected values were equal or similar (when only one of value or probability was lower). Therefore, only trials from conditions (b), (c) and (d) were included for analyzing the neural correlates of decisions.

Incentive-compatible Payment Instructions

At the beginning of the experiment, participants were provided detailed instructions about the payment procedures (see (Venkatraman et al., 2009b) for additional details). Briefly, before the first scan session, participants were instructed that their overall payment for the study was dependent on the outcomes of two randomly selected trials in the outcome phase, one from each scan session. Participants were given a sealed envelope at the first session with instructions that the envelope contained an endowment to offset any

potential losses, but they were not informed about the actual amount. As the final payment was made only at the end of the entire experiment, participants were instructed that the envelope would be kept by the experimenters and would be opened only at the end of the study. Participants were asked to sign across the seal of the envelope to ensure that it was later identifiable. Participants 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 participants expressed that they understood and believed in the procedures.

Parametric Model Analysis

We estimated parameters that best fit participants' responses using Cumulative Prospect Theory (CPT). We chose CPT (Tversky and Kahneman, 1992) over the original Prospect Theory (Kahneman and Tversky, 1979) because the latter was primarily introduced for simple two-outcome gambles and violates first-order stochastic dominance. This is a particularly important consideration in multi-outcome gambles like the ones used in this study. The gambles used in this study were of the form G = [x_1,p_1; x_2,p_2; x_3,p_3; x_4,p_4; x_5,p_5] with x_i representing the outcomes and p_i the associated probabilities The outcomes are ordered so that x_1 is the largest gain, x_5 is the largest loss, and k is the index of the smallest gain. The CPT value for each gamble is given by:

$$CPT = \sum_{i=1}^{5} v(x_i)c(i) \text{ where } v(x_i) = \begin{Bmatrix} x_i^{\alpha}, x_i \geq 0 \\ -\lambda \mid x_i \mid^{\alpha}, x_i < 0 \end{Bmatrix},$$

$$c(i) = \left\{ \begin{array}{l} w^+(p_i), i = 1 \\ w^+\left(\sum_{j=1}^{i} p_j\right) - w^+\left(\sum_{j=1}^{i-1} p_j\right),\ i = 2,..,k\ (gains) \\ w^-\left(\sum_{j=i}^{5} p_j\right) - w^-\left(\sum_{j=1+1}^{5} p_j\right),\ i = k+1,..,4\ (losses) \\ w^-(p_i), i = 5 \end{array} \right\},$$

$$w^+(p) = \frac{p^{\gamma^+}}{[p^{\gamma^+} + (1-p)^{\gamma^+}]^{1/\gamma^+}} \text{ and } w^-(p) = \frac{p^{\gamma^-}}{[p^{\gamma^-} + (1-p)^{\gamma^-}]^{1/\gamma^-}}$$

To control for the number of parameters, For the cumulative prospect theory model, we only estimated the risk (α) and loss-aversion (λ) parameters for each participant, while keeping the other values fixed based on previous experimental studies: $\gamma^+ = 0.61$ and $\gamma^- = 0.69$ (Tversky and Kahneman, 1992; Birnbaum, 2005).

Supplementary Tables

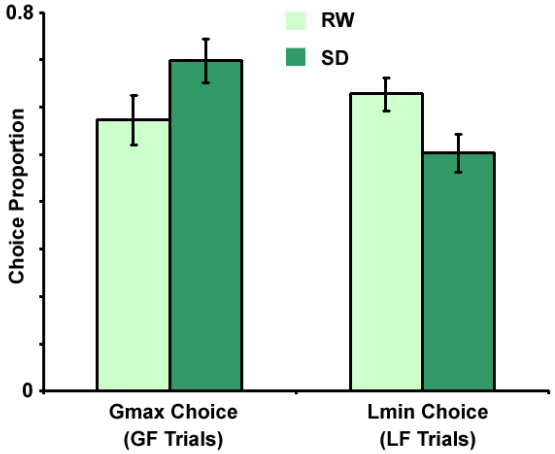
Appendix Table B-1: Regions significantly activated during the decision phase in both RW and SD sessions.

	MNI Coordinates						BA	z-value	
	RW			SD					
	x	y	z	x	y	z		RW	SD
Decision Phase									
R. Intraparietal sulcus	8	-70	43	30	-65	44	7	7.64	7.23
L. Intraparietal sulcus	-26	61	43	-28	59	42	7	7.19	7.42
R. Inf. Occipital gyrus	24	-94	-10	23	-92	-12	17	7.44	7.09
L. Inf. Occipital gyrus	-30	-90	-10	-30	-90	-9	17	7.27	6.70
L. Fusiform	-42	-63	-20	-41	-67	-17	19	7.22	6.26
R. Mid. Frontal gyrus	32	2	49	34	-1	49	6	6.79	5.71
L. Mid. Frontal gyrus	-31	1	49	-26	-4	48	6	5.96	6.07
L. Inf. Frontal gyrus	-48	9	29	-50	12	29	9	6.72	6.67
R. Inf. Frontal gyrus	48	14	29	46	12	25	9	6.32	5.83
Anterior Cingulate	1	18	46	-6	19	44	8/32	6.55	5.85
R. Anterior Insula	32	24	-2	31	20	0	13	5.41	4.50
L. Anterior Insula	-30	21	-2	-30	22	-4	13	5.32	4.61
R. Mid Frontal Gyrus	45	31	18	45	31	19	46	5.84	4.59

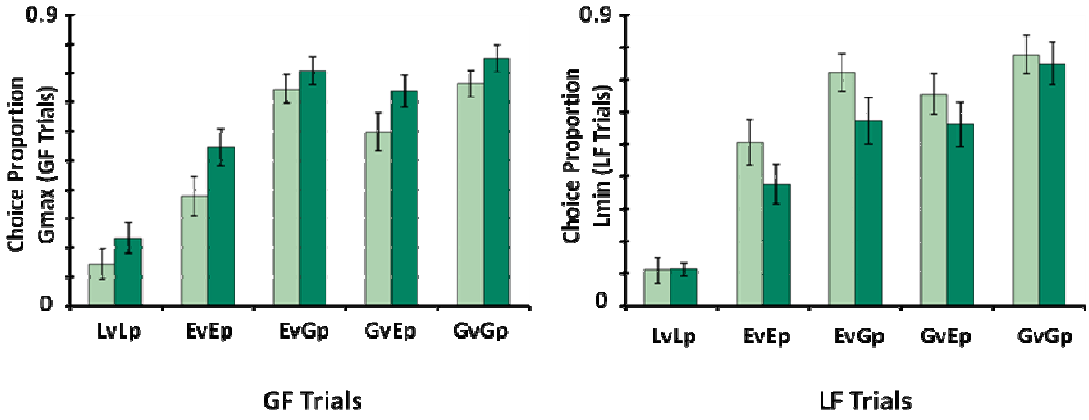
Appendix Table B-2: Regions whose activation was modulated by state during decision phase

	MNI Coordinates			Brodmann Area	z-value
	x	y	z		
Decision Phase (RW > SD)					
R. Intraparietal sulcus	20	-74	50	7	3.30
L. Intraparietal sulcus	-14	-73	50	7	2.39
R. Thalamus	14	-8	-3	-	2.92
R. Fusiform gyrus	45	-70	-15	19	2.95
L. Fusiform gyrus	-45	-50	-18	19	2.82
Decision Phase (SD > RW)					
Medial Frontal gyrus	-1	18	-14	25	3.59
	-3	33	-24	25	3.45
L. Middle frontal gyrus	-36	40	-10	11	3.30
R. Middle frontal gyrus	37	37	-16	11	2.70
Loss-focus Trials (RW > SD)					
R. anterior insula	39	19	2	13	2.95
L. anterior insula	-34	19	2	13	2.68
Dorsomedial prefrontal cortex	1	33	48	8/32	2.56

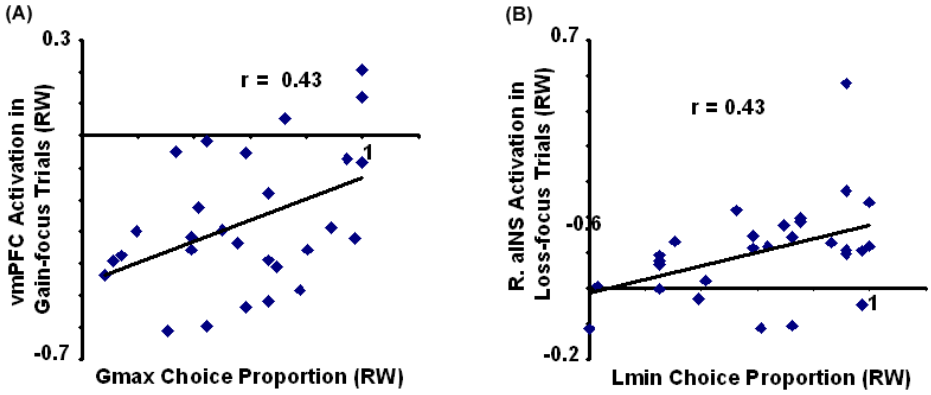
Supplementary Figures



Appendix Figure B-1: Sleep deprivation changes economic preferences.



Appendix Figure B-2: Preferences following sleep deprivation were sensitive to expected value relationship.



Appendix Figure B-3: After normal sleep, activation in vmPFC predicted Gmax choices and activation in insula predicted Lmin choices.

Appendix C: Supplementary Material for Chapter 6

Attribute-Balancing Task

Participants completed a total of 96 trials of the attribute-balancing task, split across four runs. The task was framed as a decision among stocks that varied in two attributes. The attribute values were shown by the to the percentage rankings of that stock within the set of all stocks on the major US markets. The identities of the stocks and of the attributes were hidden from the participants until the end of the experiment, so that prior knowledge about stocks and market behavior could not influence the results.

Each trial began by showing the participant three stocks. One stock was a balanced option whose attribute ratings were similar (i.e., they were either equal or differed by fewer than three points). The other two stocks were extreme options which had a better rating on one attribute and a poor rating on the other. Then, following a brief delay, one of the extreme options was eliminated, and the participant chose between the balanced option and the remaining extreme option.

There were three types of conditions: congruent, incongruent, and equal, defined based on the expected value relationship (i.e., the sum of the two attributes) between the balanced and extreme options. In the incongruent condition, the expected value of the balanced option was 8 (low-incongruence) or 16 (high-incongruence) points lower than that of the alternative extreme option while in the congruent condition, the expected value of the balanced option was 8 (low-congruence) or 16 (high-congruence) points higher. In the equal condition, the balancing and extreme options had equal expected value.

Stock attribute rankings for the balanced option ranged from 16 to 79 and the extreme alternative varied from 7 to 98, depending on trial type. For the choice trials, the extreme alternatives always had a higher score on one of the attributes and a lower score on the other compared to the balanced option. The attribute ratings for the two extreme alternatives were not identical but reversed: the numbers always varied slightly such that no two stocks on any given trial had identical ratings on any attributes. Participants completed 18 equal trials, 36 congruent trials (half low-congruence, half high-congruence), and 36 incongruent trials (half low-incongruence, half high-incongruence) for a total of 90 main choice trials. For the strategy-control analysis, we included the low-congruent and low-incongruent trials in addition to the equal trials for greater experimental power. Finally, there were 6 randomly intermixed catch trials in which the extreme alternative had higher ratings than the balanced option on both attributes and thus was the more desirable option. These trials thus served to ensure that participants attended to the task.

Participant instructions

Prior to the scanning session, participants were informed that they would make a series of choices between different stocks and their task was to predict the stock that is likely to be more profitable based on the normalized ratings on the two attributes. It was emphasized that each trial involved information about real stocks, and the attributes represented information that a financial analyst might use when making investing decisions (e.g., normalized ratings of a company's financial reserves). Participants were

told that the particular stock or attribute in each trial would not be identified while they made decisions to ensure that their prior knowledge did not influence their choice. However, as an incentive to perform well, participants were informed that a portion of their payment would depend on their performance (see Participant Payments below).

Stock Selection

All stock information presented in the task represented real stocks and their performance in a historical market (October, 2007). Stocks and their attribute rankings were identified using the website "The Motley Fool CAPS" (http://caps.fool.com/)". For each stock, the two attribute rankings were their 30-day and one-year performance, among all stocks on US markets; these corresponded to normalized attributes a1 and a2, respectively. At the end of the session, we revealed the ticker name for each available stock as well as the more profitable of the two stocks, based on its performance at the end of the identified market period. Participants received a monetary bonus if they had selected the more profitable of the two stocks (see below).

Participant Payments

Participants were informed at the beginning of the session that they would be paid a fixed amount for participation ($40) plus a variable component that would depend on their choices. For this variable component, they were given a hidden cash endowment ($10) in a sealed envelope prior to the scan; its value was unknown to the participant until the end of the session. For each of two randomly selected trials from the attribute-

balancing task, an additional $5 was added to the endowment if they successfully predicted the higher performing stock. If they did not select the higher performing stock, $5 was subtracted from the endowment. Finally, participants had the opportunity to win an additional $5 based if their performance on the counting Stroop task reached a criterion level: accuracy greater than 95% and average response time faster than 600 ms.

Behavioral Results

Participants' choices were sensitive to manipulations of expected value. In the congruent condition, where the balanced alternative was associated with higher expected value, the proportion of balanced choices was the greatest at 0.89 **(Table C-1)**. In the incongruent condition, however, this value dropped to 0.23 indicating that participants preferred the extreme alternative when it was associated with significantly greater expected value. For the equal condition, participant still showed a small, but significant, bias towards the balanced alternative preferring it in 65% of the trials. Post-experiment questionnaires indicated that participants treated our manipulations of expected value in a logical manner consistent with our experimental design.

Meta Analysis

Studies for use in the meta-analyses were identified by keyword searches through comprehensive databases (e.g., PubMed). Keywords included “cingulate”, “response”, “conflict”, “neuroimaging”, and “Stroop” for response-related control studies and “cingulate”, “decision”, “choice”, “medial frontal”, and “fMRI” for decision-related control studies. We emphasize that this meta-analysis was not intended to be a comprehensive review of all prior literature, but a way to corroborate the loci of activation identified in our experiments.

Studies selected from the search results met the following criteria. The cognitive control studies (a) utilized a task considered to elicit robust response-related control demands, such as the Stroop or Go/No-Go tasks; (b) provided three-dimensional coordinates of peak voxel activation during the response portion of the task; (c) showed peak activation in the dmPFC (BA 6, 9, 24, or 32); and (d) used fMRI or PET to acquire functional brain images from neurologically healthy individuals. The decision-related control studies (a) engaged participants in a task requiring them to decide between multiple options, (b) provided three-dimensional coordinates of peak voxel activation during the decision-making portion of the task, (c) reported areas of activation in the dmPFC (BA 6, 9,24, or 32), and (d) used fMRI to acquire functional brain images from neurologically healthy individuals. This process resulted in the selection of 28 studies for inclusion in the response-related control condition **(Table C-4)** and 25 studies for inclusion in the decision-related control condition **(Table C-5)**, yielding 48 and 38 activation foci, respectively.

Three separate activation likelihood estimate (ALE) based meta-analyses were carried out using the GingerALE software (Turkeltaub et al., 2002; Laird et al., 2005). The first consolidated response-related control studies, the second consolidated decision-related control studies, and the third generated a contrast between the first two analyses. All activation foci originally reported as MNI coordinates in the manuscript tables were converted to Talairach coordinates. ALE values were computed in Talairach space and activation foci were plotted using a full-width half maximum (FWHM) of 10.0 mm. To evaluate statistical significance, permutation testing was subsequently performed with 5000 iterations. A false discovery rate level of 0.05 was used to compute the ALE map threshold. The subtraction meta-analysis provided a map of regions where the two groups of foci are significantly different. Thresholded ALE maps were overlaid onto the colin1.1.nii anatomical template **(Figure C-7)** provided by BrainMap (Turkeltaub et al., 2002). We also transformed the peak activations for each contrast to MNI coordinates to allow direct comparisons with the functional activations in our current study **(Figure 6-6, squares)**.

Supplementary Tables

Appendix Table C-1: Mean proportion of balanced choice and response times.

	Prop. of Balanced Choices (%)		Response Time (s)	
	Mean	**S.E**	**Mean**	**S.E.**
Congruent	88.81	1.77	0.72	0.04
Incongruent	22.65	3.51	0.87	0.08
Equal	64.95	3.56	1.13	0.13

Appendix Table C-2: Regions activated during counting stroop task.

	MNI Coordinates			Brodmann Area	*z*-value
	x	**y**	**z**		
Main Effect: Incongruent > Neutral					
Dorsomedial Prefrontal Cortex	0	17	51	8	4.34
L. Dorsolateral Prefrontal Cortex	-46	13	33	9	4.61
	-40	11	24	9	4.49
L. Superior Parietal Lobule	-28	-67	43	7	4.22
L. Posterior Parietal Cortex	-37	-47	48	40	4.31
L. Middle Frontal Gyrus	-39	1	54	6	4.21
R. Middle Frontal Gyrus	36	5	54	6	3.71
Response-related control: (Incongruent – Neutral) * (Response Time)					
Dorsomedial Prefrontal Cortex	-5	10	51	32	3.41
L. Dorsolateral Prefrontal Cortex	-55	9	34	9	3.06

Appendix Table C-3: Summary of regions activated during the attribute-balancing task.

	MNI Coordinates			Brodmann Area	z-value
	X	y	z		
Decision: Equal > Incongruent					
R. Dorsolateral Prefrontal Cortex	42	38	32	9	2.81
R. Posterior Parietal Cortex	46	-41	37	40	2.91
Dorsomedial Prefrontal Cortex	-6	24	38	32	2.62
R. Inferior Frontal Gyrus	44	50	10	46	2.50
Decision: Incongruent > Congruent					
R. Inferior Frontal Gyrus	44	31	14	46	2.99
R. Precuneus	30	-50	44	9	3.42
Dorsomedial Prefrontal Cortex	-10	28	34	32	2.50
Anterior Insula	33	25	1	13	3.01
	-36	26	8	13	2.97
Choices: Extreme > Balanced					
L. Lateral Prefrontal Cortex	-46	24	12	46	3.01
R. Lateral Prefrontal Cortex	42	26	22	46	2.73
R. Anterior Insula	26	27	6	13	2.86
R. Precuneus	28	-59	54	7	2.71
L. Precuneus	-31	-50	42	7	2.51

Appendix Table C-4: Summary of response-related control studies used in ALE meta-analysis.

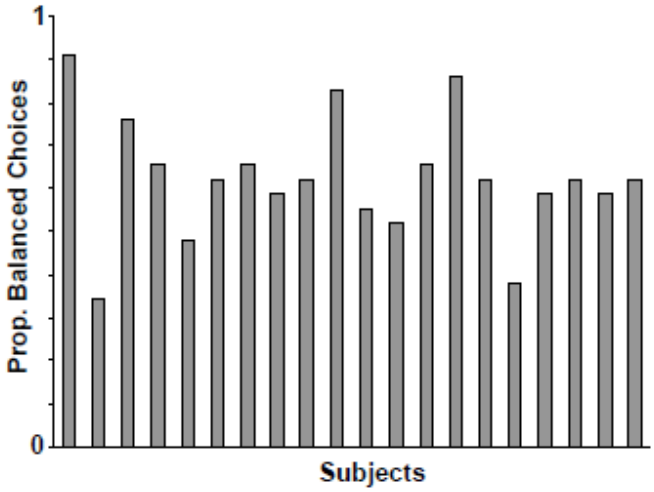
Response-related Control Studies	Talairach Coordinates		
	x	y	z
1. Bench et al. 1993	4	-4	20
	10	-4	24
	18	40	4
	20	42	8
	22	42	12
2. George et al. 1994	-22	24	32
3. Carter et al. 1995	10	8	48
	12	44	20
4. Kawashima et al. 1996	6	-11	52
	-4	-44	33
	8	-23	49
	8	6	42
	-4	9	38
	-4	5	30
5. George et al. 1997	-22	8	28
6. Bush et al. 1998	12	9	34
7. Carter et al. 1998	4	25	43
8. Derbyshire et al. 1998	-2	14	40
	0	2	48
9. Botvinick et al. 1999	-2	28	31
10. Brown et al. 1999	8	23	35
	-4	14	35
11. Bush et al. 1999	6	0	40
	6	15	43
	-3	21	37
12. Konishi et al. 1999	-5	29	32
13. Peterson et al. 1999	-7	18	26
14. Carter et al. 2000	0	15	41
15. Casey et al. 2000	-8	22	32
16. Macdonald et al. 2000	4	1	43
17. Barch et al. 2001	8	9	42
	8	21	24
	11	3	42
	5	15	39
18. Kerns et al. 2004	1	10	40

19.	Erickson et al. 2004	2	18	40
20.	Egner and Hirsch, 2004	18	8	46
21.	Milham and Banich, 2005	0	30	22
22.	Critchley et al. 2005	6	22	38
23.	Weissman et al. 2005	-2	5	43
24.	van Veen and Carter, 2005	7 1	18 26	42 28
25.	Evers et al. 2006	0	36	22
26.	Kerns, 2006	-3	8	41
27.	Lau et al. 2006	6 10	16 24	34 34
28.	Roelofs et al. 2006	-4 -8	30 36	36 28

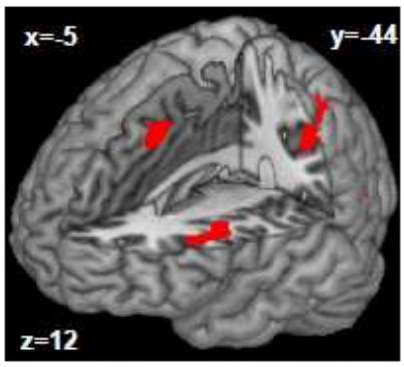
Appendix Table C-5: Summary of decision-related control studies used in ALE meta-analysis.

Decision-related Control Studies	Talairach Coordinates		
	x	y	z
1. Elliot and Dolan, 1998	-4	28	30
2. Critchley et al. 2001	8	28	24
	-6	28	20
3. Bush et al. 2002	-2	23	20
4. Paulus et al. 2002	8	44	3
	1	27	31
	6	39	10
5. Sanfey et al. 2003	4	20	36
6. O'Doherty et al. 2003	-3	21	39
	6	21	39
7. Volz et al. 2003	4	30	46
8. Rogers et al. 2004	-3	37	15
	1	38	19
9. Volz et al. 2004	1	33	41
	4	21	47
10. Walton et al. 2004	-7	16	38
	0	12	36
11. Ernst et al. 2004	-6	24	42
12. Cohen et al. 2005	5	36	29
13. Coricelli et al. 2005	-3	25	41
14. Deppe et al. 2005	-7	38	17
	6	46	11
15. Huettel et al. 2005	7	14	39
16. Fishbein et al. 2005	-8	34	15
	14	32	17
17. Paulus and Frank, 2005	8	23	28
18. Blair et al. 2006	3	16	46
19. De Martino et al. 2006	0	17	46
20. Hampton et al. 2006	6	22	40
	-3	25	26
21. Krain et al. 2006	-20	39	14
22. Marsh et al. 2006	2	25	37
23. Moll et al. 2006	-4	20	43
24. Behrens et al. 2007	-6	26	34
25. Pochon et al. 2008	-3	20	43
	-6	39	23

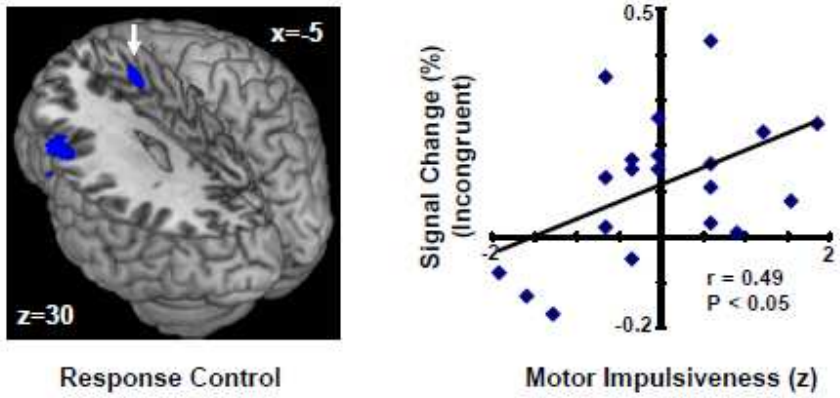
Supplementary Figures



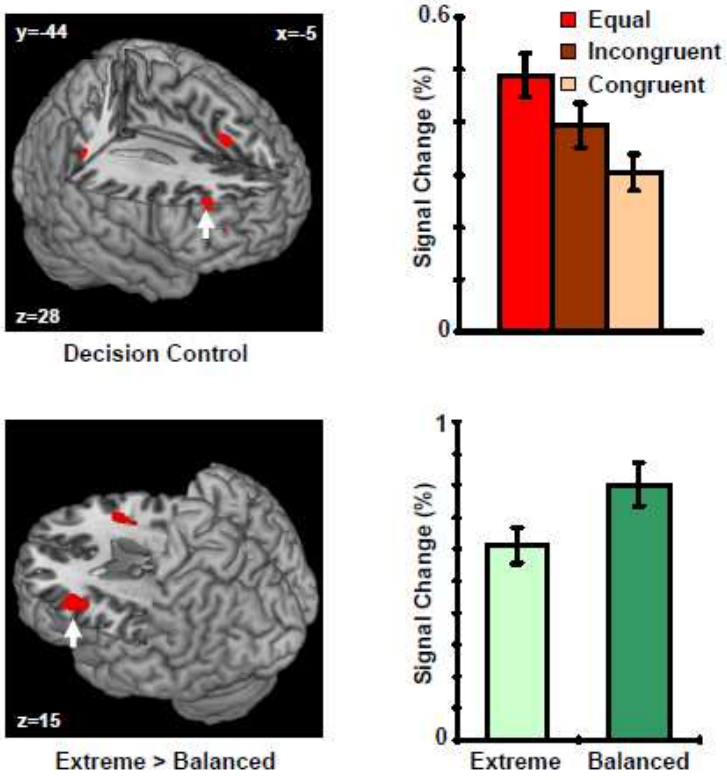
Appendix Figure C-1: Variability in preference for the balanced option in the attribute-balancing task



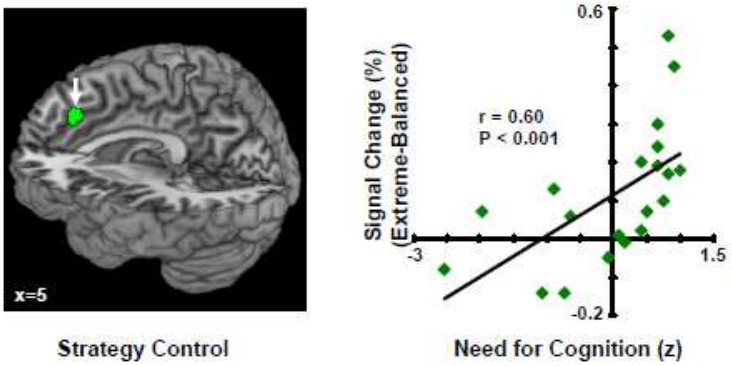
Appendix Figure C-2: Incongruent trials in the Stroop task activated lateral frontal, medial frontal, and parietal regions



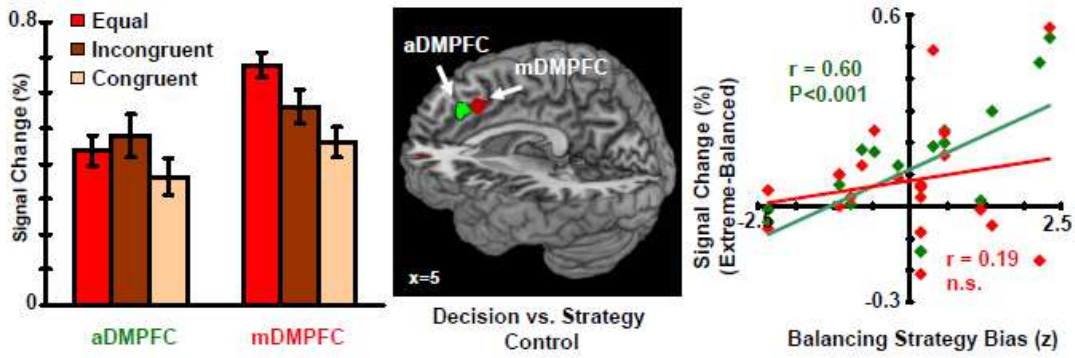
Appendix Figure C-3: Activation in pDMPFC predicts individual differences in motor impulsiveness across participants



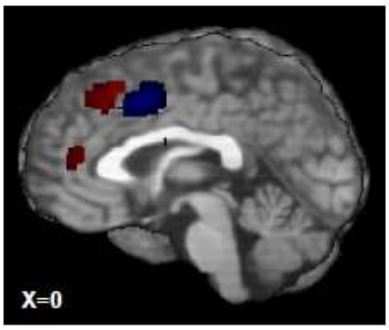
Appendix Figure C-4: Activation associated with decision-related control demands.



Appendix Figure C-5: Activation in aDMPFC predicts individual differences in the need for cognition trait across participants



Appendix Figure C-6: Anterior and middle dmPFC are associated with strategy and decision-related control respectively



Appendix Figure C-7: Functional topography in dmPFC based on meta-analysis

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Biography

I was born on April 9, 1978 in Chennai, India. After finishing my schooling in Chennai, I received a scholarship to pursue further studies in Singapore. I completed my Bachelor of Applied Science (Computer Engineering) degree with First Class Honors at Nanyang Technological University (NTU), Singapore in 1999. Subsequently, I received a Master of Engineering degree from NTU in 2001 for my thesis titled "Nonlinear Response in Functional MRI". After working as a Research Scientist at the Cognitive Neuroscience lab in Singapore studying the neural mechanisms underlying number processing and sleep deprivation, I moved to Duke University in August 2006 to pursue my PhD in Cognitive Neuroscience.

My primary research interest is in understanding the processes and mechanisms underlying decision making. I have co-authored two book chapters in the "*Handbook of Process Tracing Methods in Decision Making"* and "*Decision Making, Affect and Learning"*. I have also published extensively in several leading peer-reviewed journals including Neuron, Journal of Neuroscience, Journal of Cognitive Neuroscience, Pain, Neuropsychologia, Human Brain Mapping and Sleep. Findings from my studies have been featured in leading newspapers and radio stations around the world. I was invited to be a part of a special press conference on decision making at the annual meeting of Society of Neuroscience in 2008. I was a discussant for a round table discussion on the role of neuroscience in marketing at the Association of Consumer Research Meeting in 2008. I am currently an active member of the Society of Neuroscience, Society for Neuroeconomics and Society for Judgment and Decision Making.