A model of the neural basis of predecisional processes: the fronto-limbic information acquisition network

Bradley Charles Taber-Thomas

University of Iowa

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A MODEL OF THE NEURAL BASIS OF PREDECISIONAL PROCESSES: THE FRONTO-LIMBIC INFORMATION ACQUISITION NETWORK

by

Bradley Charles Taber-Thomas

An Abstract

Of a thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Neuroscience in the Graduate College of The University of Iowa

December 2011

Thesis Supervisor: Professor Daniel Tranel
ABSTRACT

Decision makers flexibly deploy decision-making strategies based on the specific features of the problems they face (Ford, Schmitt, Schechtman, Hults, & Doherty, 1989; Payne, Bettman, & Johnson, 1993). However, research on the neuroscience of decision making has focused on a “policy capture” approach that utilizes static decision problems to study the relationships between input (the problem presented), output (the choices made), and the brain. Since the decision problems are prepackaged, this approach does not provide information about the neural bases of predecisional processes critical for flexible decision making, such as selecting an appropriate decision-making strategy and dynamically acquiring and integrating the information needed to progress toward choice. The aim of the current project is to use the lesion method to explore the neural bases of predecisional processes. The fronto-limbic information acquisition network (FLIAN) is proposed as a neural framework critical for predecisional processes in flexible decision making. According to the FLIAN model, the ventromedial prefrontal cortex (vmPFC) represents the decision problem as currently perceived (i.e., the decision space), which is the basis for selecting a decision strategy via interactions with limbic structures. The vmPFC implements the strategy through the coordination of attribute-based information acquisition induced by the amygdala and relational, option-based acquisition induced by the hippocampus. In Chapter 1, the literature pertinent to FLIAN structures is reviewed, including the neuroanatomical and functional backgrounds of those structures, their roles in decision making, and their potential roles in predecisional processes. Chapter 2 provides a review of the behavioral literature on predecisional processes and outlines the FLIAN model in detail. Chapters 3 and 4 present studies that test, and provide partial support for, the FLIAN model using the lesion method and information board tasks. As predicted, the hippocampus is shown to be critical for relational, option-based information acquisition. The vmPFC is shown to be critical for determining how
attributes are weighted in the decision space representation and for organizing predecisional behavior. The amygdala was not found to play its role in attribute-based acquisition, but previous studies do support this function and further research is warranted on the role of the amygdala, as well as the hippocampus and vmPFC, in predecisional processes. Future research should also explore the consequences of abnormal predecisional functioning for social behavior, memory, and emotion processing.

Abstract Approved: ____________________________________________

Thesis Supervisor

________________________________

Title and Department

________________________________

Date
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Bradley Charles Taber-Thomas

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December 2011

Thesis Supervisor: Professor Daniel Tranel
CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

Bradley Charles Taber-Thomas

has been approved by the Examining Committee for the thesis requirement for the Doctor of Philosophy degree in Neuroscience at the December 2011 graduation.

Thesis Committee:

Daniel Tranel, Thesis Supervisor

Steven Anderson

Melissa Duff

William Hedgcock

Irwin Levin

Paul Windschitl
To Sarah
The universe (which others call the Library) is composed of an indefinite and perhaps infinite number of hexagonal galleries, with vast air shafts between, surrounded by very low railings.

Jorge Luis Borges
La Biblioteca de Babel
ABSTRACT

Decision makers flexibly deploy decision-making strategies based on the specific features of the problems they face (Ford, Schmitt, Schechtman, Hults, & Doherty, 1989; Payne, Bettman, & Johnson, 1993). However, research on the neuroscience of decision making has focused on a “policy capture” approach that utilizes static decision problems to study the relationships between input (the problem presented), output (the choices made), and the brain. Since the decision problems are prepackaged, this approach does not provide information about the neural bases of predecisional processes critical for flexible decision making, such as selecting an appropriate decision-making strategy and dynamically acquiring and integrating the information needed to progress toward choice. The aim of the current project is to use the lesion method to explore the neural bases of predecisional processes. The fronto-limbic information acquisition network (FLIAN) is proposed as a neural framework critical for predecisional processes in flexible decision making. According to the FLIAN model, the ventromedial prefrontal cortex (vmPFC) represents the decision problem as currently perceived (i.e., the decision space), which is the basis for selecting a decision strategy via interactions with limbic structures. The vmPFC implements the strategy through the coordination of attribute-based information acquisition induced by the amygdala and relational, option-based acquisition induced by the hippocampus. In Chapter 1, the literature pertinent to FLIAN structures is reviewed, including the neuroanatomical and functional backgrounds of those structures, their roles in decision making, and their potential roles in predecisional processes. Chapter 2 provides a review of the behavioral literature on predecisional processes and outlines the FLIAN model in detail. Chapters 3 and 4 present studies that test, and provide partial support for, the FLIAN model using the lesion method and information board tasks. As predicted, the hippocampus is shown to be critical for relational, option-based information acquisition. The vmPFC is shown to be critical for determining how
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PREFACE

Research on the neural basis of decision making has received increasing interest with recent advances in neuroimaging technology. The goal of the present project is to bring an understanding of the complex, multi-phased process of decision making to this endeavor. I became interested in this area as I studied the abnormal pattern of moral judgment observed after ventromedial prefrontal cortex damage; the question arose for me whether abnormal judgments were related to choice and evaluating options that are normally understood, or whether abnormal judgments might be related to earlier processes such as acquiring the information needed to represent (and then evaluate and choose between) options. While considering these possibilities, I was taking Irwin Levin’s psychology seminar on judgment and decision making, where he discussed process tracing, information board paradigms, and the abundant research in the psychology literature looking at predecisional behavior and information acquisition. I was excited by the potential to employ this paradigm in studying the neural basis of early decision making functions, and it was in the context of this class that I developed the ideas that were the basis of the model and studies in this dissertation. It is my hope that the reader will find a useful conceptual framework for understanding the functions of the fronto-limbic neural system in acquiring information for the purpose of guiding adaptive behavior. I thank Irwin for setting me on this path and for his support and insight along the way.

I am greatly appreciative for my advisor, Dan Tranel, who has provided support and ample resources to allow me to independently pursue my research interests. I am also thankful for the stunning Iowa pond he provided for us to contemplate on throughout the winter. I am truly grateful to my thesis committee members, Steve Anderson, Melissa Duff, Bill Hedgecock, and Paul Windschitl, who provided helpful feedback on the project and were very supportive and enjoyable to work with. Thanks to Heather Robinson, Katie
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INTRODUCTION

Decision makers flexibly deploy decision-making strategies based on the specific features of the problems they face (Ford et al., 1989; Payne et al., 1993). However, research on the neuroscience of decision making has focused on a “policy capture” approach that utilizes static decision problems to study the relationships between input (the problem presented), output (the choices made), and the brain (Billings & Marcus, 1983; Kable & Glimcher, 2009). For example, researchers have studied how input variables like risk, probability, ambiguity, and reward value are encoded in the brain, yielding advances in our understanding of the neural basis of decision making over the past two decades (Kable & Glimcher, 2009). However, because the decision problems are prepackaged, this methodology does not provide information about the neural bases of critical predecisional processes such as selecting an appropriate decision-making strategy and dynamically acquiring and integrating the information needed to progress toward a decision (Payne, Braunstein, & Carroll, 1978). The aim of the current project is to use the lesion method to explore the neural bases of predecisional processes.

Consider a hypothetical task in the mold of typical decision neuroscience studies. The participants are asked to choose between two job candidates and are presented with information about each. This binary decision is repeated over many trials that parametrically vary the information about the candidates, and correlations with fMRI activation and the candidate information can be obtained to reveal the brain networks involved in encoding the information. However, in the real world, decision making rarely involves preformulated problems like choosing between two options based on information that is fully presented. Imagine the real-world parallel of the job candidate
decision. Initially, when the pile of job applications is high, a member of a search committee for a new faculty member is likely to compare the applicants based on specific attributes, like whether they meet a cutoff number of publications. Those who fail to meet the cutoff are discarded and not examined further. When the applicant pool comes down to the last few she may switch to a different decision-making strategy in which the remaining candidates are compared across multiple attributes. In this later process, the comparison is based on more robust representations of the candidates and compromises between attributes can be made; for a given candidate, a few high profile publications may compensate for a small number of total publications. Such predecisional operations are critical in decision making, but are not captured by traditional decision neuroscience approaches.

The example of predecisional processes above also shows how decision-making strategies can be influenced by the characteristics of the decision problem being considered, such as task variables (many versus few choice options, deciding under time pressure) and context variables (how similar the options are, the wording or framing of the problem; Payne, Bettman, Coupey, & Johnson, 1992). In order to select a decision strategy sensitive to the specific problem faced, a person must form a representation of the current problem—constituting the decision space—which is used to select a decision-making strategy (Newell & Simon, 1972). The selected strategy must then be implemented through the coordination of multiple processes, such as information acquisition and integration (Payne et al., 1993). The acquisition of new information is used to update the decision space representation based on the decision strategy in use. In the example above, when implementing the cutoff strategy, the person is likely to go
about gathering information by acquiring only the information relevant to the cutoff (Payne, 1976). When the decision strategy changes and options are compared across multiple attributes, the information acquisition strategy is updated accordingly to facilitate the formation of more robust representations of the candidate options by examining the remaining candidates’ applications in depth (Olshavsky, 1979).

The flexibility of decision making allows for the optimization of behavior (Beach & Mitchell, 1978; Payne et al., 1993). Cognitive resources can be saved for when they are needed most, in the most complex task environments or when mistakes have high cost and accuracy is crucial. A failure to engage in such adaptive, strategic decision making can result in effort and resources being spent unwisely, which may lead to disadvantageous choices (Payne et al., 1992). Nonetheless, the flexibility of decision making is by no means universally advantageous; it also makes the decision process vulnerable to detrimental biases such as framing effects (Tversky & Kahneman, 1974, 1981).

Here, a model of the neural system critical for predecisional processes in flexible decision making is examined. The model centers on a fronto-limbic information acquisition network (FLIAN) model that includes the ventromedial prefrontal cortex (vmPFC), amygdala (AMY), and hippocampus (HC). Within the FLIAN model, it is argued that the vmPFC is critical for representing the currently perceived state of the decision problem (i.e., the decision space), which is the basis for selecting a decision-making strategy via interactions with limbic structures. The selected strategy is implemented by the vmPFC through the coordination of information acquisition processes induced by the amygdala and hippocampus. In this model, the amygdala is
specialized for inducing attribute-based information acquisition, which seeks information about salient attributes of the environment (or of choice options). In contrast, the hippocampus is specialized for inducing relational, option-based acquisition, which organizes information acquisition around features of the environment (or of options) that are arbitrarily related—as in the construction of an episodic memory, or the representation of an option. Information acquired by these limbic structures then feeds forward to the vmPFC where it updates the decision space representation according to the current decision making strategy. This dynamic decision space updating and information acquisition cycle proceeds until an option meets the choice criteria for the strategy in use.

In order to examine the proposed FLIAN model of predecisional processes, the effects of brain damage to the critical nodes in this network were explored in neurological patients and appropriate comparison participants. The outline for this document is as follows. Chapter 1 provides a review of the literature on the current state of knowledge of the vmPFC, AMY, and HC, their roles in decision making, and their potential roles in predecisional processes. Chapter 2 reviews the behavioral literature on predecisional processes and proposes the FLIAN model as a systems-level model of the neural bases of predecisional processes. In Chapter 3, Study 1 explores the role of the vmPFC, amygdala, and hippocampus in predecisional behavior using information board tasks in both non-social and social contexts. Study 2 is presented in Chapter 4 and examines the roles of the vmPFC in flexibly adapting predecisional behavior after training on specific decision making strategies. Studies 1 and 2 provide partial support for the FLIAN model and suggest that more research is needed on the neural bases of predecisional processes. Lastly, a Summary of these findings and their implications is presented, as well as a
discussion of future directions for exploring the implications of impairments in predecisional processes for social behavior, memory, and emotion processing.
CHAPTER 1. THE NEUROSCIENCE OF DECISION MAKING AND THE FRONTO-LIMBIC INFORMATION ACQUISITION NETWORK

The predecisional processes outlined above are fundamental to human decision making. However, little is known about their neural bases. The fronto-limbic information acquisition network (FLIAN) provides a model of the neural system critical for the coordination of information acquisition with decision-making strategies. The central nodes in this network are: the ventromedial prefrontal cortex, which is hypothesized to maintain the decision space representation and coordinate information acquisition processes; the amygdala, which is hypothesized to induce an attribute-based information acquisition mode; and the hippocampus, which is hypothesized to induce a relational, option-based information acquisition mode. In this chapter, previous research is reviewed on the functions of these structures and their roles in decision making, with a focus on how these structures might be involved in predecisional processes.

1.1 Ventromedial Prefrontal Cortex

1.1.1 Neuroanatomical and functional background

The prefrontal cortex (PFC) comprises most of the frontal cortex and lies anterior to the basic motor output regions of the precentral gyrus and premotor cortex. It has been defined as that region of cortex which receives projections from the dorsomedial nucleus of the thalamus (Fuster, 2008). These projections are specific, with the orbitofrontal cortex linked to the pars magnocellularis of the medial dorsomedial nucleus and the dorsolateral cortex with the pars parvocellularis of the lateral dorsomedial nucleus (Fuster, 2008; Rolls, 2000). The ventromedial sector of the prefrontal cortex (vmPFC)
encompasses the medial orbitofrontal cortex and roughly the ventral half of the medial prefrontal cortex (Figure 1). The vmPFC is extensively connected to limbic structures—the amygdala, insula, and hippocampus—as well as the hypothalamus and brainstem (Öngür & Price, 2000; Rolls, 2000). Through these connections it maintains higher order control over the execution of bodily components of emotions, the encoding of emotional values and the values of the consequences of actions, and the modulation of memory processing (Bachevalier & Mishkin, 1986; Fletcher, Shallice, & Dolan, 1998; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Öngür & Price, 2000; Rangel, Camerer, & Montague, 2008; Rolls, 2000).

The information processing functions of the vmPFC must be understood within the broader context of the frontal lobe, which is the cortex of action or “doing” (Fuster,
The prefrontal cortex is involved in executive functions critical for organizing action, such as planning, judgment, decision making, and self-perception (Tranel, Anderson, & Benton, 1994). To put it more generally, the prefrontal cortex is critical for adaptive behavior—the promotion of long-term survival by guiding the selection of an advantageous action among many possible courses of action (Damasio & Anderson, 2003, p. 436). This is highlighted by what happens when the prefrontal cortex is injured. Damasio and Anderson, drawing on the conceptualization of the neuropsychologist Alexander Luria, note that “patients [with PFC injury] have trouble in the choice of programs of action, that their strategy for gathering information necessary for the solution of the problem is impoverished, and that they seldom verify whether their actions meet the original intent” (2003, pp. 430-431). As a brief aside, the notion of an information acquisition impairment (a predecisional process) will be a central aspect of the research proposed here. However, as will become clear in the review below, this notion has largely been ignored in the literature as the focus has been on processes directly involved in producing choice output.

Although the operations of the PFC can broadly be understood as executive functions, the PFC is not a unified structure; there are many functions needed to support adaptive behavior, and different sectors of the prefrontal cortex perform distinct functions. At the most basic level the PFC can be divided into lateral, orbital, and medial sectors, with the orbitofrontal and ventromedial regions associated with emotion-related operations (Haber, Fudge, & McFarland, 2000). The somatic marker hypothesis, reviewed in detail below, is a neurological theory of vmPFC function that argues that the vmPFC sector is critical for integrating emotion into the process of option selection. This explains the vmPFC’s prominent role in behaviors where affective integration is critical, such as intuitive reasoning, decision making, and social behavior (Damasio, 1994). Based on this previous research, the FLIAN model proposes that the vmPFC is critical for
selecting a decision strategy based on the decision space, and implementing it by managing information acquisition via interactions with the amygdala and hippocampus.

1.1.2 Sequelae of vmPFC injury

The functions of the vmPFC are highlighted by the 19th century case of Phineas Gage. Gage, who worked as the foreman of a rock excavation group at a railroad company, was a “great favorite” among his men and was known as “a shrewd, smart business man, very energetic and persistent in executing all his plans of operation” (Harlow, 1868, p. 340). In the fall of 1848 an unfortunate accident occurred. Gage was in the process of tamping explosives into a hole when his iron tamping rod struck a spark and the explosives were set off prematurely, firing the tamping rod up and completely through his skull. At that moment his head was turned to the right and tilted slightly forward, resulting in the iron passing up through his left cheek and exiting the top of the skull. A recent study of Gage’s skull revealed that the bilateral prefrontal cortex, centered on the vmPFC, was the probable locus of his brain injury (Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994). Remarkably, Gage made a full medical recovery less than a year later. He was walking and talking and would have appeared to the casual observer to have miraculously escaped the incident without complication. However, although invisible to the naked eye, the changes in his personality and cognitive functioning were equally remarkable. He reapplied for his previous position as foreman, but, as his physician John Harlow noted at the time:

…his contractors, who regarded him as the most efficient and capable foreman in their employ previous to his injury, considered the change in his mind so marked that they could not give him his place again. The equilibrium of balance, so to speak, between his
intellectual faculties and animal propensities, seems to have been destroyed. He is fitful, irreverent, indulging at times in the grossest profanity (which was not previously his custom), manifesting but little deference for his fellows, impatient of restraint or advice when it conflicts with his desires, at times pertinaciously obstinate, yet capricious and vacillating, devising many plans of future operation, which are not sooner arranged than they are abandoned in turn for others appearing more feasible.” (Harlow, 1868)

As Harlow makes clear, Gage’s brain injury resulted in severe behavioral and personality disturbances. He seemed to have become irresponsible where he was once an example of responsibility. He lost his once natural respect for social conventions. His new behavioral patterns were ill-advised, and it seemed that he was unable to learn from the negative consequences of his mistakes. Harlow accordingly concluded that “his mind was radically changed, so decidedly that his friends and acquaintances said he was ‘no longer Gage’” (Harlow, 1868).

Changes similar to those seen in Gage have been observed in the modern patient E.V.R. studied by Damasio and colleagues (Eslinger & Damasio, 1985). E.V.R. suffered from a large bilateral orbitofrontal meningioma that was successfully removed, but left him with a disruptive behavioral syndrome that has been called “acquired sociopathy” (Eslinger & Damasio, 1985). Prior to surgery, E.V.R. was a well-respected individual and employee. After his brain injury, however, he developed profound changes to his personality and his ability to make advantageous plans and decisions. He became unreliable and unable to maintain employment, and his behavioral pattern become one of misguided business and social decisions. He had significant difficulty determining who to associate with in his business and social life (Damasio, Tranel, & Damasio, 1998). And, like Gage, he seems unable to learn from the negative consequences of his disadvantageous behavior (Damasio, 1994).
It is easy to get caught up in the remarkable behavioral changes observed in the cases of Gage and E.V.R. However, it is important to contrast them with the many domains of cognition and behavior that remain generally intact after vmPFC injury, including sensory perception, memory, language, general intellectual abilities, basic neuropsychological test performance, the ability to express basic emotions like anger, disgust, and happiness (although often at inappropriate times), and social knowledge (Damasio & Anderson, 2003). E.V.R., for example, has demonstrated post-morbid Verbal and Performance IQ scores of 129 and 135 respectively on the WAIS-R, Minnesota Multiphasic Personality Inventory scores in the normal range, and performs well on virtually all neuropsychological tests (Eslinger & Damasio, 1985). Moreover, despite his deficits in real-world social behavior, he is able to give appropriate responses to many hypothetical social and ethical scenarios (e.g., about stealing; Saver & Damasio, 1991). The point is that patients with vmPFC injury show circumscribed post-morbid changes specific to real-world decision-making and social behavior.

1.1.3 The Somatic Marker Hypothesis

since feeling is first
who pays any attention
to the syntax of things
will never wholly kiss you
—E.E. Cummings (1973)

The concomitant impairments in emotion and decision making in cases of vmPFC injury suggested a link between these two seemingly distinct mental functions (Damasio, 1994). However, despite the striking behavioral profile common in people with vmPFC injury, their generally intact functioning makes it difficult to capture and empirically
explore that profile in the laboratory (Damasio & Anderson, 2003). Tasks commonly
used for research purposes present well-structured problems with clearly defined rules
and goals, in contrast to the complex, underspecified problems ordinarily encountered in
the real world. However, patients with vmPFC injury struggle in precisely the latter
domain. Unfortunately it is inherently difficult to devise controlled tasks to study such
real-world behavior, since experimental research tasks are purposefully designed to be
highly specified with limited complexities. The absence of experimental laboratory tests
that could reveal the real-world behavioral difficulties of vmPFC patients forced early
researchers to rely on anecdote and case studies to understand the functions of the
vmPFC.

In light of this difficulty, Antoine Bechara and colleagues devised the Iowa
Gambling Task (IGT) which uses risk and ambiguity to simulate real-world decision
making in an experimental neuropsychological instrument (Bechara, Damasio, Damasio,
& Anderson, 1994). In the IGT participants are given an initial play money loan and the
goal of winning the most amount of money. They play by drawing cards one at a time
from any of four decks of face down cards. Each draw provides an immediate reward, but
punishments appear at unpredictable intervals. Also, the decks differ in their reward and
punishment schedules, with two “good” and two “bad” decks. Drawing from good decks
will result in a net profit over the course of the task, as they provide modest payoffs with
each card ($50) and the occasional punishments are modest too (totaling only $250 after
10 card draws). The bad decks, however, will result in a net loss, as they provide larger
payoffs with each card ($100) but the occasional punishments are even larger (totaling
$1250 after 10 draws). Thus, after 10 draws from a good deck the net profit would be
$250 ($500 gained and $250 lost), while there would be a net loss of $250 after 10 draws from a bad deck ($1000 gained and $1250 lost).

Over time, neurologically intact individuals demonstrate a strong preference for the advantageous behavioral strategy of drawing more from the good decks than the bad ones (Bechara et al., 1994). Participants also develop anticipatory skin conductance responses (SCRs) prior to drawing cards from bad decks, even before they report conscious awareness of the decks being disadvantageous, suggesting that covert autonomic information is informing their decision-making process (Bechara, Damasio, Tranel, & Damasio, 1997). In contrast, patients with vmPFC damage do not demonstrate a preference for selecting from good decks even after they report knowing which decks are good (Bechara et al., 1994). Moreover, although both patients with vmPFC damage and normal comparison participants generated SCRs in immediate response to gain or loss after drawing a card on the IGT, vmPFC patients failed to develop anticipatory SCRs prior to drawing from disadvantageous decks (Bechara et al., 1997; Bechara, Tranel, Hanna Damasio, & Damasio, 1996). Thus, it seems that patients with vmPFC injury continue to draw from bad decks because they do not produce anticipatory SCRs, demonstrating an impairment in using the emotional consequences of past experience to guide their behavior.

In order to succeed on the IGT, participants must learn quickly from their experiences with the four decks to discern the advantageous and disadvantageous decks, and, critically, they must use this information to guide their behavior on the task. Simply knowing which decks are good and bad is not enough; one must act on that knowledge. The inability of patients with vmPFC damage to behave advantageously on this task,
even when they have declarative knowledge of the advantageous strategy, mimics their
difficulties in real-world behavior. In spite of the large punishments and net loss provided
by the bad decks they do not learn to avoid them, just as they fail to adapt their real-world
behavior in response to the negative consequences of their decisions.

Patients with vmPFC damage also show abnormal SCRs in response to socially
meaningful stimuli, in contrast to normal responses to other stimuli (such as basic,
unconditioned emotional stimuli; Damasio, Tranel, & Damasio, 1990). As Damasio and
Anderson put it, “[social] stimuli failed to activate somatic states previously associated
with specific social situations,” and this deficit can lead to disadvantageous real-world
behavior because these somatic states “marked the anticipated outcomes of response
options as advantageous or not” (2003).

This idea is the core of Damasio’s somatic marker hypothesis, a systems-level
neurological theory of the relationship between basic motivational, affective processes
and the coordination of complex action (Damasio, 1994; Damasio et al., 1998; Naqvi,
Shiv, & Bechara, 2006). The somatic marker hypothesis holds that during decision
making the vmPFC is critical for reactivating emotional states that influence choice.
During an initial learning phase, emotions arise in the body as somatic, bioregulatory
states associated with the rewarding or punishing consequences of an option that has been
chosen, and this emotion-option relationship is encoded in the vmPFC. When similar
options are considered in the future the emotional states associated with them are
reactivated by the vmPFC through its interactions with limbic structures, producing
“somatic markers” that bias behavior. In this way, a somatic marker is the learned
anticipation of future emotional experience that may occur if one makes a certain choice
(Bechara & Damasio, 2005). When a neurologically healthy individual plays the IGT, somatic markers are activated when considering drawing from bad decks (indicated by anticipatory SCRs). The markers anticipate the negative emotional experience of losing money, which has been learned from previous draws from the bad decks. A preference for good decks is developed because somatic markers bias the choice of which deck to draw from away from disadvantageous decks.

Thus, although patients with vmPFC injuries are able to experience emotion in response to reward and punishment, their difficulties are due to a failure to use previously learned emotional information to guide their future behavior. On the IGT, they fail to develop anticipatory SCRs that are needed to bias their behavior away from the disadvantageous strategy of drawing from the bad decks. Tying this back to the case of E.V.R., Eslinger and Damasio note that “E.V.R. had a defect of analysis and integration of stimuli pertaining to real-life situations that may be due, in part, to ineffectual access to previously learned strategies of action” (Eslinger & Damasio, 1985, p. 1739). Notice again the emphasis on a deficit in strategy selection; it is not that E.V.R. cannot experience emotion, rather, he has an impairment in engaging decision-making strategies that involve the reactivation of somatic markers. When making decisions in the real world, the failure to implement somatic-marker-based strategies means that E.V.R. will not be biased away from disadvantageous options and toward advantageous options, friends, business decisions, and so on.

Psychophysiological and functional neuroimaging studies have supported the role of the vmPFC in predicting the future rewarding consequences of behavior (Naqvi et al., 2006). The vmPFC is known to be involved in reward- and punishment-related behavior,
encoding the primary reinforcing values of stimuli, and encoding the values of conditioned stimuli that predict reward or punishment (Rolls, 2000, 2004). Recent work by Wallis and colleagues in primates has shown that orbital and medial prefrontal neurons encode abstract value signals (Kennerley, Dahmubed, Lara, & Wallis, 2009; Wallis, 2007; Wallis & Kennerley, 2010). And neuroimaging studies have extended these findings to humans; a metaanalysis showed that the vmPFC was involved in the representation and monitoring of reward (Kringelbach & Rolls, 2004). One functional magnetic resonance imaging (fMRI) study found that vmPFC activation in response to conditioned stimuli is reduced by reducing the value of the unconditioned stimulus (Gottfried, O'Doherty, & Dolan, 2003). This suggests, in accordance with the somatic marker hypothesis, that the vmPFC may predict the future rewards associated with a behavior based on previous experience with its consequences (Naqvi et al., 2006). Another study showed that the vmPFC is involved in encoding the subjective values of future rewards, not only objective values like reward magnitude or temporal delay (Kable & Glimcher, 2009).

Also, body state representations have been shown to have a role in vmPFC processing, consistent with the somatic marker hypothesis (Buchanan & Tranel, 2009). For example, using magnetoencephalography, Rudrauf and colleagues found that body responses to emotionally arousing stimuli are represented in the vmPFC at the earliest stages of emotion processing (Rudrauf et al., 2009). Another study used false physiological feedback to show that information about somatic states plays a causal role in the formation of preferences (Batson, Engel, & Fridell, 1999). In sum, the somatic
marker hypothesis is an empirically supported theory of the neural mechanisms critical for integrating emotional information into the decision-making process.

1.1.4 Historical precursors to the somatic marker hypothesis

The somatic marker hypothesis presents a thorough neurological model of the role of emotion in behavior, building on ideas about the connections between emotion, the body, and complex behavior (Dalgleish, 2004). Damasio’s understanding of the role of the body in emotion is a development of the James-Lange theory, which in essence understands emotion as the perception of physiological changes in the body (Lange & James, 1922). This is the basis for the notion of a somatic marker that tags behavioral options with emotions represented in terms of the internal milieu.

In psychology and philosophy, there is a long tradition of separating emotion and the body from reason that lasted through most of the 20th century (Edwards, 1954). Following popular perceptions, emotions were often viewed as impediments to cool, rational behavior, rather than critical participants in such behavior. Nonetheless, over the years building up to Damasio’s theorizing, an increasing number of researchers came to appreciate the role of emotion in the organization of adaptive complex behavior. Echoed in Damasio’s theory is Wundt’s notion of affective primacy, which held that “the clear apperception of ideas in acts of cognition and recognition is always preceded by special feelings” (Wundt 1907, p244; Outlines of Psychology). In Wundt’s view, much like the somatic marker hypothesis, the bringing to mind of ideas (or behavioral options in the context of decision making) is inherently accompanied by affective information. Later,
Robert Zajonc developed the idea of affective primacy by arguing for a tight link between emotion and reason (Zajonc, 1980). Zajonc gave emotion an essential role in the organization of complex behavior like decision making.

The theory that most closely presaged Damasio’s somatic marker hypothesis came from the neuroanatomist and systems neuroscientist Walle Nauta. Systems neuroscience was articulated in the early 20th century by the neuropsychologist Karl Lashley in response to the various theories of central nervous function of his day. In Lashley’s view, cognitive operations are performed by the interaction of neuroanatomical units which produce behavior in a functionally interdependent way (Lashley, 1930). This systems view laid the groundwork for Nauta, and later Damasio, to understand the prefrontal cortex in terms of its tight connections with the limbic system, hypothalamus, and brain stem—nervous system structures closely linked to the internal milieu. Given this neuroanatomical situation and the deficits in behavioral organization and emotion observed after frontal cortex lesions, Nauta noted that “the behavioral effects of frontal-lobe destruction could be seen as the consequence of an ‘interoceptive agnosia’, i.e., an impairment of the subject’s ability to integrate certain informations from his internal milieu with the environmental reports provided by his neocortical processing mechanisms” (Nauta, 1971, p. 182). Foreshadowing Damasio’s notion of “somatic markers,” Nauta goes on to suggest that the interoceptive “informations” act as “navigational markers” to guide “complex goal-directed forms of behavior” (Nauta, 1971, p. 184). The somatic marker hypothesis took these early ideas and formulated a neurologically and cognitively specified theory of the role of emotion in the organization of complex behavior. This theoretical specification allowed Damasio and colleagues to
devise the hypothesis driven research program discussed above that has shown strong support for the somatic marker hypothesis over the past two decades.

1.1.5 The Role of the vmPFC in social and moral behavior

The field of social and affective neuroscience took off around the time of Damasio’s publication of the somatic marker hypothesis. Damasio highlighted that patients with vmPFC injuries have deficits in using emotions to guide their decision making toward the selection of adaptive behaviors (Damasio and Anderson 2003, p.33). From an evolutionary perspective, making adaptive, beneficial choices would clearly include engaging in socially appropriate behavior in order to maintain membership in social groups, which promote the survival of organism and species. And considering that the realms of social and moral behavior place a premium on emotional competence, it makes sense that patients with vmPFC injury show the most marked behavioral difficulties when making decisions in the personal, social, and moral domains. Patients with vmPFC injury have impairments in social emotions and moral behavior in their everyday lives (Anderson, Barrash, Bechara, & Tranel, 2006). They often display a lack of concern for others, socially inappropriate or callous behavior (e.g., inappropriate or rude comments), a reduction in the display of guilt and shame, and exhibit increased aggressive behavior (Anderson et al., 2006; Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Beer, John, Scabini, & Knight, 2011; Damasio et al., 1990; Dimitrov, Phipps, Zahn, & Grafman, 1999; Eslinger & Damasio, 1985; Fellows, 2007; Rolls, Hornak, Wade, & McGrath, 1994; Stuss & Benson, 1984). The behavior of the patient E.V.R., for example, was described as sociopathic (Eslinger & Damasio, 1985). In a case
study of a patient with childhood-onset vmPFC injury, Anderson et al. note that the patient lied frequently and unnecessarily, maintained no lasting friendships, and displayed little empathy, guilt, or remorse for his behavior (1999).

The role of the vmPFC in moral cognition has been demonstrated in a variety of laboratory experiments. Findings from functional imaging (Greene et al., 2001; Moll et al., 2002; Heekeren et al., 2003; Schaich Borg et al., 2006), behavioral (Wheatley & Haidt 2005; Valdesolo & DeSteno, 2006; Schnall et al., 2008), and lesion (Koenigs, Young et al., 2007; Ciaramelli et al., 2007; Thomas et al., 2011) studies have converged on the vmPFC as a crucial neural structure involved in integrating emotions into moral cognition (for reviews, see Casebeer, 2003; Young & Koenigs, 2007). In one of the more prominent lines of research, the vmPFC is implicated in making moral judgments about high conflict moral dilemmas that pit aggregate welfare against highly emotionally aversive acts (Greene et al., 2001; Koenigs, Young et al. 2007; Ciaramelli et al., 2007; Thomas et al., 2011). Consider, for example, the classic Footbridge dilemma in which you are standing on a footbridge over some trolley tracks and see a run-away trolley heading toward five workers on the tracks (Thompson, 1985). To save the workers, you must push a large man off of the footbridge onto the tracks where his weight will stop the trolley. In this dilemma, a large majority of people reject the utilitarian answer and say that they would not push the man, even though doing so would maximize the lives saved (Hauser et al., 2007). In contrast, in a low-conflict dilemma the competition between the choice options is reduced by limiting the social-emotional aversion to performing the action (e.g., to save the workers you must flip a switch rather than push a person). The
The majority of people tend to endorse utilitarian options in such low-conflict dilemmas (Hauser et al., 2007).

To account for these results, Greene and colleagues have developed a dual-process theory of moral judgment, which suggests that moral judgments on low-conflict dilemmas are driven by the less affective operations of the dorsolateral prefrontal cortex, which prompts the endorsement of a utilitarian outcome, while moral judgments on high-conflict dilemmas are driven by social-emotional processing performed by the vmPFC that prompts the rejection of an emotion-arousing harm (Greene 2007; Greene et al., 2004; Greene et al., 2008). The vmPFC has a well known role in social emotions, anticipating the future consequences of an action, and encoding the value of those consequences (Naqvi et al., 2006; Rangel et al., 2008). When a person considers the appropriateness of causing an emotionally aversive harm in order to secure a utilitarian outcome, as in a high-conflict dilemma, an anticipatory emotional response (or somatic-marker, cf. Damasio, 1994) is activated by the vmPFC and biases the decision away from causing harm. People who fail to properly activate this emotional information and integrate it into their decision would display an abnormal pattern of moral judgments. This is the case for patients with vmPFC injury, who have difficulty using emotions to guide their decision making (e.g., Bechara et al., 1997). Accordingly, patients with vmPFC damage lack a prepotent emotional response (Damasio et al., 1990) and are more likely to judge the utilitarian action as appropriate on high-conflict dilemmas (Koenigs, Young et al., 2007; Ciaramelli et al., 2007; Thomas et al., 2011).
1.2 Amygdala

1.2.1 Neuroanatomical and functional background

The amygdala (AMY) is a cluster of nuclei situated in the anterior-medial temporal lobe and is an important structure in the limbic system. Inputs to the amygdala can be divided into those arising from the hypothalamus and brainstem and those arising from the cortex and thalamus (Aggleton, Burton, & Passingham, 1980; Sah, Faber, Lopez de Armentia, & Power, 2003). Autonomic and somatic information that signals internal motivational states is carried to the amygdala via connections with the hypothalamus and brainstem (including the periaqueductal central gray and substantia innominata), as well as directly from spinal cord projections (Aggleton et al., 1980; Almeida, Roizenblatt, & Tufik, 2004; Klingler & Gloor, 1960). The amygdala receives primary sensory information from all modalities via cortical, thalamic, and other subcortical projections (Davis, Rainnie, & Cassell, 1994; McDonald, 1998; Sah et al., 2003). This sensory information arises in primary sensory cortex and is transmitted to the amygdala via cortical and subcortical relay centers (Sah et al., 2003). The amygdala also receives polymodal sensory information via particularly strong reciprocal connections with the hippocampus (Pikkarainen, Rönkkö, Savander, Insausti, & Pitkänen, 1999) and ventromedial prefrontal cortex (Porrino, Crane, & Goldman-Rakic, 1981). Its direct prefrontal connections are quite specific to the ventral and orbital sectors of the prefrontal cortex (McDonald, 1998).

Most of the neuroanatomical studies of the amygdala have been conducted in the rat, but cat, monkey, and human studies have shown significant overlap with rat
amygdala neuroanatomy (Sah et al., 2003). The relative amounts of information from the senses that is transmitted to the amygdala appears to be a main point of difference between species, with rats receiving more olfactory information and primates, with a higher density of cortico-amygdaloid connections, receiving more auditory and visual information (McDonald, 1998; Zald, 2003). Also, sensory information fed to the human amygdala appears to be more highly processed compared to the rat amygdala, as sensory pathways to the human amygdala involve longer projection cascades marked by more cortical waypoints (McDonald, 1998).

The central nucleus of the amygdala is its major output, with projections to a variety of hypothalamic and brainstem structures responsible for inducing the specific aspects of the fear response (Davis et al., 1994; Sah et al., 2003). For example, due to its projections to the hypothalamus, stimulation of the central nucleus induces acetylcholine release (initiating the “stress response”), tachycardia, a skin conductance response, pupil dilation, and blood pressure elevation. Projections to the trigeminal facial motor nucleus are responsible for generating facial expressions of fear.

In addition, the amygdala projects to the ventral striatum and prefrontal cortex, which exert an influence on higher complex behavior (Adolphs, 2010). For example, amygdala neurons guide reward-seeking behavior by activating the nucleus accumbens (Ambroggi, Ishikawa, Fields, & Nicola, 2008). The amygdala also sends reciprocal connections to cortical sensory areas (Sah et al., 2003). In the visual domain, processing in early visual areas in the occipital lobe is modulated by the amygdala via the inferior longitudinal fasciculus, which connects the temporal and occipital poles, and potentially through other pathways (Adolphs, 2004; Catani, Jones, Donato, & ffytche, 2003).
Similarly, the amygdala modulates memory encoding and consolidation in the hippocampus, which is the basis for emotional memory and emotion-driven enhancement of declarative memory (Buchanan & Adolphs, 2002; Davis & Whalen, 2001; Hamann, 2001).

Given its neuroanatomical situation—receiving vast sensory input and modulating the activity of many other structures—the amygdala is in good position to form associations between current sensory inputs, motivational and somatic states, and past experience, and to induce corresponding bodily and behavioral responses (Bechara, Hanna Damasio, Damasio, & Lee, 1999). One of the central findings on amygdala function is its critical role in Pavlovian fear conditioning in rats, wherein it forms a “fear memory” (an association between a conditioned and unconditioned stimulus) and induces the fear response (LeDoux, 1998; Maren & Quirk, 2004; Wilensky, Schafe, Kristensen, & LeDoux, 2006). In the wild, prey react to predatory threat by increasing vigilance or moving away (Brown, Laundré, & Gurung, 1999), likely mediated by the amygdala (Dielenberg & McGregor, 2001).

Building on fear conditioning research in rats, studies in humans and other primates have implicated the amygdala in three general functional domains: emotion, reward learning, and social behavior (Adolphs, 2010). In humans, the amygdala has been shown to be critical for fear conditioning (Bechara et al., 1995; LaBar, LeDoux, Spencer, & Phelps, 1995). An extensive case study of a patient with bilateral amygdala lesions found the amygdala to be critical for the activation of the emotional state of fear as well as its experience (Feinstein, Adolphs, Damasio, & Tranel, 2011).
Moreover, amygdala processing plays a role in a variety of psychological disorders, particularly those associated with deficits in social and emotional functioning. It is believed that amygdala dysfunction plays a major role in autism, as people with autism show deficits in amygdala processing particularly when viewing facial stimuli (Baron-Cohen et al., 2000; Baron-Cohen et al., 1999). The amygdala has been implicated in catatonia (Moskowitz, 2004) and schizophrenia as well (Schneider et al., 1998). An fMRI study showed that for individuals with schizophrenia abnormal amygdala response to fearful faces was associated with reduced emotion recognition accuracy, and for comparison participants greater amygdala activity corresponded to greater emotion recognition accuracy (Gur et al., 2007). Also, the amygdala appears to have a role in depression. For example, the 5-HTTLPR polymorphism, which is associated with depression (Caspi et al., 2003), affects interactions between the amygdala and cingulate cortex, presenting a possible mechanism for the genetic susceptibility for depression (Munafò, Brown, & Hariri, 2008). Amygdala dysfunction in directing attention to salient and potentially threatening stimuli is believed to play a critical role in anxiety, which will be discussed in more detail below (Davis, 1992; Davis & Whalen, 2001). Supporting this notion, it has been shown that in individuals with phobias there is an increase in rapid amygdala activation to fear-relevant stimuli (Larson et al., 2006).

These findings are consistent with the amygdala’s involvement in emotion and the use of motivational states to guide behavior. According to Adolphs, the amygdala is specialized for processing salient information, especially under uncertain or threatening conditions (2010). This would explain its role in emotion, reward learning, and social behavior, as these domains are likely to involve uncertainty and to place demands on
processing salient information. Below I will review research on the amygdala, which has broadly supported Adolph’s view of amygdala function. The FLIAN model builds on this previous work in holding that the amygdala is critical for inducing the acquisition of information about salient attributes of the environment, or of options during decision making.

1.2.2 Kluver-Bucy Syndrome

Early studies of amygdala functioning looked at the effects of bilateral temporal lobe removal in monkeys, which resulted in a constellation of signs and symptoms now known as Kluver-Bucy syndrome (Kluver & Bucy, 1939). The monkeys exhibited “psychic blindness,” a deficit in the ability to recognize the emotional significance of events and stimuli. They displayed a tendency to orally examine objects, increased sexual behavior, and striking changes in emotion, particularly the loss of fear. One of the most notable behavioral changes observed in monkeys after temporal lobectomy was what Karl Wernicke called “hypermetamorphosis”—the indiscriminate, compulsive, and excessive search and examination of every stimulus in the environment. However, hypermetamorphosis is reduced when the lesion is circumscribed to either the amygdala or hippocampus (Weiskrantz, 1956). Animals with circumscribed lesions exhibited excessive oral examination of objects that diminished after a week to ten days. Thus, it seems that complete medial temporal lobe lesions thoroughly disrupt the organization of information acquisition processes, and that both the amygdala and hippocampus are together critical for maintaining the orderly acquisition of information.
In humans, Kluver-Bucy syndrome has been observed after bilateral amygdala damage where the hippocampus was relatively spared (Hayman, Rexer, Pavol, Strite, & Meyers, 1998). Moreover, one study of 12 Kluver-Bucy cases showed that the primary symptoms of the disorder observed in non-human primates can also been seen in humans (Lilly, Cummings, Benson, & Frankel, 1983). However, likely due to the variable etiologies of human Kluver-Bucy syndrome, human cases typically do not display all of the symptoms seen in non-human primates and those symptoms that are observed seem to be less severe and frequently occur in combination with other symptoms, such as aphasia, amnesia, and seizures.

1.2.3 Emotion recognition and information acquisition

Lesion studies have also demonstrated an important role for the amygdala in the judgment of emotionally salient stimuli, particularly in the recognition of emotion from facial stimuli (Adolphs, 2002). Adolphs and colleagues conducted a groundbreaking study on this topic in which they examined emotion recognition in the neurological patient SM, who has bilateral circumscribed amygdala lesions (Adolphs, Tranel, Damasio, & Damasio, 1994). When viewing Ekman faces depicting various emotions, participants rated how much each face was expressing each basic emotion. SM rated five of the basic emotion categories normally, but her ratings of fear for faces in the “afraid” category were significantly below normal, revealing a selective impairment in the ability to recognize fearful facial expressions. Further studies have shown that amygdala damage (unilateral or bilateral) leads to impairments in recognizing facial expressions of complex social emotions such as guilt, admiration, and flirtatiousness (Adolphs, Baron-Cohen, &
Tranel, 2002). These complex emotion recognition impairments were even more severe than impairments in the recognition of basic emotions.

Following-up on these findings, Adolphs et al. (2005) conducted another groundbreaking study of the patient SM’s emotion perception capacities using eye-tracking while participants made emotion ratings of facial stimuli. The authors found that, relative to comparison participants, SM’s gaze fell on the eyes of the face stimuli significantly less. They also showed that the eyes are particularly important for recognizing fear as compared to recognizing other emotions, which is supported by another study showing that the eye region was most critical when distinguishing fear from other emotions (Smith, Cottrell, Gosselin, & Schyns, 2005). It has also been shown that gaze direction and pupil size modulate amygdala responses to fearful faces (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Demos, Kelley, Ryan, Davis, & Whalen, 2008). In addition, the eye region is the most effective region (i) in breaking conscious suppression of fearful face stimuli (Yang, Zald, & Blake, 2007) and (ii) in activating the amygdala (Morris, deBonis, & Dolan, 2002). Based on the importance of the eye region for fear processing, Adolphs and colleagues conclude that SM’s fear recognition impairment is due to her impairment in directing her gaze toward the critical eye region of facial stimuli. In a subsequent study of SM’s face-directed gaze, she displayed impaired eye contact during real conversations with other people (Spezio, Huang, Castelli, & Adolphs, 2007).

Conclusively demonstrating that SM’s fear recognition difficulties are due to impaired fixation to the eyes of facial stimuli, her fear recognition ability is temporarily recovered when she is instructed to fixate on the eyes of the face stimuli (Adolphs et al.,
Furthermore, Kennedy and Adolphs (2010) showed that SM’s fixation to the eyes is most abnormal at the first fixation to the face, and less abnormal in subsequent fixations, suggesting her impairment is in the initial, automatic direction of attention to the face. Supporting this notion, her fixation to the eyes is restored when a fixation dependent “search-light” presentation of face stimuli is used in which only a small portion of the face is viewed at a time (Kennedy & Adolphs, 2010). This suggests that, in the absence of bottom-up features of the face stimuli driving SM’s attention away from the eyes, she is able to use top-down control processes to guide her fixation to the eyes.

The research by Adolphs and colleagues (2005) suggests that the amygdala plays a role in determining visual input even before it arrives at the cortex. It does so via the bottom-up, stimulus-driven direction of attention toward the acquisition of salient information. I will refer to this as the information acquisition aspect of amygdala functioning. As the authors put it, SM’s emotion recognition deficits are not due to an emotion processing deficit, nor to “a basic visuoperceptual inability to process information from the eyes, but is instead a failure by the amygdala to direct her visual system to seek out, fixate, pay attention to and make use of such information to identify emotions” (Adolphs et al., 2005, p. 71). This information acquisition function of the amygdala may underlie the amygdala’s role in fear; fear enhances sensory acquisition, and the facial expression of fear maximizes the acquisition of visual and olfactory information, both of which are critical for responding to threats in the environment (Susskind et al., 2008). The fear recognition impairment in SM thus appears to be due to an impairment in the automatic induction of acquiring information about fear from facial stimuli.
Also in support of this view, it has been suggested that the central amygdala is involved in enhancing a state of general attention or arousal that boosts sensory processing (Kapp, Whalen, Supple, & Pascoe, 1992). In a magnetoencephalography study it was found that visual processing occurs early in the amygdala; there are two visual processing pathways, one of which is primarily affective and skips the traditional occipitotemporal “what” pathway (Rudrauf et al., 2008). Rudrauf and colleagues propose that this affective pathway that provides early visual input to the amygdala may be responsible for the amygdala’s constant threat monitoring function.

It is well established that emotion drives attention and is important for maintaining on-going vigilance for salient environmental cues. In arrays of fear relevant (threatening) and irrelevant pictures, fear relevant stimuli are detected more quickly than fear irrelevant stimuli (Öhman, Flykt, & Esteves, 2001). An analogous effect has been shown for threatening or angry versus friendly, happy, and neutral faces displayed in arrays, with the former faces detected faster (Öhman, Lundqvist, & Esteves, 2001).

In another study, a backward masking procedure was used in which facial stimuli expressing mild affect were displayed very briefly and followed immediately by a neutral face (Esteves & Öhman, 1993). The affective stimulus was so brief that subjects reported seeing only a neutral, expressionless face. Nonetheless, greater amygdala activation was observed when the masked stimulus expressed subtle fear than when it expressed subtle happiness. Since participants were not expecting affective stimuli, this result suggests that the amygdala automatically and carefully monitors the environment for salient information like fearful facial expressions. In this way, it maintains a state of readiness for the rapid acquisition of potentially relevant information. Accordingly, Davis and
Whalen note that “more than functioning primarily for the production of strong emotional states, the amygdala [is] poised to modulate the moment-to-moment vigilance level of an organism” (Davis & Whalen, 2001).

Indeed, the maintenance of vigilance does appear to be a critical function of amygdala. The amygdala drives enhanced sensory processing in anxious states by potentiating sensory areas, lowering the neuronal threshold for activation and heightening the readiness to receive incoming information (Whalen, 1998). The amygdala is known to modulate the processing of visual information acquired from the environment via backward projections to early visual corticies (Adolphs, 2004; Catani et al., 2003; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). The likely neurochemical mechanism for this action is the amygdala’s modulation of cholinergic neuron activity in the basal forebrain (which influences cortical processing) and the thalamus, lateral dorsal tegmental nucleus, locus coeruleus, and parabrachial nuclei (which modulate thalamic sensory relay processing; Davis & Whalen, 2001). In support of this view, stimulation of the central amygdala, which has indirect widespread effects on cholinergic neurons projecting to the cortex, produces a state of heightened attention (Kapp, Supple, & Whalen, 1994). Projections via the inferior longitudinal fasciculus also appear to be important in the modulation of early sensory processing (Catani et al., 2003).

In sum, the amygdala appears to play a critical role in driving the acquisition of salient information in the environment (Adolphs, 2008). It seems that the importance of this acquisition function for fear and threat detection explains the amygdala’s central responsibility in those domains.
1.2.4 Information acquisition in psychological disorders

The information acquisition role of the amygdala has also been found relevant in clinical contexts where amygdala dysfunction contributes to psychological disorder, as in autism and anxiety. People with autism show an absence of preferential looking to the eyes of approaching adults, and this predicts social impairment in two-year-old toddlers with autism spectrum disorders (ASD; Jones, Carr, & Klin, 2008). Abnormal gaze fixation and amygdala activity has been found in individuals with autism, and greater amygdala activity corresponded to greater time spent fixating the eye region of face stimuli (Dalton et al., 2005). Even the parents of autistic children, who may pass on a genetic predisposition to ASD, show decreased processing of the eyes of facial stimuli (Adolphs, Spezio, Parlier, & Piven, 2008). In another study, abnormal gaze fixation and reduced amygdala activity and volume were found in unaffected siblings of autistic individuals (Dalton, Nacewicz, Alexander, & Davidson, 2007). Finally, like the patient SM, high functioning individuals with autism show decreased use of eye information and a preference for directing their gaze to the mouth when viewing faces (Spezio, Adolphs, Hurley, & Piven, 2006; Spezio et al., 2007).

Amygdala dysfunction is also a prevalent feature of anxiety (Charney, Grillon, & Bremner, 1998; Davidson, 2002; Davidson, Putnam, & Larson, 2000; Davis, 1992; Rauch, Shin, & Wright, 2006). For example, Stein et al. have demonstrated increased amygdala activity in anxiety-prone people (2007). In relation to the amygdala’s information acquisition role discussed above, Davis and Whalen note that an important symptom of anxiety disorders is hypervigilance, where vigilance can be understood as a heightened mode of information acquisition that monitors the environment for potential
danger (2001). They go on to suggest that considering the amygdala’s role in vigilance (rather than fear per se) and anxiety, “pathological anxiety may not be a disorder of fear, but a disorder of vigilance.”

Supporting the importance of vigilance in anxiety, one prominent line of research has demonstrated a greater tendency among anxious individuals to interpret ambiguous information as threatening and to selectively attend to threatening information (MacLeod, Campbell, Rutherford, & Wilson, 2004). Also, trait anxious individuals are more likely to interpret ambiguous sentences as having threatening content (MacLeod & Cohen, 1993). Another study found that people with high levels of anxiety demonstrate higher vigilance for threatening faces (Bradley, Mogg, White, Groom, & Bono, 1999).

Not surprisingly, anxiety is also closely associated with uncertainty. In uncertain or ambiguous situations it is more difficult to gather needed information and to predict outcomes, and it is also important to gather that information in order to assess the potential for threat. Thus, in uncertain contexts, heightened demands are placed on vigilance and the acquisition of salient information, which are associated with the amygdala and anxiety (Adolphs, 2010). To be more specific, what exactly is the anxious individual uncertain about? According to Epstein and Roupenian, Freud associated anxiety with uncertainty about the source of one’s fear (1970). However, it has more recently been suggested that anxiety is actually due to uncertainty about unknown outcomes (Dugas, Gagnon, Ladouceur, & Freeston, 1998; Epstein & Roupenian, 1970). For example, an anxious individual might wonder, “Will I make a mistake in my lecture and be laughed at by my peers?” or “Will the snake bite me?” Davis and Whalen state the connection between uncertainty and anxiety clearly: “If one assumes that an ambiguous
stimulus requires the brain to gather more information to decide to approach or avoid that stimulus, one can imagine that a system designed to promote vigilance and attention would show greater activation, the more ambiguous the stimulus” (2001). In anxiety, an intolerance for outcome uncertainty leads to worry and anxiety, and accordingly to heightened vigilance to drive the organism to resolve the ambiguity by monitoring the environment for salient information (e.g., about the presence of threat) or by escaping. As a specific example, consider that uncertainty about whether a snake will bite can be resolved by investigating the snake for signs of whether it is in a biting mood (i.e., enhance vigilance; Davis & Whalen, 2001), or by escaping (behaviorally or cognitively; Borkovec, Alcaine, & Behar, 2004).

The role of uncertainty in anxiety has been important in the development of third wave cognitive-behavioral therapies for anxiety disorders, such as Acceptance and Commitment Therapy (Hayes, Strosahl, & Wilson, 2003). The link between anxiety and uncertainty, and ultimately the amygdala, has also been demonstrated in a variety of experimental studies. For example, people are more anxious in ambiguous as compared to structured interviews (Dibner, 1958). Unpredictability, even when separated from the overtly emotive or motivational properties of a stimulus, is sufficient to induce sustained amygdala activity and anxious behavior (Herry et al., 2007). Intolerance of uncertainty has been associated with anxiety both in individuals with psychopathology (Holaway, Heimberg, & Coles, 2006) and without (Epstein & Roupenian, 1970). In sum, it seems that in anxious individuals, the vigilance and information acquisition processing functions of the amygdala are abnormally activated due heightened intolerance of uncertainty (Dugas et al., 1998).
1.2.5 Decision making

Building on the above discussion, it has been established that the amygdala contributes to the processing of emotionally salient information during decision making, particularly under conditions of uncertainty. It also has been shown to be involved in predicting punishment and computing prediction error, which are important processes under uncertainty (Yacubian et al., 2006). In an fMRI study by Hsu and colleagues, activation of the amygdala was positively correlated with the level of ambiguity in a decision problem (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005). The Iowa Gambling Task (IGT) creates a complex decision-making environment in which the participant must overcome ambiguity in risk assessment in order to learn the contingencies of the task and make advantageous decisions. Emotional, amygdala-based processing has been shown to be critical for this process. Bechara et al. found impaired decision making on the IGT in patients with bilateral amygdala damage (1999). The researchers found that patients with amygdala damage show neither the normal skin conductance response to rewarding or punishing feedback while playing the game nor an anticipatory SCR prior to drawing from bad decks. This is in contrast to the performance of patients with vmPFC damage on the IGT, who fail to develop anticipatory SCRs, but do show normal emotional responses to feedback (Bechara et al., 1997). These findings have more recently been extended to patients with unilateral amygdala damage, revealing a gender by laterality interaction: impaired IGT performance is more pronounced in males with right damage and females with left damage (Gupta, Koscik, Bechara, & Tranel, 2010). Thus, the amygdala is critical for generating autonomic emotional responses to emotional stimuli, including the consequences of one’s decisions—a process that is an essential
precursor to the development of anticipatory responses to similar decisions in the future (Bechara & Damasio, 2005; Bechara et al., 1999). Indeed, it has been shown that information about future rewards is transmitted from the amygdala to the vmPFC, consistent with the role of these structures in guiding decision making suggested by the somatic marker hypothesis (Hampton, Adolphs, Tyszka, & O'Doherty, 2007). In the context of evaluating choice options, the vmPFC reactivates amygdala-based reward information, which feeds forward to the vmPFC to guide decision making (Bechara & Damasio, 2005).

1.2.6 The acquisition of salient information under uncertainty

The AMY is historically thought of as involved in processing emotional information, but the literature reviewed above suggests an additional critical role in acquiring salient information (Adolphs, 2008). Emphasizing an updated view of the amygdala’s processing role, Adolphs suggests that the AMY is not critical for “processing threat or fear as such, or perhaps even emotion or reward as such, but rather appears to come into play when stimuli are particularly salient (which could result from them being threatening, rewarding, or unpredictable)” (Adolphs, 2010). In addition to supporting this view, the abundant evidence reviewed above suggests that a role in acquiring salient information should be added to Adolphs’ definition of amygdala functioning.

An interesting connection exists between the amygdala’s processing and acquisition roles; the behavioral and information acquisition responses induced by the
AMY facilitate further amygdalar processing. For example, the fear response induced by the amygdala drives the acquisition of salient information in the environment, and processing information about salient features of the environment is precisely the type of processing the amygdala is specialized for. In this way, the amygdala induces a perception-action cycle (c.f., Fuster, 2008) that focuses processing on amygdala pathways. Perception-action cycles are fundamental to adaptive behavior. According to Fuster, “all adaptive behavior rests on the circular processing of information between the organism and its environment. Sensory information leads to motor actions, which produce changes in the environment, which lead to new sensory inputs, which lead to new actions, and so on” (2001, p. 329). The idea as it relates to the amygdala, taking the fear response as an example, is that an initial fear response induced by the amygdala would bring in information that will help the amygdala assess the current danger, a process which brings in further salient information, and so on.

The FLIAN model builds on these ideas, suggesting that the AMY plays a critical role in inducing the acquisition of information about salient attributes of the environment. Threat would be one such attribute. But the amygdala’s role in processing information about various attributes of options during decision making, such as ambiguity and future reward, suggests that it may also induce the acquisition of information pertaining to such attributes when they are relevant to an organism’s behavioral goals.
1.3 Hippocampus

1.3.1 Neuroanatomical and functional background

The hippocampal formation, often referred to as simply the hippocampus, is located deep within the medial temporal lobe and is a critical limbic structure for memory and relational processing (Cohen & Eichenbaum, 1995; Squire, Stark, & Clark, 2004). It has a well-known role in declarative memory, particularly for episodic events. The hippocampus incorporates the tri-layered hippocampus proper (divided into the CA1, CA2, and CA3 fields), as well as the dentate gyrus and subicular complex (Brown & Cassell, 1980; Squire et al., 2004). The main cortical input to the hippocampus comes from the entorhinal and perirhinal corticies of the parahippocampal gyrus, carrying vast unimodal sensory information from all modalities as well as polymodal sensory information (Burwell et al. 1995, Insausti et al. 1987, Lavenex & Amaral, 2000, Suzuki & Amaral, 1994). The hippocampus sends projections to limbic structures such as the amygdala and the mammilary bodies of the hypothalamus (Amaral, 1987; Van Hoesen, 1982). The HC also projects to the cortex, particularly the orbitofrontal cortex and perirhinal and parahippocampal gyri (Amaral, 1987; Van Hoesen, 1982). It has strong reciprocal connections with the vmPFC, which exert top-down control over medial temporal lobe functions (Goldman-Rakic, 1984; Tomita et al., 1999; Simons & Spiers, 2003; Wood & Grafman, 2003).

The hippocampus is thus well-situated anatomically for performing memory functions through long-term potentiation (Bliss & Lomo 1973), which forms associations between the multiple pieces of information related to a memory representation (Cohen &
Eichenbaum 1993). According to Cohen and Eichenbaum (1995), hippocampal processing generates “highly interconnected networks, with connections among informational elements forming multidimensional ‘spaces’ that capture various possible relations” (p. 62). They argue in this way that the nature of hippocampal declarative memory representations is fundamentally relational. It is because of its relational processing function that the HC is critical for declarative memory, which requires the binding together of multiple arbitrarily related pieces of information (e.g., about time, place, smells, objects, and so on) and encoding the relationships between them.

1.3.2 The HC and declarative long-term memory

The most striking historical evidence for the role of the hippocampus in memory functions came from studies of the patient HM, who underwent bilateral medial temporal lobe resection due to intractable epilepsy (Scoville & Milner, 1957; Milner, 1972; Squire, 2009). After surgery HM demonstrated preserved language, perception, and general intelligence and cognitive functioning. However, he was burdened with dense declarative anterograde amnesia and retrograde amnesia for events up to 11 years pre-surgery. Importantly, HM was not impaired in all domains of memory functioning; he retained intact nondeclarative memory (procedural memory, priming, and conditioning) as well as generally intact short-term memory (Milner, 1972; Bechara et al., 1995; Squire & Zola-Morgan, 1988). HM’s medial temporal lobe damage was not specific to the hippocampus, but subsequent studies in humans and nonhuman primates revealed the hippocampus as the critical structure, although patients with circumscribed hippocampal damage generally have less severe amnesia than HM (Zola-Morgan et al., 1986; Mishkin et al.,
Patient RB, for example, had exceedingly rare circumscribed, bilateral CA1 lesions due to stroke, and presented with dense anterograde but very mild retrograde amnesia (Zola-Morgan et al. 1986).

Functional neuroimaging studies have also demonstrated that the HC is involved in declarative memory. Studies have found that HC activation during the successful encoding of word lists correlates with subsequent recall scores (Fernandez et al., 1998). In a study of expert memory, London taxi drivers showed increased right HC and parahippocampal gyrus activation when retrieving memories of driving routes (Maguire, Frackowiak, & Frith, 1997). Moreover, the volume of the taxi drivers’ hippocampus was greater than controls, and that effect was larger the longer the participant had been driving a taxi. The role of the HC in memory retrieval has also been shown, as retrieval of successfully remembered items activates the subiculum.

Animal lesion studies primarily use the delayed non-matching to sample task to study long-term memory functions (Mishkin, 1982). In this task, a single object is presented repeatedly, then after a delay that object is presented along with a new object. To get a reward the animal must choose the novel stimulus, thus revealing its memory for the original stimulus. The interval between the initial and second presentations can be varied to test for longer- versus shorter-term memory. Using this task, a selective long-term memory impairment has been demonstrated in monkeys with bilateral medial temporal lobe damage. Moreover, the lesion size correlates with the severity of memory impairment; damage that includes the entorhinal cortex results in a more severe impairment than damage to the HC alone. The HC is the critical structure, however, as
bilateral entorhinal cortex lesions cause DNMS impairment early, but this is recovered after about a year.

1.3.3 Relational and on-line processing

The memory functions of the HC are on-line, constructive processes predicated on a system that can flexibly combine previously acquired information (Schacter & Addis, 2007). This on-line aspect of HC functioning is revealed in the finding that the HC is critical for maintaining online representations of simple objects for durations of only 6 seconds (Warren, Duff, Tranel, & Cohen, 2010). The process of spatial navigation also involves the HC in an active role (Bird & Burgess, 2008). And the HC is critical for the prediction of upcoming spatial information as an animal navigates its environment (Lisman & Redish, 2009). A similar prospective function has also been shown in humans, where the HC plays an important role in the active process of future thinking—the future construction of episodic representations (Schacter, Addis, & Buckner, 2007).

In the realm of decision making, studies using the IGT have shown that hippocampal declarative memory functions are critical for advantageous decision making (Gupta et al., 2009). Like patients with vmPFC or amygdala damage, patients with hippocampal damage failed to develop a preference for advantageous decks on the IGT. However, while their counterparts with vmPFC or amygdala damage and associated emotional impairments developed a preference for disadvantageous decks, the patients with hippocampal damage selected evenly from both advantageous and disadvantageous decks. According to Gupta and colleagues, the hippocampus is necessary on the IGT for
sustaining representations of the relations between decks and their rewarding and punishing consequences (Gupta et al., 2009).

The importance of the hippocampus for relational processing per se has been demonstrated in several experiments in humans and rats (Bunsey & Eichenbaum, 1996; Hannula et al., 2010; Konkel & Cohen, 2009). Patients with hippocampal amnesia show relational memory deficits for the relations among elements in a scene and for pairings between scene and face images, even in very short time spans (Hannula, Tranel, & Cohen, 2006). Using eye-tracking, impaired non-conscious detection of changes in scenes and impaired memory for relations between scenes and faces have also been demonstrated in patients with amnesia (Hannula, Ryan, Tranel, & Cohen, 2007). Functional neuroimaging studies have found that hippocampal activity is positively correlated with relational memory processing (Hannula & Ranganath, 2008), and that increased hippocampal activation predicts the accuracy of relational memories of scene-face pairs (Hannula & Ranganath, 2009).

Another patient study demonstrated a critical role for the hippocampus in multiple types of relational memory—spatial, associative, and sequential (Konkel, Warren, Duff, Tranel, & Cohen, 2008). And it has further been demonstrated that remembering conjunctions of information requires the hippocampus at both long and short delays (Olson, Page, Moore, Chatterjee, & Verfaellie, 2006). The relational functions of the HC have been revealed in rats as well, specifically for transitive and associative inferences (Eichenbaum & Fortin, 2009). To summarize, these results support the notion that the primary function of the hippocampus lies in the on-line processing and storage of
relational information, rather than long-term memory per se (Cohen & Eichenbaum 1993).

Several recent studies have further demonstrated the role of the hippocampus in the active, online maintenance of representations of new information. One study found that patients with damage to the hippocampus were impaired at tasks in which all of the information required to respond was fully displayed at one time, such as the Hooper Visual Organization Test (Warren, Duff, Jensen, Tranel, & Cohen, in press). The authors note that these tasks likely place demands on relational processing and, in particular, on the ongoing processing and manipulating of related information. Another study tracked the eye movements of patients with damage to the hippocampus while they visually searched a large array of complex stimuli for a match with a target stimulus (Warren, Duff, Tranel, & Cohen, in press). The patients returned to fixate on the target more frequently, and for stimuli further in distance from the target they showed a reduction in the preference to maintain fixation on stimuli more similar to the target. The HC is thus shown to be critical for the active maintenance of representations over very short delays.

1.3.4 An active role in information acquisition

As discussed in section 1.2.6, it has been suggested that the amygdala has a fundamental role in inducing information acquisition behavior. A similar possibility for the hippocampus has been largely ignored. This is a significant oversight considering the critical importance of the active acquisition of information for memory and learning processes (Bransford, Brown, & Cocking, 1999; Mayer, 2004). Moreover, hippocampal processing is sensitive to whether information is acquired actively or passively. For
example, rats form different hippocampal representations of space when actively walking around versus being carried around, and the active representations are more robust (Song, Kim, Kim, & Jung, 2005).

In a recent study of volitional memory, Voss et al. examined the neural basis of active visual exploration during learning in humans (Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011). Participants studied matrices of objects in a “spotlight,” or “viewing window,” procedure that allowed only one object to be viewed at a time. The study manipulated whether search was volitional (participants had full control over the search window) or passive (the window moved itself). The researchers found enhanced memory for objects and object locations in the volitional condition. Also, activation of the HC was greater in the volitional than passive condition. However, patients with hippocampal amnesia failed to show a memory benefit from the volitional control of information acquisition. Volitional control is thus shown to be important for exploration of and learning from the environment, and the HC is critical for the positive mnemonic effects of such active information acquisition. In discussing these findings, Voss and colleagues make a further claim:

“Rather than just being engaged in relational memory binding of incoming information, automatically and obligatorily, our findings suggest that the hippocampus has a more active role in acquiring information, presumably being involved in directing what information should be obtained next from the environment on the basis of the information already obtained.” (Voss et al., 2011, p. 120)

However, their study does not directly address this claim, as it cannot distinguish between whether the HC is involved in the active acquiring of information (as the authors suggest) or only in the processing of information that is being acquired actively. That is,
greater hippocampal activation during the volitional condition does not demonstrate that
the hippocampus is actively directing the acquisition of information—it may simply be
engaged in the on-line processing of information as it is acquired actively. A similar
problem exists in trying to interpret the results in patients with hippocampal amnesia,
where their impairment in volitional memory enhancement may be due to a deficit in
actively acquiring information from the object matrix (e.g., they search the objects
abnormally) or a deficit in processing the information acquired when the matrix is
actively searched.

The eye-tracking studies by Hannula and colleagues present a similar ambiguity.
For example, hippocampal damage results in abnormal information acquisition measured
by decreased fixation to faces that had previously been paired with a scene, which I will
call a failure of preferential fixation (Hannula et al., 2007). In the context of the
experimental task, this finding was interpreted as indicating a deficit in processing
relational information. The authors argue that face-scene relations were not encoded
properly, and thus the patients did not exhibit preferential fixation. However, the lack of
preferential fixation, understood as the abnormal acquisition of information, may simply
indicate a deficit in the induction of normal information acquisition processes. Relational
information might be encoded normally, and the failure may come in the induction of
information acquisition processes (namely, preferential fixation) that are based on that
relational knowledge. Neither the work of Voss et al. nor Hannula et al. can distinguish
the role of the hippocampus in inducing the acquisition of information from its role in
relational processing. Nonetheless, Voss et al. suggest that the HC serves an acquisition
function, while Hannula et al. interpret their results in terms of relational processing. Of
course, considering the preponderance of evidence demonstrating the role of the HC in relational processing reviewed above, it seems unlikely that in patients with hippocampal damage relational processing is fully intact and there is solely an information acquisition deficit. It is more likely that these two impairments coexist; that, like the amygdala’s proposed role in both processing information about salient attributes of the environment and inducing the acquisition of such information, the hippocampus has a role in both processing relational information and inducing its acquisition.
CHAPTER 2. FLEXIBLE DECISION MAKING AND PREDECISIONAL BEHAVIOR

Voss and colleagues observe that “human learning and memory are predominantly studied using experimental paradigms in which the participant is more a passive recipient of information than an active learner” (Voss et al., 2011, p. 115). A similar criticism applies to a majority of decision-making research, which has focused on a policy capture or structural modeling approach (Billings & Marcus, 1983; Johnson, Schulte-Mecklenbeck, & Willemsen, 2008; Payne et al., 1978; Westenberg & Koele, 1994). Indeed, the focus on such passive protocols may explain the reason the hippocampus has not been a major player in the neuroscience of decision making—passive protocols may not place sufficient demands on memory, relational processing, or the active acquisition of information to recruit the hippocampus. When more active protocols are used, as in the IGT, the HC has been shown to have a critical role in decision making (Gupta et al., 2009).

The “policy capture” approach that has been the focus of decision neuroscience research utilizes static decision problems to study the relationships between input (the problem presented), output (the decisions made), and the brain. For example, researchers study how input variables like risk, probability, ambiguity, and reward value are encoded in the brain (Glimcher, Dorris, & Bayer, 2005). In a recent review of the neural basis of decision making, the current decision neuroscience project was summarized as follows: “Any neural model of decision making needs to answer two key questions. First, how are the subjective values of the various options under consideration learned, stored, and represented? Second, how is a single highly valued action chosen from among the options
under consideration to be implemented by the motor circuitry?” (Kable & Glimcher, 2009). This view focuses on the output of decision making and entirely omits critical predecisional processes and the ongoing dynamics of real-world decision making, such as selecting an appropriate decision-making strategy and acquiring and integrating information to progress toward choice by updating the decision space (Payne et al., 1978).

The policy capture approach is right to emphasize the fact that the choice among alternative courses of action is the fundamental purpose of decision making. But decision making is a process, and producing a choice output is merely the culmination of that process. For all of our faults, it is truly remarkable that humans have the decision-making capacity (not always fully exercised!) to recognize multiple options for action, gather and evaluate evidence about them, and choose amongst them. And we are not a one trick pony equipped with one universal decision-making strategy that translates input problem variables into choice output; we flexibly select from a playbook of strategies depending on the problem we face (Einhorn & Hogarth, 1981; Loomes, 1991; Newell & Simon, 1972; Payne et al., 1993). While traditional decision-making research in psychology and neuroscience focuses on policy capture approaches, a long history of studying predecisional behavior has explored the selection of decision-making strategies and their implementation (Payne et al., 1978). This line of study began in earnest in the 1970’s, as researchers applied Newell and Simon’s (1972) information process theory of problem solving to decision making. Rather than viewing decision making simply as the choice output, it was understood as being comprised of multiple component processes that function together in decision making. The flexible aspect of the process is critical, as
it allows for adaptation to the task environment. In selecting among strategies decision makers make tradeoffs between accuracy and effort (Payne et al., 1993). Of course, in certain contexts some strategies, such as heuristics, can be quite accurate while also providing a savings on effort (Sunstein, 2005).

From the pool of decision-making strategies available to a decision maker, a strategy is selected based on the representation of the problem being faced (Gold & Shadlen, 2007; Payne et al., 1993; Rangel et al., 2008). I will refer to this representation as the “decision space,” similar to Newell and Simon’s “problem space” or Kahneman and Tversky’s “task representation” (Kahneman & Tversky, 1979; Newell & Simon, 1972). As Einhorn & Hogarth (1981) note, “different decompositions [of a problem] may lead to different task representations,” which will call for different decision strategies (p. 11). After being selected based on the decision space, a strategy is implemented primarily (i) by modulating the way acquired information is integrated into the decision space (i.e., how evaluations are formed) and (ii) by modulating how information is acquired (Einhorn & Hogarth, 1981; Payne et al., 1993).

Information integration refers to how acquired information is used to evaluate options and update the decision space representation (Billings & Marcus, 1983). Two general integration modes have been the focus of research on flexible decision making: compensatory and noncompensatory (Payne et al., 1992). In compensatory integration, tradeoffs are made across attributes such that when evaluating a given option a positive value on one attribute can make up for a negative value on another. In contrast, noncompensatory integration does not allow for such compromises—an option may be ruled out based on a negative attribute, and its positive attributes entirely ignored.
Compensatory and noncompensatory modes also differ on whether they are likely to involve consistent or selective processing of information across options or attributes (Payne et al., 1993). The question here is whether a similar amount of information is processed for all of the options being considered. Furthermore, they differ on whether explicit overall evaluations of the options are formed and maintained during the decision making process. Compensatory processing generally involves consistent processing and the explicit formation of overall evaluations, while noncompensatory processing involves selective information processing and no overall evaluation (Payne et al., 1993).

For example, in the noncompensatory elimination-by-aspects strategy, options are compared on a single attribute at a time in a “survivor”-type competition (Tversky, 1972). Information is selectively acquired for only those options that have not been ruled out, and no summary evaluation across attributes is maintained. When comparing potential apartments for rent, for example, those with anything other than 2 bedrooms might be tossed out of the running, then those with rent above $1000 may be ruled out, followed by those without a bus stop nearby, and so on, until only one apartment is left standing. Here, no summary evaluation of the apartments (integrating information across attributes) is maintained. Also, information is selectively processed—once an option is ruled out, no more information about it is acquired. In contrast, if only two apartments were under consideration and only limited information was available about them, one might use a compensatory strategy like the additive or weighted additive rule that implements summary evaluations. In this case, information is examined about each apartment and compromises are made; the expensive rent of one apartment may be bad, but that apartment might receive a positive overall rating since it is near the perfect bus...
route. Such overall, compensatory evaluations of the apartments are formed and used for option selection (Debreu, 1959; Payne et al., 1993; Tversky, 1969). Here information acquisition is consistent rather than selective, as an equal amount of information is processed about both options being considered.

As the examples given so far have illustrated, fundamental to flexible decision making is the ability to adapt information acquisition behavior to the decision-making strategy being implemented (Einhorn & Hogarth, 1981). To be clear, information acquisition is a concept that I will use to refer to the acquisition of information from the external environment (Payne et al., 1978), the body proper (such as somatic states; Rudrauf et al., 2009), or the brain itself (as in memory retrieval or the retrieval of emotional information from an “as-if” loop; Damasio, 1994; Dudai, 2002). There are two primary acquisition patterns that have been discussed: option-based and attribute-based (Payne et al., 1992). The attribute-based mode involves acquiring information about a single attribute for multiple options, whereas the option-based mode involves acquiring information about multiple attributes of a single option. Information acquired via the attribute-based mode is generally easier to process than information acquired via the option-based mode; since different attributes present different types of information, acquiring information within a given attribute at a time can to facilitate processing (Russo & Dosher, 1983).

Another aspect of information acquisition, the acquisition variability, refers to the variability in how much information is acquired about each of the available options. Acquisition variability is selective (also known as variable) when one acquires more information about some options, probably those that are most appealing, and less
information about others, probably those that have been eliminated and are no longer under consideration (Olshavsky, 1979). Acquisition is constant when an equal amount of information is acquired about all of the options under consideration. This variability in acquisition is an indicator of the integration mode being applied (Payne et al., 1992). Noncompensatory integration is indicated by the selective acquisition of information, where more information is acquired about some options than others. This is because options that are ruled out early on during the noncompensatory process end up with less information about them acquired. Compensatory integration is indicated by constant acquisition, where similar amounts of information are acquired about all options.

2.1 Information board tasks

An important approach for studying information acquisition modes and the flexible deployment of decision-making strategies is process tracing, which “uses different methods for recording what information is attended to and when that attention occurs and shifts” (Schulte-Mecklenbeck, 2007). Some process tracing methods are thinking aloud, verbal protocol analysis, eye tracking, and information boards. These methods track information acquisition and processing to provide a window into predecisional processing (Payne et al., 1993). In particular, since the acquisition of information is used to update the decision space according to the selected decision strategy (Montgomery, 1983), monitoring information acquisition is often used to examine decision-making strategies (Payne, Bettman, & Johnson, 1988).

Verbal protocol methods, for example, involve research participants verbally reporting their thought process while formulating a decision (Ford et al., 1989). This
method is limited in that it can only provide data on processes accessible to the decision maker, while it is well-known that much of the decision-making process occurs behind the veil of awareness. Information boards have been a particularly important tool in the study of predecisional processes, as they trace predecisional processes that a participant may not verbalize (Payne, 1976). In these tasks the participant is asked to decide among multiple options, each described by multiple attributes. The options and attributes are displayed in a matrix, for example, with apartment rental options A, B, C, and D occupying the columns, and their various attributes (rent, size, and number of bedrooms and bathrooms) displayed in the rows (Figure 2). Participants freely search the information until they are ready to make a choice. A participant’s information acquisition pattern throughout the decision-making process is revealed in how she searches for
information in the matrix, either acquiring information within columns (option-based) or within rows (attribute-based). And her integration mode is indicated by the acquisition variability (selective versus constant). Finally, the participant’s decision-making strategy can be characterized based on her acquisition pattern and variability (Billings & Marcus, 1983). When constant acquisition (low variability) is combined with an option-based pattern, linear and weighted additive strategies are indicated. Constant acquisition and an attribute-based pattern suggests the additive difference strategy, in which the difference between options is computed for each attribute and each option’s difference scores are summed and compared to each other (Russo & Dosher, 1983; Tversky, 1969). In contrast, selective acquisition (high variability) coupled with an option-based or attribute-based acquisition pattern suggests the conjunctive or elimination-by-aspects strategy, respectively. These categorizations are by no means meant to be decisive, but simply to indicate the general type of strategy the participant is using; a range of possible strategies fit each pattern-variability pair. For example, both the elimination-by-aspects and the lexicographic rules are indicated by attribute-based, selective acquisition. Further analysis and modeling techniques can be used to more precisely analyze predecisional behavior, and how predecisional behavior changes in the different stages of the decision process (Ball, 1997; Riedl, Brandstatter, & Roithmayr, 2008).

Information board tasks were originally performed with information on pieces of paper placed in envelopes and attached in a matrix to a cardboard poster (Payne, 1976). More recent methods have been developed to allow for these tasks to be completed on the computer. The MouseLab program in particular has been widely used, as it allows the
researcher flexibility in task design and provides an intuitive interface for research participants (Willemsen & Johnson, 2010).

2.2 Influences on predecisional processes

Flexible decision making and information acquisition have been observed to be affected by a variety of characteristics of the decision problem. This section reviews research on how a few prominent decision characteristics influence predecisional processes.

2.2.1 Task Complexity

In one of the first information board studies, Payne (1976) had participants choose among a set of apartments. Payne varied the number of apartment options (2, 6, or 12) and apartment attributes (4, 8, or 12) available in the information matrix. Examining verbal trace data and information acquisition patterns he found that participants used more compensatory information integration modes when there were only 2 apartment options, but used less compensatory modes when more options were present. Payne (1976) and others (Olshavsky, 1979) also demonstrated that the acquisition variability increases (toward a more selective mode) as the number of options increases. Thus, as the problem becomes more complex, as in Payne’s 6 and 12 option conditions, noncompensatory integration strategies (indicated by selective acquisition variability) are used to eliminate options based on limited information. In a complex problem, noncompensatory integration allows for the simplification of a complex decision space, as options are quickly removed from consideration. The increased use of compensatory strategies in binary (two-option) decision contexts and the preference for
noncompensatory strategies in multi-option contexts is now well appreciated (Biggs, Bedard, Gaber, & Linsmeier, 1985; Billings & Marcus, 1983; Olshavsky, 1979; Payne, 1982; Tversky, 1969, 1972).

Moreover, decision-making strategies are flexibly deployed within a given decision problem (Olshavsky, 1979; Payne et al., 1992). As the decision space is updated through the early stages of decision making, the problem being faced changes and new decision strategies are warranted (e.g., Olshavsky, 1979; Payne, 1976). In general, noncompensatory, attribute-based strategies are applied early and compensatory, option-based strategies are applied later (Bettman & Park, 1980; Lussier & Olshavsky, 1979; Olshavsky, 1979; Payne, 1976). Once the decision space is simplified via noncompensatory strategies, the remaining options can be examined more closely with compensatory strategies (Olshavsky, 1979). As Billings and Marcus put it, there is “evidence of an initial phase in which noncompensatory strategies are used apparently to reduce the number of alternatives, followed by a phase using compensatory strategies to evaluate the remaining alternatives and make a choice” (Billings & Marcus, 1983, p. 350). In this way, simplifying, noncompensatory strategies are often used to initiate the decision-making process (Svenson, 1979; Usher & Zakay, 1993).

Regarding the effects of task complexity on information acquisition *depth*, or the proportion of available information that is acquired, increasing the number of options or attributes led to a decrease in the depth of information acquired (Biggs et al., 1985; Payne, 1976; Stone & Schkade, 1991). Furthermore, it has been shown that the proportion of attributes about which any information is acquired decreases as the number of attributes increases (Biggs et al., 1985; Olshavsky, 1979). In some cases this may be
because attributes’ importances are weighted, and this weighting is relative to the other attribute information available (Payne et al., 1993). For example, when choosing an apartment, attribute information about the presence of a sauna might be ignored if 7 other more important pieces of information are available, but might be relied on if only 3 other similarly important pieces of information are available. When the number of attributes increases in a case such as this one, the number of attributes attended to does not increase at the same rate, leading to a decreased proportion of attributes searched (Biggs et al., 1985).

The influence of problem complexity on information acquisition patterns is less straightforward. Noncompensatory integration modes are favored when facing complex problems, but this can be coupled with an option-based or attribute-based acquisition pattern, depending on the specific decision strategy in use (Russo & Dosher, 1983). Payne (1976) showed that most participants use compensatory strategies on binary decision problems, but some implement the strategy via an option-based acquisition mode, as in the weighted additive strategy, while others implement it via an attribute-based acquisition mode as in the additive difference strategy. This finding was replicated by Billings and Marcus (1983). Nonetheless, evidence does suggest that as the number of options increases, information acquisition generally becomes more attribute-based (Stone & Schkade, 1991). This has been shown in contexts involving consumer decisions about computers (Payne & Braunstein, 1978) and risky decisions about gambles (Payne et al., 1993).
2.2.2 Dispersion

Another factor that strongly influences predecisional processes is dispersion—the variability in the weights of attributes or the attractiveness of options. Not all attributes carry equal importance. When the attributes available have similar weights (or importance), the problem is said to have low attribute dispersion. When some attributes are weighted more heavily than others, the problem has higher attribute dispersion. In an extensive study of the effects of dispersion on information acquisition modes Payne and colleagues found that participants engaged in significantly more attribute-based acquisition in the high-dispersion condition than in the low-dispersion condition (Payne et al., 1988). Their results also revealed the increased use of compensatory decision strategies in the low-dispersion condition. In a high attribute dispersion context, certain attributes are weighted more heavily than others, leading to the use of attribute-based acquisition as information acquisition is directed at the more salient attributes.

2.2.3 Time Pressure

Several studies have demonstrated consistent effects of time pressure on predecisional processes (Payne et al., 1992; Usher & Zakay, 1993). The effects of time pressure are similar to those of high option dispersion contexts. Under time pressure, people tend to use simpler strategies (Ben Zur & Breznitz, 1981; Wright, 1974; Zakay & Wooler, 1984). The elimination-by-aspects or lexicographic strategies were the most commonly used strategies under time pressure, and seemed to be the most effective (Payne et al., 1988). People tend to focused on the most important attribute and chose the alternative best on that attribute when deciding under time pressure (Edland, 1994).
Importantly, Payne et al. found that severe time pressure of a 15 second time limit seems to be needed for these effects to be observed (1988). In a 25 second time pressure condition, the influence of time pressure was significantly reduced or nonexistent.

2.3 The Fronto-Limbic Information Acquisition Network model of predecisional processes

The fronto-limbic information acquisition network (FLIAN) is a model of the neural system critical for the predecisional processes described above. The proposed model centers on fronto-limbic interactions, primarily involving the ventromedial prefrontal cortex (vmPFC), amygdala (AMY), and hippocampus (HC). Within this network, the vmPFC is critical for representing the currently perceived state of the decision problem (i.e., the decision space), which is the basis for selecting and implementing a decision-making strategy. The selected strategy is then implemented by the vmPFC via the coordination of information acquisition processes induced by the amygdala and hippocampus. The amygdala is specialized for inducing an attribute-based acquisition mode to drive the acquisition of information about salient attributes in the environment or of an option. The hippocampus is specialized for inducing a relational, option-based acquisition mode to drive the acquisition of pieces of information that are arbitrarily related to an individual event or option. Information acquired by these limbic structures then feeds forward to the vmPFC where it is integrated into an evaluation of the options to update the decision space according to the current decision-making strategy. This dynamic process proceeds until an option meets the choice criterion for the
strategy in use. The FLIAN model is described in this section in terms of what is known about the vmPFC, AMY, and HC, as reviewed in Chapter 1.

2.3.1 The role of the vmPFC in the FLIAN model

Considering its role in organizing complex behavior, the prefrontal cortex is a strong candidate region for being involved in representing the decision space and implementing a decision strategy by coordinating information acquisition during the decision-making process. Specifically, the vmPFC has been implicated in using a decision-making strategy appropriate for the problem being faced (Damasio & Anderson, 2003; Eslinger & Damasio, 1985; Fellows, 2006; Stuss & Benson, 1984). Patients with vmPFC injury have deficits in implementing advantageous plans of behavior (Eslinger & Damasio, 1985, p. 1739) and decision strategies (Bechara et al., 1997). Furthermore, the selection of a decision strategy is based on the decision space representation (Payne et al., 1993), and it has been established that the vmPFC plays a critical role in representing features that are fundamental to the representation of a decision problem, such as uncertainty, risk, and cost (Kable & Glimcher, 2009; Wallis, 2007).

One study in particular has provided support for the role of the vmPFC in implementing decision-making strategies (Fellows, 2006). Fellows used an information board task to study decision making in people with vmPFC injury. The task asked participants to choose an apartment to rent, and presented a variety of simple attribute information such as size, rental cost, and the quality of the neighborhood. Relative to comparison participants, the participants with vmPFC injury engaged in significantly more option-based information acquisition across all levels of task complexity. Adapting
information acquisition is a crucial way in which decision strategies are implemented; thus, the abnormal pattern of information acquisition suggests that the vmPFC is critical for the normal implementation of decision-making strategies. However, there is an important issue that limits the conclusions we can draw from this study: although most of the 13 vmPFC patients in this study had bilateral brain damage, the maximal lesion overlap in the vmPFC group was 4, indicating significant variability in lesion location and limiting our ability to draw conclusions about the vmPFC’s role in the findings. Nonetheless, the results are suggestive as the vmPFC group engaged in significantly more option-based information acquisition. Moreover, consistent with studies showing a link between decision strategy and choice output (Payne et al., 1992), the vmPFC group made abnormal final choices on the task. This suggests that the abnormal information acquisition mode of participants with vmPFC injury affected the outcome of their decision-making process, raising the intriguing possibility that abnormal information acquisition may be related to the abnormal decision making and social behavior in patients with vmPFC injury. However, the study by Fellows was conducted in the non-social context of choosing an apartment. Thus, in the experiments conducted here in Chapters 3 and 4 the information acquisition behavior of patients with vmPFC injury is studied in the social domain to examine whether abnormal information acquisition might be related the abnormal social decisions observed after vmPFC injury.

An important aspect of the decision space representation is the weight or value of an attribute—its salience to the decision. Certain attributes, such as threat, have inherent motivational and biological salience and thus acquiring such information to guide behavior is likely a default setting (Davis & Whalen, 2001). In contrast, for many
attributes to impact future behavior their value would have to be learned from experience with the consequences associated with past decisions that rely on those attributes. The vmPFC is a strong candidate region for learning the values of attributes as it is critical for representing the value of stimuli and the values of the consequences of actions (Öngür & Price, 2000; Rangel, Camerer, & Montague, 2008; Rolls, 2000). The somatic marker hypothesis explains how learning attribute values could occur via the vmPFC-based encoding of the affective value of information, in this case the affective value of an attribute used to guide behavior (Damasio, 1994). The affective marker can then be reactivated either to increase or decrease the weight of the attribute for future decisions. For example, consider a social decision about whether to befriend someone. A person might learn to avoid focusing on self-serving, utilitarian attributes (such as what can be gained from the friendship) due to negative consequences associated with making decisions based on that attribute in the past. When making future social decisions utilitarian information would have a lower attribute weight in the decision space representation and would receive less attention. In this way, vmPFC patients, who have impairments in reactivating somatic information related to past experience, may be less averse to integrating utilitarian information into their social decisions. They would accordingly be expected to acquire more of that information, a predecisional abnormality that could result in down-stream abnormalities in social judgment and behavior.

In sum, as the FLIAN model suggests, the vmPFC does appear to play a critical role in the predecisional processes of decision strategy selection and the coordination of information acquisition modes. It is thus argued that the underlying predecisional function of the vmPFC is the representation of the decision space, which includes the
prior learning of attribute weights and the integration of those weights into subsequent
decision space representations. Further study is warranted (i) in a group of patients with
circumscribed, bilateral vmPFC injury, (ii) to test the role of the vmPFC in the normal
predecisional weighting of attributes, and (iii) to examine how vmPFC injury affects
predecisional behavior during the different stages of the decision process. Furthermore,
the FLIAN model makes the additional claim that the vmPFC serves its function in
predecisional behavior via interactions with the amygdala and hippocampus, which, as
described below, are responsible for inducing attribute- and option-based acquisition
modes, respectively.

2.3.2 The role of the amygdala in the FLIAN model

The medial temporal lobe plays a critical role in organizing the acquisition of
information; lesions to the medial temporal lobe that include amygdala and hippocampus
produce indiscriminate, excessive, and seemingly purposeless search of the environment
(Kluver & Bucy, 1939). Monkeys with Kluver-Bucy syndrome examine their
environments excessively, but it seems as though the animals acquire no useful
information for guiding the selection of advantageous behaviors. The amygdala
specifically has been shown to be necessary for inducing the acquisition of salient
information from the environment (Adolphs, 2008; Davis & Whalen, 2001). The FLIAN
model proposes a more specific function of amygdala-based acquisition—the acquisition
of *information about salient attributes*, rather than the acquisition of “salient
information” as others have suggested (Adolphs, 2010). The idea is that the information
acquisition processes induced by the amygdala are organized around particularly salient
attributes of the environment (or of the stimulus, or of the choice options being considered). There is significant importance in specifying that amygdala acquires salient attribute information, rather than simply salient information. The latter says nothing about the process by which salient information is acquired. The former, in contrast, implies that the amygdala plays a role in a particular information acquisition mode—attribute-based acquisition.

Threat is one example of a salient attribute (under certain conditions). The FLIAN model thus explains the amygdala’s role in vigilance for threat as inducing the seeking of information about the attribute of threat in the environment. Moreover, we encounter salient attributes in many non-threatening contexts, such as during decision making. In the FLIAN model the amygdala’s role in both processing and acquiring salient attribute information extends to salient attributes wherever they are encountered, including in the context of decision making. In support of this view, the amygdala has been shown to be involved in processing information about attributes salient for decision making (Rolls, 2004; Wallis & Kennerley, 2010). And an important organizing principle behind the FLIAN model, based on the role of the amygdala in processing and acquiring threat information, is the match between the type of information the amygdala processes and the type of information whose acquisition it induces. The FLIAN model simply adds that this principle applies to salient attribute information processed by the amygdala beyond threat. In this way, the amygdala’s role in the FLIAN model is the automatic induction of attribute-based information acquisition.

An important further aspect of the FLIAN model is the explanation of how an attribute is determined to be salient. Certain attributes, such as threat, have inherent
motivational and biological salience, and thus acquiring such information is likely the amygdala’s default setting (Davis & Whalen, 2001). In the domain of decision making, however, the amygdala’s interactions with the vmPFC become critical for guiding information acquisition to salient attributes. The vmPFC represents the current state of a problem being faced, which includes a representation of the salience of the various attributes of the options. This decision space representation is the basis for selecting an appropriate decision strategy. In high-dispersion decision problems, for example, attribute-based acquisition is selected (or activated) because certain attributes are more salient than others within the decision space. In such contexts, the vmPFC activates the amygdala to induce the acquisition of information about these salient attributes. The acquired information is then processed by the amygdala and fed forward to the vmPFC to update the decision space.

2.3.3 The role of the hippocampus in the FLIAN model

The organizational principle of a match between the type of information processed and acquired is also the basis for understanding the role of the hippocampus in the FLIAN. According to the FLIAN model, the hippocampus plays a role in information acquisition behavior complimentary to its known role in information processing vis-à-vis relational memory. Namely, the hippocampus is critical for inducing relational acquisition—acquiring pieces of information that are arbitrarily related. The HC is known to be involved in declarative, relational memory, wherein arbitrarily related information is integrated into a relational representation. Such hippocampal representations are complex, flexible, and encode informational relations (Cohen &
The FLIAN model suggests a novel role of the HC in the active acquisition of information based on its arbitrary relations.

Consider the construction of prospective, future episodic representations by the HC. This is, in essence, an information gathering process whereby various pieces of arbitrarily related information are acquired from internal memory stores for the purpose of forming a representation of the future episode. Critically, the information is gathered in a relation-based mode; the reason that each specific piece of information is acquired is because of the way it relates to the others, as features of the episode being constructed. Here we can glimpse the role of the HC in acquiring information in a relation-based mode. Further consider the fact that the possible future events that we often represent are our options for action: What are the features of my option of taking this job, or buying this car, or telling this lie? In such option representations, the various attributes of an option are related to form a cohesive, relational representation of the option. Much like relational representations of an episodic memory, the aspects of an option are arbitrarily bound by the fact that they pertain to that particular option.

The HC has been shown to play a role in this type of relational processing during decision making. In the IGT, patients with hippocampal damage fail to develop relational representations that associate a choice with its outcome (Gupta et al., 2009). They thus display impaired learning and no preference for drawing from either good or bad decks. Again building on the principle of a match between the information processed and acquired, the FLIAN model holds that the hippocampus is critical for inducing an option-based acquisition mode. This is simply the relational acquisition mode applied within the context of decision making. In this mode, the various pieces of information pertaining to
the option being represented are acquired in order to generate a relational, option-based representation. In sum, the hippocampus is not only involved in processing relational information, but also in acquiring the information to be related in the first place. And it serves this function in decision making by inducing option-based acquisition.

As with the amygdala, the information acquisition function of the HC is managed by the vmPFC. All sectors of the PFC interact with the hippocampus, either directly or indirectly (Rosene and Van Hoesen, 1977; Amaral, 1987; Barbas and Blatt, 1995), and these interactions play a significant role in PFC and HC functioning (Fuster 2001). Specifically, the vmPFC is strongly connected to the hippocampus (Öngür & Price, 2000) and plays a role in modulating HC memory processing (Poldrack & Rodriguez, 2004). According to Simons and Spiers (2003), top-down PFC input is involved in “control of the encoding process, guiding, modifying and elaborating the representations in the medial temporal lobe on the basis of current goals and task demands” (p. 645). For example, greater functional connectivity between the hippocampus and lateral PFC is associated with the expression of relational memory (Hannula & Ranganath, 2009). And the vmPFC modulates HC-based memory retrieval during the on-going performance of a task (Koechlin & Hyafil, 2007). Considering such vmPFC-HC interactions, in the FLIAN model the vmPFC modulates HC-based information acquisition processes in response to the current decision space representation.

2.3.4 Summary

The FLIAN model is a systems-level model of the neural bases of predecisional processes, particularly as they relate to information acquisition processes. It proposes that
the vmPFC is critical for representing the current state of the decision space. Based on this representation, the vmPFC selects a decision strategy. The selected strategy is implemented through fronto-limbic interactions that manage the information acquisition mode. The amygdala is specialized for inducing attribute-based acquisition, while the hippocampus is specialized for inducing relational, option-based acquisition.
CHAPTER 3. STUDY 1: AN INFORMATION BOARD STUDY OF THE FLIAN MODEL

In order to explore the role of the fronto-limbic information acquisition network in flexible decision making and predecisional behavior, the effects of brain damage to the critical nodes in this network on predecisional behavior were explored in neurological patients and appropriate comparison participants. In Study 1, the roles of the vmPFC, amygdala, and hippocampus were studied using an information board task.

3.1 Aims and hypotheses

Specific Aim 1: The specific aim of Study 1 is to explore the roles of the ventromedial prefrontal cortex (vmPFC), hippocampus (HC), and amygdala (AMY) in predecisional processes (i.e., selecting a decision-making strategy and acquiring information needed to progress toward choice) in both non-social and social contexts using information board process tracing methods.

Hypothesis 1.1: For the neurologically intact comparison group, more attribute-based (and less option-based) acquisition in the social condition will be associated with a greater preference for acquiring social information, and reduced preferences for acquiring utilitarian and extraneous information. This is because the social-emotional information will be the most salient attribute, and will thus be more likely to be acquired with attribute- than option-based acquisition, whereas utilitarian and extraneous information will be less likely to be acquired with attribute- than option-based acquisition.

Hypothesis 1.2: The information acquisition patterns of patients with vmPFC damage will be less impacted by changes in decision context (i.e., Time Pressure and
Complexity) and vmPFC patients will exhibit an abnormal preference for acquiring utilitarian information, consistent with the proposed role of the vmPFC representing the decision space.

**Hypothesis 1.3:** Patients with AMY damage will be more likely than comparison participants to engage in option-based information acquisition. Consistent with the association between option-based acquisition and search quotient described in Hypothesis 1.1, the AMY group will display a greater preference for acquiring utilitarian information in the social condition relative to comparison groups. These effects will be amplified in the high complexity and time pressure conditions, where comparison participants are predicted to increasingly engage in attribute-based acquisition.

**Hypothesis 1.4:** Patients with HC damage will be more likely than comparison participants to engage in attribute-based information acquisition. Consistent with Hypothesis 1.1, the HC group will display a reduced preference for acquiring utilitarian information in the social condition relative to comparison groups. These effects will be amplified in the low complexity and no time pressure conditions, where comparison participants are predicted to increasingly engage in option-based acquisition.

### 3.2 Participants

Patients were recruited from the Patient Registry of the University of Iowa’s Division of Behavioral Neurology and Cognitive Neuroscience. There were 5 participant groups (see Table 1 for demographic information). The vmPFC group was comprised of patients with bilateral, circumscribed vmPFC damage (vmPFC group; n=8). The AMY group includes patients with (i) bilateral, circumscribed amygdala damage (n=3) or (ii)
unilateral amygdala damage that excludes other FLIAN structures (n=2). Unilateral amygdala cases were selected based on established laterality-gender interactions in limbic structures: the female patient has left unilateral amygdala damage and male patient has right unilateral amygdala damage, as these patients are most likely to manifest the phenotype of bilateral amygdala lesion cases (Gupta et al., 2010; Tranel, Damasio, Denburg, & Bechara, 2005). Two of the bilateral amygdala lesion cases were native German speakers; the task was translated into German for these participants by professional German translators and administered by fluent German-speaking research assistants. The HC group included 5 patients with bilateral, circumscribed lesions to the HC. The brain damaged comparison (BDC) group consisted of 10 patients with lesions located outside of FLIAN structures, the prefrontal cortex, and other emotion related areas such as the insula. Finally, a group of 16 neurologically healthy comparison participants formed the normal comparison (NC) group. The grouping of patients and analyses of patient data were based on data drawn from the Iowa Patient Registry under the auspices of which all patients have been extensively characterized neuropsychologically and neuroanatomically in the chronic epoch (3 or more months post lesion onset) according to the standard procedures of the Patient Registry (Tranel, 2007; Frank, Damasio, & Grabowski, 1997). Comparison participant groups were selected to match the target patient groups as closely as possible on demographic variables (see Table 1) including age, education, and chronicity (time since lesion onset for patient groups only), and all patients were studied in the chronic epoch. Participants with psychiatric or non-lesion related neurological disorders were excluded from all groups.
### Table 1: Demographic information for all participant groups. Sex indicates the number of male (M) versus female (F) participants. Means for Age and Education (Edu) are followed by standard deviations (sd).

<table>
<thead>
<tr>
<th>Group</th>
<th>N</th>
<th>Sex</th>
<th>Age</th>
<th>Edu</th>
<th>Age sd</th>
<th>Edu sd</th>
</tr>
</thead>
<tbody>
<tr>
<td>vmPFC</td>
<td>8</td>
<td>5F;3M</td>
<td>65.5</td>
<td>13.8</td>
<td>8.1</td>
<td>2.7</td>
</tr>
<tr>
<td>HC</td>
<td>5</td>
<td>1F;4M</td>
<td>55.7</td>
<td>17.8</td>
<td>4.7</td>
<td>2.3</td>
</tr>
<tr>
<td>AMY</td>
<td>5</td>
<td>3F;2M</td>
<td>53.4</td>
<td>14.2</td>
<td>18.2</td>
<td>2.8</td>
</tr>
<tr>
<td>BDC</td>
<td>9</td>
<td>4F;5M</td>
<td>65.3</td>
<td>16.2</td>
<td>11.3</td>
<td>2.8</td>
</tr>
<tr>
<td>NC</td>
<td>16</td>
<td>10F;6M</td>
<td>61.8</td>
<td>16.2</td>
<td>7.9</td>
<td>2.8</td>
</tr>
</tbody>
</table>

3.3 Materials and Methods

The information board task was designed using the MouseLabWEB program, an internet browser based application for creating information board tasks that is used widely in the process tracing literature (Willemsen & Johnson, 2010). The task was programmed in the MouseLabWEB designer (version 0.99 and the online version 1.00beta), the XAMPP software stack version 1.7.4 (PHP 5.3.5, MySQL 5.5.8, and Apache 2.2.17), and the Notepad++ text editor (version 5.8.7) using web programming languages (HTML, JavaScript, and PHP). All data were processed with MATLAB 2010b and statistics were performed in SPSS version 19. The task took approximately 1 hour for participants to complete and was administered on a PC in the Firefox 6 web browser in a testing room at the University of Iowa Neurology Department’s Division of Behavioral Neurology and Cognitive Neuroscience. The study involved a full 2 (Sociality: non-social/apartment versus social/roommate) by 2 (Complexity: high versus low) by 2 (Time Pressure: with and without) block design for a total of 8 conditions, with 4 decision
problem stimuli in each condition for 32 total stimuli. Four blocks were administered in Part 1 in the following order, all without Time Pressure: low complexity apartment, low complexity roommate, high complexity apartment, and high complexity roommate. A short break succeeded Part 1, followed by Part 2 in which the same four blocks were administered in the same order with Time Pressure applied.

The low complexity condition involved deciding between 3 options with 4 attributes describing them, and the high complexity condition involved deciding between 10 options, with 8 attributes for each. The non-social versus social manipulation is a novel information board manipulation. The non-social context asked participants to choose an apartment to rent, with the structure and content of stimuli taken directly from the literature (Fellows, 2006; Payne, 1976). The social context, in contrast, was a novel stimulus type that asked participants to select a roommate to live with. The roommates were described by three types of attributes: social, utilitarian, and extraneous. In the low complexity condition, there were 2 social, 1 utilitarian, and 1 extraneous attribute, and those numbers were each doubled in the high complexity condition. The two social attributes in the low complexity condition were “How did you meet them?” (e.g., “your best friend introduced you and thinks you two would make great roommates” or “in the classified ads”) and “How easy are they to get along with?” (from very easy to very hard). The two additional social attributes in the high complexity condition were “Number of previous roommates” (from 1 to 10) and “Cleanliness” (from very poor to very good). The utilitarian attribute in the low complexity condition was “Possible material gain they can provide for you?” (e.g., “He/she knows the owner of your favorite restaurant and you will be able to get discounts when you go there” or “He/she is starting
a ground-breaking and potentially highly profitable business venture that you could be a part of from the beginning”), and the additional utilitarian attribute in the high complexity condition was “Yearly income” (ranging from $30,000 to $1 million per year, with most values in the lower range). The extraneous attribute in the low complexity condition was “Cooking abilities” (from very poor to very good) and the additional attribute in high complexity was “Quality of car they drive” (from very low to very high). Following Payne’s (1976) original procedure, the values of each option’s attributes in both the social and non-social conditions were randomly assigned so that no one option clearly outweighed each of the other options across all attributes.

In the no-time-pressure condition participants were given unlimited time to acquire information and make a choice on each decision stimulus. In the time pressure condition, participants were given a limited amount of time to acquire information on each stimulus; after the timer expired they could no longer acquire more information, but had as much time as they wanted to make a choice. The amount of time pressure applied was computed on an individual basis for each participant in each of the four no time pressure conditions by multiplying the mean amount of time they took to complete stimuli in each no time pressure condition by a constant, 0.12. That constant was computed based on pilot data used to determine what number would need to be multiplied by the average participant’s time to complete a stimulus to yield a time pressure of 15 seconds.
3.4 Data Processing and Analysis

3.4.1 Neuroanatomical Analyses

The neuroanatomical analysis of each patient (vmPFC, HC, Amy, and BDC) was based on magnetic resonance or computerized tomography data (for participants for whom MRI data were unavailable) obtained in the chronic epoch. For the vmPFC group, Brainvox (Damasio & Frank, 1992; Frank et al., 1997) was used to reconstruct each patient's lesion in three dimensions, and the MAP-3 technique (Damasio et al., 2004) was used to manually warp each patient’s lesion contour into a single normal template brain. A lesion-overlap map, color-coded in Figure 3, was then generated by summing the number of lesions overlapping at any single voxel of the normal template brain.

![Image](image.png)

Figure 3: Lesion overlap of vmPFC patients. Mesial and frontal views of the overlap map of lesions for the 8 vmPFC patients. The color bar indicates the number of overlapping lesions at each voxel. The area of maximal overlap lies in the ventromedial prefrontal cortex.
3.4.2 Number of Reviews

The number of reviews was used as a measure of working memory load, computed by counting the number of times during the course of a given stimulus that a participant acquires a piece of information that was already acquired in that stimulus. For each participant, the mean number of reviews was computed in each of the eight conditions in the 2 (sociality) by 2 (complexity) by 2 (time pressure) experimental design. For the three target patient groups (vmPFC, AMY, and HC), separate statistical analyses were performed on mean number of reviews using mixed ANOVAs with three repeated factors: Sociality (non-social versus social), Complexity (high versus low), and Time Pressure (without versus with time pressure); and a between subjects factor of Group (target patient versus BDC versus NC).

3.4.3 Attribute Preference

Participants’ preference for each of the three attribute types in the social condition (utilitarian, extraneous, and social) was determined by calculating, out of all of the information a participant acquires on a given stimulus, what proportion was from each attribute type. These are averaged across all social stimuli to reveal the overall preference for each attribute type. This yields three proportions for each participant that represent his or her Utilitarian Preference, Extraneous Preference, and Social Preference.

Linear regressions were performed within the normal comparison group to determine whether Search Quotient predicts each of the three attribute preferences. Additionally, for the three target patient groups (vmPFC, AMY, and HC), separate statistical analyses were performed on each of the mean attribute preferences using mixed
ANOVA with two repeated factors: Complexity (high versus low) and Time Pressure (without versus with time pressure); and a between subjects factor of Group (target patient versus BDC versus NC).

3.4.4 Search Quotient

The pattern of information acquisition (attribute- versus option-based) is represented by the Search Quotient, which is calculated for a given stimulus by subtracting the number of within-attribute transitions (e.g., searching the rent for apartment A, followed by the rent for apartment B) from the number of within-option transitions (e.g., searching the rent for apartment A, followed by the number of bedrooms in apartment A), and dividing that difference by the total number of within-attribute and -option transitions (Payne, 1976). A quotient of positive 1 indicates an entirely option-based acquisition mode, whereas a quotient of negative 1 indicates an entirely attribute-based acquisition mode, and zero would indicate an equal amount of the two acquisition modes. For each participant, the mean Search Quotients were computed across the four stimuli in each of the eight conditions in the 2 (sociality) by 2 (complexity) by 2 (time pressure) experimental design.

To test the specific hypotheses for each of the three target patient groups (vmPFC, AMY, and HC), separate statistical analyses were performed on mean Search Quotients using mixed ANOVAs with three repeated factors: Sociality (non-social versus social), Complexity (high versus low), and Time Pressure (without versus with time pressure); and a between subjects factor of Group (target patient versus BDC versus NC).
3.5 Results

3.5.1 Number of reviews

For each of the three target groups (vmPFC, HC, and AMY), the 2 (Sociality) by 2 (Complexity) by 2 (Time Pressure) by 3 (Group: Target versus BDC versus NC), mixed ANOVAs revealed no significant effects of Group or significant interactions with Group for the mean number of reviews (all p’s > 0.3). In all three instances, there were significant effects of: Sociality, with a higher mean number of reviews in the apartment compared to the roommate condition; Complexity, with a higher mean number of reviews in the high compared to the low complexity condition; and Time Pressure, with a higher mean number of reviews in the no time pressure than in the time pressure condition. For example, in the vmPFC versus BDC versus NC comparison, there were main effects of Sociality, F(1,29) = 14.54, p < 0.001, Complexity, F(1,29) = 89.58, p < 0.0001, and Time Pressure, F(1,29) = 94.50, p < 0.0001.

3.5.2 Attribute preference

Search Quotient Prediction of Attribute Preferences: Within the normal comparison group, higher Utilitarian Preference was significantly predicted by a more option-based Search Quotient, b = 0.215, t(14) = 6.11, p < 0.0001, and Search Quotient explained a significant proportion of variance in Utilitarian Preference, R^2 = 0.727, F(1,14) = 37.67, p < 0.0001 (Figure 4). A higher Extraneous Preference was also significantly predicted by a more option-based Search Quotient, b = 0.20, t(14) = 4.14, p = 0.001, and Search Quotient explained a significant proportion of variance in Extraneous Preference, R^2 = 0.55, F(1,14) = 17.10, p = 0.001. Finally, a higher Social Preference was
significantly predicted by a less option-based (more attribute-based) Search Quotient, \( b = -0.414, t(14) = -5.88, p < 0.0001 \), and Search Quotient explained a significant proportion of variance in Social Preference, \( R^2 = 0.712, F(1,14) = 34.58, p < 0.0001 \).

Figure 4: The relationship between Search Quotient and Attribute Preference. Search Quotient positively predicts (a) Utilitarian Preference and (b) Extraneous Preference, and negatively predicts (c) Social Preference.
Utilitarian Preference: Comparing the Utilitarian Preference of the vmPFC to comparison groups, the 2 (Complexity) by 2 (Time Pressure) by 3 (Group) mixed ANOVA revealed significant effects of Time Pressure, $F(1,29) = 23.81$, $p < 0.0001$, with greater Utilitarian Preference without Time Pressure than with Time pressure, and Group, $F(2,29) = 4.06$, $p = 0.028$ (Figure 5). Although the vmPFC group’s increased Utilitarian Preference appears to be most prominent in the Time Pressure condition, the Time Pressure by Group interaction was nonsignificant ($p = 0.23$) suggesting the effect is independent of Time Pressure. Post-hoc t-tests showed that the vmPFC group had a significantly greater Utilitarian Preference than both the NC ($p = 0.035$) and BDC group ($p = 0.01$).

![Mean Utilitarian Preferences](image)

Figure 5: Utilitarian Preference by Time Pressure. Utilitarian Preference for the vmPFC versus comparison groups without and with time pressure. Error bars are standard error of the mean.
In examining the Utilitarian Preference of the HC compared to the NC and BDC groups, a significantly higher Utilitarian Preference in the low than in the high complexity condition was revealed, $F(1,26) = 10.09$, $p = 0.004$. The significant Complexity by Group interaction, $F(2,26) = 3.86$, $p = 0.034$, suggests that the effect of Complexity on Utilitarian Preference was driven by the HC group, which showed a higher Utilitarian Preference than comparison groups in the low complexity condition. A follow-up ANOVA with participants’ mean Utilitarian Preference in the low complexity condition as the dependent variable was supportive of this interpretation; there was a marginally significant effect of Group, $F(2,29) = 3.12$, $p = 0.06$, and in post-hoc t-tests the HC group showed a significantly higher Utilitarian Preference than the NC group ($p = 0.02$) and marginally higher than the BDC group ($p = 0.057$). Finally, there was no effect of Group or interaction with Group in an examination of the Utilitarian Preference of the AMY versus NC and BDC groups.

**Social Preference:** Comparing the vmPFC to comparison groups, there was not a significant effect of Group on Social Preference ($p = 0.11$). Significant main effects were observed for Complexity, with higher Social Preference in high than low complexity, $F(1,29) = 12.62$, $p = 0.001$, and Time pressure, with higher Social Preference when Time Pressure was applied, $F(1,29) = 48.31$, $p < 0.0001$. In comparing the Social Preference of the HC or AMY groups to the NC and BDC groups, the main effects of Complexity and Time pressure were again observed, and there were neither significant effects of nor interactions with Group.

**Extraneous Preference:** Comparing the vmPFC to comparison groups, there was not a significant effect of Group on Extraneous Preference ($p = 0.74$). Significant main
effects were observed for Complexity, with higher Extraneous Preference in low than high complexity, $F(1,29) = 17.36, p < 0.001$, and Time Pressure, with higher Extraneous Preference without Time Pressure than with Time Pressure $(1,29) = 32.26, p < 0.0001$. In comparing the Social Preference of the HC or AMY groups to the NC and BDC groups, the main effects of Complexity and Time pressure were again observed, and there were neither significant effects of nor interactions with Group.

3.5.3 Search Quotient

vmPFC versus comparison groups: For the Search Quotient dependent variable, a 2 (Sociality) by 2 (Complexity) by 2 (Time Pressure) by 3 (Group: vmPFC versus BDC versus NC) mixed ANOVA did not show a significant effect of Group ($p = 0.89$) or significant interactions with Group. In contrast to the predicted effect of Complexity, a significant effect of Complexity revealed a higher, more option based Search Quotient in the high than low complexity condition, $F(1,29) = 36.29, p < 0.0001$(Figure 6). And consistent with predictions a significant effect of Time Pressure revealed a shift toward an attribute-based Search Quotient with Time Pressure as compared to without Time Pressure, $F(1,29) = 44.09, p < 0.0001$ (Figure 6).

Follow-up analyses were performed to explore whether the shift toward option-based acquisition from the low to high complexity conditions was more prominent toward the end of a stimulus, when a participant in the high complexity condition may have narrowed their choices and be focusing on just one or two options, and whether this was more prominent in apartment or roommate stimuli. A two (Sociality) by two (Complexity) by three (Group) mixed ANOVA was performed with the Search Quotient
Figure 6: Mean Search Quotient by Complexity and Time Pressure. Mean Search Quotient for the target (vmPFC, HC, and AMY) versus comparison (BDC and NC) groups for (a) low versus high complexity and (b) without versus with time pressure. A negative search quotient (red) indicates more attribute- than option-based acquisition, while a positive search quotient (blue) indicates more option- than attribute–based acquisition. Error bars are standard error of the mean.

over the first 5 acquisitions on a given stimulus as dependent variable, and again with the Search Quotient over the last 5 transitions on a given stimulus as dependent variable. Only the stimuli without Time Pressure were examined since stimuli with Time Pressure
did not allow for enough acquisitions to examine different phases of the process. When comparing the Search Quotient for only the last 5 transitions a participant makes on a given stimulus, the low versus high complexity conditions were marked by a significant shift from attribute- to option-based acquisition, $F(1,25) = 28.64, p < 0.0001$. A significant effect of sociality also showed a more option-based Search Quotient in the apartment than roommate stimuli on the last 5 transitions, $F(1,25) = 4.74, p = 0.039$. No group effect was observed ($p = 0.83$). When comparing the Search Quotient for only the first 5 transitions, there was no difference in the low versus high complexity conditions ($p = 0.59$), and no significant effects or interactions were observed for the Sociality or Group factors.

Finally, follow-up analyses were performed to further explore how participants’ information acquisition behavior changed over the course of a given stimulus. Again only the stimuli without Time Pressure were examined so that there was sufficient data to explore different phases of information acquisition within each stimulus. The data from each participant on each stimulus was divided into quartiles. For example, the first 25 percent of transitions a participant makes on a given stimulus comprised the first quartile, and the last 25 percent of transitions comprised the fourth quartile. Group mean Search Quotients were then computed for each quartile. A 2(Sociality) by 2 (Complexity) by 4 (Quartile) by 3 (Group) mixed ANOVA revealed a significant effect of Quartile, with the Search Quotient increasing in each subsequent quartile, becoming less attribute based and more option based, $F(3,90) = 84.15, p < 0.0001$ (Figure 7). There was no effect of group ($p = 0.98$) nor any significant interactions.
Figure 7: Mean Search Quotient by Quartile. Search Quotient for Part 1 (no time pressure) for all 5 groups broken down by Quartile for the (a) low and (b) high complexity apartment conditions, and (c) low and (d) high complexity roommate conditions. A negative search quotient (red) indicates more attribute- than option-based acquisition, while a positive search quotient (blue) indicates more option- than attribute–based acquisition. Error bars are standard error of the mean.

**HC versus comparison groups:** For the Search Quotient dependent variable, a 2 (Sociality) by 2 (Complexity) by 2 (Time Pressure) by 3 (Group: HC versus BDC versus NC) mixed ANOVA did not show a significant main effect of Group ($p = 0.15$).
Significant effects of Complexity, $F(1,26) = 17.16$, $p < 0.001$, and Time Pressure, $F(1,26) = 27.95$, $p < 0.0001$ were observed as described for the vmPFC versus comparison group analyses (Figure 6). A significant Complexity by Group interaction was revealed, $F(1,26) = 4.58$, $p = 0.02$, with the HC group showing a more attribute-based Search Quotient in the high complexity condition as compared to the BDC and NC groups (Figure 6a).

Follow-up analyses were performed to explore how the HC group’s information acquisition behavior changed over the course of a given stimulus. As described for the vmPFC group, only the stimuli without Time Pressure were examined and the data were divided into quartiles. A 2(Sociality) by 2 (Complexity) by 4 (Quartile) by 3 (Group) mixed ANOVA again revealed a significant effect of quartile, with the Search Quotient increasing in each subsequent quartile, becoming less attribute based and more option based, $F(3,81) = 58.12$, $p < 0.0001$ (Figure 7). There was no main effect of Group or Sociality. However, a significant three way interaction between Sociality, Quartile, and Group did emerge, $F(6,81) = 2.429$, $p = 0.033$; the HC group had a lower, more attribute-based Search Quotient in the high complexity apartment condition, and in quartiles 2 and 3 in the roommate condition.

**AMY versus comparison groups:** For the Search Quotient dependent variable, a 2 (Sociality) by 2 (Complexity) by 2 (Time Pressure) by 3 (Group: AMY versus BDC versus NC) mixed ANOVA did not show a significant main effect of Group ($p = 0.39$). Significant effects of Complexity, $F(1,26) = 45.11$, $p < 0.001$, and Time Pressure, $F(1,26) = 45.86$, $p < 0.0001$ were observed as described for the vmPFC versus comparison group analyses (Figure 6). A significant Complexity by Time Pressure by Group interaction was revealed, $F(2,26) = 3.91$, $p = 0.033$, with the AMY group showing a lower, more
attribute-based Search Quotient than the comparison groups in the low complexity, no
Time Pressure condition and in the high complexity, with Time Pressure condition.
However, in follow-up one-way ANOVAs, there was not a significant main effect of
group in either case: F(2,29) = 1.03, p = 0.37 for low complexity without Time pressure,
and F(2,29) = 2.22, p = 0.13 for high complexity with Time Pressure.

Follow-up analyses were performed to explore how the AMY group’s information
acquisition behavior changed over the course of a given stimulus. As described for the
vmPFC group, only the stimuli without Time Pressure were examined and the data were
divided into quartiles. A 2(Sociality) by 2 (Complexity) by 4 (Quartile) by 3 (Group)
mixed ANOVA again revealed a significant effect of quartile, with the Search Quotient
increasing in each subsequent quartile, becoming less attribute based and more option
based, F(3,81) = 58.12, p < 0.0001 (Figure 7). There was no effect of Group.

3.6 Discussion

3.6.1 Search Quotient

Time Pressure and Complexity: For the Search Quotient dependent variable the
time pressure manipulation had the expected effect, with participants shifting toward an
attribute-based Search Quotient with Time Pressure as compared to without Time
Pressure. This is consistent with previous findings on the effect of time pressure on
information search behavior (Payne et al., 1992; Usher & Zakay, 1993). However, in
contrast to the predicted effect of Complexity and previous research showing greater
option-based than attribute-based acquisition in the low versus high complexity
conditions (Stone & Schkade, 1991), the present study found a more option-based Search
Quotient in the high as compared to low complexity condition. Previous research has shown conflicting results regarding the influence of task complexity on information acquisition modes. Compensatory decision strategies are favored in low complexity contexts (Biggs, Bedard, Gaber, & Linsmeier, 1985; Billings & Marcus, 1983; Olshavsky, 1979; Payne, 1982; Tversky, 1969, 1972), and compensatory strategies tend to be associated with option-based acquisition (Olshavsky, 1979; Payne et al., 1993). However, compensatory strategies can be implemented via an option-based or an attribute-based acquisition pattern depending on the specific decision strategy in use (Russo & Dosher, 1983; Billings & Marcus, 1983). Thus, further examination of the specific decision strategies being implemented may indicate the use of, for example, the compensatory additive difference strategy in the low complexity condition, which would account for the unexpectedly attribute-based pattern and would be consistent with the literature showing that compensatory strategies are favored in less complex contexts.

Another potential explanation for greater option-based acquisition in the high versus low complexity condition could have been a shift toward option-based acquisition in the later stages of information acquisition on high complexity stimuli. However, this was not the case—over the course of a decision there was a shift from more attribute-based to more option-based acquisition in both the low and high complexity conditions. Furthermore, when the data were broken down by quartile there was not a significant interaction between complexity and quartile. Each subsequent quartile was marked by a similar shift from more attribute-based to more option-based acquisition in both the low and high complexity conditions. This shift over the course of a decision supports previous research which has shown that noncompensatory strategies are favored in the early
phases of a decision in order to narrow the set of options, and more compensatory strategies are favored later in a decision (Svenson, 1979; Billings & Marcus, 1983; Usher & Zakay, 1993).

**Ventromedial Prefrontal Cortex:** Against hypothesis 1.2, the vmPFC patients did not exhibit a reduced ability to adapt their information acquisition behavior to different decision contexts (neither low versus high complexity nor with versus without time pressure). According to the FLIAN model, the vmPFC is critical for representing the decision space and, therefore, for flexibly applying decision strategies to different contexts. This led to the hypothesis that patients with vmPFC damage would show a reduced adaptation of information acquisition behavior to different decision contexts. That hypothesis was not supported by the results of the present study. Furthermore, the vmPFC group showed a normal shift from more attribute-based to more option-based acquisition over the course of a given stimulus. Previous research has shown that individuals adapt from noncompensatory processing in the early phases of a decision to more compensatory processing later in a decision (Svenson, 1979; Billings & Marcus, 1983; Usher & Zakay, 1993). The vmPFC group also engaged in an overall decision-making strategy involving this intra-decisional processing shift. Initially, these findings suggest that the vmPFC may not be critical for strategic decision making on the present task.

However, it may be that the information acquisition behavior of vmPFC patients did not reveal their underlying impairment in flexible, strategic decision making. Information acquisition modes are one aspect of a decision-making strategy and multiple strategies use the same acquisition modes. That is to say, a difference in acquisition
modes is indicative of a difference in decision strategy, but the use of the same acquisition modes does not entail the use of the same decision-making strategy. Future research should explore additional aspects of vmPFC patients’ predecisional behavior to further assess whether or not they are in fact engaging normal decision-making strategies.

Also, a limitation of the present study is that participants were required to use a computer mouse to click on pieces of information to reveal them. This is a relatively effortful way to acquire information that could have reduced the automaticity with which participants proceeded on the task (Willemsen & Johnson, 2010). In this way, the present task may have allowed higher order executive functions to influence task performance in addition to the more automatic predecisional processes of the fronto-limbic information acquisition network. Further research will be needed to explore this possibility. For example, an information board task could be conducted in which eye tracking is used to automatically reveal information in a gaze-dependent manner, thereby allowing for more precise process tracing of automatic predecisional behavior. The FLIAN model would predict that patients with vmPFC damage exhibit reduced flexibility in their information acquisition on such a task.

Finally, the results of the present study are in contrast to the results of a previous study, which found increased option-based acquisition in patients with vmPFC injury, indicating abnormal strategic decision making (Fellows, 2006). There are several differences which may account for the diverging results. Firstly, unlike the task used in the present study, the task in the previous study by Fellows did not follow conventions in the literature on predecisional processes and information board tasks which allow a participant to view only one piece of information at a time; in the study by Fellows, once
a piece of information was viewed it remained visible for the duration of the stimulus. It seems that in this alternative task context patients with vmPFC injury were (as predicted in the FLIAN model) engaging an abnormal decision-making strategy, indicated by their abnormal search behavior. This supports the proposed role of the vmPFC in strategic decision making. As discussed above, further examination of vmPFC patients’ predecisional behavior will be needed to determine whether the results of the present study do in fact indicate normal strategic decision-making, contradicting the findings of Fellows (2006) and the predictions of the FLIAN model. Secondly, most of the patients in the study by Fellows had brain damage due to trauma, suggesting that other damage resulting from trauma (e.g., to white matter and brain structures other than the vmPFC) may have factored into the results. This interpretation of an alternative neural correlate for strategic decision making would be supported if further exploration of vmPFC patients’ predecisional behavior reveals that they do engage normal decision-making strategies across varying contexts.

**Hippocampus:** As predicted in hypothesis 1.4, when the comparison groups shifted toward an option-based search mode the HC group maintained an attribute-based mode. It was predicted that the HC group would exhibit greater attribute-based acquisition relative to comparison groups especially in the low-complexity condition, where comparison participants were expected to engage in more option-based acquisition. However, the comparison groups exhibited more option-based acquisition in the high complexity condition, and it was here that increased attribute-based acquisition was observed in the HC group. This supports the hypothesized role for the hippocampus in engaging an option-based acquisition mode; in both the low and high complexity
conditions the HC group favored attribute-based acquisition. According to the FLIAN model, similar to the hippocampus’ role in relational processing (Cohen & Eichenbaum 1993), it is argued that the HC also plays a role in relational acquisition—acquiring arbitrarily related pieces of information, as in an option-based information search mode. The results of the present study support this claim. The hippocampus is not only involved in processing relational information, but also in inducing the acquisition of information that is arbitrarily related.

Finally, additional support for the increase in attribute-based acquisition after HC damage was found when the data were broken down by quartile to explore the shift in information search behavior over the course of a decision; the HC group exhibited a lower, more attribute-based Search Quotient in the high complexity apartment condition, and in the middle quartiles of the high complexity roommate condition.

Memory Load: To assess whether difficulty with the memory demands of the task might explain the abnormally attribute-based search quotient of the hippocampus group, the number of reviews was used as an initial measure of memory performance on the task. The number of reviews is the number of times a participant acquires a piece of information that was already acquired during the course of a given stimulus. An abnormally high number of reviews relative to comparison groups would be indicative of a memory impairment affecting information acquisition behavior. For the mean number of reviews of each target group (HC, vmPFC, and AMY) as compared to those of the BDC and NC groups, there were neither main effects of nor interactions with group. This suggests that memory load did not differentially affect the target patient groups as compared to the comparison groups. Thus, although short term memory undoubtedly
plays a role in the tasks used in this study, effects of memory load are not likely to account for the findings discussed above.

**Amygdala:** Hypothesis 1.3 was not supported, as the amygdala group did not engage in more option-based acquisition. The patients with amygdala damage engaged option- and attribute-based acquisition normally relative to comparisons across the various contexts studied. Moreover, the amygdala group showed a normal intra-decisional shift from attribute- to option-based acquisition. Initially, this may suggest that the amygdala may not play the critical role hypothesized in the FLIAN model in inducing an attribute-based information acquisition mode. However, recent research has supported the idea that the amygdala is critical for acquiring information about salient attributes in the environment (e.g., Kennedy & Adolphs, 2010) and maintaining vigilance for salient information (Öhman, Flykt, & Esteves, 2001; Öhman, Lundqvist, & Esteves, 2001; Esteves & Öhman, 1993). Furthermore, some indirect support for the role of the amygdala in inducing attribute-based information acquisition can be taken from the increase in attribute-base acquisition after bilateral damage to the hippocampus. According to the FLIAN model, in that case the amygdalar, attribute-based acquisition mode would be the only acquisition mode available for activation by FLIAN mechanisms—and consistent with the results, an increase in attribute-based acquisition would be expected. Thus, future research is warranted to further explore the potential role of the amygdala in predecisional information acquisition processes.

Also, there are limitations to the present study which may account for the lack of support for Hypothesis 1.3. Kennedy and Adolphs (2010) showed that the amygdala’s role in information acquisition can be driven by bottom-up input from the environment,
which automatically directs attention to salient information; in a patient with bilateral amygdala lesions they found that an impairment in fixating the eyes of face stimuli was restored when a fixation dependent “search-light” procedure was used. They suggest that this procedure allowed for top-down control processes to direct gaze independently of bottom-up input from face stimuli. Thus, future research should focus on exploring the amygdala’s role in predecisional behavior using tasks that place more demands on automatic processing and leave less room for higher-order executive control processes to affect task performance, such as a gaze dependent information board task. Finally, the amygdala group was small (n=5) and thus the heterogeneity in the group may have played a role in the negative findings.

3.6.2 Attribute preference

Search Quotient Predicts Attribute Preferences: In support of Hypothesis 1.1, in the normal comparison group participants who had a higher, more option-based Search Quotient showed a greater Utilitarian Preference, and those with a lower, more attribute-based Search Quotient showed a greater Social Preference. Extraneous Preference was also positively predicted by Search Quotient, with a greater extraneous preference associated with a more option-based Search Quotient. Thus when an attribute-based acquisition mode is engaged and participants are likely focusing on the attributes most important to them (Tversky, 1972), social attributes are preferred. In this way, engaging an attribute-based acquisition mode may shift attention toward more crucial information. Conversely, engaging in an option-based mode, which predicts increased utilitarian and extraneous preferences, may result in attentional resources being expended on less important attributes, which could negatively impact decision making in situations where
focusing on the most important attributes is crucial. This demonstrates the importance of information search behavior for the decision-making process; using different acquisition modes is not equivalent to acquiring the same information in different ways—how one goes about acquiring information influences what information is viewed as important and is acquired.

The significant effect of Time Pressure on preferences for each of the three attribute types in the social condition also supports the interpretation that the Social attribute was viewed as more important. Under time pressure people are more likely to focus on their most important attribute (Edland, 1994); adding time pressure here was associated with reduced Utilitarian and Extraneous Preferences, but greater Social Preference. Similarly, Social Preference was greater and Extraneous Preference less in the high as compared to low complexity condition, suggesting that in the more complex context social information was viewed as more important. Thus, when under a time crunch or making a highly complex decision and needing to acquire the most crucial information, participants focus in on social information and shift away from utilitarian and extraneous information.

Accordingly, it seems that the preference for different types of information (e.g., social versus utilitarian) is constructed depending on the decision context and what information search strategy one is engaging in. The construction of preferences and values during choice is a well-known phenomenon in social psychology (Kahneman, Knetsch, & Thaler, 1991; Slovic, 1995). In the predecisional realm, Query Theory holds that preferences to retrieve various pieces of information from memory and factor them into the decision-making equation are influenced by the context of the decision (Johnson,
Häubl, & Keinan, 2007). Also, the cognitive-ecological sampling approach argues that the acquisition of information from the external environment can be influenced by biases in the way a decision-maker searches for information (Fiedler, 2000). In support of that view, the results from the present study show that preferences to acquire information from external stores are influenced by information acquisition modes; the preference for social information over utilitarian and extraneous information is greater when searching in an attribute- than option-based mode.

**Increased Utilitarian Preference After vmPFC Damage:** In support of Hypothesis 1.2, the vmPFC group displayed a significantly greater utilitarian preference than the BDC and NC groups. Patients with vmPFC place a greater weight on utilitarian information than comparison participants. Thus, the vmPFC is shown to be a critical neural region for the normal predecisional weighting of attributes, particularly those pertaining to utilitarian information. Previous research has shown that the vmPFC is involved in value representations (Öngür & Price, 2000; Rangel, Camerer, & Montague, 2008; Rolls, 2000) and affectively marking stimuli on the basis of past experience (Damasio, 1994). Whereas neurologically intact individuals may activate learned somatic markers via a vmPFC-based process that drive their information acquisition behavior away from utilitarian information, participants with vmPFC damage may lack this aversion and thus exhibit a stronger preference to acquire utilitarian information when making social decisions. Thus, the increased weight placed on utilitarian information by vmPFC patients suggests that vmPFC damage may result in a loss of the aversion to integrating utilitarian information into social decisions.
An abnormal preference for utilitarian information may play a role in the social-emotional impairments observed after vmPFC injury. For example, several studies have shown an increase in utilitarian moral judgments after damage to the vmPFC (Koenigs, Young et al., 2007; Ciaramelli et al., 2007; Thomas et al., 2011). It may be that because patients with vmPFC injury attend more to utilitarian information than neurologically healthy individuals, they are more likely to make utilitarian judgments. Furthermore, as reviewed in Chapter 1, it is well-known that vmPFC injury results in abnormal, maladaptive social behavior (Anderson et al., 2006; Beer, John, Scabini, & Knight, 2011; Dimitrov, Phipps, Zahn, & Grafman, 1999; Eslinger & Damasio, 1985; Fellows, 2007; Rolls, Hornak, Wade, & McGrath, 1994; Stuss & Benson, 1984). When making decisions in the social sphere, an abnormal weighting of different types of information available for consideration could have a devastating effect on the choices one makes. Further research will be needed to explore the potential link between predecisional processes, such as an increased preference to attend to utilitarian information, and social behavior.

**Utilitarian Preference and the Hippocampus:** The hippocampus group exhibited a greater utilitarian preference than the comparison groups in the low complexity condition, but a normal utilitarian preference in the high complexity condition. Interestingly, in the high complexity condition the HC group engaged in less option-based acquisition than the other groups—since less option-based acquisition is associated with a lower utilitarian preference, the lack of an effect of HC damage on utilitarian preference in the high complexity condition may be due to the HC group’s less option-based search quotient. Thus, although the HC group exhibited a greater utilitarian preference in only the low complexity condition, there may be an underlying increase in the preference to
acquire utilitarian information that is masked in the high complexity condition. It was expected that the HC group would have a greater social preference due to an increase in attribute-based acquisition. A potential explanation for the opposite finding is that HC patients acquire more information overall in an attempt to compensate for a deficit in forming representations of options—which are relational representations, the formation of which is known to involve the hippocampus (Bunsey & Eichenbaum, 1996; Hannula et al., 2010; Konkel & Cohen, 2009). This deficit is amplified by the HC group’s reduced engagement of option-based, ‘relational’ acquisition. In an attempt to compensate and generate more robust representations of options, HC patients’ may acquire more of the available information, thereby acquiring information from utilitarian attributes that other groups are more likely to ignore. Further research will be needed to explore the possibility that patients with HC damage explore a greater amount of available information.

**Attribute Preference and the Amygdala:** Hypothesis 1.3 was not supported, as the amygdala group did not exhibit an increased utilitarian preference. This finding was consistent with the normal search quotient observed in the amygdala group. As in that case, there are limitations to the present study (perhaps not sufficiently tapping automatic predecisional processes) and with the amygdala group that could account for the negative findings. Further research will be needed to continue to explore the role of the amygdala in predecisional processes and the acquisition of salient attribute information during decision making.
3.6.3 Summary

The results of Study 1 are partially supportive of the FLIAN model. The hypothesized roles of the vmPFC in strategic information acquisition and the amygdala in engaging in attribute-based information acquisition were not supported. Future research should further explore the predecisional functions of these structures. The vmPFC was shown to be critical for the normal weighting of attributes, as vmPFC patients showed an increased preference to acquire utilitarian information. Attribute weighting is an essential process during the formation of a representation of the decision space, suggesting that the vmPFC is critically involved in this aspect of representing the decision space. The abnormal emphasis on utilitarian information may play an important role in the social-emotional deficits observed after vmPFC injury.

The hippocampus was demonstrated to play a necessary role in engaging a relational, option-based information acquisition mode. This finding suggests a novel role for the hippocampus in not only relational information processing, but also in bringing in arbitrarily related information for processing. Further research should explore the potential role that a deficit in relational acquisition may play in the memory and decision-making impairments observed after HC damage.
CHAPTER 4. STUDY 2: THE EFFECTS OF TRAINING ON PREDECISIONAL BEHAVIOR

This study was designed to examine the role of the vmPFC in the ability to strategically implement specific decision-making strategies in different contexts. In this study, patients with vmPFC damage and brain damaged and normal comparison participants were trained to use two decision-making strategies, an option-based strategy in the low complexity condition and an attribute-based strategy in the high complexity condition. Participants then performed an information board task like the one used in Study 1 Part 1 (without time pressure), with manipulations of Sociality (apartment versus roommate) and Complexity (low versus high).

4.1 Aims and hypotheses

Specific Aim 2: The specific aim of Study 2 was to examine the role of the ventromedial prefrontal cortex (vmPFC) the predecisional process of adaptively applying option- and attribute-based decision-making strategies to different contexts using information board process tracing methods.

Hypothesis 2.1: The vmPFC group will be less likely than the BDC and NC groups to use the appropriate strategy (according to the training session) for the context.

4.2 Participants

The participants were culled from the vmPFC (n=6), BDC (n=8), and NC (n=10) groups in Study 1 based on whether they were able to participate in a second testing session. The group definitions were as described for Study 1.
4.3 Materials and Methods

The study took approximately 1 hour to complete. The task design was the same as that described for Part 1 (without time pressure) of Study 1, again with manipulations of Sociality (apartment versus roommate) and Complexity (high versus low), and no time pressure. Thus, there were 4 conditions with 4 stimuli in each condition for a total of 16 stimuli. To begin Study 2, participants were first trained to use two decision-making strategies, the weighted additive rule (a compensatory strategy implemented via option-based acquisition) and the elimination-by-aspects rule (EBA; a noncompensatory strategy implemented via attribute-based acquisition) based on the methods described by Bettman, Johnson, and Payne (1990). The former strategy was renamed the “Option Evaluation Strategy” (OES) for clarity. Participants were trained that the OES was best to use on the simpler, low complexity stimuli, where there are only a few options and attributes, while the EBA strategy was best to use on the more complicated, high complexity stimuli, where there are many options and attributes. And they were asked to do their best to use the strategies as they learned them.

The training session began by having participants read descriptions of each strategy. After each description, a real-life example of a situation of selecting a job candidate from among few resumes (for the OES explanation) or many resumes (for the EBA explanation) was provided, and it was explained how the recommended strategy could be applied to that situation. Next, participants completed a training set of 8 information board stimuli asking them to select a vehicle to purchase. The vehicle stimuli alternated quasi-randomly between a low complexity (3 options, 4 attributes) and high complexity (10 options, 8 attributes) context. The experimenter explained how to use the
OES strategy on the first low complexity stimulus and the EBA strategy on the first high complexity stimulus. The participant then worked on the stimuli with the experimenter answering questions and providing feedback about how to apply the recommended strategy in each context. The training session ended when the participant was able to indicate that they understood the strategies, and how and when to use them, by independently using each strategy at least one time in the appropriate context. For all participants the training session was completed within one round of the 8-stimulus training set. Participants were then reminded to do their best to use the strategies as they learned them, and the experimenter left the room while the participant completed the full task.

4.4 Data Processing and Analysis

The pattern of information acquisition (attribute- versus option-based) was the primary dependent variable of interest. The acquisition pattern is revealed by the Search Quotient, which is calculated by subtracting the number of within-attribute transitions from the number of within-option transitions, and dividing that difference by the total number of within-attribute and -option transitions (Payne, 1976).

To assess the effectiveness of the training session, participants’ Search Quotients were compared between Part 1 of Study 1 (no training) and the round completed after training using a mixed ANOVA with three repeated factors: Training (no training/Part1 of Study 1 versus training), Sociality (non-social versus social), and Complexity (high versus low); and a between subjects factor of Group (vmPFC versus BDC versus NC).
4.5 Results

For the Search Quotient dependent variable, the 2 (Training) by 2 (Sociality) by 2 (Complexity) by 3 (Group: vmPFC versus BDC versus NC) mixed ANOVA confirmed the effectiveness of the training session, revealed by a significant interaction of Training and Complexity, $F(1,20) = 62.25, p < 0.0001$; participants shifted toward a more option-based search quotient after training in the low complexity condition, and a more attribute-based Search Quotient after training in the high complexity condition (Figure 8). A significant Complexity by Training by Group interaction was also observed, $F(2,20) = 4.88, p = 0.019$, with the vmPFC group being less impacted by the training in only the low complexity condition (shifting less toward an option-based Search Quotient). For the low complexity condition after the training session, a follow-up one-way ANOVA found a marginally significant effect of group, with the vmPFC group showing the least option-based Search Quotient, $F(2,23) = 3.18, p = 0.06$. Post-hoc t-tests show that this effect was significant for the vmPFC versus NC group contrast ($p = 0.020$), but not the vmPFC versus BDC group contrast ($p = 0.18$).

Follow-up analyses were performed to further explore how participants’ information acquisition behavior changed over the course of a given stimulus after training, and, in particular, whether this differed between groups. The data from each participant on each stimulus was divided into quartiles. A 2 (Sociality) by 2 (Complexity) by 4 (Quartile) by 3 (Group) mixed ANOVA revealed a significant effect of Complexity, $F(1,21) = 21.26, p < 0.001$, with a more option-based Search Quotient in low complexity, and more attribute-based Search Quotient in high complexity. The effect of quartile was also significant, $F(3,63) = 55.63, p < 0.0001$, with a shift toward a more option-based
Figure 8: The effect of training on Search Quotient for (a) the low complexity condition, in which training recommended the use of an option-based strategy, and (b) the high complexity condition, in which training recommended the use of an attribute-based strategy. Error bars represent standard error of the mean.

(less attribute-based) Search Quotient in each subsequent quartile. Finally, there was a significant three-way interaction of Complexity, Quartile, and Group, $F(6,63) = 2.90, p = 0.01$ (Figure 9); in the low complexity condition, the NC and BDC groups maintained an option-based acquisition mode from quartile 1 through quartile 4, while the vmPFC
group began with a significantly more attribute-based Search Quotient and shifted toward option-based acquisition in each subsequent quartile; in the high complexity condition, all three groups began with an attribute-based Search Quotient and shifted toward option-based acquisition with each subsequent quartile.

Figure 9: Search Quotient with training broken down by quartile for (a) the low complexity condition and (b) the high complexity condition. Error bars are the standard error of the mean.
Finally, to explore the effect of training on each quartile of information acquisition, the mean search quotient with training was subtracted from the mean search quotient without training in each quartile. A 2 (Complexity) by 4 (Quartile) by 3 (Group) mixed ANOVA revealed a significant 3-way interaction of Complexity, Quartile, & Group, $F(6,60) = 2.36, p = 0.04$ (Figure 10). The vmPFC group was not affected by the
low-complexity training in any of the quartiles while the BDC and NC groups shifted toward a significantly more option-based acquisition mode in the early quartiles.

4.6 Discussion

The training session was successful in driving participants’ search behavior. Within-subject analyses comparing participants’ search quotients without training (from Study 1) to with training (Study 2) showed shifts consistent with the training toward more option-based acquisition after training in the low complexity condition, and more attribute-based acquisition after training in the high complexity condition. Consistent with predictions the vmPFC group was less impacted by the training session, shifting less toward an option-based Search Quotient in the low-complexity condition. This supports the critical role of the vmPFC in the flexible implementation of decision making strategies.

In the low complexity condition the NC and BDC groups successfully executed the trained strategy, maintaining an option-based acquisition mode from quartile 1 through quartile 4. However, the vmPFC group began with a significantly more attribute-based Search Quotient in quartiles 1 and 2, shifting toward option-based acquisition in each subsequent quartile—just as all groups did prior to training in Study 1. The FLIAN model holds that the vmPFC is critical for representing the decision space, and thus for adaptively implementing different predecisional strategies depending on the context. Study 1 showed that vmPFC patients can engage different information acquisition modes in different contexts, but further research was warranted to explore if there was in fact an underlying deficit in which decision-making strategies they used (even though those strategies may have relied on the normal acquisition modes). The results of Study 2
suggest that the vmPFC is indeed critical for implementing specific decision-making strategies in the appropriate context. In particular, the vmPFC group was impaired in their use of the weighted additive (or “option evaluation”) rule in the low complexity condition. This strategy involves integrating overall evaluations of multiple options into the decision space representation, holding those evaluations online simultaneously, and then comparing them to generate choice (Payne, et al., 1993). The vmPFC plays a critical role in implementing this strategy, a finding consistent with the FLIAN model’s proposed role for the vmPFC in representing the decision space.

In the high complexity condition, the training session was less successful in eliciting an attribute-based acquisition mode throughout the course of each stimulus. All three groups engaged in more attribute-based acquisition after training, but shifted from attribute-based acquisition toward option-based acquisition with each subsequent quartile as they did prior to training. That is, participants did engage a more attribute-based strategy overall after training, but they deviated from the training by continuing to shift toward more option-based acquisition in the later stages of a decision. It seems that the tendency to shift from more attribute-based to more option-based acquisition is particularly strong in the high complexity condition. It may be that high complexity stimuli were particularly taxing on participants’ cognitive resources, and thus they were less able to engage in the trained strategy.
SUMMARY

Several decades of process-tracing research have demonstrated that decision makers flexibly adapt their predecisional behavior to the specific features of the problems they face (Ford et al., 1989; Payne et al., 1993). This view is further supported in the present work, with time pressure driving a shift toward attribute-based information acquisition (Payne et al., 1988; Payne et al., 1992; Usher & Zakay, 1993; Ben Zur & Breznitz, 1981; Wright, 1974; Zakay & Wooer, 1984).

However, in contrast to previous research on the effects of complexity on acquisition behavior (Biggs, Bedard, Gaber, & Linsmeier, 1985; Billings & Marcus, 1983; Olshavsky, 1979; Payne, 1982; Tversky, 1969, 1972), there was not an increase in attribute-based information acquisition in the high versus low complexity condition; participants’ acquisition mode shifted in just the opposite direction, with more attribute-based acquisition in the low complexity condition and more option-based acquisition in the high complexity condition. This is likely accounted for by the use of specific decision making strategies, such as the compensatory additive difference strategy (which involves attribute-based acquisition), in the low complexity condition and a noncompensatory option-based strategy in the high complexity condition. Future research will be needed to further examine the decision strategies participants rely on.

In accordance with previous findings it was demonstrated that participants tend to use more attribute-based acquisition early in the decision process and shift toward option-based acquisition later, likely after the options under consideration have been narrowed down. Previous work has shown that it is common for the decision space to be simplified
during early predecisional operations and then examined more thoroughly later (Olshavsky, 1979; Billings & Marcus, 1983; Payne et al., 1992).

A novel relationship between information acquisition modes and the preference to acquire different types of information was found when participants made social decisions. An attribute-based acquisition mode has been associated with increased focus on attributes that are weighted most heavily in a decision, while option-based acquisition is associated with the distribution of attention to attributes with a variety of levels of importance or weights (Tversky, 1972; Edland, 1994; Payne et al., 1993). In Study 1, this finding was extended to social decisions and attributes, where a more attribute-based acquisition mode predicted a greater preference to acquire social information. In contrast, the preference to acquire utilitarian and extraneous information when making a social decision was predicted by more option-based acquisition. Thus, the preference to acquire different types of information (e.g., social versus utilitarian) appears to be influenced by the information search strategy one is engaging in, consistent with previous research showing that how information is acquired influences what information is acquired (Fiedler, 2000). This supports the critical role that predecisional processes play in decision making.

Regarding the neural basis of predecisional, information acquisition processes, the hippocampus was revealed as a critical neural structure for engaging in option-based acquisition. Consistent with the FLIAN model, patients with HC damage show a reduction in option-based acquisition and more engagement of an attribute-based acquisition mode. This was revealed in the high complexity condition in Study 1, when comparison participants shifted toward a more option-based mode and HC patients failed
to do so, instead maintaining a more attribute-based acquisition strategy. This finding also provides some indirect support for the proposed role of the amygdala in the FLIAN model in inducing attribute-based information acquisition; according to the model and consistent with the current findings, when the hippocampus is damaged the attribute-based acquisition mode induced by the amygdala would be prominent. However, effects of bilateral amygdala damage on predecisional processes were not observed. Future research should explore the possible role of the amygdala in attribute-based information acquisition using tasks that place greater demands on automatic predecisional behavior and leave less room for higher-order executive processes to affect task performance.

The vmPFC was demonstrated to play a critical role in flexible predecisional behavior, particularly in the use of specific decision strategies in different contexts. Patients with vmPFC damage showed a deficit in the use of an option-based strategy in the low complexity condition after training. The trained option-based strategy places demands on integrating information into the decision space representation. In this strategy, options are not just eliminated and the decision space simplified; rather, representations of the options under consideration are maintained online and then compared. Thus, the reduced engagement of this option-based strategy supports the proposed role of the vmPFC in representing the decision space.

Finally, both the vmPFC and HC groups showed an increased preference to acquire utilitarian information, further supporting the role of these structures in predecisional behavior. It is likely that these findings are due to different underlying cognitive processes. According to the FLIAN model, the vmPFC, in its role in representing the decision space, is critical for the process of weighting attributes. Further
research will be needed to understand what about utilitarian attributes makes them more important to patients with vmPFC injury. One possibility is that neurologically intact individuals experience a social-emotional aversion to utilitarian attributes that reduces the probability that they will acquire such information. For example, considering what material gain a roommate can provide might be considered selfish and elicit feelings of guilt, and thus drive the avoidance of that information. The vmPFC is known to be critical for social-emotional processing and anticipating the future consequences of behavior. Thus patients with vmPFC injury may favor utilitarian information due to a lack of aversion to integrating utilitarian information into their social decisions. This finding suggests that an important avenue for future study will be to examine the potential effects of abnormal attribute weighting for social decision making and real-world socio-moral behavior.

In sum, I have proposed and discovered partial support for a model of the neural system critical for predecisional processes in flexible decision making. The model centers on a fronto-limbic information acquisition network that includes the ventromedial prefrontal cortex, amygdala, and hippocampus. Within the FLIAN model, the vmPFC is argued to play a role in representing the currently perceived state of the decision problem (i.e., the decision space). The model suggests that a selected decision-making strategy is implemented by the vmPFC through the coordination of information acquisition processes induced by the amygdala and hippocampus. The role of the hippocampus in inducing relational, option-based acquisition was supported. The potential effect of impaired option-based acquisition on memory impairments caused by hippocampus damage warrants future investigation. The possibility of higher-order executive processes
compensating for an information acquisition deficit is intriguing and may provide a novel approach to typically intractable memory impairments by intervening at the stage of information acquisition. Although the amygdala was hypothesized to be responsible for inducing an attribute-based information acquisition mode, only indirect support for this claim was found. Considering the interconnectivity of the vmPFC, amygdala, and hippocampus, future research should continue to explore the role of all of these regions in predecisional behavior. Overall, the FLIAN model is a promising model of the neural basis of predecisional processes. Future research in the neuroscience of decision making should continue to explore decision making as a process and include studies of predecisional behavior.
REFERENCES:


