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To My Mother

Acknowledgments

“Few are those who see with their own eyes and feel with their own hearts.”

Albert Einstein

My mother is one of the few. First and foremost I thank my mother for her generosity and for her unconditional support. This thesis serves as a dedication to her.

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List of Abbreviations

ACC	Anterior Cingulate Cortex
Amyg	Amygdala
BOLD	Blood Oxygenation Level-Dependent
CAPM	Capital Asset Pricing Model
dorsal	from <i>dorsum</i> (Latin: Pertaining to the back or posterior)
e.g.	Exempli gratia (Latin: For example)
et al.	Et alii (Latin: And others)
EU	Expected Utility
EV	Expected Value
fMRI	functional Magnetic Resonance Imaging
ibid	Ibidem (Latin: At the same place)
i.e.	Id est (Latin: That is)
L ins	Left (anterior) insula
R ins	Right (anterior) insula
mb	Midbrain
md	Mediodorsal thalamic nucleus
LOFC	Bilateral Orbitofrontal Cortex
R-OFC	Right Orbitofrontal Cortex
L put	Left putamen
R put	Right putamen
ventral	from <i>venter</i> (Latin: Pertaining to the front or anterior)
L vst	Left ventral striatum
R vst	Right ventral striatum
vs.	Versus (Latin: Turned against)

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CHAPTER 1

Introduction

“[F]inance and economic research has hit a wall. We can not answer any more questions by running another regression analysis. Now, we need to get inside the brain to understand why people make decisions.”

Andrew Lo

Interview in [Bloomberg Markets \(2006\)](#)

With the benefit of hindsight economists have become accustomed to the fact that financial decisions and conditions of uncertainty intertwine. Until the advance of the early fifties of the twentieth century, Neoclassical Finance has treated humans as a black box, resting on the assumption that behavioral rules are imposed by rational choice theory. Notwithstanding this normative theory of choice, in the late seventies – in allusion to miscellaneous psychologically constructed evidence of both experimental and observational studies of hypothetical choice – Behavioral Finance has reached a consensus on individuals’ choices diverging from the prediction that economic and financial decisions are taken on immaculately rational grounds, perpetually contemplating humans as a black box.

In contrast, the nascent field of Neurofinance precludes a daring challenge to the deeply entrenched conundrum of the black box, by making attempts to find a computational model of choice (i.e., to understand behavior) by scrutinizing the indispensable neural correlates of decision making when exposed to financial risk.

For instance, where does choice in earnest originate from? Is it a foregone conclusion that choice is the outcome of a utility maximization process? Are emotions to impair financial decision making or are they necessary for reasoned choice? In recent years, this genre of question has been addressed making use of fruitful collaborations with neuroscientific methods to implement neuroimaging experiments. It is pertinent to elaborate on the issue of *in vivo* localization of choice since it possesses the ability to provide some intriguing insights into the involvement of multiple specific neural circuitries in a large preponderance of individuals.

Although the precise role of the neural substrate underlying financial decision making – partly due to its highly intricate structure – has not been understood in extenso, one of the main objectives of this thesis is to attempt to ably elucidate the interdisciplinary endeavor of Neurofinance in the realm of cognitive neurosciences. Thus, to provide constraint on the perennially adjuvant adjudication among neuroanatomically and perhaps neurophysiologically distinct and spatially separated neural structures, the collective dynamics of neural networks in the human brain is not to be regarded as a nuisance.

At the core, following the landmark studies of [Preuschoff et al. \(2006a,b\)](#) and of [Preuschoff et al. \(2008\)](#), this thesis aims to warrant an understanding of the neural basis of financial decision making, namely by focusing on the actual processing of risks and rewards in the human brain.

The remainder of this work is structured as follows. The second Chapter contrasts Expected Utility Theory, which is the major normative theory of decision making under risk, with Prospect Theory as a descriptive analysis, including an extensive segment on psychological biases and decision heuristics. Chapter 3 presents the anatomical and the chemical foundations of the processes in the human cerebrum, needed for the understanding of neural evidence of decision making under risk. Chapter 4 investigates the perception of risk and reward in the human cerebrum. I conclude with a short summary and with some discussion of future research directions in Chapter 5.

CHAPTER 2

The Basic Tenets of Neurofinance

Neurofinance investigates the neural mechanisms underlying human decision making under uncertainty. In recent years, ample experimental evidence has accumulated arguing that choice is the outcome of complex neurophysiological processes. Before opening the black box of the human brain in the third chapter, a natural question to ask is what has led to the emergence of Neurofinance. Hence, in order to depict the basic tenets of Neurofinance, this chapter aims at exploring and contrasting the foundations of two distinctive approaches in finance attempting to characterize human choice, namely Neoclassical and Behavioral Finance. Both approaches treat the human agent as a black box, interpreting choices “as if” they maximize some utility.

2.1 The Foundations of Neoclassical Finance

The assumption about investor preferences, or about how investors evaluate risky gambles is an integral part of any model in the quest of understanding asset prices or trading behavior. Neoclassical Finance in terms of studying decision making under uncertainty is motivated by the premise that economic agents exhibit stable and coherent preferences and act rationally with their choices being in consistence with Expected Utility Theory (von Neumann and Morgenstern, 1944). The following section provides the reader with a comprehensive explanation of the main elements of Neoclassical Finance.

Expected Utility (EU) Theory (von Neumann and Morgenstern, 1944) as a normative model of rational choice, has dominated the analysis of decision making in the presence of uncertainty. According to EU theory, there is an equivalence between choices (i.e., when satisfying a number of rationality requirements) and maximization of an *expected utility index*. Before I delve into the issue of highlighting the core utility paradox regarding non-rational behavior of actual decision-makers in detail, I will devote considerable space to covering the utility function and the EU Rule.

Rational choice theory traces its origins to the prominent St. Petersburg essay in which [Bernoulli \(1738\)](#) suggested that if choosing among a set of uncertain alternatives, people prefer the lottery yielding the greatest expected utility rather than the lottery with the highest expected value.¹ [Samuelson's \(1938\)](#) crucial achievement which lies at the heart of decision theory, was to identify rules for decision makers to be obeyed if they are making choices in order to maximize some utility function. His advance was to show that utility maximization implies restrictions identified by the Weak Axiom of Revealed Preference (see, also [Houthakker, 1950](#)). This “revealed preference” methodology in its simplest form states that if some object x is chosen over another object y , in some other experiment y can not be chosen over x . If and only if this condition holds does a decision maker behave as if making choices in order to maximize some fixed utility function.

From the perspective of [von Neumann and Morgenstern \(1944\)](#) who pioneered the derivation of an expected utility representation of preferences under uncertainty, it is of fundamental significance to state that the basic objects involved in the characterization of available choice are lotteries. By definition, a lottery is a random variable with specified payoffs and specified probabilities. Traditionally, the measurement of utility is based on rational behavior which is established as behavior in accordance with a systematic set of preferences. Thus, a rational agent's decision problem essentially boils down to the following four elements:²

- (1) a set of states $(1, \dots, s, \dots, S)$ available to Nature;
- (2) a set of actions $(1, \dots, x, \dots, X)$ available to him;
- (3) a consequence function $c(s, x)$ showing outcomes under all combinations of states of nature s and actions x ;
- (4) a probability function $p(s)$ representing his beliefs (as to the likelihood of Nature choosing each and every state) by a “subjective” probability distribution – to wit, a degree of belief assigned to each state s in the form of numerical weights p_s lying between zero and one inclusive, and summing to unity: $\sum_{s=1}^S p_s = 1$.

¹ [Pascal's \(1948\)](#) theory of Expected Value postulates a first formal description of decision making. Expected value provides a common metric that individuals can assign to various options and then use to choose between them. As I will focus on the identification of neural correlates of expected value in order to predict choice in the fourth chapter of my thesis, I will shed light on the theory of Expected Value starting on page 25.

² This section predominantly draws on the first chapter of the following book by [Hirshleifer and Riley \(1992\)](#) and on the ninth chapter of the following book (in german) by [Eisenführ and Weber \(2003\)](#).

In assuming that each consequence c takes the form of a basket (vector) of consumption goods, it has to be emphasized that initial individual preferences are described as a ranking or “preference ordering” among choices, that is, in ordinal terms (Arrow, 1951). As opposed to an “ordinal” relation, a “cardinal” relation is one which contains information about how much better one alternative is than another, by the assignment of real numbers to consequences. An essential property of cardinal variables is that they allow quantitative measurement, leaving the relative magnitudes of differences unchanged (e.g., altitude, time, temperature).

Correspondingly, a rational agent will take action x as given and denote $c(s, x)$ in short hand as c_s and $p(s)$ as p_s . An inductive argument can be used to show that the lottery L that results from action x is defined by the vector $C = (c_1, \dots, c_s, \dots, c_S)$ of possible consequences of x and its vector $P = (p_1, \dots, p_s, \dots, p_S)$ of the probabilities of each consequence in C .

Four substantive assumptions on preferences over lotteries underlying Expected Utility Theory are revealed by axiomatic analysis: completeness, transitivity, continuity and independence. At this point, we introduce the symbol \sim to indicate indifference, the symbol \succeq for weak preference, and the symbol \succ to explain preference relations.

Axiom 1: “Completeness”

For all L_1, L_2 , either $L_1 \succeq L_2$ or $L_2 \succeq L_1$ or both.

Axiom 2: “Transitivity”

For any L_1, L_2, L_3 , if $L_1 \succeq L_2$ and $L_2 \succeq L_3$, then $L_1 \succeq L_3$.

Axiom 3: “Continuity”

For any $L_3 \succ L_2 \succ L_1$, there exists a unique α , $0 \leq \alpha \leq 1$ such that $\alpha L_3 + (1 - \alpha)L_1 \sim L_2$.

Axiom 4: “Independence”

For any L_1, L_2 and L_3 such that $L_1 \succ L_2$, then for any $\alpha \in (0, 1)$, $(1 - \alpha)L_1 + \alpha L_3 \succ (1 - \alpha)L_2 + \alpha L_3$.

Representation Theorem. *If the four axioms presented above hold, then there exists a cardinal utility index u such that ranking according to expected utility accords with actual preference over lotteries.*

$$\begin{aligned} U(x) &= p_1u(c_1) + p_2u(c_2) + \dots + p_Su(c_S) \\ &= \sum_{s=1}^S p_s u(c_s) \end{aligned} \tag{2.1}$$

Equation (2.1) says that the utility $U(x)$ of an act x is obtained as the mathematical expectation (the probability-weighted average) of the elementary utilities $u(c_s)$ of the associated consequences. The von Neumann and Morgenstern (1944, pp. 15-31) utility function u is unique up to a strictly increasing affine transformation (i.e., cardinality requirement), with the implication that u can be replaced by $a + bu$ for any constants a and $b > 0$ without changing the preference ordering of u . Importantly, EU theory assumes that outcomes c_s are valued nonlinearly by a utility function u , but are weighted by their objective probabilities (Savage, 1954).

The standard utility function, derived from Expected Utility Theory, has two essential characteristics: first, it captures the decision maker's risk attitude, that is, concavity of the utility function implies risk aversiveness of the decision maker (Jensen, 1906), and second, it captures the decision maker's attitude toward certain outcomes, that is, concavity of the utility function implies a decreasing marginal utility of wealth. In this manner a *risk-averse* agent prefers to receive the expected value of every lottery rather than face a lottery, while a *risk-preferring* decision maker prefers a random distribution of every lottery over its expected value. In the intermediate case of *risk neutrality*, the expected utility of wealth equals the utility of its expected value. As opposed to the risk-averse agent who is equipped with a concave utility function, meaning that its slope becomes flatter with the increase of wealth, the risk-preferring decision maker displays a convex utility function, with its slope getting steeper as wealth increases. Generally we can state that the more concave the utility function, the more risk averse the individual will be, and the more convex the utility function, the more risk preferring the individual will be. The Arrow-Pratt coefficient of absolute risk aversion r is a measure of the curvature of the utility function (Pratt, 1964 and Arrow, 1965) and is retained by normalizing the second derivative of the expected utility function by dividing by the first:

$$r(c) = -\frac{u''(c)}{u'(c)}$$

Rabin (2000) shows that an expected utility maximizer who is risk-averse to gambles at low wealth levels, would have extraordinarily high risk aversion over gambles with medium and high stakes.

Is Expected Utility Theory a good approximation to how people evaluate a risky gamble like the stock market or does it make invalid predictions? Allais (1953) was instrumental in the establishment of the “common ratio effect” which can be reconciled by reliable evidence ably proving that the hypothesis of expected utility being linear in probabilities displays systematic inconsistency with individuals’ conscious patterns of choice.

The “ambiguity aversion effect” illustrates that most decision makers seem to express a preference for risky prospects with equal outcome probabilities to ambiguous ones. The classic demonstration of it is the Ellsberg paradox (Ellsberg, 1961) as a violation of the axioms of rational choice. In its simplest form, the classic experiment would be an urn (I) with red and black balls of an unknown proportion, out of which one ball is to be drawn at random. In urn (II) the red and the black balls are in equal number and the proportion of red and black balls is known. Therefore, in both cases the indifference between choosing Red or Black can be regarded as an expression of assigning equal probabilities to both colors. As far as urn (II) is concerned, the probability of drawing a red ball, for example, is objectively given as 0.5, and as far as urn (I) is taken into consideration, only the subjective probability of the same event can be asserted as being 0.5, as the objective probability is unknown. Ellsberg (1961) documents that people prefer to have the ball drawn from urn (II) (with known proportion), displaying deviant behavior incompatible with the expected utility principle.

2.2 The Foundations of Behavioral Finance

This section aims to provide a comprehensive survey of the growing interdisciplinary area of Behavioral Finance, where insights from psychology are used to improve the realism of classical financial models (Barberis and Thaler, 2003). As documented in the Behavioral Finance literature, individuals’ choices show considerable deviation from the expectation of rational behavior implied by normative decision analysis (see, for example, Shefrin, 2002 and Camerer and Loewenstein, 2003).

2.2.1 Behavioral and Cognitive Psychologists

Literature on behavioral psychology seldom emphasizes the crucial role of developmental psychology on neural mechanisms of the human mind. Academic thinking

on the mental origin of individuals' behavioral patterns vaguely bears in mind that Darwin (1872) laid the foundations for the application of evolutionary theory to the human behavioral sciences.

Behaviorism could be argued to originate as early as 1877 from Darwin's notations on the nature of expressions observed for different emotions. He kept accurate records on the early mental development of his first-born son William Erasmus Darwin, introducing the notion of emotions such as anger, fear (including anxiety), helplessness, affection, and moral sense. One seminal idea noted in Darwin (1877) is that most of our emotions are innate. Darwin had not solely made an observation about William's smiling as an expression of affectionate behavior; he witnessed that infants who are blind from birth begin smiling without practice or prompting at the same age as normal infants.³

The theory of Pavlovian conditioning has heralded the beginning of neurophysiological and psychophysiological studies of the reflex mechanisms of long-term cerebral activity. Russian physiologist Ivan Pavlov – Nobel laureate in medicine in 1904 in recognition of his investigations of digestive glands – merely by coincidence made headway in introducing the theory of *Conditioned Reflexes* as being composed of orchestrated physiological processes. In general, Pavlov (1927) refers to the conditioned stimulus which comes to evoke a response of the unconditioned stimulus, and under these circumstances the conditioned stimulus calls forth behavior that has ably adapted to the behavior that had previously been elicited by the unconditioned stimulus – with the magnitude of the response depending on the intensity of the stimulus.⁴ Pavlov and his colleagues paved the way for the emergence of cognitive neuroscience analyzing the genetic contributions to the development of cerebral asymmetry, formulating the heritability of lobar and cerebral hemispheric volumes correlating with handedness.

The genesis of Behaviorism as a science of objectively observable behavior (excluding the study of mental processes) can be traced back to John B. Watson with

³ For evidence on the recognition of multiple emotions from facial expressions accompanied by asymmetries in muscle movement, see Adolphs et al. (1994). Apart from focusing on the criterion of phylogenetic contexts, they demonstrate that lesions of the human amygdala impair the evocation of emotional responses.

⁴ Cortical inhibition processes shielding (the cortex) from overstimulation are exemplified through the elicitation of salivation of dogs under study by a conditioned stimulus (the sound of a bell) that has repeatedly preceded presentations of an unconditioned stimulus (food). The unconditioned (i.e. initial inborn) reflexes are constantly supplemented by the conditioned ones routed through the cerebral hemispheres.

his magnum opus *Psychology as the behaviorist views it* (Watson, 1913). The basic premise of his research is to evoke psychology into a general science of behavior, arguing that all complex human behavior is learned by unique adaptation to the environment in contrast to the inheritance of traits. Watson (1913) rejects the concepts of consciousness and of introspection as being intersubjectively unverifiable, suggesting that complex functional behaviors could be conditioned via Pavlovian principles. In applying Pavlov's (1927) model of classical conditioning in the first instance to humans with phobic and other behavioral disorders, Watson (1913) provides a mechanism for prescriptive psychotherapy, in which patients with simple phobias of hereditary origin (mediated by genetic factors) are systematically challenged to face clinical exposure.

In contrast to the model of classical (respondent) conditioning, Skinner (1938) studies the impact of human behavior in terms of the operant conditioning paradigm. In operant behavior analysis, the basic association takes place between the operant response and the reinforcer, with the emission of antecedent (discriminative) stimuli depending on its past consequences instead of on the unconditioned (eliciting) stimuli. Given this finding that the environment molds behavior, it can be expected that characteristic patterns of responding are revealed as reinforcement contingencies are subsequently varied. As operant behavior is shaped and maintained by the consequences of current responses for the individual, its study is essential in specifying what aspects of behavior are to be attributed to hereditary endowment.⁵

The theory of *cognitive dissonance* was introduced by Festinger et al. (1956), who noted that individuals holding two or more cognitions (i.e., attitudes and beliefs) that are psychologically inconsistent will experience an uncomfortable state of cognitive dissonance. Individuals will therefore strive to reduce dissonance by changing one or more of the cognitions so that they are no longer inconsistent. Kahneman and Tversky (1972) and Tversky and Kahneman (1973, 1974) made headway in the empirical study of human judgment under uncertainty, by documenting three heuristics – representativeness, availability, and anchoring and adjustment – that people employ in assessing probabilities and in predicting values.

⁵ Advances in the study of the biologic underpinnings of complex cognition are highlighted in Gazzaniga (2004). The author(s) profoundly covers the analysis of intellectual capacity in (developmental) cognitive neuroscience examining the role of environmental factors in intelligence, suggesting that with nearly half of the variance attributable to genetic factors, IQ scores are strongly heritable.

2.2.1.1 Prospect Theory

Behavioral Finance rejects the idea that choice reflects maximization of a rational (expected) utility function. In Behavioral Finance, the rules that govern the workings of the black box are derived from observation of actual or hypothetical choice (i.e., maximization of prospect utility). The year 1979 saw the formulation of Prospect Theory by [Kahneman and Tversky](#) as a descriptive model of decision making under uncertainty.

[Kahneman and Tversky's](#) (1979) original version of Prospect Theory is concerned with simple prospects with at most two non-zero outcomes. The authors propose that when offered a prospect of the form

$$(c_1, p_1; c_2, p_2),$$

to be read as “get outcome c_1 with probability p_1 , outcome c_2 with probability p_2 , and nothing with probability $1 - p_1 - p_2$,” where $c_1 \leq 0 \leq c_2$ or $c_2 \leq 0 \leq c_1$, and where $p_1 + p_2 \leq 1$, people assign it a value of

$$V(c_1, p_1; c_2, p_2) = \pi(p_1)v(c_1) + \pi(p_2)v(c_2),$$

where $v(0) = 0$, $\pi(0) = 0$, and $\pi(1) = 1$. Or in a condensed notation

$$V(x) = \sum_{s=1}^S \pi(p_s)v(c_s). \quad (2.2)$$

Equation (2.2) shows that the over-all value of a prospect denoted V , is expressed in terms of two scales, π and v . The first scale, π , associates with each probability p a decision weight $\pi(p)$, which reflects the impact of p on the overall value of the prospect. The second scale, v , assigns to each outcome c a number $v(c)$, which reflects the subjective value of that outcome (see, [Kahneman and Tversky, 1979](#)). Correspondingly, when deciding between different gambles, agents choose the gamble with the highest value.

In comparison with Expected Utility Theory (as in Equation 2.1) u is replaced by v as denoting the value function – being defined on outcomes – in a prospect theoretical context. Also, risk-sensitivity in Prospect Theory results from a combination of nonlinearities in the value function and the presence of a probability-weighting function π , whereas in standard Expected Utility Theory, nonlinearities in u predominantly generate risk attitudes ([d’Acromont and Bossaerts, 2008](#)).

The essential feature of the value function is that it is defined on gains and losses rather than on final asset positions, which captures the notion that people in general treat outcomes as departures from some reference point, rather than in terms of total wealth (for a seminal discussion, see [Markowitz, 1952b](#)). The relevance of this assumption to the cognitive analysis of individual perception and judgment can be seen by considering the capability of adaptation to attributes such as brightness, loudness, or temperature relative to past concepts in the same context, rather than to the evaluation in absolute terms.

A second salient characteristic of the value function is that the marginal value of both gains and losses commonly decreases with their magnitude, that is, the value function for changes of wealth is concave above the reference point ($v''(c) < 0$, for $c > 0$) and frequently convex below it ($v''(c) > 0$, for $c < 0$).

A third significant property of the value function – called “loss aversion” – is that it is steeper for losses than for gains (i.e., the disutility of giving up an object is greater than the utility associated with acquiring it). The common reluctance to accept a fair bet (i.e., a bet with expected gain or loss of wealth equal to zero) on the toss of a coin suggests that the displeasure associated with losing a c number of money exceeds the pleasure associated with gaining the same amount, or $v(c) < -v(-c)$ (most notably, see, [Kahneman and Tversky, 1979, 1984, 2000](#) and [Tversky and Kahneman, 1991](#)).⁶ It can be therefore proposed that the S-shaped value function in Prospect Theory is steepest at the reference point, in marked contrast to the utility function postulated by [Markowitz \(1952b\)](#).

[Kahneman and Tversky \(1979\)](#) and [Tversky and Kahneman \(1992\)](#) confirm an aversion to equiprobable gambles of the form:

Problem 1

$$(110, 0.5; -100, 0.5)$$

to be read as “win \$110 with probability 0.5, lose \$100 with probability 0.5, independent of other risks”. [Kahneman and Tversky \(1979, p. 279\)](#) view loss aversion as follows: “An individual is loss averse if she or he dislikes symmetric 50-50 bets and, moreover, the aversiveness to such bets increases with the absolute size of the stakes.”

⁶ In particular, [Samuelson \(1963\)](#) first finds evidence of loss aversion, by offering the following bet to an economist colleague over lunch: a 50% chance to win \$200 and a 50% chance to lose \$100. The colleague gave the following answer: “I won’t bet because I would feel the \$100 loss more than the \$200 gain. But I’ll take you on if you promise to let me make 100 such bets”.

Prospect Theory posits that individuals' simultaneous demand for both lottery tickets and insurance can be inferred from overweighting very low probabilities, that is, $\pi(p) > p$ for small p . In that vein, consider the following two choice problems that illuminate the features of Prospect Theory – as a violation of Expected Utility Theory – as in [Kahneman and Tversky \(1979\)](#).

The authors use $-c$ to denote the loss of c , and \succ to denote the prevalent preference, that is, the choice made by the majority of people. For example, the majority of subjects prefer one chance in a thousand to win \$5000 over a certain \$5, whereas they are not willing to accept a risk of 0.001 to lose \$5000, in preference to a sure loss of \$5.

Problem 2

$$(5000, 0.001) \succ (5, 1)$$

Problem 3

$$(-5, 1) \succ (-5000, 0.001)$$

In problem 2, the preference for a small probability of a large gain – which can be viewed as a lottery ticket – over the expected value of that ticket, contributes to the concavity of the value function in gains. In contrast, in problem 3, individuals prefer a small loss, what is in effect the payment of an insurance premium, over a small probability of a large loss. Similarly, the payment for insurance implies convexity of the value function for losses ([Kahneman and Tversky, 1979](#)).

Importantly, people seem to exhibit a larger amount of sensitivity to differences in probabilities at higher probability levels. For example, the following pair of choices (as in [Kahneman and Tversky, 1979](#)) where subjects tend to prefer a certain \$3000 to (\$4000, 0.8), but also prefer (\$4000, 0.2) to (\$3000, 0.25),

Problem 4

$$(3000, 1) \succ (4000, 0.8),$$

and

$$(4000, 0.2) \succ (3000, 0.25),$$

violating Expected Utility Theory, imply

$$\frac{\pi(0.25)}{\pi(0.2)} < \frac{\pi(1)}{\pi(0.8)}.$$

Problem 4 demonstrates that outcomes which are obtained with certainty are overweighted relative to uncertain outcomes. [Kahneman and Tversky \(1979\)](#) refer to this situation as the “certainty effect”. As seen above, the 20% increase in probability from 0.8 to 1 appears to be more striking to people than the 20% increase from 0.2 to 0.25, emphasizing that people are placing more weight on outcomes that are certain relative to outcomes that are merely probable (see, for example [Barberis and Huang, 2007](#)).

[Tversky and Kahneman \(1992\)](#) introduce a generalization of Prospect Theory which can be applied to gambles with more than two outcomes. This version is termed the “Cumulative Prospect Theory” since the transformation of probabilities is first applied to the cumulative density function instead of directly to the probabilities. Specifically, if a gamble pays off c_s with probability p_s – and where π_s is the decision weight associated assigned to outcome s – the authors propose that people assign the gamble the value

$$\sum_{s=1}^S \pi_s v(c_s), \quad (2.3)$$

where v is called the value function with

$$v(c) = \begin{cases} c^\alpha & \text{if } c \geq 0 \\ -\lambda(-c)^\beta & \text{if } c < 0, \end{cases}$$

and with w being the probability weighting function,

$$\pi_s = w(p_s) - w(p_s^*),$$

$$w(p) = \frac{p^\gamma}{(p^\gamma + (1-p)^\gamma)^{\frac{1}{\gamma}}}.$$

Above, p_s (p_s^*) denotes the probability of the gamble yielding an outcome at least as good as (strictly better than) c_s , where $\alpha=\beta=0.88$, $\lambda=2.25$, and $\gamma=0.65$ ([Tversky and Kahneman, 1992](#)). It is substantial to note that λ represents the coefficient of loss aversion, which is as previously mentioned, a measure of the relative sensitivity to gains and losses (also, see [Benartzi and Thaler, 1995](#)).

To illustrate the importance of *framing*, consider the following experiment in [Tversky and Kahneman \(1981\)](#) where they ask 150 subjects the following question:

Problem 5: Imagine that you face the following pair of concurrent decisions. First examine both decisions, then indicate the options you prefer.

Decision (i). Choose between:

- A. a sure gain of \$240
- B. a 25% chance to gain \$1000 and a 75% chance to gain nothing

Decision (ii). Choose between:

- C. a sure loss of \$750
- D. a 75% chance to lose \$1000 and a 25% chance to lose nothing

In decision (i), A is chosen by 84% of respondents over B. The choice is consistent with risk aversion, since the expected \$250 gain of B is greater than the sure \$240 gain of A. In contrast, in decision (ii), the majority (with 87%) of respondents opt for D over C. The choice is consistent with risk seeking, since the expected \$750 loss of D (which is riskier than C since it can impose a \$1000 loss) is equal to the sure \$750 loss of C. [Kahneman and Tversky \(1979\)](#) refer to this situation as “aversion to a sure loss”, since C imposes a sure loss while D does not.

In particular, 73% of subjects chose the combination of A & D, which offers

- a 25% chance to win \$240 and a 75% chance to lose \$760,

while only 3% of respondents chose the combination of B & C, which offers

- a 25% chance to win \$250 and a 75% chance to lose \$750.

The choice of the most common pattern (A and D) is surprising, given that the combination of A and D is inferior to the combination of B and C. Problem 5 shows that the respondents fail to take into account the possibility of the conjunction of two choices, although the instructions of the experiment indicate that the choice among A, B, C and D is concurrent. Instead, they frame the choice as a pair of separate choices.⁷ Furthermore, the underweighting of moderate and high probabilities

⁷ For evidence of framing effects see also [Tversky and Kahneman \(1986\)](#). The authors describe that subjects who choose optimally when problems are framed in a transparent form often choose suboptimally when problems are framed in an opaque form.

contributes to the relative attractiveness of the sure gain in decision (i) and to the relative aversiveness of the sure loss in decision (ii).

Tversky and Kahneman (1981) emphasize that instead of focusing on the outcome that determines their final wealth, subjects analyze choices in isolation from the other aspects of their financial situations. By establishing a separate mental account (*psychological or mental accounting*) for each choice, namely by framing mental accounts as gains and losses, these gains and losses are determined in terms of a reference point (see, also Thaler (1985) for implications to marketing).

Endowment effect (or *inheritance effect*) refers to the fact that people often demand a much higher price for their assets (willingness to accept or WTA) than they would be prepared to pay to acquire them (willingness to pay or WTP) (Thaler, 1980). People seem to give preference to their current situation when comparing it with a new one that they do not know well, even if the current one does not seem the most appropriate to them (Thaler, 1980). Kahneman et al. (1990) conduct a series of experiments to determine whether the endowment effect survives when subjects face market discipline and where learning takes place over successive trials.⁸

Shefrin and Statman (1985) apply Kahneman and Tversky's notion of framing to the realization of losses. They label this phenomenon the "disposition effect", arguing that investors are predisposed to holding losing investments (relative to their purchase price) too long while selling winners too early.⁹ Subsequently, Odean (1998a) – by studying the trading activity over the 1987 to 1993 period of 10,000 households – confirms that over a one year period investors are more likely to sell stocks that have increased their value relative to their purchase price, rather than stocks that have decreased their value.

De Bondt and Thaler (1985, 1987, 1990) apply Tversky and Kahneman's (1974) notion of representativeness to market pricing. They argue that investors overreact to both bad news and good news. Therefore, overreaction leads past losers to become underpriced and past winners to become overpriced. Huberman and Regev (2001) observe herding in the context of a contagious speculation associated with a potential breakthrough in cancer research, although the latter had already been reported more than five months prior in scholarly publications.

⁸ Subjects are for example either given a coffee mug and then asked if they would be willing to sell it, or not given a mug and then offered the chance to buy one. Kahneman et al. (1990) argue that mug owners demand more than twice as much to sell their mugs as non-owners are willing to pay to acquire one.

⁹ In a recent paper, Barberis and Xiong (2009) support Shefrin and Statman's (1985) decision to implement prospect theory over realized gains and losses.

2.2.1.2 Overconfidence and Excessive Trading

Extensive experimental and observational evidence compiled by behavioral psychologists concerning the psychology of beliefs has emerged from the cognitive analysis of individual judgment and financial decision making. A significant tenet in the behavioral finance literature is overconfidence, suggesting that people tend to be overconfident about their ability to make good investment decisions (Fischhoff and Slovic, 1980; Griffin and Tversky, 1992; Daniel et al., 1998; Odean, 1999; Barber and Odean, 2001). Odean (1998b) and Gervais and Odean (2001) predict that investors display overconfidence in the sense that they trade too much (i.e., trading, at the margin, reduces their expected utility).¹⁰

Barber and Odean (2000) support the view that excessive trading emanates from investor overconfidence. Figure 2.1 graphs the monthly turnover and the annual performance of 78,000 households. Mean monthly turnover ranges from 0.19% (households of the low turnover quintile) to 21.49% (households of the high turnover quintile). Households that trade frequently (households of the high turnover quintile) earn a net annualized geometric mean return of 11.4%, while households that trade infrequently (households of the low turnover quintile) earn 18.5%.

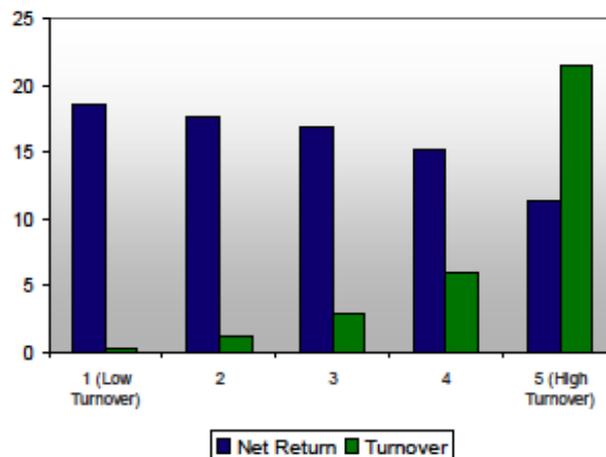


Figure 2.1

Monthly Turnover and Annual Performance of Individual Investors.

The blue bar represents the net annualized geometric mean return in percent for February 1991 through January 1997 for individual investor quintiles based on monthly turnover (the average of sales and purchase turnover). The green bar represents the mean monthly turnover in percent. Quintile 1 contains households with the lowest turnover (highest net return), quintile 5 contains households with the highest turnover (lowest net return).

Source: Lecture notes by Odean (2005).

¹⁰ In contrast, the rational expectations model predicts that investors whose expected trading is greater (i.e., those who trade more) will have the same expected utility as those who trade less. For detailed information please refer to Grossman and Stiglitz (1980).

Barber and Odean (2001) study whether overconfidence contributes to excessive trading and to lower returns by partitioning 37,664 investors on gender. Figure 2.2 depicts turnover rates for common stock portfolios held by women and men. Some interesting facts concerning the difference in turnover between women and men emerge. Barber and Odean (2001) find empirical evidence suggesting that women, who are inclined to be less overconfident than men, trade less than men (as measured by annual portfolio turnover). Men trade 45% more actively than do women, who turn their portfolios over 52.8% annually, while men turn their portfolios over 76.9% annually. However, if single households are taken into account, Figure 2.2 shows that single men – at an annual turnover of 84.6% – trade the most. This compares with an annual turnover of 50.6% for single women, who trade 67% less than single men, respectively.

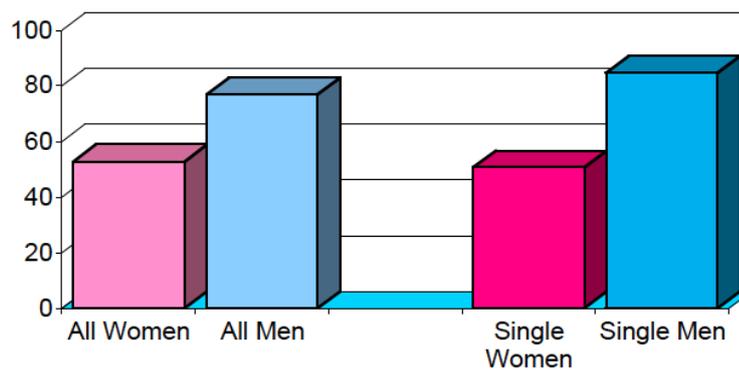


Figure 2.2

Turnover of Common Stock Investments of Female and Male Households.

Households are classified as female or male based on the gender of the person who opened the account. The pale pink bar (pale blue bar) represents the annual portfolio turnover of 8,005 female households (29,659 male households) in percent for February 1991 through January 1997. The pink bar (blue bar) represents the annual portfolio turnover of 2,306 *single* female households (6,326 *single* male households) in percent for the identical time period.

Source: Lecture notes by Odean (2005).

In Figure 2.3 the own-benchmark annual abnormal net returns for common stock portfolios held by women and men are presented. Barber and Odean (2001) illustrate that women earn annual net returns that are 1.72% lower than those earned by the portfolio they held at the beginning of the year, while men lower their annual net returns by 2.65%, respectively. Correspondingly, if taking single households into consideration, single men underperform single women by annually 1.45%. Trading reduces single women's annual net returns by 1.45% as opposed to 2.90% for single men.

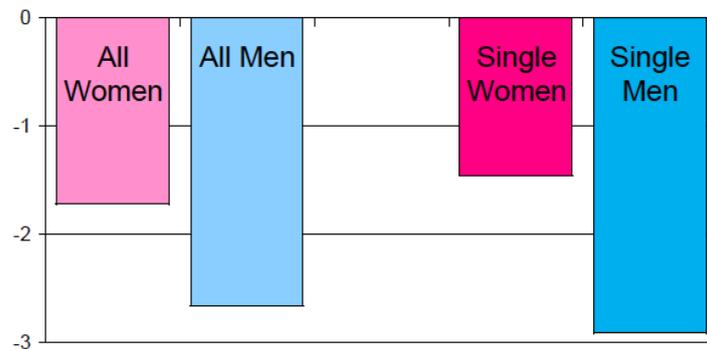


Figure 2.3

Return Performance of Common Stock Investments of Female and Male Households.

Households are classified as female or male based on the gender of the person who opened the account. The pale pink bar (pale blue bar) represents the own-benchmark annual abnormal net returns of 8,005 female households (29,659 male households) in percent for February 1991 through January 1997. The pink bar (blue bar) represents the own-benchmark annual abnormal net returns of 2,306 *single* female households (6,326 *single* male households) in percent for the identical time period.

Source: Lecture notes by [Odean \(2005\)](#).

2.2.2 Affect and Financial Decision Making

Astonishingly meager literature in economics interrelated with behavioral psychology has been devoted to illuminate affective cues tightly linked to diverse anomalies in the behavior of stock market prices and returns. For example, [Schwarz and Clore \(1983\)](#) find that affect negatively influences individuals' ratings of life satisfaction particularly on rainy days. [Hirshleifer and Shumway \(2003\)](#) show that the occurrence of sunshine is strongly positively correlated with market index returns at 26 international stock exchanges from 1982-1997. In this respect, [Hirshleifer and Shumway \(2003\)](#) illustrate that in New York City for instance, the annualized nominal market return on perfectly sunny days is 24.8% per year, versus 8.7% return per year with respect to cloudiness.

Research in psychology strongly supports the view that daylight has a far-reaching effect on individuals' moods, and in turn individuals' moods are related to risk aversion. [Kamstra et al. \(2003\)](#) analyze the effects of seasonal variation in length of day in 9 stock markets at different latitudes and in both the Northern and Southern Hemisphere. By observing stock market returns during the three months between the autumn equinox and the winter solstice and the three months between the winter solstice and the spring equinox, [Kamstra et al. \(2003\)](#) conclude that stock market returns are significantly related to season. Specifically, lowest annual returns commence with the autumn quarter and are followed by highest annual returns in the month after winter solstice (see, also [Kamstra et al., 2009](#)).

CHAPTER 3

The Human Cerebrum

A major foundation of neurophysiological processes in the human brain is the profound comprehension of the anatomy of the human cerebrum. Therefore, the aim of this chapter is first, to explain the neuroanatomy and second, to shed light on the neurochemistry. Before we advance our understanding of the human brain, the impetus of this first section is to give a rigorous underpinning of the imaging technique applied in the vast majority of the studies introduced in this thesis, which has hitherto been given scant attention.

3.1 Neural Imaging Techniques

The past decade has seen a proliferation of illuminating human studies confirming the stringent tenacity of functional brain mapping in the clinical neurological sciences (Logothetis et al., 2001 and Logothetis, 2008). The advent of functional magnetic resonance imaging (fMRI) provides an indirect measure of neuronal activation by dint of recording the ratio of oxyhemoglobin (i.e., oxygenated form of hemoglobin) to deoxyhemoglobin (i.e., hemoglobin that has donated its oxygen).¹ Eminently, fMRI renders possible to monitor that blood oxygenation-level-dependent (BOLD) contrast to sequence *in vivo* changes (i.e., delays in onset occurring about 2 seconds after neuronal activity) in hemodynamic responses in regions of the cerebral cortex as small as $2mm^3$ on the order of seconds (Fecteau et al., 2007 and Knutson and Gibbs, 2007).

It is a conceptual advance, because the non-invasivity of fMRI allows to stipulate brain activation that occurs not only during or after the performance of a specific task, but also before decisions. This “crossing of the rubicon” enables researchers to put herculean effort into investigating neural circuitries and its correlates, which have long been believed to play crucial roles in financial decisions.

¹ For prescient early insights, see Kwong et al. (1992) and Ogawa et al. (1992).

3.2 Neuroanatomy²

The human cerebrum – as displayed in Figure 3.1 – at the coarsest level, is composed of two hemispheres (with the right hemisphere controlling the left side of the body, and vice versa) which again can be divided into the (cerebral or neo-)cortex and into three evolutionary older subcortical structures: the *basal ganglia*³ (facilitates the initiation of willed movements, such as walking or writing), the *hippocampus*⁴ located deep along the medial surface of the temporal lobe (involved in episodic or autobiographical memory and in navigation), and the *amygdala*⁵ as part of the “limbic system” specializing in emotional memories (LeDoux, 1995).

Each cerebral hemisphere is segmented into four major lobes – from anterior to posterior – namely the frontal, parietal, occipital, and temporal lobes (as can be seen in Figure 3.1). *Anterior* and *dorsolateral* regions of *prefrontal cortex* are largely continuous to the upper and front most surfaces of the frontal lobes, which are thought to be the locus of higher cognitive faculties, including deliberative thought, abstract reasoning, judgment, problem solving, planning and language (see, for example, Koechlin et al., 1999; Smith and Jonides, 1999; Miller and Cohen, 2001 and Coricelli and Nagel, 2009). Parietal areas govern motor action, that is, they play a crucial role in somatosensory processes. The occipital lobe is where visual processing occurs. The temporal lobes are involved in the processing of auditory information and semantics, or word meaning. A fifth area of the cortex, called the *insula* (or insular cortex, as displayed in Figure 3.1), lies between the frontal and temporal lobes (Reynolds and Zahm, 2005), and it has been known to be activated during the observation of negative emotions such as revulsion, pain and disgust (Singer et al., 2004 and Stein et al., 2007).⁶

² Parts of this section have been adapted from O’Brien et al. (2008).

³ A collection of neurons deep in the cerebrum forms the basal ganglia, consisting of three major structures covering the thalamus in each hemisphere: the caudate nucleus, putamen, and globus pallidus (lateral and medial divisions). Together, the caudate nucleus and the putamen are frequently referred to as the striatum.

⁴ Derived from Greek: “hippokampos”, since its curved shape in coronal sections resembles a seahorse. Patients suffering from Alzheimer’s disease exhibit initial symptoms of memory absence and of disorientation as a result of damage to the hippocampus. Also, the hippocampus – through the process of neurogenesis – retains its ability to regenerate neurons throughout life.

⁵ The amygdala, as seen in Figure 3.1 (almond-shaped) sits anterior to the hippocampus (not pictured) in the temporal lobes. The amygdala is important in memory consolidation, but primarily it detects danger and activates fear and the stress response. The role of both antidepressants and psychotherapy is of great significance in reducing the sensitivity and reactivity of the amygdala.

⁶ Nearly all studies of decision making under risk and uncertainty have assigned a prominent role to insular activations. Insula activation has primarily been linked to the anticipation of monetary loss (see, for example Kuhn and Knutson, 2005 and Bechara and Damasio, 2005).

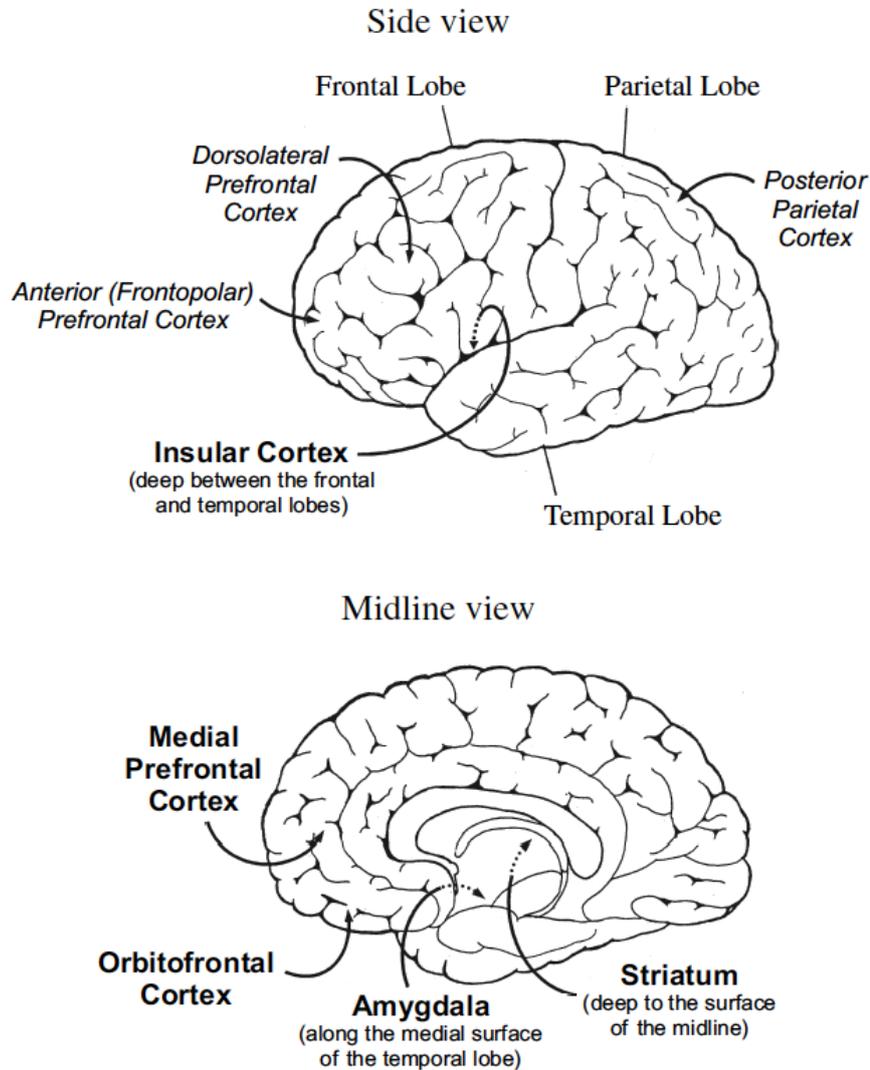


Figure 3.1
Regions of the Human Cerebrum.

(Top and Bottom) Side (lateral) view and midline (medial) view of the human cerebrum, identifying areas censoriously associated with decision making. Areas in bold depict key neural substrates underlying emotional processing, while areas in italics have uniformly been associated with higher level cognitive processes.

Source: [Cohen \(2005\)](#).

Cardinal attention will in this thesis be confined to the sound neurophysiological underpinnings of the *limbic system* ([Broca, 1877, 1878](#)) – which is an evolutionarily ancient brain structure known to be engaged in self-preservation behaviors in primitive settings, that has evolved 150 million years ago – where reward centers can be located, and of the *frontal lobe* – which as part of the neocortex was exaggerated in humans 2 to 3 million years ago – where cognitive decision making occurs ([Robson, 2001](#)).

3.3 Neurochemistry

This section advocates consideration of the neurochemical foundations of choice, thus we will not concern ourselves greatly with the peripheral nervous system, but for the purposes of description will first of all concentrate on the histology of the central nervous system comprising the brain and spinal cord.

In essence, a nerve cell (a *neuron*) is the primal functional unit of the central nervous system. Azevedo et al. (2009) find that the average adult male human brain – with a mass of 1508 gramms – contains 86.1 billion neurons. Inimitably, since Pakkenberg and Gundersen (1988) the authors arrestingly adumbrate that the average human cerebral cortex – with a mass of 1233 gramms – contains 16.3 billion neurons. Neurons are composed of three morphologically and molecularly distinct domains: the *cell body*, *axon*, and *dendrites* (as illustrated in Figure 3.2).

The cell body (perikaryon or *soma*) of a neuron houses a *nucleus* surrounded by cytoplasm inclosing dissimilar organelles such as lysosomes, mitochondria, Nissl substance, neurofibrils, and a Golgi complex. On the one hand, each neuron has singly one axon (or *nerve fiber*), which in specific is an elongated cylindrical projection conducting an electrical discharge, that is, the *action potential* (the nerve impulse) away from the soma towards *axon terminals*. The axon may evoke divisive ramifications – termed *axon collaterals* – facilitating its parent cell to sway various other cells. Axonal *ensheathment* or myelination by oligodendrocytes (node of Ranvier) expedites the velocity of propagation of nerve impulses, a process known as “saltatory conduction” (Na^+ and K^+ exchange pump). On the other hand, there are habitually multiple branches of unmyelinated dendrites, cultivating “dendritic trees” which receive stimuli from other neurons and conduct nerve impulses toward the soma (see, for example Brodal, 2004).

The area where transmittal of information occurs is called a *synapse* which represents a region of solely functional continuity between the outpouching of the terminal aspects (synaptic knob or *bouton*) of the axon of one *pre-synaptic* neuron and the dendrites, soma or axon of another *post-synaptic* neuron. The *vesicles* of the pre-synaptic neuron contain a *neurotransmitter* substance which diffuses unidirectionally across a physical gap called the *synaptic cleft* about 20nm wide (that is, 2/100,000mm) between the membrane of the bouton and the post-synaptic membrane.

Histochemical studies have indicated dendritic synthesis, storage and release of *dopamine* from the nigro-striatal dopaminergic neurons (Geffen et al., 1976 and Chermany et al., 1981). The human dopamine system is a collection of merely 450,000 neurons in the pars compacta of the substantia nigra (German et al., 1983).

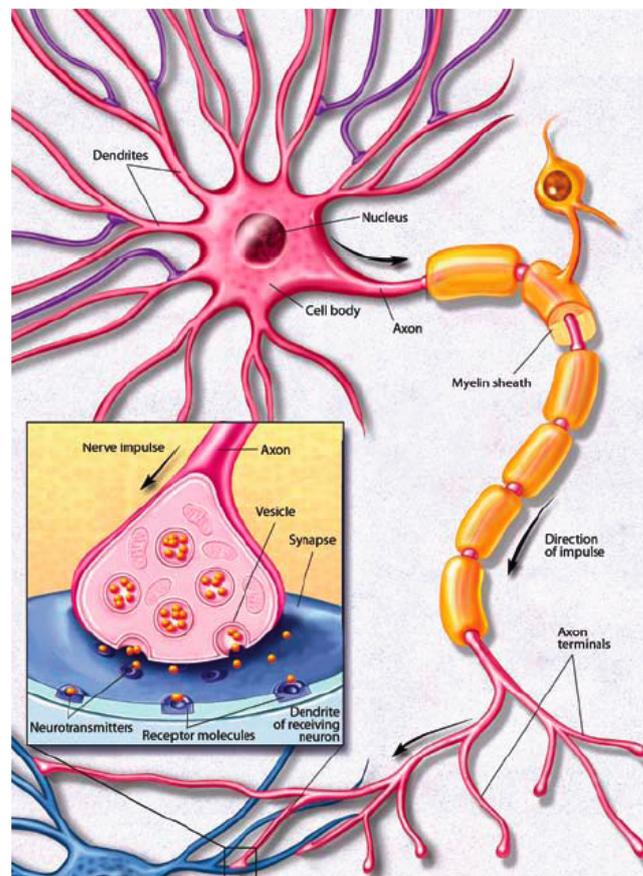


Figure 3.2

Anatomy of a Dopaminergic Neuron.

Nerve terminals, or *boutons* forming axosomatic and axodendritic synapses. The action potential – that is, an electric current – is conveyed into a chemical signal through the presynaptic release of a *neurotransmitter* by binding to *receptor molecules* in the postsynaptic membrane (increase in intracellular Ca^{2+}).

Source: [Society for Neuroscience \(2008\)](#).

Only in the fifties, dopamine was identified as a crucial neurotransmitter⁷ ([Carlsson et al., 1958](#)). A plethora of studies – which will be discussed in detail in Section 4.1 – have effectually corroborated the involvement of dopamine in reward-based decision making (see, also, [Schultz, 2002](#); [Montague et al., 2004](#); [Knutson and Peterson, 2005](#) and [Caplin et al., 2009](#)). Concisely, considerable evidence indicates that in the brain, dopamine plays an important role in the anticipation of reward and learning, in the regulation of voluntary movements and postural reflexes, attention, and motivation (see [Wise, 2004](#); [Pessiglione et al., 2006](#) and [Tobler et al., 2007a](#) for grave reviews).

⁷ Others for instance include serotonin, norepinephrine, acetylcholine, glutamate and γ -aminobutyric acid.

In addition to the aforementioned interactions, dopamine neurons have been associated with the involvement in symptoms of attention deficit hyperactivity disorder, mood disorders such as unipolar depression and bipolar disorder, anxiety and Tourette's disorder, cognitive dysfunction such as dementia (e.g., Parkinson's and Alzheimer's disease as a common cause of dementia) and schizophrenia, and precarious substance disorders, such as addictive behaviors of cocaine, heroin, nicotine and amphetamines (see, for example, Saal et al., 2003; Nestler, 2005 and Naqvi et al., 2007).

Of primary interest in all the studies that I highlight in my thesis are two dopaminergic pathways in the midbrain. Figure 3.3 depicts the *mesostriatal* pathway which originates in the *substantia nigra pars compacta* innervating the striatum (i.e., specifically the *caudate nucleus* and *putamen*) and the *mesolimbic* pathway which originates in the *ventral tegmental area* – which contains about 80% dopamine neurons and measures about 60mm^3 in volume – projecting to the amygdala, the *nucleus accumbens*, and the *prefrontal cortex* (D'Ardenne et al., 2008).

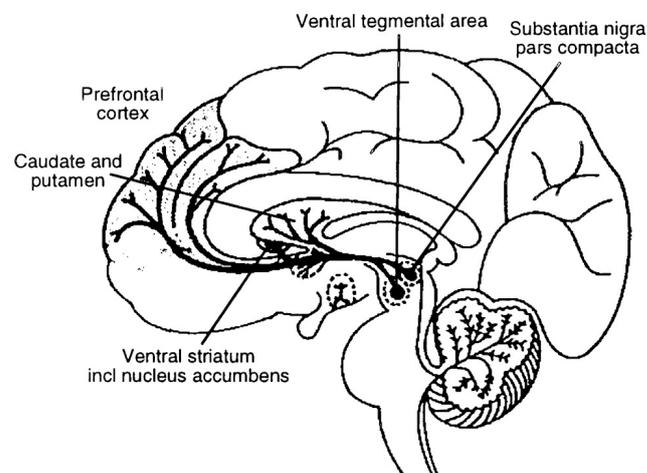


Figure 3.3

Projection Pathways of Midbrain Dopamine Neurons.

Neuronal somata of dopaminergic neurons are located mainly in the pars compacta of substantia nigra and the medially adjoining ventral tegmental area. Their nerve fibers project mainly to the striatum (caudate nucleus and putamen), ventral striatum including nucleus accumbens, and frontal cortex (dorsolateral, ventrolateral and orbital prefrontal cortex).

Source: [Schultz \(1999\)](#).

CHAPTER 4

Perception of Risk and Reward from a Neural Perspective

A key contribution of this thesis is aimed at unraveling the neural and metabolic mechanisms of the human brain underlying decision making under uncertainty. However, the quest for understanding the neural processing of the core parameters of antecedent neural activation in order to predict upcoming financial decisions has remained elusive. A foundational component of decisions in microeconomic theory is represented by [Pascal's \(1948\)](#) theory of Expected Value (EV). [Pascal's](#) framework postulates that since outcomes of choices possess specific magnitudes and occur with specific probabilities, they can be appropriately characterized by probability distributions of outcome magnitudes. [Pascal \(1948\)](#) conjectured that when deciding between different options, individuals tend to choose the option with the highest expected (mean) value of the probability distribution of outcomes (expected value as sum of all probability-weighted values of the distribution, the first moment of a probability distribution).

Equation [4.1](#) denotes that expected value is the summed product of reward outcome and probability:

$$EV(x) = \mu_s = \sum_{s=1}^S p_s c_s \quad (4.1)$$

where p relates to the probability of reward; c refers to the outcome of reward; and s refers to the underlying states of nature. Thus, economic models of decision making also incorporate uncertainty involved in choice behavior. Uncertainty – as in Equation [4.2](#) – can be denoted by the variance of the probability distribution (variance as sum of probability-weighted differences from expected value, the second moment of a probability distribution):

$$Var(x) = \sigma_s^2 = \sum_{s=1}^S p_s (c_s - \mu_s)^2 \quad (4.2)$$

where p relates to the probability of reward; c refers to the outcome of reward; μ stands for the expected value; and s refers to the underlying states of nature. Variance refers to the spread of the probability distribution and indicates how far each possible value is away from the expected value. Variance is perceived as “risk” and denotes how much a decision maker in uncertain situations risks to gain or to lose relative to the expected (mean) value of the known probability distribution.

However, probability is not a monotonic measure for risk. In a two-outcome situation, such as reward versus no reward, expected reward (measured as mathematical expectation of reward) increases linearly with the probability of reward p ; it is minimal at $p = 0$ and maximal at $p = 1$. In contrast to expected reward, risk (measured as reward variance, or as its square root, standard deviation) follows an inverted U-function of probability and is maximal at $p = 0.5$ and minimal at $p = 0$ and $p = 1$.¹

To this date, numerous economic studies of decision making under uncertainty (e.g. Holt and Laury, 2002; Bossaerts and Plott, 2004; Knutson and Bossaerts, 2007 and Platt and Huettel, 2008) have emphasized the crucial relevance of risk consideration in addition to expected reward.² In the following sections I refer to neuroscientific studies that play a decisive role in confirming the neurobiological representation of expected reward and risk in human (*sub*-)cortical structures. On the one hand, neural representation of expected reward is investigated in detail in Section 4.1. On the other hand, the studies examined in Section 4.2 provide a basis for understanding the precise neural representation of risk. Furthermore, in Section 4.3 a rigorous neurophysiological underpinning of the perception of expected utility is given. Section 4.4 focuses on the neural treatment of ambiguity. Ultimately, in Section 4.5 we will put grave emphasis on the role of emotions in financial decision making and discuss their neural correlates, respectively.

4.1 Neural Representation of Expected Reward

There is a growing literature which ascertains neuronal activation correlating with expected reward (Elliott et al., 2000, 2003; Berns et al., 2001; Breiter et al., 2001; O’Doherty et al., 2002; McClure et al., 2004, 2007; Dreher et al., 2006; Zink et al.,

¹ Please refer to Figure 4.2B from Preusschoff et al. (2006a) for further details.

² To provide elemental insights into the field of neuroeconomics, I have benefited from an early paper by Camerer et al. (2005). For a profound confrontation with neurofinancial issues the following book by Glimcher et al. (2009) served a great purpose.

2006; Knutson et al., 2000, 2001, 2003, 2008a; Balleine et al., 2007; Kepecs et al., 2008; Mainen and Kepecs, 2009). These papers are related to this thesis as they study the engagement of the human and nonhuman *sub*-cortical dopaminergic structures such as (the dorsal and) ventral striatum (including the nucleus accumbens), amygdala and prefrontal cortex (e.g., medial orbitofrontal cortex) in reward-related processes and provide interesting and important findings on this matter.

Neurophysiological evidence on the perception of risk and reward in the human brain is primarily based on electrophysiological studies of the nonhuman primate brain by Fiorillo et al. (2003) in support of the classic Pavlovian experiment outlined in Section 2.2.1. The authors document that single dopaminergic neurons in groups of the *substantia nigra pars compacta* and the medially adjoining *ventral tegmental area* in the ventroanterior midbrain show an increase in response (by spiking) to stimuli – during the interval between stimulus and reward – with the probability of reward. Following the reward itself, the impulse activity decreases monotonically with increasing probability, leading to the proposal that the information encoded by these neurons reflects the reward prediction error, or the difference between actual and predicted rewards. The prediction error (signal) is used to update the expected reward associated with a certain stimulus or cue in the environment (similarly to the arguments in terms of temporal difference models of learning, see Fiorillo et al., 2005 and on a more fundamental level, see Rescorla and Wagner, 1972).

From the plethora of experiments in connection with the identification of brain regions tracking reward prediction errors pioneered by Schultz et al. (1997), O’Doherty et al. (2003) have found activations in the ventral striatum (left ventral putamen) and in the orbitofrontal cortex to correlate with reward prediction error. Scaling of rewards in the nonhuman primate orbitofrontal cortex and in striatal areas (ventral striatum and putamen) was demonstrated by Tremblay and Schultz (1999) and Cromwell and Schultz (2003) while in the human medial orbitofrontal cortex and in dorsal striatum (i.e., caudate nucleus) it was recently observed by Elliott et al. (2008); De Martino et al. (2009) and Valentin and O’Doherty (2009), respectively.

In a set of experiments Tobler et al. (2005) demonstrate “adaptive encoding” (i.e., scaling) of rewards by presenting three pseudorandomly alternating visual stimuli indicating a 50% chance of gustatory (i.e., juice) reward to two adult female *Macaca fascicularis* monkeys. The observation that the responses of dopamine neurons in the *ventral tegmental area* to three liquid volumes spanning a tenfold range appear to be identical is depicted in Figure 4.1A and 4.1B. Interestingly, the sensitivity or gain of the neural responses as a function of liquid volume evoked an adaptation according to the prediction made by the visual stimulus, so that responses appeared to be equivalent regardless of their absolute magnitude (Figure 4.1C).

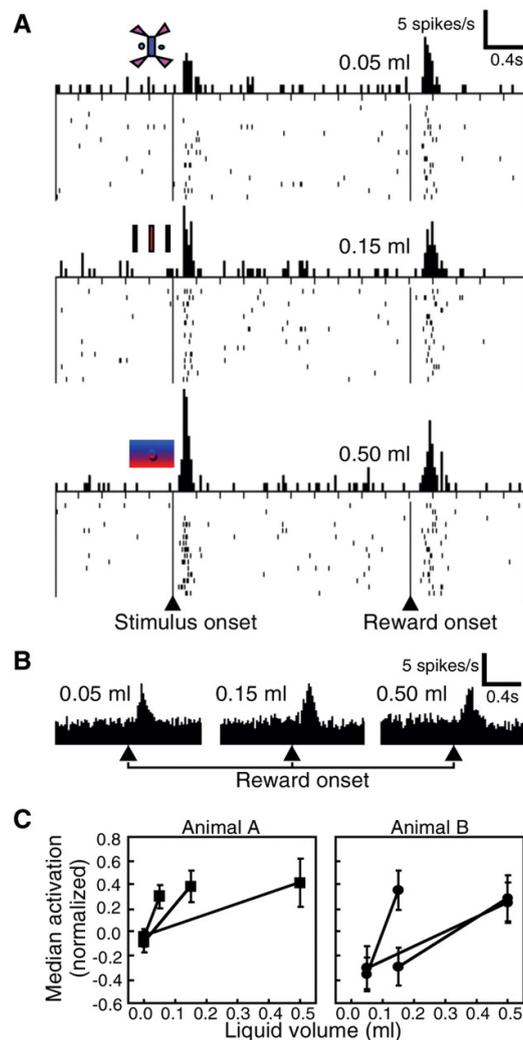


Figure 4.1

Adaptive Encoding of Reward in the Nonhuman Primate Brain.

(A) Single Neural Firing Patterns in Ventral Tegmental Area.

Almost identical neural responses of a single dopamine neuron to three liquid volumes spanning a 10-fold range. Each of three distinct visual stimuli (as shown on the left hand side in color), presented on pseudorandomly alternating trials, predicts that one of two potential liquid volumes (top, 0.0 or 0.05 ml; middle, 0.0 or 0.15 ml; bottom, 0.0 or 0.5 ml) will be delivered with $p = 0.5$. The dopamine responses after visual stimuli onset increase with their associated expected reward values. Results for only rewarded trials are shown.

(B) Population Histograms of Responses.

Histograms of group firing rates (of animal A) for the three different liquid volumes from the experiment in (A).

(C) Plots of the Median Neural Responses as a Function of Liquid Volume.

Straight lines connect the data points which represent the median response ($\pm 95\%$ confidence intervals) of the population taken after normalizing the response (percentage change in activity) within each neuron to the response following the delivery of unpredicted liquid (0.15 ml) recorded in a separate block of trials. The slope of these lines provides an estimate of the neurons' gain or sensitivity with respect to liquid volume. (Left) The experiment in (A) and (B). (Right) Identical experiment performed in animal B with two nonzero liquid volumes per conditioned stimulus at $p = 0.5$ (stimulus 1: 0.05 vs. 0.15 ml, stimulus 2: 0.15 vs. 0.5 ml, stimulus 3: 0.05 vs. 0.5 ml).

Source: [Tobler, Fiorillo, and Schultz \(2005\)](#).

4.1.1 The Approach by Preuschoff, Bossaerts and Quartz (2006)

Preuschoff et al. (2006a) examine whether and how activation in subcortical dopamine regions in the human brain correlates with changes in expected reward and risk.³ In accordance with financial decision theory (i.e., portfolio theory), expected reward is measured as mathematical expectation of reward (for example, as in Knutson et al., 2003), and risk is measured as reward variance, namely as the mean squared deviation from the expected outcome (Markowitz, 1952a). The combination of functional magnetic resonance imaging (fMRI) with a simple gambling task allows for the simultaneous variation of expected reward and risk.

4.1.1.1 Data and Methods

Figure 4.2 reveals the experimental procedure with subfigure (A) displaying the timeline of the gambling task for a single trial and with subfigure (B) exhibiting the risk and reward profile, respectively.

A total of nineteen subjects played a simple card game. Ten cards (as seen in subfigure (A)), numbered 1 through 10, were randomly shuffled. In each trial, two cards were drawn consecutively (and without replacement within each trial) from the deck of cards. Before seeing either card, subjects were asked to place a bet (\$1 per trial) on one of the two options, “second card higher” or “second card lower”. If guessing the right card, subjects could earn \$1 and if they were wrong, they lost \$1. About 3 seconds later, the first card was displayed, followed about 7 seconds later by the second card. To ensure that subjects paid attention, at the end of each trial, they were asked to indicate whether they won or lost on the according trial. A penalty of \$0.25 was imposed if they incorrectly reported the outcome of their bet or if they did not respond.

Subfigure (B) demonstrates expected reward and risk as a function of the probability of reward. Expected reward (dashed line), modeled as mathematical expectation of reward (i.e., mathematical expectation of payoff), increases linearly in reward probability p . Risk (solid line), measured as reward variance, is quadratic in reward probability p , exhibiting a symmetric, inverted U-shaped pattern. Variance attains a maximum at $p = 0.5$. Due to the fact that the level of reward was kept constant across all rewarded trials, expected reward and risk (variance) upon display of card 1 vary only as a function of the probability of winning.

³ Please refer to Figure 3.3 for details on the subcortical dopaminergic structures of the human brain.

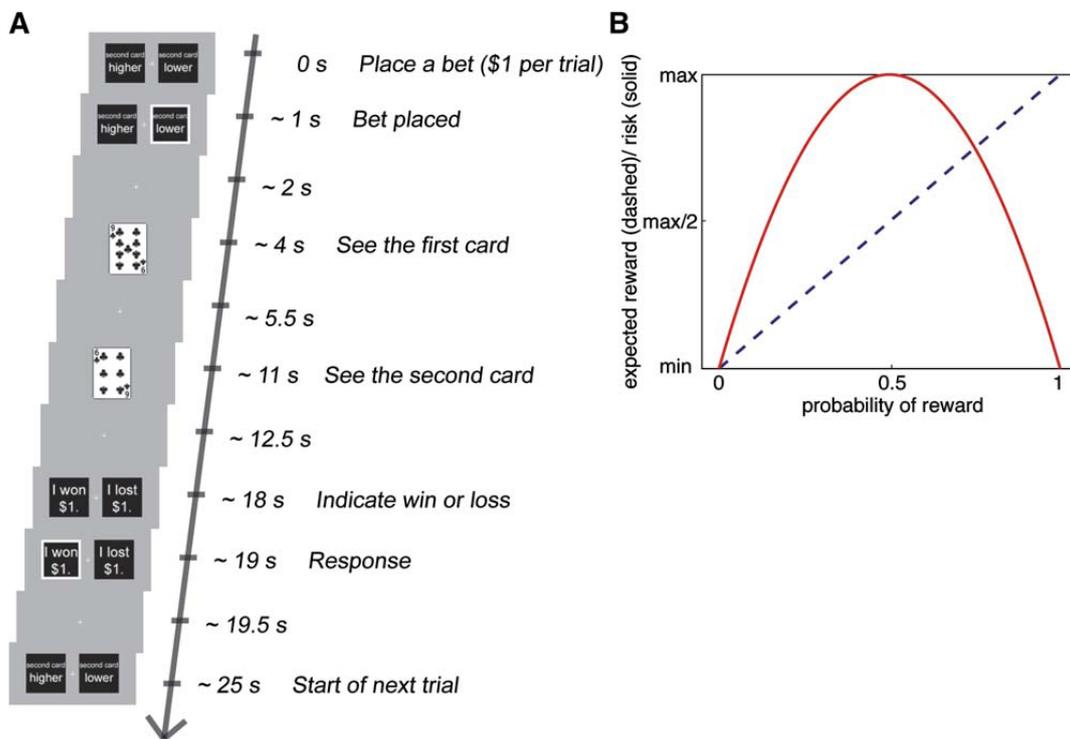


Figure 4.2
Experimental Procedure.

(A) Timeline of the Gambling Task for a Single Trial.

Screenshots that were seen by the subjects at each stage of a trial, are displayed to the left. 19 subjects (10 male, 9 female; aged 18-30, mean age 21.4 years) performed the gambling task. Subjects started out each session with the provision of an initial endowment of \$25. Subjects played three sessions of 30 trials each, with their final payoff being determined by the selection of one of the three sessions at random.

(B) Expected Reward and Risk Profile of the Gambling Task.

The horizontal axis depicts the probability of reward p ranging from $p = 0$ to $p = 1$. On the vertical axis, expected reward is represented by the dashed line (in dark blue) and risk is represented by the solid line (in red). Expected reward is minimal at $p = 0$ and maximal at $p = 1$. Risk attains minimums at the extremes $p = 0$ and $p = 1$, peaking at $p = 0.5$.

Source: [Preuschoff, Bossaerts, and Quartz \(2006a\)](#).

[Preuschoff et al. \(2006a\)](#) emphasize that their focus is on the time interval between display of card 1 and card 2, being referred to as the *anticipatory period*. In that vein, their aim is to find regions of interest whose activity is modulated by expected reward and risk (reward variance), by decomposing the anticipatory period into (i) a response at the initial subperiod (i.e., at the onset of card 1), followed by (ii) a response at the subsequent subperiod (i.e., until the onset of card 2). In accordance with the previous findings of [Fiorillo et al. \(2003\)](#) and [Tobler et al. \(2005\)](#), the duration of the initial response (i) was set at 1 s and the duration of the subsequent response (ii) was set at 6 s.

4.1.1.2 Results from the Approach by Preuschoff, Bossaerts and Quartz (2006)

Figure 4.3 reveals anticipatory period activation in subcortical dopaminoceptive regions correlating with expected reward. Figure 4.3A displays two cross-sections of the human brain through the (ventral) *striatum* (top, in coronal format, and bottom, in axial format), where immediate neural responses (i.e., within 1 second of display of the first card) related to expected reward were detected. The coronal cross-section through the (ventral) striatum depicts the *nucleus accumbens* (circled) and the axial cross-section depicts the *putamen* and the *globus pallidus* (both are circled).⁴ In Figure 4.3B activation in striatal areas (ventral striatum and putamen) is shown to increase linearly in reward probability.

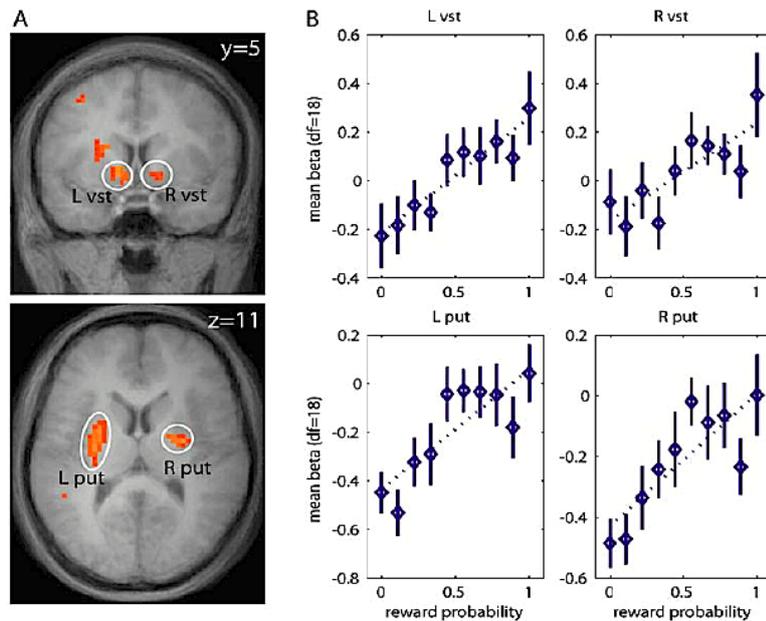


Figure 4.3

Immediate Encoding of Expected Reward in Dopaminoceptive Structures.

(A) Neural Responses Related to Expected Reward.

Regions showing activation within 1 s of display of the first card (in orange), including bilateral ventral striatum (L vst, R vst; displayed in coronal format) and putamen (L put, R put; displayed in axial format).

(B) Mean Activations Stratified by Level of Reward Probability.

Activation increases linearly in reward probability. Betas are slope coefficients for dummy variables that are set equal to one for a 1 s period after cue presentation (i.e., presentation of the first card). Vertical bars indicate 95% confidence intervals (df=degrees of freedom) and the dashed lines indicate the best linear fit.

Source: [Preuschoff, Bossaerts, and Quartz \(2006a\)](#).

⁴ The minor activation seen in the coronal cross-section displays the anterior cingulate cortex (upper left corner in Figure 4.3A).

4.2 Neural Representation of Risk

Unambiguous correlation between risk and activation in human and nonhuman *cortical* regions as (the anterior) insula, prefrontal cortex (i.e., frontoparietal cortex) and anterior cingulate cortex is highlighted in neuroscientific studies (Critchley et al., 2001; Paulus et al., 2001, 2003; McCoy et al., 2003; Kuhnen and Knutson, 2005; Huettel et al., 2006; Paulus and Frank, 2006). Furthermore, activity in human *subcortical* dopaminergic structures such as (the dorsal and ventral) striatum (e.g. Hsu et al., 2005; Dreher et al., 2006; Grinband et al., 2006; Knutson et al., 2008b) and in the nonhuman primate brain (e.g. Lauwereyns et al., 2002 and Takikawa et al., 2002) was found to correlate with risk.

As elucidated in the second chapter of this thesis, Expected Utility Theory posits that risk sensitivity is ascertained by the curvature of the utility function. Studies that observe neuronal activity in terms of the expected utility of an option (Knutson et al., 2005 and Yacubian et al., 2006, 2007) identify neurocorrelates of probabilities and of utilities assigned to outcomes principally in the medial prefrontal cortex and the nucleus accumbens.

Admittedly, within the framework of financial decision theory, in the mean-variance concept, risk aversion is the consequence of the penalty imposed on risk. This mathematical model of decision making under uncertainty postulates a separate assessment of expected value and variance (most notably, Tobin, 1958; Levy and Markowitz, 1979 and Markowitz, 1991). Specifically, Sharpe (1964), Lintner (1965), and Mossin (1966) suggest that expected returns on risky securities should increase not as a function of their own risk, but only to the extent that they contribute to the risk of the securities market as a whole (Capital Asset Pricing Model, CAPM). Pivotaly, the notion of prices of options (to purchase or sell securities) increasing as a function of risk (variance) was pioneered by Black and Scholes (1973) marking the cornerstone of modern option valuation theory. Thus, studies in support of the mean-variance approach (McClure et al., 2003; Paulus et al., 2003; O'Doherty et al., 2004; Huettel et al., 2005 and Rolls et al., 2008) correlate activation with expected value and variance in striatal loci and insula, respectively. Taken together, the observation of neural correlates of value and risk in the ventral striatum and anterior cingulate (Christopoulos et al., 2009) further seems to corroborate the validity of the mean-variance analysis in neurally determining choice under uncertainty.

To complicate matters further, the striatum and the cingulate gyrus are found to encode a nonlinear probability term (Berns et al., 2008 and Hsu et al., 2009) in a manner predicted by Prospect Theory (for a comprehensive comparison between mean-variance and Prospect Theory see, Boorman and Sallet, 2009).

4.2.1 Results from the Approach by Preuschoff, Bossaerts and Quartz (2006)

Figures 4.4A to 4.4C show three cross-sections of the human brain, namely through the (ventral) *striatum* in (A) (in coronal format), through the brainstem (*midbrain* is located between the forebrain and the brainstem) in (B), and through the *thalamus* exhibiting the *thalamic nuclei* and the (bilateral) *insula* in (C) (both are displayed in axial format). In each of these regions delayed neural responses (i.e., after 1 second of display of the first card and until display of the second card) related to risk were registered. The responses in all regions increase towards medium reward probabilities, with a maximum at $p = 0.5$, and decrease towards low and high reward probabilities (as in 4.4D).

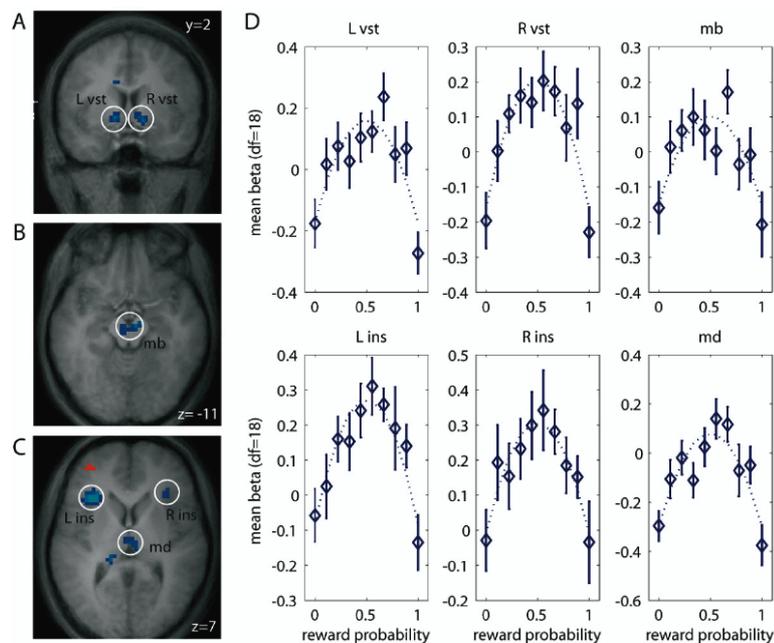


Figure 4.4
Delayed Encoding of Risk in Dopaminergic Structures.

(A to C) Neural Responses Related to Expected Risk.

Regions showing activation after 1 s of display of the first card and until display of the second card (in blue), including bilateral ventral striatum (L vst, R vst; displayed in coronal format in (A)) extending into the subthalamic nucleus, midbrain (mb; displayed in axial format in (B)), mediodorsal thalamic nucleus and bilateral insula (md; L ins, R ins; displayed in axial format in (C)).

(D) Mean Activations Stratified by Level of Reward Probability.

Activation changes quadratically with reward probability. Betas are slope coefficients for dummy variables that are set equal to one for a period starting 1 s after cue presentation (i.e., presentation of the first card) and running until presentation of the second card. Vertical bars indicate 95% confidence intervals (df=degrees of freedom) and the dashed lines indicate the best quadratic fit.

Source: [Preuschoff, Bossaerts, and Quartz \(2006a\)](#).

4.2.2 Results from the Approach by Preuschoff, Quartz and Bossaerts (2008)

The notion of human subjects adjusting their learning rate to changing risk implies tracking of risk one way or another (Behrens et al., 2007 and Preuschoff and Bossaerts, 2007). Although in the past researchers have already documented activation in insula in the context of uncertainty, they did so with respect to risk-related characteristics of gambles and not with an emphasis on the precise neural responses to risk prediction errors, nor on the differentiation of their occurrence from that of the risk prediction signals (see, for example, Elliott et al., 2000; Critchley et al., 2001; Ernst et al., 2002; Hsu et al., 2005; Huettel et al., 2006 and Grinband et al., 2006). With respect to evidence for reward processing in the dopaminergic system, which encodes both reward prediction and reward prediction errors, Preuschoff et al. (2008) investigate activation in the human insula to correlate with risk prediction and risk prediction errors.⁵

Preuschoff et al. (2008) employ the same experimental paradigm as in their seminal article two years prior that can be reflected on in Figure 4.2A (Preuschoff et al., 2006a). Within each trial, predictions occur twice: once before the first card, and again before the second card. This means that both predictions generate corresponding prediction errors, namely that the risk prediction before the first card is followed by a risk prediction error when the first card is displayed, and subsequently the risk prediction before the second card is revealed, is followed by a risk prediction error when the second card is displayed.

Figure 4.5A depicts that activity in bilateral anterior *insula* correlates positively with risk prediction errors as of display of both cards 1 and 2. Furthermore, as shown in subfigure 4.5B, increasing activation levels in right anterior insula reflect a linearly increasing relationship with the level of risk prediction error upon display of both cards 1 (in red) and 2 (in blue). Most notably, Preuschoff et al. (2008) demonstrate that the relative magnitudes of the activations after the first and the second card are commensurate with the relative magnitudes of the risk prediction errors. Trials where there is no risk after seeing the first card and, hence, there is no risk prediction error at the second card, constitute an outlier (both attributes are clearly visible in Figure 4.5B). These results are in consistence with novel findings by d’Acromont et al. (2009), observing risk prediction errors in insula and importantly, in other cortical structures such as the *inferior frontal gyrus*.

⁵ Mathematically, the risk prediction error is the difference between the squared reward prediction error and reward variance. For details on autoregressive conditional heteroscedasticity (ARCH) processes please refer to Engle (2002).

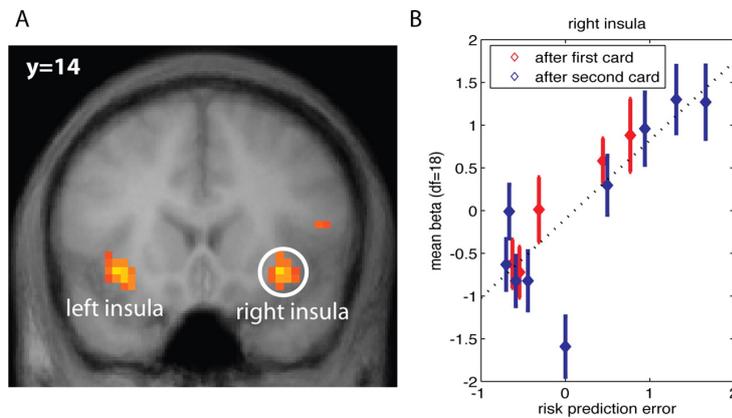


Figure 4.5

Encoding of Risk Prediction Error in Cortical Areas.

(A) Neural Responses Related to Risk Prediction Errors.

Region showing activation as of display of the first and of the second card (in orange) is identified as the bilateral anterior insula (left insula, right insula appears circled; displayed in coronal format).

(B) Mean Activation Stratified by Level of Risk Prediction Error.

Activation in right anterior insula increases linearly with the level of risk prediction error upon display of the first card (in red) and of the second card (in blue). The average activation at zero risk prediction error constitutes an outlier, referring to trials when no risk remained after the first card. Vertical bars indicate 95% confidence intervals (df=degrees of freedom) and the dashed line indicates the best linear fit.

Source: [Preuschoff, Quartz, and Bossaerts \(2008\)](#).

[Preuschoff et al.'s \(2008\)](#) findings indicate activation in bilateral anterior *insula* correlating with both risk prediction and risk prediction error. This spatial separation is highlighted in [Figure 4.6](#) in three cross-sections of the human brain ([top panel](#)) through the insular cortex, whereby the risk prediction error signals (in orange) are detected in an area slightly more inferior and posterior than risk prediction signals (in blue).

Corroborating evidence not only on the spatial but also on the temporal differentiation of the signals reflecting risk prediction and risk prediction error in bilateral anterior insula comes from the paper by [Preuschoff et al. \(2008\)](#). The authors allegorize the two signals of risk prediction and risk prediction error as of showing a late onset followed by a fast onset signal at the time of the outcome, respectively. [Figure 4.6 \(bottom panel\)](#) depicts the time courses for activation in right anterior insula at the first card. Risk prediction between placing the bet and seeing the first card is constant across all trials and subjects. However, the risk prediction error at the first card emerges instantaneously after the first card appears (in the bottom right panel, displaying an U-shaped pattern). In contrast, activation correlating with the risk prediction preceding the second card emerges with an approximate delay of five seconds after the first card (in the bottom left panel, displaying an inversely U-shaped pattern).

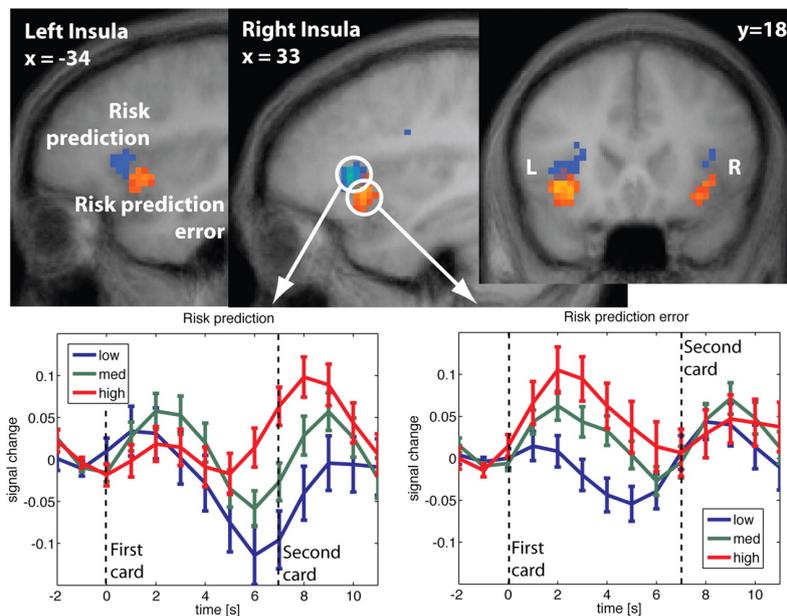


Figure 4.6

Encoding of Risk Prediction and of Risk Prediction Error in Cortical Areas.

(Top) Neural Responses Related to Risk Prediction and to Risk Prediction Errors.

Bilateral anterior insula (left insula, right insula) activation correlates with risk prediction (in blue) as well as with risk prediction error (in orange). Risk prediction error signals are reported in an area slightly more inferior and posterior than risk prediction signals. The orange and blue clusters both picture positive correlations in anterior insular cortex.

(Bottom) Temporal Patterns for Representations of Risk Prediction and of Risk Prediction Error.

Averaged adjusted time courses in right insula showing different temporal patterns at the first card. Before the first card is seen, risk prediction is constant across all trials independent of the probability of winning after the first card. The risk prediction error at the first card is a function of the first card and the subject's bet. It is pictured in the time course immediately after the first card is shown (bottom right panel). Before the second card is seen, the risk prediction is pictured in the time course after the first card but only after a short delay (bottom left panel).

Source: [Preuschoff, Quartz, and Bossaerts \(2008\)](#).

This paper by [Preuschoff et al. \(2008\)](#) has a profound impact on the understanding of the exact role of the anterior insula in the processing of risk. As discussed above, on the one hand, the neural response to risk prediction is delayed after the risk cue (first card) and is remaining active at the time of the outcome, suggesting that risk prediction may function as an anticipatory signal before risk is realized. On the other hand, the authors observe that the neural response to risk prediction errors is promptly present after risk is realized and is remaining active only for a brief period, suggesting that risk prediction error may effectuate learning. As I will elaborate on future challenges of Neurofinance in the concluding section of my thesis, I will at this point merely suggest to put an emphasis on the clinical implications of pathological inconsistencies, eventually considering psychiatric disorders in risk prediction learning.

4.3 Neural Representation of Expected Utility

Taken together, the perspective that evolves from the compelling contributions by Preuschoff et al. (2006a) and Preuschoff et al. (2008) argues for the human brain to value risky gambles by evaluating their expected reward and risk by means of spatio-temporal separation (see Figures 4.3, 4.4 and Figure 4.6). Before we further advance our understanding of the neural coding of basic decision parameters, a next step is to consider the presence of total valuation signals functioning as the common denominator between the separate evaluation signals, and then put the findings into the larger perspective (for a study in a similar vein, see Bruguier et al., 2008).

In this vein, Tobler et al. (2007b) take cognizance of valuation signals in the context of gambles in *prefrontal cortex*. Their study points to a distinct role of the lateral part of the prefrontal cortex, because it appears to not solely be separately sensitive to the two main components of expected utility, namely expected reward and risk, but also sensitive to subjective attitudes towards risk (see Tobler et al. 2009 as a fruitful extension of Tobler et al. 2007b).

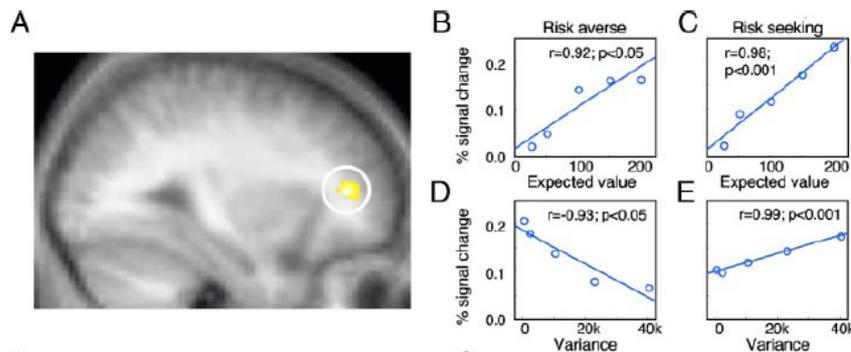


Figure 4.7

Encoding of Expected Utility in Cortical Areas.

(A) Neural Responses Related to Expected Utility.

Lateral orbitofrontal cortex (in yellow, circled) activation correlates with expected utility of a gamble.

(B to E) Activation in the Orbitofrontal Cortex as a Function of Expected Reward and Reward Variance Stratified by Individual Risk Attitude.

Activation increases in expected reward for both risk averse (in (B)) and risk seeking subjects (in (C)). Activation decreases with risk of the gamble (measured as reward variance) for risk averse subjects in (D) while it increases with risk for risk seeking subjects in (E).

Source: Tobler, O'Doherty, Dolan, and Schultz (2007b).

Figure 4.7A locates the common neural signals correlating with expected utility of a gamble in *lateral orbitofrontal cortex* (activation is located above the left orbita in the bottom right corner and is circled in yellow for better visualization). Integrated expected utility signals show increased activation in lateral orbitofrontal cortex in ex-

pected reward irrespective of individuals' risk attitude (Figure 4.7B and C). However, activations in the same voxels decrease with risk (variance) in risk-averse subjects (Figure 4.7D) but increase with risk in risk seekers (Figure 4.7E).

4.4 Neural Representation of Ambiguity

The results in this fourth chapter of the thesis suggest that distinct risk signals for monetary rewards with different time courses occur in separate human brain structures, thus fulfilling the requirements for the mean variance concept in financial decision theory. Upon further examination of the neural processing of key decision variables and the brain mechanisms underlying the computation of choices under uncertainty, the evidence exemplifies that in some choices, such as in weather forecasts for distant tourist destinations or betting in games whose rules are not perspicuous, probabilities are based on meager or conflicting evidence, where vital information is absent (Schultz et al., 2008). At the other extreme, such as in gambling on a roulette wheel, probability can be confidently judged from relative frequencies, event histories, or an accepted theory (Hsu et al., 2005). These two forms of uncertain events are called ambiguous and risky, respectively. Ambiguity refers to situations of uncertainty in which the probabilities of outcome are incompletely known, as opposed to risk where probabilities are known (Ellsberg, 1961).⁶

The impetus of the standard decision theory, however, rests on the notion that the preclusion of agents from acting differently in the face of pure risk and ambiguity emerges from the availability of a constant level of information about probabilities to the decision maker. Nevertheless, in the literature various empirical papers can be found that find evidence for individuals' aversion to ambiguity (see, for example, Camerer and Weber, 1992). The connection of the revelation of ambiguity aversion in choices with the identification of neural ambiguity signals is illuminating in light of findings of *amygdala* and of *striatal activation* in Hsu et al. (2005). By contrasting choices between certain and uncertain monetary outcomes involving three experimental treatments in which the uncertain option dissociates between ambiguity and risk based on different amounts of information, the authors observe two forms of neural distinction between ambiguity and risk.

On the one hand, Hsu et al.'s (2005) findings suggest graded coding of uncertainty in amygdala and in parts of frontocortical circuits (e.g., dorsomedial prefrontal cortex), which may reflect a unified neural treatment of ambiguity (i.e., unknown or

⁶ The primary model existing that accounts for decisions under ambiguity is the maxmin expected utility model by Gilboa and Schmeidler (1989) and subsequently, the " α -maxmin" expected utility model by Ghirardato et al. (2004).

partially known probabilities, higher signal) and risk (i.e., fully known probabilities, lower signal). Figures 4.8A and 4.8B show two cross-sections of the human brain, namely through the (bilateral) *amygdala* in (A), and through the (bilateral) *orbitofrontal cortex* in (B) (both are displayed in coronal format) – with these brain structures exhibiting stronger responses during the ambiguous condition relative to the risk condition. Importantly, as depicted in Figure 4.8C, the hemodynamic responses of the respective (sub-)cortical regions are synched to the onset of the stimulus, with the activations in bilateral amygdala (top panel) and in the orbitofrontal cortex (bottom panel) occurring at the beginning of the trial, and peaking before the decision epoch.

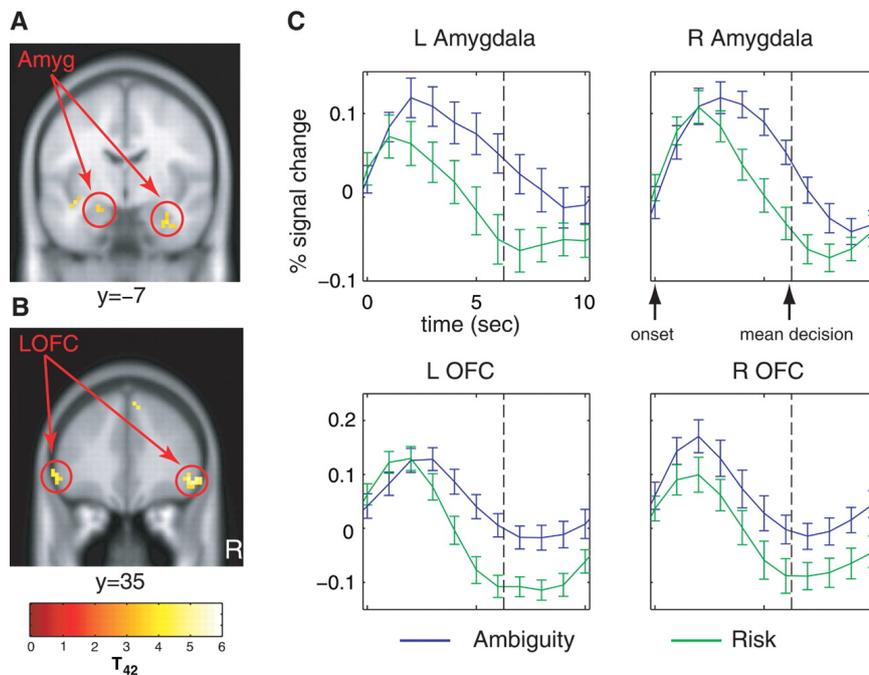


Figure 4.8
Encoding of Ambiguity in Subcortical and Cortical Areas.
(A and B) Neural Responses Related to Ambiguity.

Bilateral amygdala (Amyg; left amygdala, right amygdala extending into the parahippocampal gyrus, in yellow, circled in red; displayed in coronal format in (A)) and bilateral orbitofrontal cortex (LOFC; left orbitofrontal cortex, right orbitofrontal cortex, in yellow, circled in red; displayed in coronal format in (B)) reveal greater activation in response to stimuli-predicting ambiguous outcomes than in response to those outcomes involving pure risk.

(C) Temporal Patterns for Representations of Ambiguity.

Mean time courses of bilateral amygdala (top panel) and of bilateral orbitofrontal cortex (bottom panel) responses to onset of stimuli-predicting ambiguous or risky outcomes (dashed vertical lines are mean decision times; blue lines indicate average activation in trials with ambiguity; green lines indicate average activation in trials with pure risk; error bars are standard error of the mean, SEM; $n = 16$ participants).

Source: [Hsu, Bhatt, Adolphs, Tranel, and Camerer \(2005\)](#).

On the other hand, [Hsu et al. \(2005\)](#) were able to detect risk signals in dopaminergic areas such as dorsomedial *striatum* (caudate nucleus), *precuneus* and *premotor cortex* exhibiting higher hemodynamic responses during risky compared with ambiguous gambles. Furthermore, the striatal activations correlated positively with the expected values of subjects' actual choices, while inducing slower time courses with significantly delayed peaks in comparison with the ambiguity signals in amygdala and orbitofrontal cortex. Thus, the present results point to the presence of two interacting neural circuits – a “vigilance”/evaluation circuit in the amygdala and orbitofrontal cortex responding instantly to the stimuli and grading uncertainty, and a reward anticipation circuit in the striatum that appears further downstream.

Taken together, striatum, parietal cortex, and parts of frontal cortex encode risk, versus amygdala and more eminent frontocortical areas are uniquely demonstrated to encode ambiguity distinctively, consistent with a scheme of dual dissociation (in the context of learning under ambiguity, see [Payzan Le Nestour, 2009](#)). In effect, corroborating the results from subsequent empirical research by [Huettel et al. \(2006\)](#), [Preuschoff et al. \(2006a\)](#) and very recently by [Asparouhova et al. \(2009\)](#) and [Bossaerts et al. \(2010\)](#) it is of severe relevance to point out the fact that a general neural circuit seemingly evaluates qualitatively different degrees of uncertainty, which appears to be incompatible with simplistic theories of decision making ([Hsu et al., 2005](#)).

4.5 Neural Representation of Emotions

The large body of research in neuroscience and psychology provides a wealth of information about emotions as a major factor in the interaction between environmental conditions and human decision processes. The Somatic Marker Hypothesis ([Bechara and Damasio, 2005](#)) proposes that the process of decision making is influenced by marker signals arising in bioregulatory processes, especially those underlying emotions. A plethora of research highlights that in the absence of a somatic marker, patients with focal lesions in specific components of neural circuitries that have been shown to be critical for the processing of emotions take risks even when they result in catastrophic losses.

Specifically, [Bechara et al. \(1997, 1999\)](#) find that impairment of the (*ventromedial prefrontal cortex*, of *insula*, and of *amygdala*) preclude the ability to use somatic (i.e., emotional) signals that are necessary for advantageous decision making. However, individuals deprived of normal emotional reactions may, under certain circumstances, behave more efficiently than those not deprived of such reactions (see, for example, [Damasio, 1994](#) and [Shiv et al., 2005](#)).

There is ample evidence of the necessity of emotional experience for reasoned choice (Feng and Seasholes, 2005). Recent studies suggest an important link between rationality in decision making and emotion, implying that the two notions are not antithetical but, in fact, complimentary. In this strand of literature, most authors emphasize the specific interaction between automatic emotional responses such as fear and greed (i.e., responses mediated by the amygdala) which seem to trump “higher-level” or more controlled responses (i.e., responses mediated by the prefrontal cortex).

For example, Lo and Repin (2002) measure the real-time psychophysiological responses of ten securities traders during live trading sessions and observe that traders’ physiological reactions⁷ correlate with periods of market volatility. The authors also hypothesize that less experienced traders exhibit a relevantly higher number of physiological responses (i.e., in the number of skin conductance responses, blood volume pulse amplitude⁸, and in the number of body temperature increases) to market volatility than traders with high experience. In this respect, their evidence provides further corroboration of the somatic mediation of changes in cardiovascular variables and in electrodermal activity. Or to put it in their words, “Contrary to the common belief that emotions have no place in rational financial decision-making processes, physiological variables associated with the autonomic nervous system exhibit significant changes during market events even for highly experienced professional traders.” (ibid, p. 332). In a study in the same vein, Lo et al. (2005) extend the findings of Lo and Repin (2002) by showing that extreme emotional responses are counterproductive from the perspective of trading performance.

From the preceding discussion, it becomes obvious that emotions and reasoned choice are interrelated. This means that studying the role of the endocrine system in financial risk taking could provide valuable insights into the neural basis for rational choice. This is exactly the novel path that the study by Coates and Herbert (2008) takes and contributes to the literature. By taking saliva samples before and after the bulk of the day’s trading from 17 male traders for 8 consecutive business days on a trading floor in London, the authors analyze the levels of two steroids: testos-

⁷ At this point, I would like to emphasize that the vast majority of the studies of the neurobiological basis of how emotions influence behavior was until Lo and Repin’s (2002) study confined to methods measuring epiphenomenal physiological parameters such as the skin conductance response.

⁸ The two cardiovascular variables measured in the study by Lo and Repin (2002) are blood volume pulse and heart rate. The latter variable refers to the frequency of the contractions of the heart muscle or *myocardium*, initiated by the *pacemaker cells*. Heart rate deceleration frequently results in an increase in blood volume pulse, which is the rate of flow of blood through a particular blood vessel and alludes to both blood pressure and the diameter of the vessel.

terone and cortisol. Coates and Herbert (2008) find a significant relationship between testosterone and financial return and between cortisol and financial uncertainty, the latter being measured by the variance of economic return and the expected variance of the market. These results point to an intriguing possibility – if the acutely elevated steroids observed in the study were to persist or eventually increase as volatility rises, they might have cognitive and behavioral consequences, especially by shifting risk preferences and possibly altering a trader’s ability to make optimal decisions.

Consistent with the view that the insula is an arbitrative relay of the information about bodily states (i.e., emotions) to the cortex, Critchley et al. (2004) find that activation of the right anterior insula is uniquely correlated with subjective perception of heartbeat timing, which is a classic test of interoceptive awareness. These results corroborate the hypothesis of Kuhnen and Knutson (2005) that anterior insula activation precedes risk averse choices (such as buying insurance), while nucleus accumbens activation precedes risk seeking (such as gambling at a casino) choices (for a conceptual study on consumers’ purchasing decisions see, Knutson et al., 2007).

Inquiring whether the experience and anticipation of regret as a high-level emotion has an impact on the process of choice, Coricelli et al. (2005) confirm the role of the *orbitofrontal cortex* which seemingly integrates cognitive and emotional components of decision making. Specifically, the activity of the regret circuitry is found in situations where the experimental subjects know, prior to making a decision, that they will get information about the outcomes of the rejected alternatives (i.e., complete feedback trials). The authors also report an increase of the proportion of regret-avoiding choices over time with the cumulative effect of the experience of regret.

As demonstrated in the second chapter of this thesis, the notable susceptibility of human choices to the manner in which available options are presented, can be explained by the “framing effect”, which is a key aspect of Prospect Theory (Kahneman and Tversky, 1979 and Tversky and Kahneman, 1981). In this vein, De Martino et al. (2006) investigate the neurobiological basis of the framing effect and report increased activation in the *amygdala* associated with subjects’ tendency to be risk seeking for gambles involving losses but risk averse for gambles involving gains (as displayed in Figure 4.9 in the left panel). Importantly, when subjects’ choices ran counter to their general behavioral tendency, enhanced activation in the *anterior cingulate cortex* (ACC) was identified (as depicted in Figure 4.9 in the right panel).



Figure 4.9

Encoding of the Framing Effect in Subcortical and Cortical Areas.

(Left) Bilateral amygdala (Amyg) activation (left amygdala, right amygdala, in yellow, circled) reflects subjects' behavioral tendency to choose in accordance with the framing effect.

(Right) Anterior cingulate cortex (ACC) activation (in yellow, circled) reflects the decision to choose counter to subjects' general behavioral tendency.

Source: [De Martino, Kumaran, Seymour, and Dolan \(2006\)](#).

[De Martino et al.'s \(2006\)](#) findings indicate that the framing effect has a pervasive impact on amygdala activity, supporting an emerging role for the amygdala in mediating decision biases. It is noteworthy that there appears to be an opponency between the anterior cingulate cortex⁹ and the amygdala, with the anterior cingulate cortex being involved in “analytic” response tendencies (i.e., logically reasoned choice underlying slow response timing) and with the amygdala exhibiting more “emotional” responses (i.e., intuitive choice signaling fast response patterns).

Furthermore, *orbital* and *medial prefrontal cortex* activation is shown to predict the substantial intersubject variability in terms of behavioral susceptibility to the framing effect (Figure 4.10A).¹⁰ Specifically, [De Martino et al. \(2006\)](#) calculate a “rationality index” (i.e., level of sensitivity to the framing effect) for each subject from the difference between the proportion of trials in which a given subject chose the gamble option in the Loss frame, as compared to the Gain frame. This value is then linearly transformed into an index, ranging from 0 (least rational) to 1 (most rational).

These results reveal that across individuals, right orbitofrontal cortex activation decreases with subjects' tendency to become risk seeking for monetary losses (Figure 4.10B), i.e., more “rational” individuals exhibit greater activation in *orbital* and

⁹ The region around the paracingulate sulcus in the *medial prefrontal cortex* contains a large concentration of spindle cells – large projection neurons shaped like spindles, which are almost unique to human brains ([Allman et al., 2001](#)).

¹⁰ For a discussion on the involvement of the *paracingulate cortex* in the encoding of an “influence update” see, [Hampton et al. \(2008\)](#).

medial prefrontal cortex, having a more refined representation of their own emotional biases. This is a conceptual advance, because *amygdala* activation seems to reflect these emotional biases imposed by some kind of “default action” deeply ingrained in organisms trying to maximize the probability of survival in the face of adverse events.¹¹

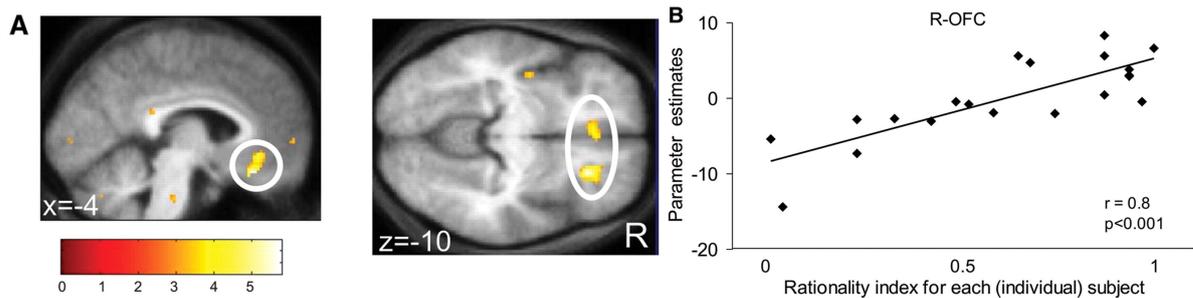


Figure 4.10

Encoding of the Framing Effect in Cortical Areas.

(A) Neural Responses Related to the Framing Effect.

Interaction contrast in ventromedial prefrontal cortex activation (in yellow, circled in left panel), and in orbital and medial prefrontal cortex and in right orbitofrontal cortex (R-OFC) activation (in yellow, circled in right panel) significantly correlates with subjects’ rationality index (i.e., between-subjects measure of susceptibility to the framing manipulation).

(B) Plot of the Correlation of Parameter Estimates for Right Orbitofrontal Cortex with the Rationality Index for Each Subject.

Interaction contrast increases in right orbitofrontal cortex (R-OFC) with the rationality index for each subject.

Source: [De Martino, Kumaran, Seymour, and Dolan \(2006\)](#).

In contrast, the *orbitofrontal cortex* seems to evaluate and integrate emotional and cognitive information – more generally, it is engaged in “high-level” cognitive functions, overriding the initial emotional reactions or “default actions” as for example when such choices might lead to suboptimal decisions.¹²

Contrary to previous findings (see, for example, [Sanfey et al., 2003](#)), the necessity of amygdala and of anterior insula activation in the context of loss aversion is not corroborated. In a remarkable task contrasting neural loss aversion and behavioral loss aversion, [Tom et al. \(2007\)](#) link *ventral* striatal and *ventromedial* prefrontal cortical activation to loss aversion.

¹¹ In this vein, the short commentary by [Kahneman and Frederick \(2007\)](#) sheds light on the psychological propositions of [De Martino et al.’s \(2006\)](#) study.

¹² Similarly to the arguments on differences in prefrontal cortex and amygdala interactions in the course of genetic variation, see [Roiser et al. \(2009\)](#).

CHAPTER 5

Conclusion and Future Directions

“[I]f you feel you are on the cusp of disaster, you will tend to want to take more risk ... Pilots are trained (very often actually) to ignore their own cognitive input when they are for instance flying through the clouds, because the brain is not made for flying through the clouds. They actually need instruments and they know beforehand, that they cannot possibly rely on their own senses.”

Peter Bossaerts

Interview with [Private Banking Innovation](#) (2008)

Uncertainty is endemic in human decision making, peculiarly, in contemplation of financial risks. Thus, characterized retrospectively through the lens of evolutionary biology, financial risks are a novel phenomenon. This thesis tries to advocate consideration of the neurophysiological antecedents of risk perception and eventually of the neural correlates of underlying choice parameters by cataloguing canonical findings in the aspiring frontier of neurofinance.

The second chapter focuses on the basic tenets of neurofinance by introducing and contrasting two models attempting to characterize choice, namely expected utility theory with prospect theory. It finds tentative support for the latter theory in the sense that the preferences of people are not entirely reflected in their choices, to wit, humans are prone to psychological biases and decision heuristics.

The third chapter sheds light on the neuroanatomical and neurochemical bases of reward and decision making processes which have hitherto been given scant attention in the literature. Importantly, this chapter provides *prima facie* evidence that the prefrontal cortical areas which are known to serve as the substrate for higher cognitive functions, are inherently constrained through phylogenetic differentiation. The second part of this chapter reveals that the neurotransmitter dopamine is an integral component of reinforcement learning, belief formation, and choice within the human and nonhuman brain.

The last chapter of this thesis raises the seminal question of how the human cerebrum computes choices. Eminently, this chapter integrates an extensive debate of recent neuroeconomic work on the basis of the expected utility approach and on the basis of the mean-variance approach to educating choice under uncertainty. In our analysis of neurobiological studies of cortical and subcortical activation we coherently confirm the presence of valuation signals in the *orbitofrontal cortex*. However, we cannot corroborate the neural contemplation of either model in the computation of values. Pivotaly, it is not a foregone conclusion that the models are neurally represented mutually exclusive of one another.

In a miscellaneous vein, the body of the fourth chapter of this thesis builds on prior findings of in vivo lesion localization studies. It is particularly striking that in a prolonged preponderance of probands enrolled in clinical trials, the *cingulate cortex* and the *amygdaloid nuclei* – which are prominent parts of the “limbic system” – occupy an integral role in reasoned decision making. In a nutshell, ample research has provided decisive evidence that adaptation – fostered by the impact of emotions – is a rigorous feature of neural activity. Our main insight is that affect can influence financial decisions without coercion, therefore, emotions (e.g., anxiety and excitement) and rationality are not to be placed in mutual opposition.

Much has happened in the conversation between economics and neuroscience over the past five years. Professor Peter Bossaerts and his colleagues have been instrumental in the establishment of neurofinance to come to the conclusion that financial decision making at its coarsest level can be understood, not as a matter of implementing existing preferences, but rather as the resolution of interaction between multiple comprehensively complex neural systems. In light of this fact, it is a welcome challenge for me to describe current research perspectives in but a few sentences.

[Kuhnen and Chiao \(2009\)](#) and [Cesarini et al. \(2009\)](#) have made considerable headway in the endeavor of addressing the genetic determinants of financial risk taking. [Kuhnen and Knutson \(2009\)](#) confirm that emotions modify risk preferences, as well as the learning process itself. This is akin to a quest for adding a greater impetus on the effect of aging and financial choice. Preliminary evidence by [Samanez-Larkin et al. \(2010\)](#) suggests that aging may disrupt rational financial choice. To conclude, human (sub-)cortical networks may vastly be “maladaptive” for today’s financial markets (for example, see, [Biais et al., 2010](#) and [Bruguier et al., 2010](#)).

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Deutscher Abstract

Diese Diplomarbeit beschäftigt sich mit den neuronalen Korrelaten von Investorenentscheidungen (“Neurofinance”). Die prägnante Erkenntnis, daß finanzielle Entscheidungen mit Unsicherheiten verknüpft sind, dient als Ausgangsthese des ersten Kapitels dieser Arbeit. Es enthält zunächst eine Vorstellung und anschließend eine synoptische Gegenüberstellung der Erwartungsnutzentheorie und der Prospect Theorie. Weiters werden systematische Verzerrungen im menschlichen Entscheidungsverhalten ausführlich betrachtet.

Das zweite Kapitel behandelt die funktionelle Anatomie des Cerebrum, der Schwerpunkt der Untersuchung liegt aber in der Darstellung der dopaminergen Innervation des Mittelhirns. Essentiell ist nicht zuletzt aufgrund der extremen Komplexität (sub-)kortikaler Strukturen die Abgrenzung des *frontalen Assoziationskortex* gegenüber anderen neuronalen Strukturen. Insbesondere gilt festzuhalten, daß der dorsale und laterale frontale Assoziationskortex – dem strategische Vorgehensweisen zugeschrieben werden – zu den phylogenetisch jüngsten Hirnregionen zählen.

Das letzte Kapitel dieser Arbeit beschäftigt sich mit der Wahrnehmung von Risiken und Belohnungen im Kontext finanzieller Entscheidungen. Es werden jüngere Studien mit funktionellen bildgebenden Verfahren vorgestellt, die einerseits auf der Erwartungsnutzentheorie, und andererseits auf dem Erwartungswert-Varianz-Prinzip aufbauend, sich mit der Lokalisierung von neuronalen Korrelaten dieser Modelle befassen. Die Forschungsergebnisse bestätigen nicht exklusiv das Vorhandensein der spatio-temporalen Separation in der Wahrnehmung von Risiken und Belohnungen, vielmehr zeigen sie, daß es sich um eine entweder/oder Abbildung handelt. Im zweiten Teil des dritten Kapitels wird, basierend auf neuropsychologischen Untersuchungen von Patienten mit selektiven bilateralen Läsionen die eine differenzierte Erregung der *Amygdala* und des *orbitofrontalen Kortex* feststellen, gezeigt, daß emotionale Variablen bei der rationalen Entscheidungsfindung unverzichtbar sind.

Evolutionsbiologisch determiniert ist, daß die subkortikale Amygdala – die eine entscheidende Rolle bei Gedächtnisprozessen mit affektiver Konnotation spielt – eine unmittelbare, präkognitive Einschätzung eines Stimulus auf seine emotionale Relevanz vornimmt, um zur Aktivierung instinktiver Reaktionsprogramme beizutragen. Daher kann abschließend festgestellt werden, daß obwohl rationale Entscheidungen ohne Affekt-Unterstützung nicht adäquat darzustellen sind, die amygdaloide Aktivierung unter Umständen einen divergenten Ansatz der Maladaption in Bezug auf rationale Investorenentscheidungen zu verfolgen scheint.

Curriculum Vitae

Réka Heim wurde am 15. August 1976 in Budapest, Ungarn, als Tochter von Mag. Eva Adamik und D.I. Dr. Lajos Hegyesi geboren. Sie besuchte das Realgymnasium in der Wenzgasse in Wien-Hietzing, und verbrachte währenddessen ein Jahr als Austauschschülerin an der Lambert High School in Montana, USA. Nach Abschluss der Matura studierte sie zunächst Medizin an der Universität Wien und begann anschließend mit dem Studium der Internationalen Betriebswirtschaftslehre ebenfalls an der Universität Wien. Während des Studiums war sie kontinuierlich von 2003-2009 Studienassistentin am Institut für Finanzwirtschaft der Universität Wien bei Herrn Professor Dockner. Ihre Vertiefungen absolvierte sie aus Internationalem Management und aus Public Utility Management. Réka Heim verfasste ihre Diplomarbeit über “The Neural Foundations of Financial Decision Making” unter Betreuung von Professor Engelbert Dockner (Wirtschaftsuniversität Wien).