What Decision Neuroscience Teaches Us About Financial Decision Making

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Abstract
Financial decision making is the outcome of complex neurophysiological processes involving, among others, constant re-evaluation of the statistics of the problem at hand, balancing of the various emotional aspects, and computation of the very value signals that are at the core of modern economic thinking. The evidence suggests that emotions play a crucial supporting role in the mathematical computations needed for reasoned choice, rather than interfering with it, even if emotions (and their mathematical counterparts) may not always be balanced appropriately. Decision neuroscience can be expected in the near future to provide a number of effective tools for improved financial decision making.
1. INTRODUCTION

Finance studies decision making under uncertainty. For a long time, this study has been normative, addressing the question, How should one choose when faced with uncertain outcomes? This has led to the development of utility theory and, more specifically, expected utility theory and mean-variance analysis. The latter has proven to be most helpful when multiple options can be chosen at one time (portfolio analysis).

Normative decision analysis still dominates asset pricing theory, based on the idea that there is a marginal investor (or an aggregate investor) and that somehow she must be doing things right. From experiments, however, we know that this is far from a foregone conclusion. For instance, in situations of ambiguity (some of the outcome probabilities are unknown), the irrational investor may determine prices even if he is clearly not the marginal investor (Bossaerts et al. 2009).

At the individual level, normative analysis has long been known to make invalid predictions. For example, ever since Allais (1953), choices have been consistently found to violate the two foundational axioms of expected utility, namely, the independence axiom and the sure-thing principle. This, together with ample evidence of miscalibrated beliefs (often evident even at the market level) (Bossaerts & Hillion 2001, Michaely et al. 1995, Ritter & Welch 2002), has led to the emergence of behavioral finance.

Behavioral finance also starts from choice, but it rejects the idea that choice reflects maximization of a rational (expected) utility function. Nevertheless, it has one important feature in common with normative finance: Choices still are interpreted “as if” they maximize some utility. Even the choice of utility profile is suggestive of nostalgia toward expected utility; there are underlying states of nature, and utility is obtained as the summation over these states of state probabilities (perhaps weighted) and utilities of state-specific outcomes.

Indeed, prospect theory (Kahneman & Tversky 1979) can be viewed as an attempt to characterize actual human choice (and recently also nonhuman primate choice; Chen et al. 2006) within the constraints of a rule that combines judgment (beliefs) and value (utility) in a multiplicative way. A reference point needed to be introduced, probabilities needed to be biased in specific ways, and the idea of decreasing marginal utility had to be abandoned for the loss domain.

But is it really true that choice is the outcome of a utility-maximization process? Take risk seeking for losses, for instance. What if this is a bias that comes about because of the way decisions are made, and not really the result of increasing marginal (hedonic) utility for outcomes below the reference point? Indeed, as is argued below, one could envision a process theory of decision making based on anticipations (expectancy, fear, etc.) of various emotional reactions to outcomes (elation, regret, envy, etc.), each contributing differentially to the choices that we now interpret in terms of utility maximization.

Ostensibly innocuous consequences follow from practical implementation of the idea that choice under uncertainty reflects maximization of (prospect theory) utility. For example, wealth managers should encourage their clients to buy “structured products” that implement short positions in put options.¹ This is all right if prospect theory reflects what investors want, but not if it merely reveals what people choose.

¹A “put option” rewards the writer (seller of the option) with a fixed payment in good states of the world and penalizes him with varying losses in bad states of the world. This fits well with prospect-theoretic preferences, which are risk averse in the gain domain, but risk seeking in the loss domain.
But how could we know where choice really comes from? It is here that neuroscience comes in. Neuroscience allows us to study the entire process of decision making, from initial perception of a “stimulus” (which conveys new information and/or new investment options), to valuation and motivation, and the very act of choosing.

When looking for inspiration in neuroscience, it is important from the outset to realize that neuroscience is a subfield of biology and, hence, that it uses an overarching principle to understand neurobiological phenomena (analogous to absence of arbitrage or the efficient-markets hypothesis of neoclassical finance), namely, evolutionary fitness. Specifically, the brain is viewed as an organ that is well adapted, through evolutionary pressure, to do things right in its natural environment.

There is ample evidence for this in sensory processing in the brain. For instance, auditory signals are optimally mixed with visual signals to generate accurate guesses of the localization of the source of the signals (Shams et al. 2005). Optimal in such cases indicates accordance with Bayes’s law.

Evidence has been mounting that the same applies to higher cognition. Humans have long had to deal with a changing (nonstationary) environment, and evolutionary neurobiologists (Ash & Gallup 2007) have argued that the astonishing expansion of the modern human brain coincided with an increase in the need for humans to adapt quickly to changing environments. Recent evidence converges on the theory that the cytoarchitecture of cerebral additions is optimized to harness the power of old emotions and new cognition to respond adaptively to changing conditions (Allman et al. 2001). Imaging of these modern brain regions has uncovered signals that indeed track the instability of the environment (Behrens et al. 2007).

When choice under uncertainty is concerned, however, the types of risks that the brain would be adapted to may be very different from risks routinely encountered in the financial sphere. Indeed, whereas many ecologically relevant risks (e.g., temperature changes) can readily be described as Gaussian and predictable, returns generated through organized financial markets are distinctly leptokurtotic and unpredictable. So, it makes sense to ask whether there is a mismatch between the brain and financial markets. But we cannot tell as long as we do not know how decisions come about in the brain. That is one of the tasks of an area of neuroscience called decision neuroscience.

When exploring decision neuroscience, one is immediately confronted with an inspiring differentiation. In decision theory as well as equilibrium game theory, all risks are the same—there is no distinction by source. Yet, the brain evidently distinguishes between (at least) two types: uncertainty generated by an unintentional source (“nature,” a random number generator, a financial market without insiders) and that generated by an intentional source (a strategic opponent, a financial market with insiders). The distinction manifests itself in the engagement of different functional regions of the brain, the behavioral effects when lesions selectively affect these regions, and differences across humans in attitudes toward either source. Still, the separation is not extreme; common regions do get involved (as discussed below). Here, I deal mainly with uncertainty from an unintentional source, leaving intentional uncertainty for a later section.

Decision neuroscience has progressed dramatically over the past ten years, following the discovery of the role of dopamine neurons in prediction under uncertainty (Schultz et al. 1997). The speed of discovery has been growing over the past five years, so that surveying the accomplishments becomes like describing a moving target. By the time this
review is published, some claims made here will be outdated, and questions raised may have been answered.

The increase in speed is in large part due to the introduction of concepts, theories, and results from economic theory and experimental economics. Hence, some would refer to decision neuroscience as neuroeconomics or, when it concerns risk and uncertainty, as neurofinance. I refrain from using these terms here, primarily to emphasize that neuroscience had much to say about decision making even before the advent of neuroeconomics.

On the matter of neuroeconomics, a number of reviews have recently appeared. All too often these reviews are not surveys but critical assessments instead—from both proponents and opponents of the field—based on only a few articles with a distinct economics angle, effectively bypassing the vast and sophisticated literature in decision neuroscience. The goal in this review, in contrast, is to let not only the economist talk, but also the decision neuroscientist.

2. EXPERIMENTAL FINANCE

Virtually all empirical work in finance uses historical data from the field, i.e., data as they are generated by “naturally occurring (financial) markets.” This is in contrast with decision neuroscience, where controlled experimentation is the norm. Although this sometimes involves the field (Camerer 1998), it mostly means laboratory experiments. If finance is to be enlightened by decision neuroscience, it needs to appreciate the merits of controlled experimentation. This is far from a foregone conclusion, so it is pertinent to elaborate.

The use of experiments is dictated not only by practical considerations (it would be hard to have a trader perform his daily duties while in an fMRI scanner), but also foremost by the necessity to control parameters. Indeed, nature rarely cares about our interests. We may want to study the basic principles underlying the Capital Asset Pricing Model (Bossaerts & Plott 2004), yet nature may have decided to provide us with an environment (multiperiod securities with skewed payoffs, delegated portfolio management, etc.) least propitious for the Capital Asset Pricing Model to emerge. To generate financial uncertainty caused by an intentional source, one may want to control the number of insiders (A. Bruguier, S. Quartz & P. Bossaerts, manuscript under review), yet the number of insiders is generally unknown in field markets, even if their presence may be suspected at times (and exploited) (see Bossaerts & Hillion 1991).

Lack of external validity is perhaps the most important reservation one can have about laboratory experimentation. In experimental finance, this mostly concerns the size of payments and risks, which are generally thought to be inadequate for the results to have any relevance for the “real world”—as if a laboratory were not real, but that is not the point. Rather, critics allege that behavior of individuals and of markets would look significantly different at higher levels of risk than anything hitherto tried in the lab (including asset pricing experiments where subjects could earn on average $500 in real terms and up to $2500 for a 3-hour effort) (see Bossaerts et al. 2007). Unfortunately, the dispute cannot be settled so long as critics do not state exactly what level of risk they would consider “real.”

Interestingly, decision neuroscience gives an indication of how to think about this issue. Indeed, one of the key brain regions that tracks reward prediction errors has recently been
demonstrated to encode rewards adaptively: When the high reward of a binary gamble is delivered, firing of dopamine neurons in the brainstem is independent of the size of the reward; even when the reward is increased tenfold, activation remains the same. The converse is seen for delivery of the low reward of such gambles (see Figure 1). In terms of the reward-prediction system in the brain, working with small gambles or with large gambles is the same; everything is just scaled.

There is, of course, a simple explanation for adaptive encoding (or scaling): There is a physical constraint on the amount of firing a given type of neuron can achieve. Since the range of stimuli that neurons may be confronted with is far beyond that of their firing, the brain has opted for scaling.

Adaptive encoding of rewards can also be observed elsewhere, such as in the orbito-frontal cortex (the region right above the eyes), which encodes utility (more on that later). Although this was first demonstrated for the monkey brain (Tremblay & Schultz 1999), it has recently been confirmed for the human brain (Elliott et al. 2008). The evidence is far from isolated (for a survey, see Seymour & McClure 2008). Further support for adaptive encoding emerges from behavioral experiments that demonstrate how attitudes toward risk are better captured with preferences that involve a relative measure of risk (the coefficient of variation; see Weber et al. 2004).

Adaptive encoding may not be sufficient to establish external validity of laboratory experiments. Indeed, although adaptive encoding has been observed for the ranges of outcomes and risks in the laboratory, there is no guarantee that it extrapolates without limit. Specifically, beyond a certain range, brain regions may become involved that are typically not activated in the laboratory.

But the belief that decision making under uncertainty in the “real world” is fundamentally different requires proof that the brain regions that are activated in the laboratory become disengaged. This is highly unlikely, because the regions that are active inside the

Figure 1
Median firing of dopamine neurons in the brains of two macaque monkeys after receiving no or little reward versus various higher rewards (juice). Reward magnitudes changed from one trial to another, but were perfectly anticipated, and the monkey had learned that the higher reward would be delivered with 50% chance in all cases. Firing shows adaptation to a situation: Reaction to delivery of 0.05 ml is no different from that when ten times the amount is delivered (0.50 ml; Animal A and B). Likewise, delivery of a low reward of 0.15 ml causes the same firing as when a low reward of 0 ml is anticipated (Animal B). Source: Tobler et al. (2005).
laboratory are powerful and pervasive, as discussed below, involving crucial neurotransmitters (such as dopamine) and triggering strong emotional reactions (e.g., arousal, fear) that would need to be offset or neutralized to become irrelevant.

In fact, all evidence points to the contrary. Decision making by professional traders is highly emotional (Lo & Repin 2002), and it activates hormones such as testosterone and cortisol (Coates & Herbert 2008) that have a direct influence on the very brain regions we see at work in the laboratory. Likewise, the alleged widespread use of pharmacological “enhancers” such as cocaine suggests attempts by professional traders to impact directly the dopamine neurons referred to above. Indeed, cocaine affects the synaptic strength of dopamine neurons, causing projection neurons to become hypersensitive, specifically to positive reward prediction errors (Saal et al. 2003).

Field studies such as the ones just mentioned could actually play the role of benchmarks against which artificially created financial events (such as bubbles and crashes) could be evaluated. That is, they could provide crucial information about how to realistically simulate financial events and to better study how humans cope with them, just like earthquake simulation is used to probe how physical structures respond to seismological forces.

Many financial decision problems, such as retirement portfolio allocation, have a significant time component. It is a serious challenge to emulate such problems in the lab. The time horizon in recent experiments has been extended to several weeks (Kable & Glimcher 2007, McClure et al. 2004), but not years. Nevertheless, a clever choice of experimental design allows experimenters to expose subjects to multiyear horizons, even if only indirectly. For instance, when subjects are faced with nutritious food and tasty food, choice effectively implies a substantial time dimension, because consequences for health lie far into the future (Hare et al. 2009).

Of course, one could always resort to “thought experiments,” by asking subjects for hypothetical choice in imagined situations (as in the original experiments in Kahneman & Tversky 1979). The problem here is that thought experiments may not engage the same brain processes as those that are activated when experiencing the outcomes. In the context of (risk-free) consumer choice, preliminary evidence has supported this conjecture (Min et al. 2009). Moreover, when uncertainty is involved, emotions, for instance, are an integral part of reasoned decision making. If the hypothetical questions cannot induce the same emotional reaction as when the risks are experienced first hand, predicted effects may not emerge. This could explain why experimental economists have noticed that they obtain better results when they pay for performance. Field data also tell us that outcomes may need to be experienced before they significantly influence choice (Feng & Seasholes 2005).

3. PERCEPTION OF RISK AND REWARD

One of the most fascinating findings of the past two or three years is that the brain separately encodes the risk and the reward when confronted with a gamble. This suggests that the brain engages in mean-variance analysis, whereby gambles are represented in terms of their statistical properties (moments) rather than as random variables living on an abstract state space. The suggestion is all the more credible because the metric of risk encoded in the brain appears to be variance. (Ongoing work extends this to higher moments, such as skewness and kurtosis.)
Experiments such as the following provide evidence for this: Subjects are presented with a deck of ten randomly shuffled cards, numbered 1 to 10. Two cards will be drawn from the deck, without replacement. Subjects are asked to bet whether the second card is going to be lower than the first. Once the subject posts her bet (for $1), the two cards are displayed, one after the other. We are interested in brain activation when the cards are revealed, because that is when the brain should encode the corresponding changes in expected reward and risk (Figure 2a).

Notice that this is a very simple game involving cards, with which most subjects should be intimately familiar. Probabilities are not mentioned explicitly, to shortcut the “mathematical” region of the brain that would be summoned to translate the abstract numerical data into something the reward and risk processing regions can deal with. Indeed, explicit representation of probabilities would add a layer of complexity, which would be interesting, but which we may not be ready to venture into yet.

Figure 2
(a) Timeline of card game. Of interest are brain activations resulting from the display of card 1 (and card 2) when beliefs (expected reward, reward variance) are updated as a function of the number on the card and the bet. (b) Expected reward and reward variance as a function of probability of reward. Brain signals that encode these statistical features should show similar relationships. Source: Preuschoff et al. (2006).
Also, notice that subjects do not have to make any decision at the points in time that interest us (revelation of the two cards). Again, this is deliberately done. There is a long path in the brain from perception to choice, and we are at first interested in perception. Does that mean that the resulting activations are irrelevant for choice? No: By now, it is known that these activations predict choice (Christopoulos et al. 2009, Kuhnen & Knutson 2005). As a matter of fact, activations in a purely perceptual task such as ours provide better predictions of choice than (past) choice itself, especially when one is close to indifference (Berns et al. 2008). That is, perceptual neural signals of valuation parameters provide better forecasts than preferences revealed through (past) choice. This is not to say that the perceptual activations determine choice. In situations of free choice, additional engagement is needed, both subcortical (O’Doherty et al. 2004) and cortical (Hampton et al. 2006).

In our card game, expected reward (mathematical expectation of payoff) and reward risk (measured as variance) change each in their own way as a function of probability of reward. Specifically, expected reward increases linearly and risk displays a symmetric, inverted U-shaped pattern, with a peak at probability 0.5 (Figure 2b). If expected reward and risk are encoded somewhere in the brain, activation ought to exhibit the same patterns.

Figure 3a (see color insert) displays a cross section of the human brain highlighting areas that were identified because activation in an fMRI scanner increased linearly in reward probability. Reward probability was computed from the bet that the subject chose and the number on the first card. Activation is measured in the first second after the display of card 1 (modulo the hemodynamic response delay). Figure 3b shows mean activations across 19 subjects and 95% confidence intervals, stratified by level of reward probability. This verifies that the activation patterns are indeed increasing and linear, which is required if the activations are to be associated with expected reward.

With the exception of a small activation in the upper-left part of the brain, the regions highlighted in Figure 3a are subcortical projection areas of the dopamine neurons in the brainstem, in particular, the ventral striatum. The importance of the dopamine neurons in tracking rewards is discussed above. Traditionally, however, they were thought to cause arousal. The link between this emotional reaction and prediction errors is intriguing (I elaborate on this below). Figure 3c situates the reward-tracking dopamine neurons in the ventral tegmental area of the brainstem, and they project to the ventral striatum. There are also dopamine neurons in the substantia nigra, but these are primarily engaged in other tasks (and damage to these neurons leads to Parkinson’s disease).

The results of Figure 3 have been replicated many times. In fact, we now know that this activation reflects reward prediction errors, i.e., the difference between what was expected before the display of the stimulus (card 1) and the updated expectation or outcome (Hare et al. 2008, McClure et al. 2003, O’Doherty et al. 2003). As such, the activation is backward looking, and consistent with this finding, it is phasic (meaning of short duration) and time locked to the stimulus display. That the activations represent reward prediction errors has recently been confirmed in an analysis that required minimal assumptions about the prior expectation (A. Caplin, M. Dean, P.W. Glimcher & R.B. Rutledge, manuscript under review; Y. Niv J.A. Edlund, P. Dayan & J.P. O’Doherty, manuscript under review).

Figure 4a (see color insert) shows a cross section of the human brain with regions where activation changes quadratically with reward probability. Figure 4b displays the pattern of activation in one of those regions, namely, the right insula. As required if this
activation is to reflect reward variance, mean activation is lowest for zero and unit reward probability, highest at approximately 0.5, and symmetric around 0.5. The regions indicated in Figure 4a (left and right insula and the thalamus) are involved in relaying information about “bodily state”—emotions—and sensory input (e.g., visual cues) to cortical areas. The results have been replicated many times (e.g., Dreher et al. 2005). Activation in at least two additional cortical regions correlates with risk (Huettel et al. 2005). One of them, the inferior frontal gyrus, is briefly mentioned below: Its shallow location allows for direct electrical or magnetic manipulation, with interesting behavioral effects.

The timing and modulation of the signals displayed in Figure 4 are significantly different from those in Figure 3. Specifically, the signals emerge later, are sustained, and seem to be time locked to the display of card 2. This is consistent with the interpretation that they reflect expectation of risk that is to be resolved upon revelation of card 2. As such, it is forward looking and therefore not a prediction of error, but anticipation. Thus, the brain also encodes a corresponding prediction error, which, in this case, should be referred to as the risk prediction error.

In our card task, probabilities are “known,” in that subjects should be familiar with basic features of card games. The contrast of activation when probabilities are known (which economists would refer to as pure risk) against when these are not known (ambiguity) shows that the dopamine projection areas such as the ventral striatum are less activated under ambiguity (Hsu et al. 2005). Interestingly, another activation emerges, namely, in the amygdala (located approximately where the number three is displayed in Figure 3c, but more lateral).

The amygdala forms part of a circuit (which includes the dopamine system) that has been associated with goal-directed learning (Balleine et al. 2003). The amygdala also appears to signal a need to start learning. Econometricians would refer to this signal as parameter estimation uncertainty (or its inverse, precision), to be distinguished from the irreducible risk that remains in any stochastic environment even when probabilities are perfectly known. It is interesting to observe that the brain likewise differentiates between these two aspects of uncertainty. It confirms behavioral evidence that humans treat pure risk and ambiguity differently, but the link with fundamental concepts from econometrics suggests that the differentiation should not necessarily be interpreted negatively, in contrast with tradition (Ellsberg 1961). Indeed, a recent experiment demonstrates that humans manage to exploit the differentiation to optimize learning under ambiguity (Payzan & Bossaerts 2009). Furthermore, patients with lesions in the orbitofrontal cortex do not distinguish between ambiguity and risk, further supporting the idea that the distinction is biologically natural and important (Hsu et al. 2005).

Although the amygdala has been associated with learning only recently, it has always been viewed as the “fear center” of the brain (Adolphs et al. 1995, LeDoux et al. 1990, Morris et al. 1996). However, the two views are not mutually exclusive. Fear may be the emotional expression of estimation uncertainty, just like arousal accompanies positive reward prediction errors (and relates to activation of the dopamine system). That is, fear may act as a dual signal, relaying both a caution not to bet on things unknown and a directive to find out more (Hsu et al. 2005).

As mentioned above, the dopamine system encodes a reward prediction error and, therefore, plays a crucial role in learning expected rewards. Signals correlating with risk prediction error in our card game have also been located, in the insula (Preuschoff et al. 2008), overlapping with the areas where risk prediction was found in prior studies.
Mathematically, the risk prediction error is simply the difference between the squared reward prediction error and its anticipation, namely, reward variance. Econometricians would recognize this as the driving term of an ARCH (autoregressive conditional heteroskedastic) process (Engle 2002). Risk prediction errors can also be observed in the other cortical structures where risk signals have been found (d’Acremont et al. 2009).

One of the striking aspects about brain activation in our card game is that signals of expected reward and risk (and corresponding errors) appear every time the game is played. Evidently, the brain insists on re-evaluation of basic statistical features rather than simply retrieving some valuation (utility) number from memory. If this is a general property, the brain is best viewed as a computer with incredible processing capacity but a small hard disk. This should inspire new modeling of bounded rationality.

But constant re-evaluation of the statistics of a gamble takes time. One therefore wonders whether this has an effect on choice when subjects are forced to make decisions before all neural computations can be completed (which would be within 2–3 s after stimulus display). Revealed preferences are indeed significantly different when subjects have to indicate their choice at second 2, compared with their choice at second 4 or 6 (A. Bollard, R. Liu, A.D. Nursimulu, A. Rangel & P. Bossaerts, manuscript under review). This has important implications for the design of continuous-trading mechanisms, where profit opportunities can sometimes be achieved only if action is taken in a split second.

So far, the encoding of statistical features of a gamble in the human brain has been discussed. In financial decision theory, these are merely the inputs to valuation, i.e., to expected utility. Where, then, are the value signals in the brain?

Perhaps the activation displayed in Figure 3 actually does not reflect expected reward prediction (errors), but expected utility (errors). We do not see any nonlinearity, however (concavity for risk-averse and convexity for risk-seeking subjects). Then again, one should not overinterpret the evidence, as it is not entirely clear whether the fMRI signal is linear to the firing of individual neurons. As a matter of fact, even patterns in neuronal firing (see Tracking Neuronal Firing, sidebar below) should be interpreted with care. Indeed, because signal precision decreases with firing rate, one could expect to observe a convex relationship between reward probability and firing, even if the neuron at hand merely encodes expected reward (see The Mathematics of Neuronal Information Transmission, sidebar below).

Also, in our card game, only probabilities were varied. Significantly, we kept (reward) magnitude the same: Bets were always for $1. One recent study manipulated magnitudes. This revealed strict concavity in the reward prediction error signals in the ventral striatum. Moreover, the degree of concavity increased with risk aversion (Tom et al. 2007).

But if this means that the signals in the ventral striatum reflect expected utility, and not expected reward, what do the risk signals in the insula or inferior frontal gyrus indicate? Do these reflect variance of utility? At this moment, we do not know. Preliminary evidence (Christopoulos et al. 2009) suggests that the risk-induced activations in the insula and inferior frontal gyrus correlate with risk aversion, and, hence, reflect subjective variance. Although the idea of separately encoding utility variance and expected utility may seem strange at first, recall that Allais (1953) was the first to suggest it as an explanation for the violations of expected utility axioms that he observed in human choice.

To complicate matters, in the ventral striatum, signals encoding probability of reward and magnitude of reward appear to live alongside signals that correlate with expected
reward (Tobler et al. 2007, Yacubian et al. 2006). Probability and magnitude are the crucial ingredients of expected utility. The probability signal in the ventral striatum even shows biases that are reminiscent of probability weighting in prospect theory (Berns et al. 2008, Hsu et al. 2009).

Why has the brain chosen to encode all four features of a gamble: expected reward, reward variance, reward probability, and reward magnitude? After all, (expected) utility can be computed either by summing magnitudes after multiplication with probabilities or by combining expected reward and risk. Perhaps these two approaches are not equivalent, in contrast to received wisdom (Kroll et al. 1984). Potential fundamental differences have recently been explored both theoretically and empirically (d’Acremont & Bossaerts 2008).

Separate encoding of the key decision-theoretic features of a problem is not limited to gambles. The human brain, likewise, separately tracks equity and efficiency in problems of moral judgment (Hsu et al. 2008). Interestingly, equity correlates with activation in regions engaged in risk encoding, such as the insula, whereas efficiency activates the ventral striatum, which is involved in expected-reward encoding. This finding is unlikely to be coincidental. It certainly lends support to models of moral decision making based on a trade-off of equity against efficiency, similar to the evidence in Figures 3 and 4 supporting mean-variance analysis as a model of human financial valuation.

**TRACKING NEURONAL FIRING**

Firing of individual neurons can be tracked by inserting an electrode in the brain, a rather invasive procedure done in humans only if there is a medical need and even then the location of the electrode is determined by medical concern and not scientific value. Recently, a number of imaging techniques have become available that allow one to noninvasively but indirectly measure firing of clusters of neurons or, more accurately, activation of projection areas triggered by firing of upstream neurons (Goense & Logothetis 2008). Functional magnetic resonance imaging (fMRI) is one of them. Basically, fMRI localizes the presence of oxygen-rich blood. Although oxygen-rich blood concentrates where there is activation, the effect comes with some delay (approximately 4 s), referred to as hemodynamic response delay. The “functional” in fMRI stands for the fact that a large part of the brain is scanned in its entirety approximately every 2 s, so that changes in activation can be picked up at different stages of a task. Pictures of brain activation such as those in Figure 3a are effectively maps of $t$ statistics of the treatment effects, whereby only activations beyond a cut-off $p$ level (generally 0.001 or less) are retained.

**THE MATHEMATICS OF NEURONAL INFORMATION TRANSMISSION**

Neurons relay information to downstream brain structures strictly in binary form, by “firing.” Mathematically, neurons thus generate outcomes of a Poisson process. The message that is being transmitted consists of changes in the mean firing rate over short time intervals. Downstream brain regions, however, never observe the true mean firing rate that the upstream neuron is trying to convey. Instead, they observe only a noisy sample mean firing rate. Basic mathematics of Poisson processes implies that the precision of the sample mean decreases as the true mean increases. As such, it is harder for downstream brain regions to pick up significant changes in firing rates when their true averages are high. Upstream neurons could compensate for this by spacing out firing rates more as the signal they attempt to convey increases. As a result, firing rates are convex in the underlying intended signal.
4. EMOTIONS

The regions of the human brain where we see clear risk and reward signals include the dopamine system, insula, and amygdala. These regions have in common one important feature of the human condition, namely, emotions. Above, I mention arousal in the context of dopamine (sometimes inflated artificially through cocaine use, for instance). The amygdala has been associated with fear, and the insula (or at least the anterior part, where we observe risk signals) provides a crucial relay of emotions to the cortex.

The evidence surveyed in the previous section also suggests that activation in these same brain regions reflects encoding of “cool” mathematical quantities such as expected reward, risk (measured as variance), reward prediction errors, ARCH-like risk prediction errors, estimation uncertainty, etc. Has the brain decided to relate these mathematical quantities, usually associated with cool-headedness, to emotions?

In the same vein, recent studies have shown that strong emotions such as disappointment, elation, regret, relief, envy, and gloating are associated with mathematical error signals such as (negative and positive) reward prediction errors, fictive-play prediction errors, and prediction errors relative to other people’s rewards, respectively (Bault et al. 2008, Coricelli et al. 2005). All these can be found in the brain structures discussed above.

In the context of the insula, I mention a study where the ability to sense one’s own heartbeat was found to correlate with the size of the insula (Critchley et al. 2004). Together with the findings that (a) the heartbeat of professional traders correlates with risk (Lo & Repin 2002) and that (b) the insula encodes risk (Figure 4), one may conjecture that the human body has chosen to employ a somatic marker (heartbeat) to encode risk.

When that somatic marker is absent, the consequences may be harmful. Bechara et al. (1997) showed that subjects who fail to express emotional anticipation when making risky decisions (because of specific brain lesions) consistently opt for inferior financial choices. This led the authors to posit that emotional processes guide reasoned decision making, which they referred to as the somatic marker hypothesis (Bechara & Damasio 2005). Because of the mathematical accuracy of the signals encoded in the emotional regions of the human brain, an updated interpretation of the findings would be that emotions are somehow subsumed in the mathematics of optimal decision making. This would explain why (emotional) experience is important for rational choice (Feng & Seasholes 2005).

Another way to put this is that reasoned choice is the result of the balancing of emotional inputs. Human decision making under uncertainty thus takes on features of the celebrated multiattribute choice theory (Lancaster 1966), albeit with “characteristics” replaced by the emotional aspects of a gamble. Normal emotions are not bad per se, and abnormal (irrational) behavior such as regret avoidance, ambiguity aversion, and the like are to be viewed as the result of maladapted weighing of the different emotional aspects of a gamble.

It is important to realize that emotion-based decision making may be entirely subconscious. As a matter of fact, its speed may preclude conscious brain processes from interfering. At times, such decision making may conflict with choice based on explicit reasoning, and the fact that humans often show signs of both fast, emotion-based decision making as well as slow, logically reasoned choice has led many to propose a dual-system theory (Evans 2003, Kahneman & Frederick 2002). According to this theory, humans are capable...
of opportunistically switching back and forth between these two ways of generating decisions. Prefrontal and lateral orbitofrontal cortical regions as well as the adjacent anterior cingulate cortex are thought to be involved in explicit, conscious decision making, but the precise neurobiology remains poorly understood.

A recent study on framing (De Martino et al. 2006) illustrates how this may work. When prospects were framed in terms of losses, subjects appeared to take on more risk, and this behavior was associated with increased activation of the amygdala. Nevertheless, subjects who showed the least (or no) impact from framing also simultaneously displayed increased prefrontal activation, suggesting attempts by the conscious system to control quick emotional reactions (Bossaerts et al. 2008, Kahneman & Frederick 2007).

How do we know that the secondary activation is really conscious? As yet, we do not. However, because it allows for better time resolution, electroencephalograms (EEGs) may provide insight. In a recent study on the impact of disappointment on subsequent decision making, a secondary EEG signal emerged in frontal regions after 375 ms but only in individuals who successfully overcame the detrimental effect of reflexive reaction to disappointment (Tzirnopulos et al. 2009). Although the arrival of this secondary signal is surprisingly quick, it is not too fast for conscious experience.

It should be repeated that emotion-based decision making need not be bad or unsophisticated. The mathematical precision with which activation in the insula correlates with an ARCH-like risk prediction error (Figure 5) underscores this, as do the reward prediction errors that dopamine neurons encode. Indeed, the latter reveal a learning algorithm that is exquisitely adapted to environments with multiple stimuli, action possibilities, and reward opportunities (Montague et al. 1996, Schultz et al. 1997). This very same algorithm, called temporal difference learning, is used in machine learning to solve complex dynamic programming problems.

5. VALUE SIGNALS

Standard economic thinking (including behavioral finance) starts from the premise that choice results from maximization of value. Partly under the influence of economists, one of the main issues that decision neuroscientists have been interested in is whether there are value signals in the brain. The first handbook in neuroeconomics is mostly devoted to this issue (Glimcher et al. 2009).

At one level, the existence of a value signal is likely to be confirmed. Indeed, if acts follow the instructions of motor or premotor neurons that fire most intensely, this firing must be in accordance with maximization of some utility function if the resulting acts satisfy the axioms of revealed preference. That is, neurons generate specific actions from a list of possible actions by winning firing contests, not by looking up values and picking the action with the highest values (as in Bernheim 2009). Consistent with this conjecture, Platt & Glimcher (1999) found that the firing of neurons in the intraparietal sulcus (a fold in the lateral cortex beyond the brain midline) of the macaque brain correlated with expected utility.

But what about the executive regions in the front of the brain, far removed from the motor cortex? By now, the evidence in favor of signals that economists would recognize as “value” is well established. Valuation signals have been discovered in the orbitofrontal cortex of the macaque monkey (Padoa-Schioppa & Assad 2006, Tremblay & Schultz 1999). This has recently been confirmed (Plassmann et al. 2007) and extended (Hare et al. 2008) for the human brain: Activation in medial prefrontal cortex correlates with

**Electroencephalogram (EEG):** recording on the scalp of electrical activity generated by the brain, with excellent time resolution, but difficult source localization.
willingness to pay (WTP), and more lateral activation (and corresponding to the activation identified in the macaque brain) correlates with economic surplus (i.e., utility net of cost), whereas activation in the ventral striatum represents value prediction errors (as discussed above).

In the context of gambles, the signals in the lateral orbitofrontal cortex exhibit the characteristics one would expect if they are to convey expected utility: Although they increase with expected reward, yet decrease with risk (variance), for risk-averse subjects, they increase with risk for risk-seeking subjects (Figure 6, see color insert).

The presence of value signals is handy in many respects. For one thing, evolution of this signal over time teaches us many things about learning. For example, Hampton et al. (2006) showed that value signals in a randomly reverting two-armed bandit task reveal learning that is distinctly Bayesian. It is true that the behavioral data only marginally favored Bayesian updating (over simple reinforcement learning), but the value signals show the correct properties at the right time so that even the most skeptical mind would be convinced of the hypothesis of Bayesian learning.

Value signals have also shed light on the endowment effect. Specifically, this cognitive bias is not directly reflected in the above value signals, but it may be the result of reference-based encoding in the ventral striatum and insula (De Martino et al. 2009). In the context of gambles, activation in the insula suggests that the endowment effect is the consequence of the level of risk that the subject perceives. Specifically, the WTP is lower because the subject perceives less risk in her starting position (cash endowment). The willingness to ask (WTA) is higher, because she is now endowed with the gamble and is faced with the option of exchanging this for another risky position. The latter may seem strange, because the gamble is to be sold for cash (i.e., a risk-free position), but this ignores the fact that WTP is generally elicited using the Becker-DeGroot-Marshak mechanism, which induces risk. The finding suggests novel hypotheses, such as the dependence of the difference between WTP and WTA on risk aversion. It also demonstrates that the endowment effect in this case results from a fundamental misconception of the Becker-DeGroot-Marshak mechanism (or a violation of the independence axiom). Hence, it should be avoidable through appropriate training—which is precisely what has been shown recently (Plott & Zeiler 2005).

6. UNCERTAINTY CREATED BY AN INTENTIONAL SOURCE

So far, we have considered uncertainty that is “objective,” in the sense that it is generated by a source without goal directness or intention behind it. Opposed to this are situations where a strategic agent (e.g., an animal, human, sophisticated computer, or perhaps a market with insiders) causes the uncertainty. Equilibrium game theory has long had to cope with this type of uncertainty, but it has settled on analyses that do not distinguish between these two types of uncertainty.\(^2\) Valuation is performed using standard expected utility, and updating follows Bayesian principles. The resulting equilibrium concepts are straightforward Bayesian extensions of Nash equilibrium.

But neuroscience has suggested that there are fundamental differences in the way humans approach uncertainty from an intentional choice. For instance, activation in a

\(^2\)Nonequilibrium analysis sometimes deals with strategic uncertainty explicitly and in a way that is different from nonstrategic uncertainty (see, e.g., Goeree & Holt 2004).
simple game of imperfect information is more like that in situations of ambiguity, not pure risk (Hsu et al. 2005). Likewise, psychology has long differentiated dealing with an intentional opponent. Assessing the risk in such a situation has become known as theory of mind or mentalizing, and specific regions of the brain seem to be dedicated to it, most importantly, the paracingulate cortex (the region of the frontal cortex above the orbitofrontal cortex), which is cytoarchitecturally a relatively recent brain region (Gallagher & Frith 2003).

The paracingulate cortex is preferentially activated during play of strategic games with other humans, more so than with computers programmed with a simple rule (Gallagher et al. 2002, McCabe et al. 2001). Hampton et al. (2008) explored the mathematical computations in this region during game play and discovered that it encoded an “influence update,” namely, the error from predicting how one’s opponent would shift strategy as a result of one’s own moves.

As such, this signal effectively pushes human game play beyond simple reinforcement learning, fictitious play, or some mixture thereof (experience weighted attraction learning; Camerer & Ho 1999). Most significantly, it demonstrates that humans recognize the intentionality of the target (opponent) about which they are learning, a possibility that has been raised only occasionally in the game-theory learning literature (Camerer et al. 2002, Stahl 2000).

Exploiting the simple formal structure of the “beauty contest,” Coricelli & Nagel (2009) recently confirmed this finding. Significantly, in no study were the regions traditionally associated with formal mathematical and logical thinking engaged. Indeed, Coricelli & Nagel (2009) showed how skill in the beauty contest and mathematical proficiency were unrelated, despite the fact that the mathematics tests required the very calculations that are implicit in successful game play. This discovery is still obtained when the game is far more complex. In financial markets with insiders, skill in predicting future price movements does not correlate with mathematical proficiency (A. Bruguier, S. Quartz & P. Bossaerts, manuscript under review).

7. DISCUSSION

What should a finance scholar make of all this neurobiology? To begin, it provides plausibility and discipline to modeling of human decision making. For instance, it suggests where one should place emotions or conscious control. It teaches us that values are not merely retrieved from memory, but recomputed every time, with the risk of occasional misestimation. That is, choice is the outcome of a process, from perception to action, not maximization of utility. Likewise, it suggests why humans can be good at, say, playing strategic games even if, when asked explicitly, they do not seem to be good at the mathematical computations implicit in their play.

Neurobiology does ask us to evaluate everything in terms of a single criterion, namely, evolutionary plausibility. Alleged cognitive biases remain suspect until they make sense in an ecologically relevant setting. The use of an overarching criterion should be familiar to finance scholars, who have been applying their own to evaluate pricing patterns in financial markets, namely, absence of arbitrage opportunities, as well as to neoclassicists, who have used the efficient-markets hypothesis.

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1In the beauty contest, subjects are asked to guess a number that comes closest to a fraction (e.g., two-thirds) of the average guesses. As in Keynes’s (1964) description of financial markets, the goal is therefore to guess what others are guessing rather than estimating some exogenously determined number.
Novel conjectures will be the by-product of any insistence that theories of human decision making be validated neurobiologically. For instance, it is well known that humans envy and gloat and that these emotional reactions appear to affect utility and, hence, future choice (Bault et al. 2008). But, why would envy and gloat affect utility? Perhaps this leads the area of the brain that encodes the reward prediction error (the difference between experienced utility and expected utility) to react, not only to what an individual did herself (as in traditional reinforcement learning) or what she failed to do (fictive learning as in Lohrenz et al. 2007), but also to what others chose to do. As such, the reward prediction error automatically includes options chosen by others. Learning of optimal strategies is thereby enhanced dramatically. This should matter especially in situations when the consequences of unchosen actions are hard to assess, so that fictive learning is ineffective. In addition, imitation learning is known to be powerful in animals and children alike, and its neurobiological foundations are slowly being understood (Heyes 2001). The alternative for the brain would be to set up a costly parallel learning system that simulates the utility of others, without reference to one’s own utility. Or it could choose a “mirror system” (Rizzolatti & Craighero 2004) that stores actions of others without recording their value, but the blindness of such a system renders its cognitive use questionable.

Choice biases can be expected to arise when the brain faces a new adversary or an unknown environment. Financial markets may be a prime example of the brain charting new territory. Nevertheless, even within novel environments, humans often appear to do remarkably well. For instance, the success of the continuous double auction in generating efficient outcomes despite its strategic complexity (Friedman & Rust 1993) and the facility with which humans can detect and exploit insider information in it (Bruguier et al. 2008) suggest that certain designs exploit the computational capabilities of the human brain better than others.

But the development of the double auction was accidental, in the sense that it did not emerge from a thorough study of the human brain and its capacity. It is hoped, however, that future discoveries in decision neuroscience will facilitate the targeted development of new tools for improved financial decision making and exchange. For instance, further study of how long it takes the brain to re-evaluate gambles each time they are presented should inspire timing restrictions on trading platforms with the aim of avoiding choice biases induced by time pressure.

Among such tools, one can also envisage simple affect control (Kuhnen & Knutson 2008). Pharmacological remedy is also within reach (e.g., glucocorticoid receptor agonists block the synaptic effects of stress on dopamine neurons in the ventral tegmental area; see Saal et al. 2003). And investors should be warned that the side effects of medication (such as L-Dopa; Gschwandtner et al. 2001) that interferes with the brain systems involved in decision making under uncertainty. Direct control of risk attitudes is now possible through electrical (Fecteau et al. 2007) or magnetic (Knoch et al. 2006) stimulation of the inferior frontal gyrus, where a risk signal resides (discussed above), but such control raises ethical issues.

One also wonders whether it is possible to teach humans to become better financial decision makers, without resorting to tools such as double auctions, timing restrictions, or pharmacological remedies? To the extent that decision making under uncertainty engages powerful emotional processes and pervasive neurotransmitter release that are difficult to counter, the answer should be, No. Still, we can teach tricks, such as looking for generalized ARCH features to detect the presence of insiders (A. Bruguier, S. Quartz & P. Bossaerts, manuscript under review), similar to the way autistic patients can now be instructed to look in the eyes of others to overcome their handicap in discerning the intention of others (Spezio et al. 2007). Such tricks are useful, but their scope is limited, because what we are asking for is the equivalent of controlling a visual bias. A visual bias
is harmless if one knows when it occurs, but because such a bias never disappears completely, the brain will be fooled any time it is inattentive.

The forgoing also answers a commonly raised question: Should computers replace humans in financial markets? The answer is, No. Humans are much better at certain tasks than computers, but humans have clear limitations when asked to solve problems for which their brains are maladapted. The goal of decision neuroscience is to identify these limitations and to introduce computers only when necessary to overcome them.

The focus of this discussion has been on implications for investments and trading. However, decision neuroscience is bound to impact all of finance. Whereas its impact on household and consumer finance as well as college and retirement savings is more obvious, new insights into the neurobiological foundations of ambiguity aversion, reward, and risk learning will also clarify issues ranging from venture capital to capital market engagement and disengagement and on to overpricing of deep out-of-the-money put options (“volatility smiles”). Better understanding of strategic uncertainty could also help shape corporate finance, microfinance, market microstructure analysis, and other subfields of finance where strategy is key. Eventually, improved comprehension of the true nature of human decision making under uncertainty will enable us to design better resource allocation and incentive mechanisms that could even exploit well-known deficiencies and turn them into a virtue, as exemplified in Meloso et al. (2009), where overconfidence spurred market-based intellectual discovery.

**SUMMARY POINTS**

1. Choice is the outcome of a long neurophysiological process, from perception to action. In the context of gambles, this process includes constant re-evaluation of statistical features.

2. From the statistics of gambles, the brain constructs the very valuations (utilities) that are at the core of modern economic thinking. These valuation signals can be found in executive areas of the human brain that are remote from the motor cortex and, hence, that are not directly involved in the acts that implement a choice, but in the evaluation of the options at hand.

3. Brain regions that encode the mathematical features of a decision problem are often also involved in the corresponding emotional reactions, suggesting that emotions may largely be subsumed in the mathematics of decision models.

4. Emotions are an integral part of reasoned decision making. Choice can be viewed, to a large extent, as the result of a delicate balancing of the emotional features of a decision problem, such as disappointment, elation, regret, relief, envy, and gloating.

5. The claim that laboratory experiments in finance do not have external validity can be upheld only if it is demonstrated that the brain circuitry engaged in the laboratory somehow becomes neutralized. This is highly unlikely, because that circuitry is in control of pervasive neurotransmitters and of strong emotional responses.

6. Cognitive biases need to be evaluated against evolutionary fitness, similar to the way financial market phenomena are judged against absence of arbitrage (or the efficient markets hypothesis). Cognitive biases need to be understood as a mismatch between a novel environment and a neurobiological system that is optimized for a different, ecologically more relevant, problem.
7. Although the theory of games of imperfect information borrows largely from financial decision theory, the human brain deals differently with uncertainty generated by an intentional source than with “objective” uncertainty.

8. An improved understanding of the neurobiological foundations of human decision making under uncertainty should lead to the development of effective tools of assistance, such as appropriate emotional control, trading interfaces that exploit natural skills, and even pharmacological decision support.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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LITERATURE CITED


Figure 3

(a) Location of (some of the) activations that increase linearly in reward probability: left and right ventral striatum.
(b) Mean activation in left ventral striatum across 19 subjects (orange circles) stratified by reward probability; vertical lines indicate 95% confidence intervals. (c) Cross section of the brain from front (right) to back, showing key projection areas of dopamine neurons in the midbrain. Dopamine neurons encoding reward prediction errors can be found in the ventral tegmental area. They project, among others, to the ventral striatum (region activated in panel a). Sources: Preuschoff et al. (2006) and http://openlearn.open.ac.uk.
Figure 4

(a) Location of (some of the) activations that are quadratic in reward probability: left and right anterior insula and mediodorsal nucleus of the thalamus (md) (front of the brain is on top). (b) Mean activation in right anterior insula across 19 subjects (blue circles) as a function of reward probability shows the inverted U-shaped pattern needed for it to encode reward variance; line segments indicate 95% confidence intervals. Source: Preuschoff et al. (2006).

Figure 5

(a) Location of activation that correlates with risk prediction error upon display of card 1: left and right anterior insula. (b) Mean activation in the right anterior insula across 19 subjects as a function of risk prediction error upon display of card 1 (red circles) and card 2 (blue circles). Outlier at zero risk prediction error refers to trials when no risk remained after card 1. Line segments indicate 95% confidence intervals. Source: Preuschoff et al. (2008).
Figure 6

(a) Location of activation correlating with expected utility of gambles: prefrontal cortex, slightly to the right of the medial line (eye ball is visible in bottom right corner). (b–e) Activation in this location as a function of expected reward and reward variance, per subject, stratified by revealed risk attitude. Source: Tobler et al. (2007).
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Errata

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