Valuation for Risky and Uncertain Choices

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INTRODUCTION

This chapter provides an overview of the neuroeconomics of decisions under risk and uncertainty. Choice under risk and uncertainty is distinguished from other forms of decision making by the fact that choice options yield different rewards on different occasions; they yield different outcomes with different probabilities. A particular stock will pay different amounts of dividends in different years, and flowers of a certain genus will provide differing amounts of nectar to feeding bees on different visits. Despite this uncertainty, decision makers must assign a value to available choice options, in order to select the one that is most advantageous. In addition to reviewing different modeling approaches to describe risk and uncertainty (some of which are also covered in Chapters 1 and 3), the chapter reviews key findings in the neuroeconomic literature that provide neural correlates of both risky choice model components

and the conceptual distinctions that underlie those models. Neuroscience evidence is provided by results from fMRI studies of decisions under risk and uncertainty made by human respondents and from single cell recording analyses of risky choices made by non-human primates and rats. The findings suggest that key valuation structures of the brain, such as the striatum and medial prefrontal cortex, process components of the formal models describing risk and uncertainty.

Importantly, this chapter distinguishes between, and describes, two basic modeling approaches. One decomposes risky choice options into outcomes and probabilities, as for example in the expected utility framework of economics. The other decomposes the distribution of possible outcomes into first and second (or higher) order moments, as for example in the risk-return framework of finance. Moments are quantitative measures that describe the shape of a probability distribution and include the mean (1st moment), the
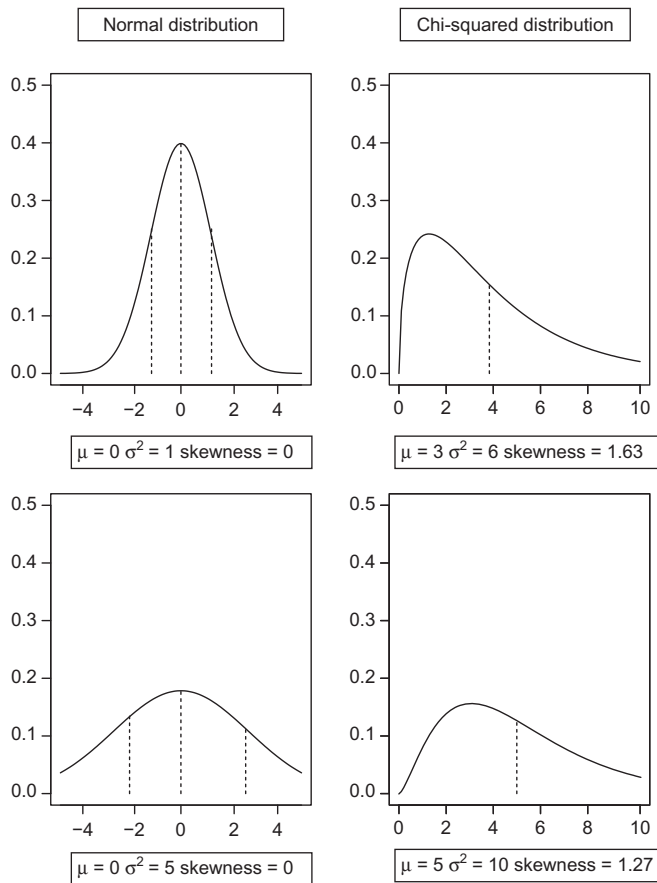
FIGURE 9.1 Distributions varying in mean, variance, and skewness.

variance (2nd moment) and the skewness (3rd moment) of a distribution. As shown in Figure 9.1, the symmetric normal distribution, for example, is characterized by a mean that is at the center of the distribution, by its variance, and by zero skewness. The larger its variance, the more dispersed are its outcomes away from the mean. A chi-squared distribution, in contrast, is positively skewed, its skewness is greater than zero, and the mean is closer to the lowest possible outcome than the highest possible outcome. Just as for the normal distribution, the larger its variance, the more dispersed are its outcomes away from the mean.

Both modeling approaches have normative-rational versions as well as descriptive-behavioral versions that account for a broader range of observed choices. This chapter provides evidence for the neural coding of both types of representations in the brain. It also distinguishes between decisions under uncertainty/ambiguity versus under risk and discusses the implications of different ways of learning about reward value and probability, from experience across species, or from description for human respondents.

DECISIONS UNDER UNCERTAINTY AND RISK

Types of Uncertainty

Benjamin Franklin famously stated that the only things certain in life are death and taxes. If anything, the amount of uncertainty in our world has increased between the 18th and the 21st centuries. A common distinction is made between *aleatory* uncertainty, i.e., objective and irreducible uncertainty about future occurrences that is due to inherent stochasticity in physical or biological systems, and *epistemic* uncertainty; which is subjective and reducible, because it results from a lack of knowledge about the quantities or processes identified with a system. The uncertainty associated with the outcome of the toss of a coin is an everyday example of aleatory uncertainty, whereas not knowing the chlorine level of your swimming pool is an example of epistemic uncertainty. While epistemic uncertainty is reducible in principle, many domains may have limits to the precision of predicting events far into the future, due to the complex or chaotic nature of the processes that give rise to them (Lempert *et al*., 2004). The social world provides uncertainties beyond those of the physical world, and game theory, both classical and behavioral, is a way of coping with the uncertainties that arise out of our limited ability to predict the behavior of others, a point covered in detail in Chapters 2, and 25 respectively.

Degrees of Uncertainty

The economist Frank Knight was the first to make a conceptual distinction between decisions under *risk* and under *uncertainty* (Knight, 1921, Ch.7). Risk refers to situations where the decision maker knows with certainty the mathematical probabilities of possible outcomes of choice alternatives, such that these can be described as a set of outcomes and their probabilities (usually for discrete outcome distributions with a small number of possible outcomes) or by the mean, variance, and skewness of the distribution of possible outcomes (typically for continuous distributions, as shown in Figure 9.1). Uncertainty refers to situations where the likelihood of different outcomes cannot be expressed with any mathematical precision. Traditional rational-economic analysis assumes that uncertain situations can be reduced to risky situations. In the absence of any information about probabilities, all possible values (in the extreme, between 0 and 1) should be assumed to be equally likely, with the midpoint of the range of possible likelihoods (e.g., 0.5) as the best estimate, a line of reasoning referred to as the "ignorance prior." Contrary to this assumption, Ellsberg (1961) showed that people

clearly distinguish between risky and uncertain options and have a clear preference for the former, a behavior that Ellsberg called *ambiguity aversion* (Box 9.1).

Knowledge about the probability distribution of possible outcomes of a choice can lie anywhere on a continuum, from complete ignorance (not even the possible outcomes are known) at one end, through various degrees of partial ignorance (where outcomes may be known, but their probabilities not precisely specified, denoted as uncertainty or ambiguity), to risk (where the full outcome distribution is precisely specified), to certainty (where only a single, deterministic outcome is known to result).

Ambiguity aversion has been observed in both laboratory experiments and in real-world health, environmental, and negotiation contexts (see Curley and Yates, 1989; Hogarth and Kunreuther, 1989). While ambiguity aversion is a very stable phenomenon, it is not universally observed (Camerer and Weber, 1992). If the ambiguous choice option is in a domain in which the decision maker believes him- or herself to have expertise, ambiguous options (e.g., sports bets) are often preferred to equivalent risky monetary lotteries (Fox and Tversky, 1995).

Ways of Resolving and Quantifying Uncertainty

Epistemic uncertainty can be resolved in different ways, particularly through learning (various forms of which are described in Section 3 of this volume). Personal experience powerfully affects memory and subsequent behavior: a single painful touch of a hot stove can prevent similar mishaps for a lifetime. Trial and error can improve the accuracy with which outcome-probability distributions are represented.

Observational or vicarious learning allows the observer to learn from the observed. It is an evolutionary innovation available primarily to humans, primates, and a few other species (Zentall *et al.*, 1988), while other forms of social learning may be more common. Cultural learning, the ability to understand other's cautionary tales and anecdotes, extends the range of vicarious experience even further and across generations. Individuals who live in cooperative groups with the ability to communicate information in symbolic form can use the experience of others not just by direct observation, but can receive it in condensed form. The possible outcomes of investing in a particular company stock, for example, can be provided as a probability distribution of possible outcomes or as a time-series of past outcomes.

MODELS OF RISKY CHOICE

Outcome-Probability Decomposition of Risky Options

Models of risky choice that decompose choice options into possible outcomes (or rewards) and their associated likelihoods of occurrence are described elsewhere. Such models range from normative models that maximize expected value or (subjective) expected utility (Samuelson *et al.*, 1947; Chapter 1) to descriptive models like *prospect theory* (PT: Kahneman and Tversky, 1979; Chapter 3 and the Appendix).

Expected Value Theory

The expected value of a risky choice option is the same for all decision makers, as it uses the objective

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BOX 9.1

ELLSBERG PARADOX

The Ellsberg paradox involves an "urn" with 30 red balls and 60 other balls that are either black or yellow. You don't know how many black or yellow balls there are, but that the total number of black balls plus the total number of yellow balls equals 60. The balls are well mixed so that each individual ball is as likely to be drawn as any other. You are given the choice between (A1) winning $100 if you draw a red ball or (B1) winning $100 if you draw a black ball. Which option do you select? In a second choice, you can choose between (A2) winning $100 if you draw a red or yellow ball or (B2) winning $100 if you draw a black or yellow ball. Which option do you select?

Most people choose option A1 (the red ball) in the first decision and option B2 (the black or yellow ball) in the second decision, which is inconsistent. Selecting A1 (red ball) for the first choice signals a belief that there are more red balls (30) than black balls (<30), which implies that there are more yellow balls (>30) than red balls (since black and yellow balls add up to 60). If so, then A2 (red or yellow ball, >60) would be the dominant option for the second decision. Instead, respondents prefer the option in each choice set for which they know the precise number of balls (A1, 30 balls; B2, 60 balls) and avoiding those options for which there is ambiguity about the number.

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outcome amount and probability level, multiplying each outcome by its likelihood of occurrence and adding over all probability-outcome pairs:

$$EV(X) = \sum_x p(x) \cdot x. \qquad (9.1)$$

In this equation, expected value (EV) of a gamble X is computed as the sum of all possible outcomes (x) weighted by their respective probability (p(x)). The maximization of the (monetary) EV of gamble X, first considered in the mid 17th century, was rejected as an universally applicable decision criterion based on the so-called St. Petersburg paradox, where people are found to be willing to pay only a small price (typically between $2 and $4) for the privilege of playing a game with a highly skewed payoff distribution $(1/2 \times 2 + 1/4 \times 4 + 1/8 \times 8 + \ldots)$ that has infinite expected value, as shown in Figure 9.2.

Expected Utility Theory

To resolve the St. Petersburg paradox, Bernoulli (1954/1738) proposed that people maximize expected utility (EU) rather than expected value,

$$EU(X) = \sum_x p(x)u(x) \qquad (9.2)$$

postulating that money and wealth are diminishing in the value they impart to a decision maker, as shown in Figure 9.3. The function that maps actual wealth (x) on the x-axis into utility for wealth (u(x)) is no longer linear but is "concave" in this formulation. An increase in wealth of $1000 is worth a lot more at lower initial levels of wealth (from $0 to $1000) than at higher initial levels (from $2000 to $3000). In power functions, $u(x) = x^\theta$, for example, the exponent θ is a parameter that describes the function's degree of curvature $(\theta = .50$ in Figure 9.3) and serves as an index of an individual's degree of risk aversion. Such an individual difference parameter has some face validity, as some individuals seem to resolve choices among options that differ in risk in very cautious ways $(\theta < 1)$, while others seem willing to take on great risks in the hope of even greater returns $(\theta > 1)$. Formally however, this representation of risk attitude is problematic, as discussed below in the section on Risk Attitude.

The expected utility of a risky choice option can differ between decision makers, because the same objective outcomes can map into different levels of subjective utility. von Neumann and Morgenstern (1947) provided an intuitively appealing axiomatic foundation for expected utility maximization which is covered in more detail in Chapter 1. Its axiomatic foundation made expected utility maximization a normatively attractive decision criterion not only for
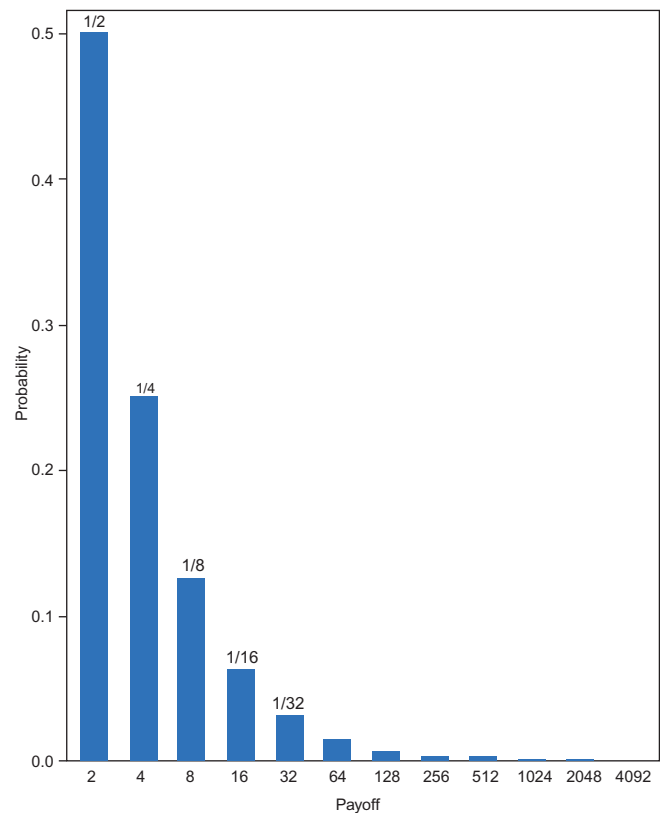

FIGURE 9.2   Payoff distribution for St. Petersburg paradox game, where a fair coin is tossed until the first "head" is scored. The payoff depends on the trial at which the first "head" occurs, with $2 if on the first trial, $4 if on the second trial, and 2^n if on the nth trial.
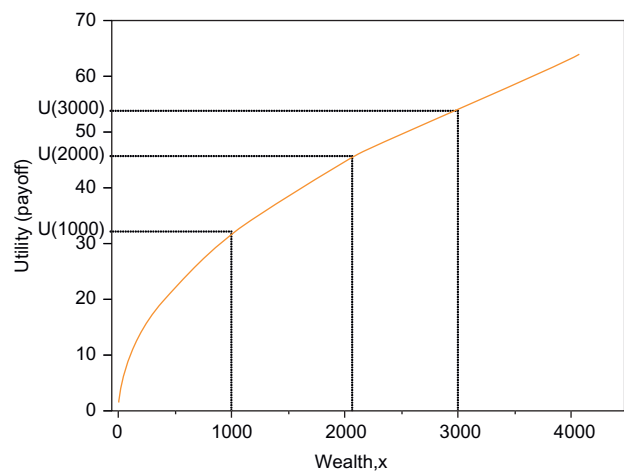
FIGURE 9.3   Concave utility function $u(x) = x^5$ which converts wealth, x, into its utility u(x). An increase in wealth from $0 to $1000 is shown to result in a greater increase in utility than an increase in wealth from $2000 to $3000.

repeated decisions in the long run, but also for unique risky decisions, so much so that it became the dominant assumption in the economic analysis of choice under risk and uncertainty for nearly half a century.

The valuation of risky choice options in PT allows for an even broader range of ways in which objective outcomes map into subjective value and objective probabilities into subjective decision weights, a model covered in Chapter 3 and in the Appendix, thus providing a broader range of processes, captured by separate model parameters, that can account for individual differences in apparent risk taking. More specifically, PT no longer assumes that the valuation of outcomes is "reference-independent"; does not depend on what the outcome can be compared to. Unlike expected utility theory, prospect theory does not assume that receipt of a $100 has the same value to a given individual, when it is the top prize in the office basketball pool or when it is the consolation prize in a lottery for $1million dollars.

Risk-Return Decomposition of Risky Options

The second basic approach to the valuation of risky choice options comes out of finance, and assumes that risky options are not represented as outcome-probability pairs but as outcome distributions that can be described by their moments, their mean as the first moment, their variance as the second moment, and their skew as the third moment. Markowitz (1959) modeled people's *willingness to pay* (WTP) for risky option X as a tradeoff between the option's first moment, its mean return $V(X)$ and its second moment, i.e, its risk $R(X)$ defined as the variance of outcomes, with the assumption that people will try to minimize level of risk for a given level of return:

$$WTP(X) = V(X) - bR(X) \qquad (9.3)$$

Traditional risk-return models in finance thus equate $V(X)$ with the EV of option X and $R(X)$ with its variance. Model parameter b describes the precise nature of the tradeoff between the maximization of

return (EV) and minimization of risk (variance) and serves as an individual difference index of risk attitude, with positive b coefficients denoting risk-aversion and negative coefficients denoting risk seeking. Figure 9.4 shows how WTP varies for two risky prospects as a function of the tradeoff parameter b. This risk-return tradeoff model is widely used in finance, for example in the *Capital Asset Pricing Model* (CAPM; Sharpe, 1964; see Bodie and Merton, 1999, for more detail). Interestingly, this model is fairly closely related to the axiomatic approaches described in Chapter 1. Recall from that chapter that the axioms of expected utility theory basically require that choosers behave as if they had monotonic utility functions. If one relaxes those axioms to allow for quadratic utility functions (functions that basically are inverted "U" shapes and thus not monotonic across the full range of outcomes), then one can show that these two approaches are equivalent (Levy and Markowitz, 1979). Other classes of utility functions derived from axiomatic approaches also have risk-return interpretations, where returns, $V(X)$, are typically modeled as the EV of the risky option, and different kinds of utility functions compatible with a given set of axioms (like monotonic, non-monotonic, quadratic non-monotonic) imply different functional forms for risk, $R(X)$ in this framework (Jia and Dyer, 1997).

Despite their normative strengths, both EU maximization and mean-variance optimization have encountered problems as descriptive models for decisions under risk and uncertainty. Experimental evidence as well as choice patterns observed in the real world suggests that individuals often do not behave in a manner consistent with either of these classes of models (Camerer 2000; McFadden 1999). Human choice behavior deviates in systematic ways, as captured originally in two classical demonstrations, the Ellsberg (1961) paradox described above and the Allais (1953) paradox. Human performance in movement tasks, where
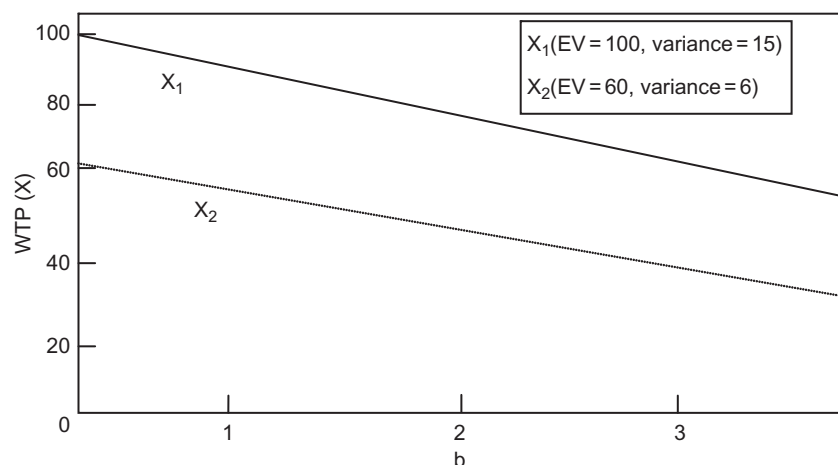

FIGURE 9.4 Willingess-to-pay (WTP) for risky investment options X_1 (EV = 100, Variance = 15) and X_2 (EV = 60, Variance = 6) as predicted by risk-return model in Eq. 9.3, for different values of b.

uncertainty of outcomes arises from the inherent variability of the motor system, has traditionally shown closer adherence to the normative EU model (Trommershauser *et al.*, 2008) and mean-variance tradeoff models (Braun *et al.*, 2011; Nagengast *et al.*, 2011), though closer analysis has revealed some deviations of observed behavior from normative model predictions there as well (Wu *et al.*, 2009).

Normative risk-return models that predict risk taking based on the first and second moment (i.e., mean/EV and variance) have been suggested not only in finance (Markowitz, 1959) but also for risky foraging decisions in evolutionary biology (Caraco, 1980). Psychophysical risk-return variants on these models (Sarin and Weber, 1993; Weber and Hsee, 1998; Weber and Milliman, 1997) attempt to do for the normative mean-variance model what prospect theory did for expected utility, namely to generalize the model to account for a broader range of behavior, making the predictions of the normative model just a special case. Weber *et al.* (2004) proposed to substitute the coefficient of variation (CV = standard deviation/EV) for the variance as a measure of risk, to explain systematic deviations in observed levels of risk taking by people and other species.

At least in some situations, extensions of risk-return models that add higher-order moments, in particular the third-order moment skewness, explain behavior better than two-moment models (and expected utility models), even if one corrects for the larger number of free parameters (e.g., Shafir *et al.*, 2003; Symmonds *et al.*, 2011). Skewness takes on a comparable role for risk-return models as probability distortion for prospect theory. Indeed, in gambles with binary outcomes, the two probability levels and the skewness of the gamble are strongly correlated. It is possible to approximate any expected utility index by a mathematical operation called Taylor series expansion that consists of a weighted sum of moments (from 1 to n), thereby providing a conceptual link between the two classes of theories (e.g., D'Acremont and Bossaerts, 2008, for more details).

This and other behavioral models of risk-taking attempt to use 150 years of psychological insights into attentional and perceptual processes to better describe and predict risk perception and risk taking (Weber and Johnson, 2009) within the category of risk-return models. People share basic perceptual, encoding, and associative processes with other animals, but also have evolved to employ abstract, symbolic representations and the ability to manipulate and communicate such representations, abilities not found in lower animals. Comparative studies that compare what people versus song birds or honey bees do in risky foraging situations can be instructive both about the similarities and the differences in behavior.

Risk Taking and Risk Attitudes

Both the EU and the traditional risk-return approach to risky decision-making model differences in choice behavior with a single parameter, referred to as "risk attitude" or "risk tolerance." This parameter simply describes the curvature of the utility function or the slope of the risk-return tradeoff and is identified empirically from a person's choices. For example, someone who is indifferent between $45 for sure and a 50/50 gamble between $0 and $100 is risk averse. The $5 difference between the EV of the gamble (which is $50) and the certainty equivalent of $45 is referred to as the risk premium. Greater risk aversion results in a larger risk premium.

The label "risk attitude" suggests that such behavior is motivated by an attitude, typically a stable construct, a personality trait. Unfortunately for the interpretation of risk-attitude as a personality trait, risk taking is far from stable across situations for most individuals (Bromiley and Curley, 1992). The same person often shows different degrees of risk taking in financial, career, health and safety, ethical, recreational, and social decisions (Hanoch *et al.*, 2006; MacCrimmon and Wehrung, 1986; Weber *et al.*, 2002). This leaves two options. Either there is no stable individual difference in people's attitude towards risk, contrary to the intuition that people differ on this dimension, or we need to find a way to measure risk attitude in a way that shows stability across domains by factoring out other (more situationally determined) contributors to apparent risk taking.

Constant and Relative Risk Aversion in EU

EU explains the fact that people's certainty equivalents for lotteries typically are below the lotteries' EV by a concave function that turns objective amounts of money into their utility equivalent, with increasing amounts of money generating increased utility (positive slope; a positive first derivative), but less and less so (thus a negative second derivative). There are a large number of functions that have this general characteristic, not just the power function shown in Figure 9.3. Economists Kenneth Arrow and James Pratt thus tried to derive some measures of risk aversion independent of the utility function's functional form. They did so by linking risk aversion and the risk premium described above and, in particular, defined two

indices that specified how a person's risk taking would change as her wealth increases. With more detail in Chapter 1, we will only describe two types of effects here. The Arrow−Pratt (Arrow, 1965; Pratt, 1964) measure of absolute risk aversion is defined as:

$$\text{ARA}_u(x) = -\,u''(x)/u'(x) \qquad (9.4)$$

where u' and u'' denote the first and second derivative of utility function u. This measure specifies the absolute value of the risk premium associated with a given lottery. As shown in Figure 9.5 (left column), exponential utility functions have the property of constant absolute risk aversion (CARA), meaning that the decision maker would pay the same risk premium to avoid the uncertainty of a given lottery (for example, $5 for the 50/50 lottery between $100 or nothing) at all levels of wealth. Arrow (1965) more realistically assumed that most people show decreasing absolute risk aversion; they would be more likely to play the gamble at higher levels of wealth, and thus pay a smaller risk premium to avoid it.

The other Arrow−Pratt measure, relative risk aversion, defined as:

$$\text{RRA}_u(x) = -(x \cdot u''(x))/u'(x) \qquad (9.5)$$

specifies the percentage value of wealth the EU maximizer is willing to put at risk. As shown in Figure 9.5 (right column), power utility functions have the property of constant relative risk aversion (CRRA), meaning that the decision maker is willing to put the same percentage of wealth at risk (e.g., 40% in Figure 9.5), at all levels of wealth. Arrow (1965) assumed that instead, most people would show increasing relative risk aversion.

Accounting for Domain Differences in Risk Taking

An early attempt to restore cross-situational consistency to the construct of risk-attitude argued that utility functions derived from risky choices, u(x), consist of two components: The first one measuring the (typically decreasing) marginal value (v(x)) of the outcome dimension (i.e., two bananas not being twice as rewarding as one banana). The second one measuring the (typically averse) attitude towards risk, u(v(x)); a disliking of the fact that in a lottery one does not know for sure what one will get, resulting in the risk premium discussed above. In such case, u(v(x)) is not as large as v(x), and gets increasingly smaller the more v(x) is at stake. If the index of the curvature of risky utility functions is the sum of these two contributions, then domain differences in curvature could be the result of different marginal values for different outcomes dimension
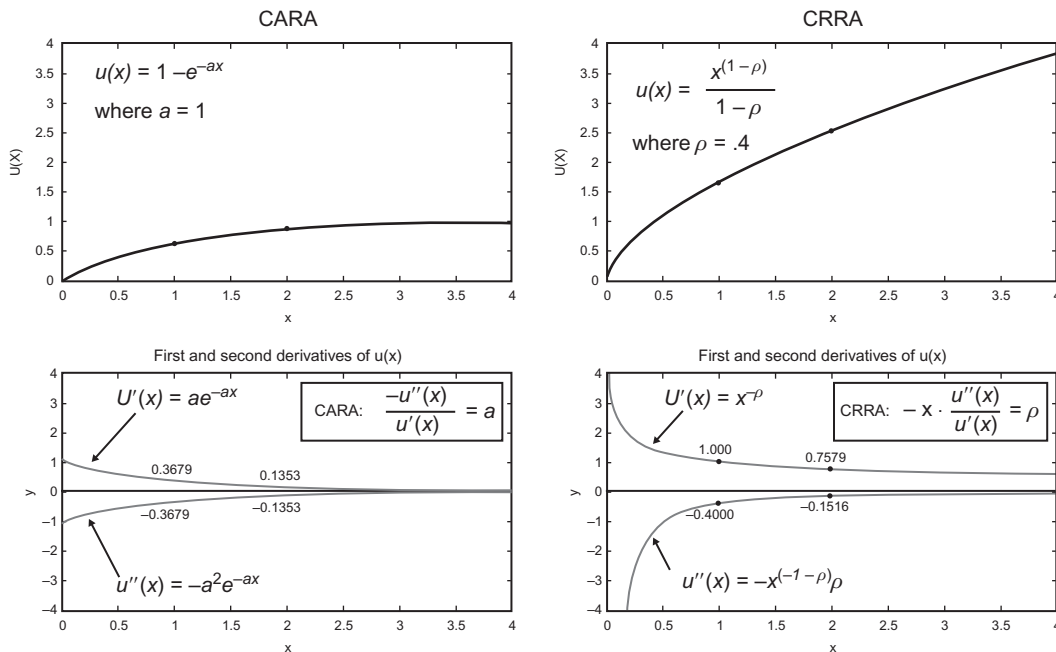

FIGURE 9.5 Constant absolute risk aversion (CARA, left column) and constant relative risk aversion (CRRA, right column). The top panel shows the described utility function, the bottom panel its first and second derivative.

(e.g., the incremental value of an additional dollar versus the incremental value of an additional life saved), while the true attitude towards the risk or uncertainty with which these outcomes were obtained could be the same across domains. Figure 9.6 provides an example from a hypothetical person who has a decreasing marginal value for additional bananas (shown in the top left panel) and slightly increasing marginal value for additional glasses of wine. As indicated in the middle panels by the straight line that maps marginal value into utility, this person happens to have a completely neutral attitude towards risk, her anticipated enjoyment of bananas or glasses of wine is the same, regardless of whether these are acquired for certain or as part of a lottery. Because of the difference in

marginal value, however, a utility function inferred from risky choices will show her to be risk-averse for bananas (bottom left panel) but risk seeking for glasses of wine (bottom right panel). Dyer and Sarin (1982) suggested that possible domain differences in riskless marginal value to be factored out of an assessment of risk attitude, and thus replaced the Arrow−Pratt measure of ARA with what they referred to as *relative risk attitude*:

$$-u''(v(x))/u'(v(x)) \qquad (9.6)$$

where $v(x)$ denotes the riskless marginal value function. When Keller (1985) compared people's Arrow−Pratt measure of risk attitude (inferred from risky choices in
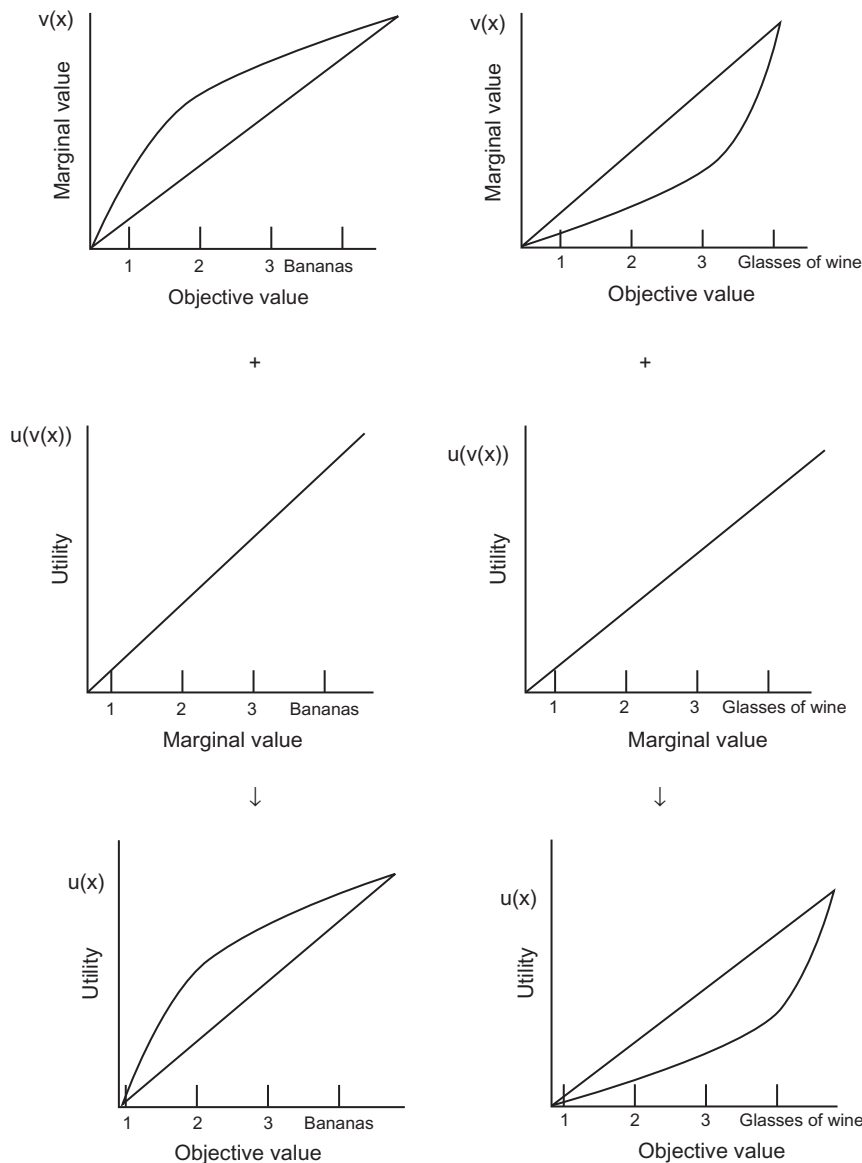

FIGURE 9.6 Decomposition of utility function u(x) (bottom row) into marginal value function v(x) (top row) and attitude towards risk function u(v(x)) (middle row).

various decision domains) to their relative risk attitudes (inferred from choices and marginal value functions in the same domains), she found that the two agreed in only a small number of cases, supporting the usefulness of unconfounding attitude towards uncertainty from nonlinear marginal value. Unfortunately, relative risk attitudes did not show any more consistency across decision domains for any given respondent than the Arrow−Pratt ARA measure.

PT does not directly address the issue of inconsistency in risk taking in different decision domains, but suggests other reasons we might see different risk-taking behavior. Because a reference point divides outcomes into relative gains and relative losses, decreasing marginal utility produces a concave function and thus risk-averse choice for gains, but a convex function and thus risk seeking choices for losses. In addition, the loss function has a steeper slope than the gain function in prospect theory (a relationship that produces *loss aversion*) and in this theory probability weighting is nonlinear. Thus PT, to the extent it is a descriptive theory of choice, suggests many reasons why risk taking may seem unstable: first, the representation of the problem might change reference points, changing the apparent risk attitude; second, to the extent that a person's decreasing marginal value or degree of loss aversion differs for outcomes in different domains, PT could account for domain differences in risk taking. Gaechter and colleagues (2007) provide evidence that loss aversion can differ for different attributes, in their case as a function of attribute importance and the decision-maker's expertise in the domain.

Behavioral extensions of risk-return models (Sarin and Weber, 1993) account for domain differences in risk taking by questioning the equating of return with EV and of risk with outcome variance. While studies of financial decisions typically find that the EV of risky investment options presented in decisions from description is a good approximation of expected returns (Weber *et al.*, 2005), survey data assessed in populations known to differ in actual risk-taking behavior suggest that risk takers judge the expected benefits of risky choice options to be higher than control groups (Hanoch *et al.*, 2006). A large and growing literature has also examined perceptions of risk, both directly (by assessing people's judgments or rankings of the riskiness of risky options and modeling these, often on an axiomatic basis) and indirectly (trying to infer the best fitting metric of riskiness from observed choices under the assumption of risk-return tradeoffs: See Weber, 2001, for more details). These studies are unanimous in their verdict that the variance or standard deviation of outcomes fails to account for perceived risk, for a variety of reasons. First, deviations above and below the mean contribute symmetrically to the mathematically defined variance, whereas perceptions of riskiness tend to be affected far more by downside variation (e.g., Luce and Weber, 1985). Second, variability in outcomes is perceived relative to average returns. A standard deviation of $+/-\$100$ is huge for a risky option with a mean return of $50 and amounts to rounding error for a risky option with a mean return of $1M. The *coefficient of variation* (CV), defined as the *standard deviation* (SD) that has been standardized by dividing by the EV:

$$\mathrm{CV}(X) = \mathrm{SD}(X)/\mathrm{EV}(X) \qquad (9.7)$$

provides a relative measure of risk, i.e. risk per unit of return. It is used in many applied domains and provides a vastly superior fit to the risk taking data of foraging animals and people who make decisions from experience (Weber *et al.*, 2004). Weber *et al.* importantly show that simple reinforcement learning models that describe choices in such learning environments predict behavior that is proportional to the CV and not the variance. Kacelnik and colleagues have explained animal risk taking that is proportional to the CV with a model called Scalar Utility Theory, which postulates that the cognitive representation of outcomes follows Weber's Law (1834), namely that the spread of the distribution of expected outcomes is proportional to its mean (e.g., Marsh and Kacelnik, 2002). While scalar utility theory can account for risk-averse foraging decisions, it fails to provide a mechanim for risk-seeking decisions that are regularly observed when sure rewards are insufficient to guarantee survival (Weber *et al.*, 2004).

Finally, affective (i.e., nonrational or non-consequential) responses to risky situations have been shown to play a large role in both the perception of the riskiness of risky choice options and in risky choice. The greater volatility in responses observed in decisions from experience relative to decisions from description, for example, where behavior is influenced more by more recent experiences, an adaptive learning rule in nonstationary environments, can be seen as resulting from the salience of emotional reactions to recent outcomes. The emotional salience of recent events, which decays over time, facilitates and mediates such learning. Familiarity with risky choice options or a risky choice domain lowers the perceptions of the choice options' riskiness.[1] The so-called *home bias effect* in investing, the tendency to invest a larger than prudent amount of

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[1]In evolutionary times, safer options provided longer periods of survival, with longer opportunities to acquire familiarity with choice options.

one's assets into stocks in one's home country or into stock of the company one works for, has been shown to be mediated by perceptions of lower risk of familiar investment opportunities (Weber et al., 2005).

Decisions from Description Versus Decisions from Experience

One important recent distinction that has resulted from such studies is that between risky decisions made from experience versus from description (Hertwig et al., 2004). In decisions-from-experience, people, birds, and bees find out about the different outcomes of available choice alternatives by repeatedly sampling them and experiencing their consequences. Positive consequences increase the likelihood that the option is chosen again, whereas negative consequences decrease it. Decisions-from-description are available primarily to human decision makers; people commonly use and process summaries about the outcomes of different choice options and their likelihood, communicated in graphic or numeric form, as in the prospectus of an investment fund or the pie charts that describe different choice options in an experiment.

When small probability events are involved, people's choices can differ drastically when decisions are made either from experience or from description (Weber et al., 2004). As noted in Chapter 3 and the Appendix, prospect theory was developed to account for choices made under description and predicts that rare events tend to be overweighted, relative to their likelihood of occurrence. Weber and colleagues (2004) showed that the reinforcement learning models that predict decisions from experience tend to underweigh rare events, an observation confirmed by Hertwig and colleagues (2004). Weber and colleagues (2004) also explored the implication of learning about outcome variability from description versus from experience for risk-return decomposition models. In a direct comparison of decisions under the two learning conditions, they empirically showed the CV to be a far better predictor of risk taking in decisions from experience for both people and other animals, but at best marginally better than the variance or standard deviation in decisions from description. As previously mentioned, they also showed more generally that associative learning of which choice options result in better outcomes from personal experience leads to choices consistent with mean-CV tradeoff models rather than mean-variance models.

The distinction between risky decisions from experience versus from description also helps explain apparent differences in risky choices between different types of decision, in particular between risky economic decisions (e.g., monetary lotteries) and risky motor tasks

(e.g., pointing tasks similar to dart throwing, where the inherent variability of the motor system gives rise to probabilistic rewards). Outcome and probability information of choice options in studies of risky economic decisions is almost exclusively communicated by description, whereas the probabilities of different outcomes of choice options for risky motor decisions are by necessity only learned from personal experience. Paralleling the results of Weber and colleagues (2004) for monetary lottery choices from description versus from experience described above, Wu and colleagues (2009) found that respondents overweighed small probability events in their risky economic decisions from description, but underweighed small probability events in their (equivalent) risky motor decisions, where the likelihood of achieving different payoffs had been learned from personal experience in a previous training session.

NEURAL REPRESENTATION OF UNCERTAINTY AND RISK

The previous sections of this chapter have shown that uncertainty and risk are important factors that impact value-based decisions. In this section, we describe what is known about how these factors are represented by the brain, and how they influence value-related brain processes. In as far as risk impacts value and value is represented in a specific set of brain regions, such as the striatum and medial prefrontal cortex, risk-mediated changes in value would be expected to be represented in these brain regions, which is indeed the case (e.g., Levy et al., 2010). Investigating and dissociating specific risk factors at the neural level can, however, be difficult because of noise in neural recordings and correlations in variants of some factors, such as CV, variance and standard deviation. For clearly distinguishable factors of uncertainty or risk, a typical approach is to manipulate one factor, while keeping the others constant, and examine the effects of such manipulation on both behavior and brain activity. This approach has revealed neural signals representing probability, risk (in the sense of variance or skew) and uncertainty in a variety of structures, both at the level of single neurons and of brain regions (for general reviews, see Bach and Dolan, 2012; Burke and Tobler, 2011a; D'Acremont and Bossaerts, 2008; Mohr et al., 2010a; Platt and Huettel, 2008; Rushworth and Behrens, 2008; Schultz et al., 2008, 2011).

In reviewing the neural correlates of choice under risk and uncertainty and of the valuation of risky choice options, we consider both animal single cell and human neuroimaging data and follow the conceptual

distinction introduced above of decomposing risky options either into outcomes and probabilities or into mean-variance-skew. Given that direct comparisons have shown that choice and no-choice tasks can elicit similar activations (Christopoulos *et al.*, 2009; Tobler *et al.*, 2009) and that choice can be predicted from no-choice activations (Lebreton *et al.*, 2009; Levy *et al.*, 2011; Tusche *et al.*, 2010), we occasionally include both types of tasks. Finally we review the differential brain activations in tasks where decisions are made from description or from experience. This last part is, by necessity, limited to human literature.

To study the neural representation of risky choice options or future outcomes in animals, their meaning needs to be signaled somehow to the animals. This is typically done by using distinct sensory stimuli that more or less probabilistically lead to larger or smaller outcomes, a relationship that is learned by trial-and-error, and thus a decision from experience. If the sensory stimuli are visual, their position on the screen is typically varied from trial to trial. Moreover, a fixed delay usually occurs between every task event. This makes it easier to dissociate stimulus- or option-related neural signals from movement- or movement preparation- and outcome-related neural activity. Alternatively, the meaning of going left or right can be kept constant within a given block of trials without using distinct stimuli. In this case, the meaning of actions or locations needs to be learned. As a consequence, in both no-choice and choice tasks, neural signals can be related to stimuli, delays, movements, or outcomes (Figure 9.7). Moreover, predictive or retrospective value signals can be attached to all of these trial events. Accordingly, value-modulating probability or risk processing would impact signals reflecting the value of stimuli presented, of the actually chosen (or the unchosen) option, or of actions (Lau and Glimcher, 2008; Matsumoto *et al.*, 2003; Padoa-Schioppa, 2007; Wunderlich *et al.*, 2010).

This chapter reviews select studies in which probability, risk (variance or skew), or uncertainty was varied. Sometimes the evidence for decomposition into components as opposed to non-decomposed value coding is somewhat difficult to ascertain. This occurs for example with increasing risk signals when subjects are risk seeking. Here separate tests of decomposed factors such as risk-free magnitude help in dissociating value from component processing. In general, one can conceive of neural decompositions in time, where the same neuron or region processes different components at different points within a task. Alternatively, decompositions can occur in space or kind, where neurons with different inputs, different neuron types or different regions preferentially process one of several tested components. In any case, it should be noted that it is

notoriously difficult to dissociate different decompositions of risky choice or representations of risk factors and evidence for one should not be taken as evidence against the other. Indeed it is perfectly possible that the brain represents risk in multiple ways and implements more than one decomposition. It should thus always be kept in mind that the observation that a single brain area represents both risk and reward does not necessarily mean that it represents risk and reward separately. It is often the case that these two properties are combined, even at the level of single neurons.

Correlates of Outcome-Probability Decompositions

Several regions have been found to encode the two main components of outcome-probability decompositions of risky options. However, because the two components have not always been tested together and directly compared, we proceed according to brain structure rather than according to component. We start with dopamine neurons (which may correspond to what has been called the "retina of the reward system", a system discussed in detail in Section 3 of this volume). Then we consider their primary projection sites in the basal ganglia and frontal cortex before finishing with structures in frontal and parietal cortex that are closer to the motor output, but likely also serve other functions such as the allocation of attention. When possible, we first consider electrophysiological recordings from non-human primates, followed by functional neuroimaging in humans.

Single dopamine neurons in the midbrain of the non-human primate show phasic (about 100 millisecond duration) responses to unpredicted liquid and food rewards delivered outside of any task. These responses increase with the magnitude of the unpredicted rewards (Tobler *et al.*, 2005). In Pavlovian and operant conditioning situations studied also in the non-human primate, rewards are delivered typically about 2 seconds after the presentation of sensory stimuli (in operant situations conditional upon a response by the animal). By repeated pairing with rewards, the animals come to learn that these sensory stimuli predict the reward. Concurrently, dopamine neurons come to show phasic activations to the reward-predicting stimuli rather than the now predicted rewards (as discussed in Chapter 14; see also Bromberg-Martin *et al.*, 2010a; Schultz, 1998).

The phasic dopamine responses to reward-predicting stimuli increase with the magnitude of reward these stimuli predict (Tobler *et al.*, 2005). Moreover, when different stimuli indicate the subject will receive either a reward of a known (strictly
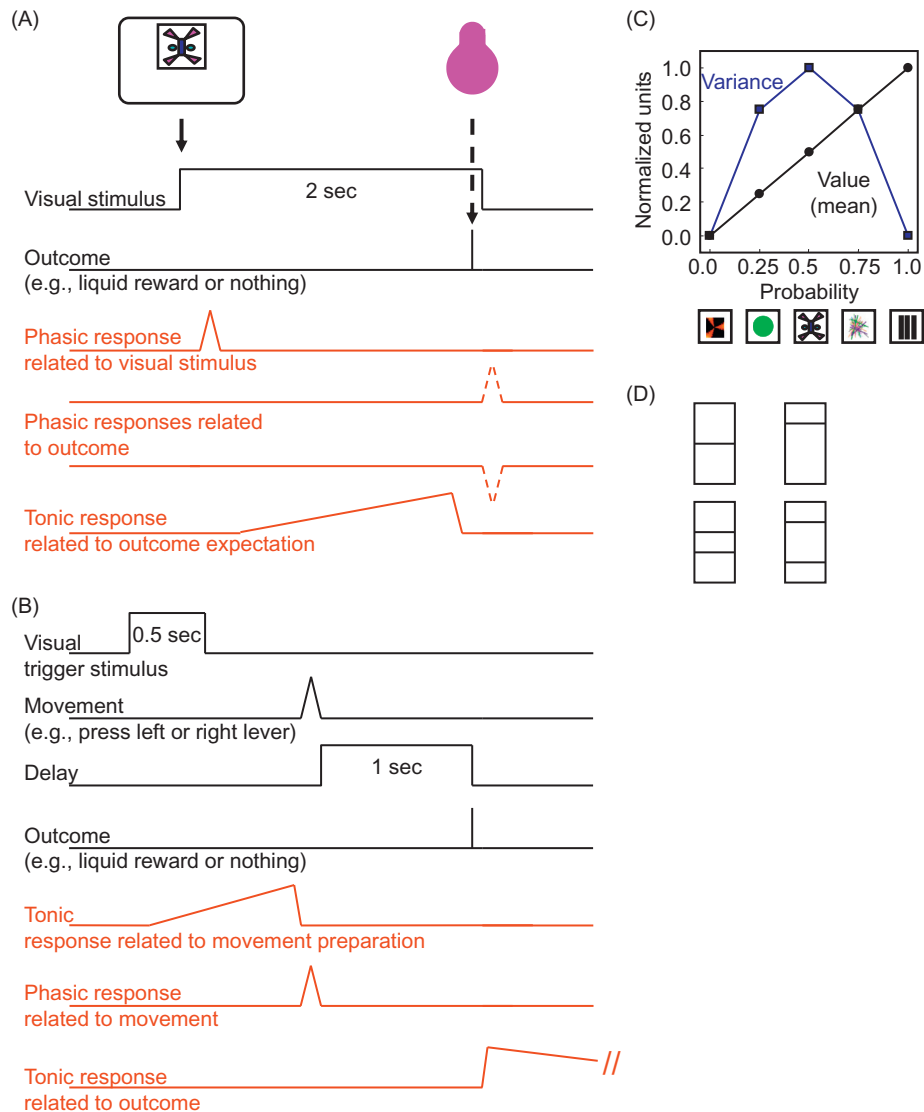
FIGURE 9.7   Typical task events and responses in electrophysiological experiments. (A) In the simplest form, visual stimuli (or stimuli from a different modality) are followed by outcomes with different probabilities or magnitudes. Outcomes can for example be juice or no juice. Typical neural responses are shown in red and can correspond to activation increases or decreases (dotted lines, only one example given). (B) Choices are often triggered by a non-specific stimulus indicating to the decision maker that a movement should now be performed and choice thereby be implemented. Sometimes, instruction stimuli precede trigger stimuli and provide information about the upcoming options (not shown). Movements are typically performed with the eye or the hand. To dissociate response-related from outcome-related activity, a delay (here 1 sec) can be used. (C) Dissociation of mean and variance by variation in probability. As probability increases from p = 0, both mean and variance increase up to p = 0.5. As probability increases further, the mean increases but variance decreases. At the bottom, example stimuli are shown, predicting reward at p = 0, 0.25, 0.5, 0.75 and 1 (see also Figure 9.10). (D) Dissociation of mean and variance by instruction stimuli. The height of horizontal bars corresponds to reward magnitude, the number of these bars corresponds to the number of different, equiprobable, outcomes. The stimuli on top are associated with different reward magnitude at certainty (difference in mean, no difference in variance risk of zero). The stimuli at the bottom are associated with different variance risk (left smaller than right) but no difference in mean (see also Figure 9.11).

positive) constant magnitude or no reward with different probabilities in binary reward distributions, the phasic dopamine responses elicited by these stimuli increase with the probability at which the reward is predicted (Fiorillo *et al.*, 2003). Finally, when both components are varied (both probability of reward and reward magnitude), the stimulus-induced responses of these neurons combine reward probability and magnitude such that reductions in one parameter can be compensated by increases in the other (Tobler *et al.*, 2005). Thus these phasic responses are indicative of value coding reminiscent of EV in Equation 9.1 and EU in Equation 9.2. Accordingly, across cells, the sensitivity to probability correlates with sensitivity to magnitude. However, some cells are more sensitive to one than the other
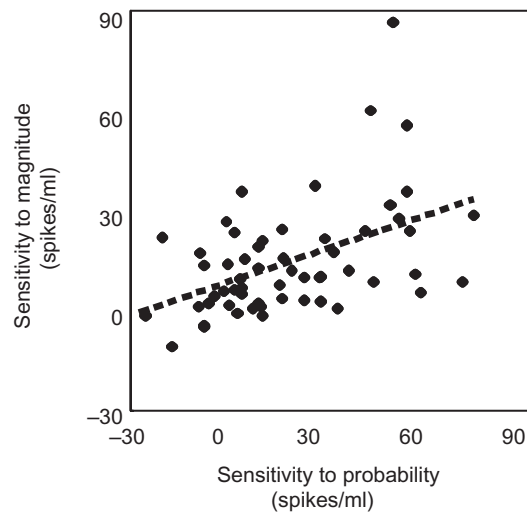
FIGURE 9.8 Positive but moderate correlation between the sensitivity of individual dopamine neurons to reward probability and magnitude ($R^2 = 0.23$). Each neuron (n = 57 neurons) was tested in situations in which distinct stimuli predicted liquid reward with increasing probability (0.15 ml at p = 0.0, 0.5, and 1.0) and magnitude (0.05, 0.15, and 0.50 ml at p = 0.5). Phasic activity induced by these stimuli was measured. A line was fit in each case, and the slopes provided independent estimates of the sensitivity of that neuron to reward probability and magnitude. For each neuron, the slopes are plotted against each other. Some neurons were more sensitive to magnitude than probability and vice versa. *Adapted with permission from Tobler et al., 2005.*

component (Figure 9.8). Together, the data suggest substantial coding of the value of risky choice options, with both outcome and probability information being coded, but with perhaps somewhat differential sensitivity to one or the other component within the population of dopamine neurons.

Primary target regions of dopamine neurons are the striatum and prefrontal cortex. In many of these regions, the decomposition question remains to be addressed fully, especially in light of the fact that many studies typically only look for a single representation of the decision variable or a single component of the decision variable. With this caveat, here is a rough summary of what is currently known: some phasically active (presumably GABAergic medium spiny projection) cells in the dorsal striatum of the rat code reward probability at the time of reward predicting stimuli with increasing firing rates (Oyama *et al.*, 2010). At reward delivery, the opposite pattern of activation occurs, i.e. activity is highest with least probable rewards and stays at baseline when reward occurs with p = 1.0 (Oyama *et al.*, 2010). Both of these findings mirror how dopamine neurons encode reward probability (Fiorillo *et al.*, 2003). By contrast, tonically active (presumably cholinergic inter-) neurons of the primate putamen are increasingly suppressed with increasing levels of reward probability (Apicella *et al.*, 2009).

Thus, they show an opposite response profile to that of dopamine and striatal projection neurons. The representation of magnitude by tonically active neurons largely remains to be studied.

Phasically active neurons in monkey striatum encode reward probability, magnitude, *and* the value of actions (e.g., Cromwell and Schultz, 2003; Hollerman *et al.*, 1998; Kawagoe *et al.*, 1998; Lau and Glimcher, 2008; Samejima *et al.*, 2005). In one task (Samejima *et al.*, 2005), for example, monkeys chose in each trial between turning a handle to the left or the right. Across blocks of trials, the value of turning left or right was changed independently by varying the probability with which each movement would result in large or small magnitudes of liquid reward. The activity of phasically active neurons in the striatum was measured during a 1 second delay period, before an unspecific signal triggered movement execution. During this preparatory phase, activity of about 40% of task-related neurons changed in an increasing or decreasing fashion with the value of one of the two possible actions either turning left or right (Samejima *et al.*, 2005). The activity of other phasically active striatal neurons reflects not the value of possible actions but the value of the chosen action, expressed around and after the time of movement execution (Lau and Glimcher, 2008). Moreover, activation increases or decreases in response to larger reward magnitude occur at the time of stimuli predicting different reward magnitudes, as well as during later task events, such as the time of delay, movement-triggering stimuli and reward (Cromwell and Schultz, 2003). Taken together, phasically active neurons of the striatum show value coding reminiscent of EV and EU in Equations 1 and 2, often specifically during action preparation or for chosen actions.

Functional neuroimaging has revealed similar outcome and probability signals in the striatum as those identified by dopamine and striatal neuron single cell recordings. Dopamine areas are somewhat more difficult to image because of their smaller size and susceptibility to MRI-related artifacts, but blood oxygenation level dependent (BOLD) signals in the striatum are likely to at least partly be due to the effects of dopamine (Düzel *et al.*, 2009; Pessiglione *et al.*, 2006). This is consistent with the notion that dopamine neurons encode probability and magnitude information primarily in an increasing fashion, making such activation more easily detectable with functional magnetic resonance imaging methods than the often equal proportions of neurons that show either increasing or decreasing activation in other regions, also within the striatum (see above and below). In any case, for a variety of tasks in which different stimuli predict rewards with different probability and magnitude, stimulus-

induced BOLD activations increase with predicted probability, magnitude and their combination (Abler et al., 2006; Berns and Bell, 2012; Breiter et al., 2001; Burke and Tobler, 2011b; Christopoulos et al., 2009; Delgado et al., 2004; Hsu et al., 2005; Knutson et al., 2001, 2005; Levy et al., 2010; Preuschoff et al., 2006; Shenhav and Greene, 2010; Studer et al., 2012; Tobler et al., 2007, 2008; Tom et al., 2007; Yacubian et al., 2006, 2007). Accordingly, reductions in one parameter can be compensated, in units of BOLD signal, by increases in the other (Tobler et al., 2007).

Precise tests between competing representations of value need to be performed but some findings suggest that value-related BOLD-activations in the striatum are well-captured by a value function of the kind proposed by prospect theory (Tom et al., 2007) and show features not contained in the many alternative theories. For example, at least some striatal activations are now known to be reference-dependent (e.g., Breiter et al., 2001; Tom et al., 2007; Park et al., 2012), to increase more steeply for losses than for gains (Tom et al., 2007) and to reflect probability distortion (Hsu et al., 2009; see also below), all features of the representation of outcome and probability information in prospect theory but not EU theory.

While the fMRI studies mentioned so far support the notion that a single decision variable capturing both probability and magnitude is encoded in these areas, some studies have shown spatial decomposition of risky options into probability and magnitude information within the striatum, in the sense that some subregions are preferentially active to one or the other of these components (Berns and Bell, 2012; Tobler et al., 2007; Yacubian et al., 2007). In one example, Yacubian et al.s' subjects had to place a bet of adjustable magnitude (either €1.00 or €5.00) on either one or four out of eight hidden cards as specified by the experimenter. If the bet was placed on a hidden card that turned out to be the previously selected 'target card,' subjects won the amount of the bet, else they lost it. Activity was analyzed during an anticipatory period, before the outcome was revealed. Probability-related activations arose in more anterior and lateral regions of the ventral striatum whereas magnitude-related activations arose in more posterior and medial regions (Figure 9.9; Yacubian et al., 2007). Thus, when assessed with fMRI, magnitude and probability information about risky choice options are at least sometimes spatially decomposed within the human striatum. Despite this decomposition, it is worth keeping in mind that probability- and magnitude-related activations overlap substantially in large subparts of the striatum.

Reward value-related information is also processed in immediate target regions of the striatum, such as the pallidum, and their target regions, such as the
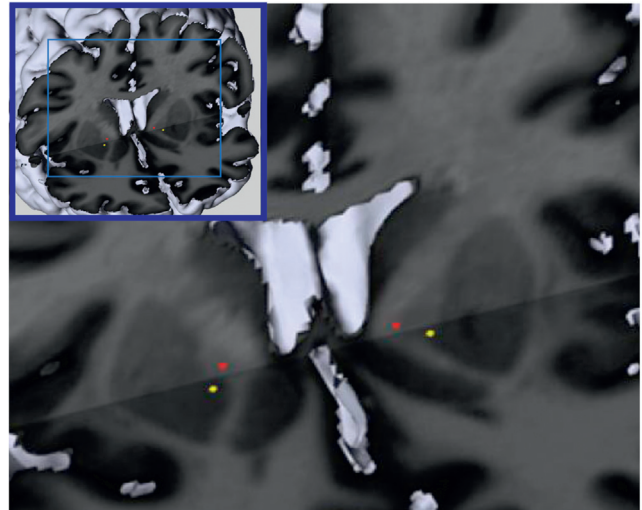

FIGURE 9.9　Spatial decomposition of probability and magnitude in the human ventral striatum. Probability-related peak activation is shown in yellow, magnitude-related peak activation in red. The probability-related peak was significantly more lateral and anterior than the magnitude-related peak. The view is from the front to the back of the brain. Inset on top left shows how brain has been sectioned to reveal the striatum. *Adapted with permission from Yacubian et al., 2007.*

lateral habenula. Neurons in the internal globus pallidus, the substantia nigra pars reticulata (Joshua et al., 2009) and the lateral habenula (Matsumoto and Hikosaka, 2009) respond to reward (and punishment: Bromberg-Martin et al., 2010b) probability. Neurons in the lateral habenula code reward probability in an inverse manner to dopaminergic neurons, showing increased suppression of firing rates to stimuli predicting reward with increasing probability (Matsumoto and Hikosaka, 2008). The habenula could feed this probability information to dopamine neurons (for example via a glutamatergic projection to the primarily GABAergic rostromedial tegmental nucleus: Hong et al., 2011; Jhou et al., 2009). Together, a variety of subcortical regions process reward probability but decomposition into probability versus magnitude largely remains to be investigated.

Prefrontal cortex is connected to both the striatum and the dopaminergic midbrain. Simultaneous recordings from neurons in lateral prefrontal cortex (lPFC), orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC) have revealed reward probability and magnitude signals in all three regions (Kennerley et al., 2009, 2011; for magnitude in OFC see also Padoa-Schioppa and Assad, 2006; Morrison and Salzman, 2009; for probability in OFC Van Duuren et al., 2009). About equal numbers of responsive neurons fire in an increasing or decreasing fashion to increasing probability or magnitude (Kennerley et al., 2009; 2011),

although some studies also find primarily increasing relations to magnitude, for example in the dorsal ACC (Hayden and Platt, 2010). When found, increasing and decreasing neuron types tend to be spatially inter-mingled rather than clustered (Kennerley et al., 2009, 2011). Similar proportions of neurons in the different areas encode probability and magnitude. However, the ACC contains a higher proportion of probability and magnitude responsive neurons than lPFC and OFC. Moreover, ACC neurons are more likely to encode both probability and magnitude (and even further value-modulating parameters such as effort) than neurons in the other two regions. It is therefore conceivable that lPFC and OFC may in this setting decompose probability and magnitude more strongly than ACC.

The coding of both outcome and probabilities in single ACC, OFC and lPFC neurons could form the neural substrate of risky option value computations such as the EV or EU combination of outcomes and probabilities described in Equations 9.1 and 9.2. In line with this prediction, dorsal ACC neurons appear to integrate overall reward probability and magnitude of choice options during choice trials (Amiez et al., 2006). However, in principle it is also conceivable that separate neurons encoding either probability or magnitude both innervate neurons elsewhere and that these latter neurons perform the combination. In any case, assuming that motor output should be affected by both rather than only one of these decision variable components, neurons or regions (and activities within them) closer to the motor output should show less decomposed and more combined coding of probability and magnitude. And in fact this seems to be the case. One example comes from the supplementary eye field (SEF), a region involved in processing eye movements that is also innervated by the OFC. SEF neurons respond in an increasing or decreasing fashion to increases of probability and magnitude during saccade preparation (So and Stuphorn, 2010). The measured activations always change with the combination of magnitude and probability and reflect value, both in choice and no-choice situations. The majority of probability and magnitude coding SEF neurons also process the specific direction of upcoming saccades, compatible with a neural signal that combines value with motor aspects of future actions.

BOLD activations related to probability or magnitude occur in cingulate cortex (Fujiwara et al., 2009; Studer et al., 2012), medial prefrontal (Breiter et al., 2001; Kahnt et al., 2010; Kim et al., 2006; Knutson et al., 2005; Plassmann et al., 2007, 2010; Tobler et al., 2007; Tom et al., 2007) superior frontal (Studer et al., 2012) and lateral prefrontal (Mohr et al., 2010b; Plassmann et al., 2007, 2010; Tobler et al., 2007, 2009) regions. Moreover, OFC responses to rewards as well as to reward-predictive stimuli represent high versus low reward magnitude information in distributed patterns (Kahnt et al., 2010). Thus, even though electrophysiological recordings in animals report more heterogeneous signals in cortical regions (firing rate both increases and decreases with magnitude) than say dopamine neurons (which primarily show firing increases), neuroimaging methods can nevertheless be used to study the representation of magnitude in such regions. Common or combined coding of both components has been observed in cingulate cortex for error magnitude and probability (Brown and Braver, 2007), in medial orbitofrontal (Studer et al., 2012; Symmonds et al., 2010) and in lateral prefrontal cortex for reward magnitude and probability (Tobler et al., 2007). By contrast, preferential activations to probability rather than magnitude arise in parts of medial prefrontal cortex (Knutson et al., 2005).

In the parietal cortex, probability and magnitude information is typically spatially restricted to response fields. For example, neurons in the lateral intraparietal area reflect probability in blocks of trials in which the probability of a rewarded saccade varies (Platt and Glimcher 1999) or the probability that a saccade to a target would result in a reward (Sugrue et al., 2004). Moreover, they also respond to expected reward magnitude and in several cases it has been shown that single neurons respond to both probability and magnitude (Platt and Glimcher, 1999). The activity of single neurons in a more medial and dorsal region of parietal cortex (the parietal reach region) reflects reward probability and magnitude between the sensory and motor phases of a memory-guided reaching task. The activity of these neurons correlates with differential reward information during a memory period (1.2−1.8 seconds) after a stimulus, the size of which predicts reward at high or low probability or high or low magnitude (Musallam et al., 2004). Thus, value components are coded in a common representation by parietal neurons.

Accordingly, there appears to be relatively little evidence for separate coding of probability and magnitude in parietal cortex although preferential BOLD activation to probability rather than magnitude arises in the junction of parietal and temporal cortex (Studer et al., 2012). Note though, that neurons in the posterior parietal cortex represent the number of items presented on a screen irrespective of the sensory properties of the items (e.g. Nieder et al., 2006; Roitman et al., 2012). In other words, activations under many conditions scale with numerical magnitude, which may contribute to decomposing outcome magnitude of countable rewards, such as might occur in a more naturalistic analysis of the number of fruits on a tree. And indeed, human research has confirmed a role for

parietal cortex in numerical cognition (e.g., Piazza et al., 2007; for review see Nieder and Dehaene, 2009; Roitman et al., 2012). Such numerical representations could in turn suggest that some parietal regions may preferentially code magnitude.

In summary, a wide variety of regions and neurons encode the components of outcome-probability decompositions. Importantly, probability and outcome information is also processed where it should be processed, in value-coding regions of the brain such as dopamine neurons, striatum, OFC and medial prefrontal cortex. Although encoding of the two components has not always been studied simultaneously, it seems plausible to assume that at least some neural substrates combine them in a way roughly equivalent to the manner described in Equations 9.1 and 9.2. In the domain of value and decision regions, these include dopamine neurons, striatum and regions of lateral and medial prefrontal cortex. When combined with spatial or motor information, such representations may also contribute to the representation of action value in striatal, frontal and parietal regions.

Although hemodynamic responses appear to support decomposition into probability and magnitude to at least some degree, single cell evidence for this decomposition is scarce. While some neurons in regions coding both factors may be more sensitive to one than the other factor, to our knowledge no single neuron recording study has so far identified a brain region that codes probability in the absence of coding magnitude. Accordingly, the dissociations reported in the fMRI domain await confirmation by single cell electrophysiology. In principle it is conceivable that in some subregions of the striatum, neurons coding one factor are more prevalent than those coding the other, but so far this has not been found. In this sense, it remains an open question whether probability and magnitude are decomposed at the level of brain regions when investigated with single cell electrophysiology in tasks where animals learn magnitudes and probabilities from experience.

Correlates of Risk-Return Decompositions

Experimentally distinguishing risk-return decompositions from outcome-probability decompositions is difficult because the two are usually strongly correlated. Studies attempting to test between these decompositions, have used two types of design. In the first one, magnitude is kept constant and probability is varied such that variance risk can be dissociated from probability, because variance risk is highest at p = 0.5 and lower at both lower and higher probabilities (Figure 9.7C; exemplified in Fiorillo et al., 2003;

Preuschoff et al., 2006; Tobler et al., 2007). In the second type of design, probability is kept constant but magnitude varies such that variance risk varies (Figure 9.7D; exemplified in Christopoulos et al., 2009; McCoy and Platt, 2005; Mohr et al., 2010b; O'Neill and Schultz, 2010; Tobler et al., 2009). This latter approach follows the notion of increases in risk using a mean-preserving spread (Rothschild and Stiglitz, 1970), and thus it cannot simultaneously assess sensitivity to differences in returns (mean rate-of-reward).

There is at least some evidence that the decomposition of risky options into mean, variance and skew is implemented in the brain. While the above described phasic response of dopamine neurons may encode the mean, a more sustained activity has been shown to reflect a risk parameter (Fiorillo et al., 2003; but see Niv et al., 2005 for an alternative, model-inspired, view, according to which the activity reflects errors in the prediction of reward traveling back from the time of reward to the time of the reward predicting stimulus, Fiorillo et al., 2005 for further elaboration on the data contradicting the alternative view and Pan et al., 2005 for models not requiring back-propagation). This more sustained activity is low for probabilities predicting the occurrence of reward or no reward with a probability close to 0 or 1, and high for maximal variance or standard deviation (a probability of 0.5 for the occurrence of reward or no reward; Figure 9.10). Sustained activity thus corresponds to the inverted
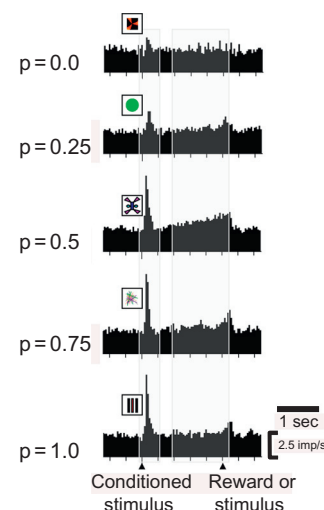

FIGURE 9.10 Temporal decomposition of value and risk in population of dopamine neurons. Different conditioned stimuli (at time of left arrowhead) predicted reward (2 s later, right arrowhead) of a given magnitude at the probabilities indicated on the left. Value of stimuli increases with probability and so does phasic response induced by reward-predicting stimuli (left shading). By contrast, variance risk and sustained response building up to time of outcome (right shading) are highest at p = .5. *Adapted with permission from Fiorillo et al., (2003).*

U-shape with which variance changes as a function of probability (Figure 9.7C). The sustained activity of dopamine neurons also increases when probability is kept constant at p = 0.5 but variance is increased by increasing the magnitude range of the two possible outcomes (similar to Figure 9.7D; Fiorillo et al., 2003). If the faster phasic responses are taken as coding the mean, these slower tonic activations suggest a dissociation between first and second-order moments (mean and variance) in the temporal domain.

The dissociation of mean and variance in phasic and tonic dopamine responses is mirrored in corresponding phasic and sustained striatal BOLD responses (Dreher et al., 2006; Preuschoff et al., 2006). Just like phasic dopamine responses, striatal activations have been found which scale with the probability that a reward will ensue, whereas sustained responses increase with variance risk. This pattern could correspond to the temporal dissociation of mean and variance shown by dopamine neurons. Note though, that dissociating phasic and tonic components is more difficult with fMRI than with single cell electrophysiology, because of the lower temporal resolution of fMRI.

Variance risk signals also occur in single neurons of the OFC (O'Neill and Schultz, 2010). Following the rationale of employing a mean-preserving spread, O'Neill and Schultz associated distinct visual stimuli with different levels of variance risk, but the same mean in a no-choice task (Figures 9.7D and 9.11). In separate tests, risk (variance) was kept constant but the mean was varied. They found that OFC activity increased or decreased with variance risk, most prevalently for cue presentation and reward delivery. Of course, a monotonic increase in activity in response to increasing variance risk in risk-seeking individuals could also indicate a value response. However, the separate tests with constant (zero) variance but varying magnitude, revealed both decomposed and combined value and variance signals in single neurons of the monkey orbitofrontal cortex (Figure 9.11; O'Neill and Schultz, 2010). Interestingly, some of these cue-induced variance activations have a relatively short latency (100 milliseconds). This suggests that the OFC could be the source of the later risk-dependent activity modulations in dopamine neurons (Fiorillo, 2011; Fiorillo et al., 2003; Sugam et al., 2012).

In risk-seeking monkeys, the activity of neurons in the posterior cingulate cortex is sensitive to risk as captured by the CV (CV = standard deviation/EV) (McCoy and Platt, 2005). The firing rates of these neurons have been shown to scale with the CV of the options monkeys choose with eye movements, particularly when the risky target was in the neuron's receptive field. In the McCoy and Platt experiment, the probability of
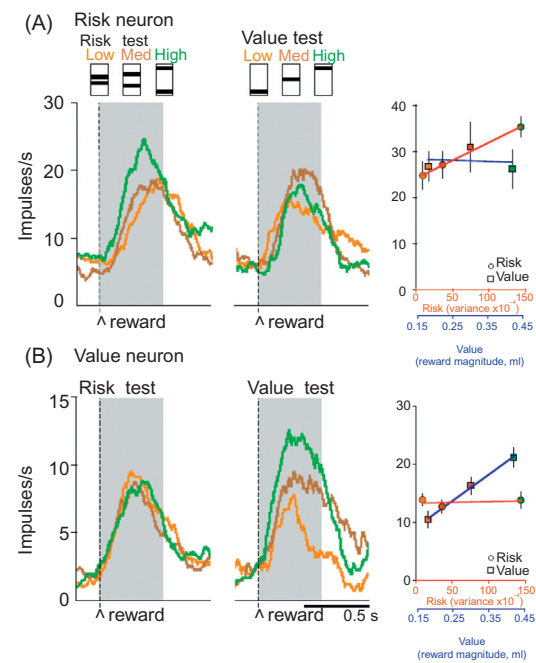

FIGURE 9.11 Separate processing of risk and return in OFC neurons. (A) Example of OFC neuron that coded risk but not return (labeled as value). (B) Example of OFC neuron that coded return but not risk. Neurons were tested in situations with increasing risk (e.g., standard deviation: 0.03, 0.06 and 0.12 ml at constant mean of 0.3 ml) and return (0.18, 0.3, 0.42 ml at constant standard deviation of 0 ml). Left panels show firing rates during risk trials, right panels during value (return) trials. In both examples, activations occurred upon reward delivery, even though risk has actually returned to 0 at this point in time; such activation patterns could correspond to an unsigned prediction error (see also Ogawa et al., 2013). Separate responses as the ones shown here were more prevalent (n = 183) than common responses (n = 13). *Adapted with permission from O'Neill and Schultz, (2010).*

reward remained constant at p = 0.5 and risk varied by variation of a mean-preserving spread. Yet, the degree of decomposition of the neural signal into mean and variance (or CV), and comparison with outcome-probability dissociations remain to be investigated. Some of the cells they studied maintained increased firing rates preceding risky choices also during delay periods before the onset of eye movements, suggesting a role for the posterior cingulate in biasing eye movements to options with higher subjective value or salience. And it is conceivable that this information may subsequently be passed on to posterior parietal cortex which codes the relative subjective value of eye movements (Dorris and Glimcher 2004; Sugrue et al 2004) and contributes to directing attention (e.g., Arcizet et al., 2011; Reep and Corwin, 2009). Although the parietal cortex has been discussed primarily in terms of outcome-probability approaches to value (see above), a formal assessment of the two types of decomposition is pending also for this region.

In addition to the tonic variance-risk signals mentioned above, fMRI evidence has also revealed phasic variance-risk signals. These occur particularly in the insula (Burke et al., 2013; Mohr et al., 2010b; Preuschoff et al., 2006, 2008), the lateral orbitofrontal cortex (Preuschoff et al., 2006, Tobler et al., 2007), the cingulate cortex, preferentially during choice as opposed to no-choice situations (Burke and Tobler, 2011b; Christopoulos et al., 2009; Smith et al., 2009), and the posterior parietal cortex (Symmonds et al., 2011). Together with phasic mean signals in the striatum (e.g., Burke and Tobler, 2011b; Christopoulos et al., 2009; Hsu et al., 2005; Yacubian et al., 2007) and elsewhere, these phasic variance activations result in a spatial decomposition of risk and return. Thus, at least in some situations, the two first moments of outcome distributions seem to be coded separately (see next paragraph for data on the third moment). Moreover, risk signals are combined with mean signals in the lateral prefrontal cortex such that higher variance reduces mean-related activity in risk-averse subjects and enhances it in risk-seeking subjects (Tobler et al., 2009).

Neuroimaging studies have investigated not only the first and second moment but also the third one, skewness, or skew. Skew captures how asymmetric outcome distributions are, as shown in Figure 9.1. Although there is individual variation, at least some evidence suggests that animals and investors seek positive skew (Caraco and Chasin, 1984; Kraus and Litzenberger, 1976; Shafir et al., 2003), which roughly corresponds to the possibility of very large gains. Human subjects in the lab are similarly sensitive to skewness (Burke and Tobler, 2011b; Symmonds et al., 2011; Wu et al., 2011a). The insula appears to play a multi-faceted role in skew processing. Some insula subregions show activation increases with increasing skew, such that activation follows the pattern positive skew > no skew > negative skew, irrespective of preferences (Burke and Tobler, 2011b), a finding taken to suggest that skew is coded in these areas explicitly. Others are primarily active for positive skew (Symmonds et al., 2011) or scale with skew preference such that activation for positive skew is stronger the more subjects seek positive skew (Burke and Tobler, 2011b; Symmonds et al., 2011). Still others act like asymmetry detectors such that activation follows (positive ∼ negative skew) > no skew (Burke and Tobler, 2011b; Wu et al., 2011a). Skew-like signals have been observed also in the striatum (increasing activation with increasingly positive skew; Symmonds et al., 2011; Wu et al., 2011a) and dorsomedial prefrontal cortex (increasing activation for increasingly negative skew only; Symmonds et al., 2011).

In summary, knowledge about mean-variance-skewness decompositions of risky choice options as distinct from outcome-probability decompositions is relatively scarce, in part because the two decompositions are correlated for many experimental designs and many studies only look for evidence for one type of decomposition. However, both single cell electrophysiological and neuroimaging have found some evidence for risk-return decompositions, using specialized designs. More specifically, mean-variance decompositions appear to be implemented in the OFC and the temporal profile of phasic (mean) and tonic (variance) dopamine firing and striatal BOLD-responses can be described by a mean-variance approach (but see below). The insula appears to decompose risk processing by separate representations of variance and skewness risk and to represent both the objective level of skewness as well as people's skewness preference.

Neural Basis of Risk Attitude

Risk attitude determines whether risk enhances or reduces the value of options, either by determining the curvature of the utility function in outcome-probability decompositions or by the weights given to higher-order moments in mean-variance-skew decompositions. Monkeys are commonly risk seeking in laboratory situations that provide relatively small rewards, despite the fact that this reduces the overall income from their decisions under at least some conditions (Fiorillo, 2011; Hayden et al., 2011; McCoy and Platt, 2005; O'Neill and Schultz, 2010; So and Stuphorn, 2010). Given the two alternative decompositions of risky choice option representation, the question arises how individual differences in risk attitude impact the neural activations during risky choice. Take dopamine neurons, for example. Does the degree of risk seeking exhibited by monkeys affect the phasic responses that scale with probability and magnitude, or the tonic responses that scale with variance risk? Just as the two representations are not mutually exclusive, the effects of individual or group differences in risk attitude on the respective representations do not need to be mutually exclusive, of course. However, at first sight modulation of phasic responses may appear more compatible with an outcome-probability account, and modulation of tonic responses with a mean-variance account. In agreement with the former, the stimulus-induced phasic activation of dopamine neurons is enhanced in risk-seeking monkeys when the stimulus is associated with risky outcomes, compared to a safe outcome of the same expected value (Fiorillo, 2011). Moreover risk enhances phasic dopamine release as measured with voltammetry in risk-preferring rats but reduces it in risk-averse ones (Sugam et al., 2012). These findings could suggest that phasic value

activations of dopamine neurons track individual risk attitude and thus provide evidence for an outcome-probability approach in describing the activity of dopamine neurons. Still, since the study did not examine evidence for an effect of risk attitude on the representation of a mean-risk decomposition, this is not necessarily evidence against such a decomposition. Another monoamine, serotonin, also appears to play a role in the subjective valuation of risk. Reducing serotonin levels below normal levels induces risk seeking in monkeys, suggesting that more serotonin renders them more risk averse (Long *et al.*, 2009).

Orbitofrontal activations induced by large variances, or risks, are enhanced in risk-seeking animals (Roitman and Roitman, 2010). Consistent with this result, patients with OFC-lesions are risk- and ambiguity-neutral and thus less ambiguity- and risk-averse than IQ-matched control patients with temporal lobe lesions (Hsu *et al.*, 2005). Variance risk-related BOLD signals in lateral and medial prefrontal cortex before a risky choice or after presentation of stimuli associated with variable outcomes are modulated by risk attitude (Christopoulos *et al.*, 2009; Mohr *et al.*, 2010b; Tobler *et al.*, 2007, 2010). Since risk-averse subjects would have a positive coefficient b that multiplies the variance risk according to Equation 9.3 above (where $-b \times R(x)$ takes value away from the gamble as a function of its riskiness, and risk-seeking ones a negative b (where $-b \times R(x)$ adds value to the gamble as a function of its riskiness), these results have been taken as evidence that the risk attitude parameter proposed by the risk-return model of finance theory appears to be represented in the brain. However, note again that it is difficult to experimentally separate the curvature of the utility function from risk attitude processing as proposed by risk-return decompositions — these are highly collinear properties under most of the experimental conditions examined so far. Accordingly, the data of this paragraph are compatible with either mathematical approach to the study of risk.

Correlates of Ambiguity Versus Risk

Outcome responses of dorsal anterior cingulate neurons are reduced when the probabilities with which the outcomes would occur are unknown as opposed to when they are known (Hayden *et al.*, 2011). Given that one and the same outcome elicits more or less surprise depending on how much it was expected, this response pattern could indicate reduced surprise with these kinds of outcomes, which are often called ambiguous. Compared to risk, such ambiguity elicits higher mean BOLD signals in orbitofrontal cortex (Hsu *et al.*, 2005; Levy *et al.*, 2010), amygdala (Hsu *et al.*, 2005) and

in some studies also in parietal cortex (Bach *et al.*, 2011; Huettel *et al.*, 2006). Some of these regions may, by this increased activity, signal that information is missing. But in any case, the distinct preferential activations to risk versus ambiguity suggest some neural separation of traditional probabilities (and described by variance and risk) and ambiguity.

Although some of the components of risky choice models may be represented separately, it is likely that once they are valued, common regions are engaged (particularly when value is combined with motor information as mentioned above). One illustration of this principle comes from a neuroimaging experiment on risk and ambiguity. Subjects chose between a constant reference option that had a 50% chance of winning $5 and an option that varied in both the amount and either the winning probability (risk) or the level of ambiguity. In such a task, the subjective value of risky and ambiguous choice options is commonly coded in the striatum, the medial prefrontal cortex and the posterior cingulate cortex (Figure 9.12; Levy *et al.*, 2010). This latter finding converges with the notion that the striatum and medial prefrontal cortex play a general role in the valuation of choice options. Moreover, these results raise the possibility that regions representing different decomposed factors as discussed above feed into regions for determination of the subjective value of choice options.

Experience Versus Description

The research giving rise to prospect theory used primarily symbolically described probabilities rather than probabilities learned through repeated experience, and
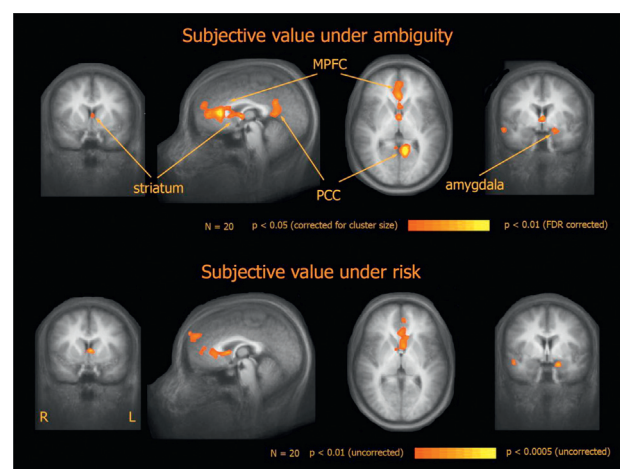

FIGURE 9.12 Common processing of subjective value (SV) under risk and ambiguity. Acitvation in similar areas correlated with SV under ambiguity (top) and under risk (bottom). MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; L, left; R, right. *Reprinted from Levy* et al., *(2010).*

adhered to the outcome-probability decomposition of risky options. Comparing the neural correlates of experience-based and description-based decisions is an exciting but novel field. Accordingly, when Hsu et al. (2009) symbolically communicated probabilities to human subjects they found that activity in the left dorsolateral PFC activation showed a probability distortion corresponding to the inverted-S shape suggested by prospect theory (see Chapter 3 and the Appendix), an overvaluation of small and undervaluation of large probabilities. In agreement with this notion, a second study has shown that when probability is initially described symbolically to subjects, this same region in dorsolateral PFC shows inverted-S coding (Tobler et al., 2008). By contrast, when experience with such outcomes is prolonged, the fit of activation with an inverted-S decreases while at the same time the fit with a linear probability encoding function increases, suggesting that experience changes the representation of reward probability in dorsolateral prefrontal brain regions. Interestingly, a similar but contralateral dorsal prefrontal region is also activated as ambiguity gradually turns into risk with experience (Huettel et al., 2006).

Activation of dorsomedial prefrontal regions matches distortions as they arise when probabilities are described symbolically in a classical lottery task. By contrast, activation of more ventromedial regions matches distortions as they arise when probabilities are experienced in an equivalent motor task (Wu et al., 2011b). Similarly, S-shaped disortions of probability, which are common when probabilities are experienced (see above, Hertwig et al., 2004; Weber et al., 2004), occur in ventral prefrontal regions (Tobler et al., 2008). Finally, striatal activity may reflect distorted probabilities primarily when they are described (Hsu et al., 2009) rather than experienced (Tobler et al., 2008; see also Abler et al., 2006).

The impact of experience has also been studied with respect to risk as variance in the context of mean-variance-skewness decompositions of risky options (FitzGerald et al., 2010). Variance learned from experience accelerates choice reaction time and activates anterior cingulate cortex more than described variance; by contrast, described variance activates anterior insula cortex more than learned variance. At the time of outcomes the cingulate cortex also tracks volatility and may use this information to adjust learning rates (Behrens et al., 2007). Taken together, regions involved in implementing behavioral flexibility such as the prefrontal cortex (but see Schoenbaum et al., 2007) and the anterior cingulate cortex, appear to mediate the effects of experience on the representation of decomposed parameters.

CONCLUSIONS

Much of the literature we have reviewed shows how widespread the representation of value information is in the brain. Sensory and motor regions receive such information from value-coding regions. Given that value is influenced by a variety of factors, it is not very surprising to find scaling of neural activity with such factors also in sensory and motor regions. Which approach the core value processing regions use to decompose the value of risky options may appear at first sight to be a rather arcane question. Nevertheless, for successful behavior, gauging the risk of outcomes is often just as important as predicting how valuable they will be. We have reviewed two approaches to decomposing risky options: outcome-probability and mean-variance-skewness. The former represents risky choice options as a set of outcome-probability pairs; the latter represents the outcome distributions of risky choice options with its first three statistical moments. It is still a matter of investigation what type of decomposition is preferentially implemented by behavior and by the brain, under what type of conditions and potentially by what types of people. Indeed research that tries to discriminate between these two approaches, or to control for one while investigating the other, is relatively scarce (Burke and Tobler, 2011b; Christopoulos et al., 2009; Dreher et al., 2006; Fiorillo et al., 2003; Mohr et al., 2010b; O'Neill and Schultz, 2010; Preuschoff et al., 2006, 2008; Tobler et al., 2007, 2009; Weber et al., 2004) and more of these studies are currently needed. As both approaches have distinct advantages and disadvantages, they are not fully redundant. Outcome-probability decompositions are particularly useful for learning about simple choice options, whereas mean-variance-skewness decompositions facilitate handling cases where many outcomes are possible (D'Acremont and Bossaerts, 2008). Accordingly, it would not come as a surprise if both types of decomposition were implemented in the brain.

So far, the literature suggests that risk signals occur in the brain's valuation system, including dopamine neurons, striatum, OFC and medial prefrontal cortex but also more dorsal and posterior regions such as posterior cingulate and parietal cortex. However, value and risk signals seem to be partially separated in time (phasic value versus sustained risk responses in dopamine neurons and the striatum) and in spatial location within the brain (e.g., mean in striatum versus variance and skewness risk in cingulate and insula). Regions and neurons sensitive to subjective value combine various components, for example in the phasic responses of dopamine neurons, general value representations of the striatum and the medial prefrontal cortex and risk

attitude-dependent integrations in the lateral prefrontal cortex. It is noteworthy that the brain represents decompositions of risky options in a way that can be elegantly described with approaches from economics and finance theory, and by their often less elegant but more descriptively accurate generalizations from psychology. In turn, such neural representations may lend face-value to these theoretical approaches in the form of biological plausibility.

Acknowledgments

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