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# Research report

# Prospect theory on the brain? Toward a cognitive neuroscience of decision under risk

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#### **Abstract**

Most decisions must be made without advance knowledge of their consequences. Economists and psychologists have devoted much attention to modeling decisions made under conditions of risk in which options can be characterized by a known probability distribution over possible outcomes. The descriptive shortcomings of classical economic models motivated the development of prospect theory (D. Kahneman, A. Tversky, Prospect theory: An analysis of decision under risk. Econometrica, 4 (1979) 263–291; A. Tversky, D. Kahneman, Advances in prospect theory: Cumulative representation of uncertainty. Journal of Risk and Uncertainty, 5 (4) (1992) 297–323) the most successful behavioral model of decision under risk. In the prospect theory, subjective value is modeled by a value function that is concave for gains, convex for losses, and steeper for losses than for gains; the impact of probabilities are characterized by a weighting function that overweights low probabilities and underweights moderate to high probabilities. We outline the possible neural bases of the components of prospect theory, surveying evidence from human imaging, lesion, and neuropharmacology studies as well as animal neurophysiology studies. These results provide preliminary suggestions concerning the neural bases of prospect theory that include a broad set of brain regions and neuromodulatory systems. These data suggest that focused studies of decision making in the context of quantitative models may provide substantial leverage towards a fuller understanding of the cognitive neuroscience of decision making.

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# 1. Introduction

Most decisions entail some degree of risk. Should one purchase an extended warranty on a new car or take one's chances? Dash through the middle of a busy street or take the long way via a crosswalk? Opt for surgery or radiation therapy for a tumor? Invest retirement savings in the stock market or treasury bills? From mundane dilemmas to life-defining decisions, we are usually forced to choose without knowing in advance what the consequences will be.

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The study of decision making under risk has been a major thrust of microeconomics for most of the last century; however, it has only received significant attention from psychologists in the last few decades. Early behavioral studies provided simple cognitive accounts of preferences between chance gambles, with more recent studies exploring the role of affect, motivation, and social context in such decisions. The newest, and possibly most exciting, frontier in this research area is the effort to understand the ways in which neural processes mediate risk-taking behavior. The last few years have seen a tremendous push by neuroscientists and their collaborators to apply modern neurophysiology methods (e.g., ERP, fMRI, and animal models) to economic decisions. The purpose of this paper is to take

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stock of some of these early efforts and relate them to more traditional behavioral research on decision making under risk.

The lay concept of "risk" is associated with hazards that fill one with dread and/or are poorly understood [112]. In a financial context, people tend to think of risk as increasing with the magnitude and probability of potential losses [79]. Decision theorists, in contrast, view risk as increasing with the variance in the probability distribution of possible outcomes. Thus, a bet that offers \$100 if a fair coin lands heads and nothing if it lands tails is more "risky" than an option that offers \$60 if a fair coin lands heads and \$40 if it lands tails. Economists following Knight [68] distinguish risk from uncertainty. Decisions under risk entail options that have well-specified or transparent outcome probabilities, such as a bet on a coin toss or a lottery with a known number of tickets. Decisions under uncertainty, by contrast, entail options whose outcomes depend on natural events such as a victory by the home team or a rise in interest rates, so that probabilities must be estimated by the decision maker with some degree of vagueness or imprecision. In the present paper, we focus our attention primarily on decisions under risk for the following practical reasons: (1) Risk is a simpler domain that is better understood and more thoroughly characterized by behavioral decision theorists, (2) most extant work in cognitive neuroscience at this early juncture speaks more directly to decisions under risk than to decisions under uncertainty.

The following section of this paper provides a brief historical overview of traditional models of decision making under risk, culminating in prospect theory [61,123], the most influential descriptive account that has emerged to date. Next, we distill the most important facets of prospect theory and map them onto relevant neuroscience studies. In particular, we draw on basic neurophysiology, computational modeling, and clinical neuroimaging to advance a novel framework that describes several candidate mechanisms underlying risky choice behaviors. Finally, we conclude by suggesting promising avenues for future research. Naturally, at this early juncture, our conclusions are preliminary and highly speculative.

#### 2. The Classical theory of decision under risk

The primitives in most traditional models of decision under risk and uncertainty are acts, states, and consequences. An *act* is an action that is associated with a set of possible *consequences* that depend on which one of a set of possible *states* of the world obtains. To illustrate, consider a gambler who considers betting a dollar on a single spin of a roulette wheel (see Table 1). The gambler considers two possible acts: Bet on "red" or bet on "black." The consequence of this decision depends on which state of the world will occur after the roulette wheel is spun: The ball will land in one of the 18 red numbers, one of the 18

Table 1 A decision matrix for a hypothetical roulette gambler

ACTS	States			
	Red $(P = 18/38)$	Black (P = 18/38)	Green $(P = 2/38)$	
Bet \$1 on red Bet \$1 on black	Gain \$1 Lose \$1	Lose \$1 Gain \$1	Lose \$1 Lose \$1	

Acts are listed as row headings, states as column headings and possible consequences are listed as cell entries (in italics).

black numbers, or one of the two green numbers (0 or 00). Our roulette gambler faces a decision under *risk* because the objective probabilities of each relevant state of the world are transparent. If she were instead considering a bet on either the home team or visiting team winning an upcoming basketball game, our hypothetical gambler would be facing a decision under *uncertainty* because she would be forced to assess the probability that each team wins with some degree of subjectivity and vagueness.

The origin of decision theory is usually traced back to a 17th century correspondence between Pascal and Fermat that laid the mathematical foundation for probability theory. Following this work, theorists asserted that decision makers ought to choose the option that offers the highest expected value (EV).

$$EV = x_1p_1 + x_2p_2 + ... + x_np_n$$

$$=\sum_{i=1}^{n}x_{i}p_{i}\tag{1}$$

where  $x_i$  is the (monetary) outcome of state i and  $p_i$  is the probability of state i.

A decision maker is said to be "risk neutral" if she is indifferent between a gamble and its expected value; she is said to be "risk averse" if she prefers a sure payment to a risky prospect of equal or higher expected value; she is said to be "risk-seeking" if she prefers a risky prospect to a sure payment of equal or higher expected value. Thus, expected value maximization assumes a neutral attitude toward risk. For instance, a decision maker who employs this rule will prefer to receive \$100 if a fair coin lands heads (and nothing otherwise) to a sure payment of \$49, because the expected value of the gamble ( $\$50 = .5 \times \$100$ ) is higher than the value of the sure thing (\$49). Expected value maximization is problematic because it does not allow decision makers to exhibit risk aversion—it cannot explain, for example, why people would prefer a sure \$49 over a .5 probability of \$100 or why they would purchase insurance. Swiss mathematician Daniel Bernoulli [17] advanced a solution to this problem when he asserted that people do not evaluate options by their objective value but rather by their utility or "moral value." Bernoulli observed that a particular amount of money (say, 100 ducats) is valued more when a person is poor than when she is wealthy and, therefore, marginal utility decreases as wealth increases. This gives rise to a utility function that is concave over states of wealth (see Fig. 1). In Bernoulli's model, decision makers choose the option with highest expected utility (EU):

$$EU = \sum_{i=1}^{n} u(x_i)p_i \tag{2}$$

where  $u(x_i)$  represents the utility of obtaining outcome  $x_i$ . For example, a concave utility function implies that the utility gained by receiving \$50 is more than half the utility gained by receiving \$100 and, therefore, a decision maker with such a utility function should prefer \$50 for sure to a .5 probability of receiving \$100.

Expected utility gained greater currency in economic theorizing when von Neumann and Morgenstern [124] articulated a set of axioms that are necessary and sufficient to allow one to represent preferences by expected utility maximization. The axioms were relatively simple and on their surface seemed unassailable. For instance, one prominent formulation of expected utility theory [107] relies on an axiom known as the "sure-thing principle": If two acts yield the same consequence when a particular state obtains, then a person's preferences among those acts should not depend on the particular consequence (i.e., the "sure thing") that they have in common. To illustrate, consider a game in which a coin is flipped to determine which fruit will be included in your lunch. Suppose that you would rather receive an apple if a fair coin lands heads and a cantaloupe if it lands tails (a, H; c, T) than receive a banana if the coin lands heads and a cantaloupe if it lands tails (b, H; c, T). If this is the case, you should also prefer to receive an apple if the coin lands heads and dates if the coin lands tails (a, H; d, T) to a banana if it lands heads and dates if it lands tails (b, H; d, T).

The sure-thing principle is necessary to establish that utilities of outcomes are weighted by their respective probabilities. However, it was not long before the descriptive validity of expected utility theory and its axioms were called into question. The most powerful challenge has come to be

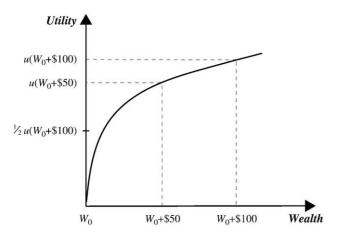


Fig. 1. A hypothetical utility function, demonstrating the concave relationship between wealth and utility.

Table 2
The Allais Paradox presented as a lottery

	Ticket numbers		
	1	2–11	12-100
A	\$1 M	\$1 M	\$1 M
В	0	\$5 M	\$1 M
C	\$1 M	\$1 M	0
D	0	\$5 M	0

known as the "Allais Paradox" [4,5]. Consider the following choices:

**Decision 1.** Choose between (A) \$1 million for sure and; (B) a 10% chance of receiving \$5 million, an 89% chance of receiving \$1 million, and a 1% chance of receiving nothing.

**Decision 2.** Choose between (C) an 11% chance of receiving \$1 million and; (D) a 10% chance of receiving \$5 million.

Most people choose (A) over (B) in the first decision and (D) over (C) in the second decision, which violates the sure-thing principle. To see why, consider options (A) through (D) as being payment schemes attached to different lottery tickets that are numbered consecutively from 1 to 100 (see Table 2). Note that one can transform options (A) and (B) into options (C) and (D), respectively, merely by replacing the common consequence (receive \$1 M if the ticket drawn is 12–100) with a new common consequence (receive \$0 if the ticket drawn is 12–100). Thus, according to the sure-thing principle, a person should favor option (C) over option (D) if and only if he or she prefers option (A) to option (B), and the dominant pattern of preferences violates this axiom. Typically, people explain their choice in decision (1) as a preference for certainty over a possibility of receiving nothing; meanwhile, they explain their choice in decision (2) as a preference for a higher possible prize given that the difference between a probability of .10 and .11 is not very large.

The Allais Paradox is perhaps the starkest and most celebrated violation of expected utility theory. In the years since it was articulated, numerous studies of decision under risk have shown that people often violate the principle of risk aversion that underlies much economic analysis. Table 3 illustrates a common pattern of risk aversion and risk seeking exhibited by participants in studies of Tversky and Kahneman [123]. Let C(x, p) be the *certainty equivalent* of the prospect (x, p) that offers to pay x with probability p (i.e., the sure payment that is deemed equally attractive to the risky prospect). The upper left-hand entry in the table shows that the median participant was indifferent between receiving \$14 for sure and a 5% chance of receiving \$100. Because the expected value of the prospect is only \$5, this observation reflects risk-seeking behavior.

Table 3a reveals a fourfold pattern of risk attitudes: Risk seeking for low-probability gains and high-probability

Table 3
Depiction of risk attitudes for pure and mixed gambles (from [123])

	Gain	Loss
(a) Pure gambles		
Low probability	C(\$100, .05) = \$14 risk seeking • Overweight low probabilities • (Concave value function)	C(-\$100, .05) = -\$8 risk aversion • Overweight low probabilities • (Convex value function)
High probability	C(\$100, .95) = \$78 risk aversion • Concave value function • Underweight high probabilities	C(-\$100, .95) = -\$84 risk seeking  • Concave value function  • Underweight high probabilities
(b) Mixed gambles		
	0 ~ (-\$100, 0.5; \$202) risk aversion • Loss aversion	

The primary mechanisms driving these risk attitudes, according to prospect theory, are listed as bullet points below each entry (with mechanisms that temper these patterns listed in parentheses). (a) The fourfold pattern of risk attitudes for pure gain or pure loss gambles. C(x, p) is the median certainty equivalent of the prospect that pays x with probability x. (b) Acceptability pattern for mixed (gain/loss) gambles. The median participant required a 50% probability of \$202 to make up for a 50% probability of losing \$100 (that is, a possible gain of \$202 made this gamble equally attractive to receiving nothing).

losses, coupled with risk aversion for high-probability gains and low-probability losses. Choices consistent with this fourfold pattern have been observed in several studies [41,52,61,92]. Risk seeking for low-probability gains may contribute to the attraction of gambling, whereas risk aversion for low-probability losses may contribute to the attraction of insurance. Risk aversion for high-probability gains may contribute to the preference for certainty, as in the Allais [4] paradox, whereas risk seeking for high-probability losses is consistent with the common tendency to undertake risk to avoid facing a sure loss.

# 3. Prospect theory

The Allais Paradox and fourfold pattern of risk attitudes are accommodated neatly by prospect theory [61,123], the leading behavioral model of decision making under risk, and the major work for which psychologist Daniel Kahneman was awarded the 2002 Nobel Prize in economics. According to prospect theory, the value V of a simple prospect that pays x with probability y (and nothing otherwise) is given by

$$V(x,p) = v(x)w(p), \tag{3}$$

where v measures the subjective value of the consequence x, and w measures the impact of probability p on the

attractiveness of the prospect (see Fig. 2). Prospect theory differs from expected utility theory in a number of ways. First, the utility function u(.) over states of wealth is replaced with a value function v(.) over gains and losses relative to a reference point (usually the status quo), with v(0) = 0. Second, this subjective value function is not weighted by outcome probabilities but rather by a decision weight, w, that represents the impact of the relevant probability on the valuation of the prospect. Decision weights are normalized so that w(0) = 0 and w(1) = 1. Note that w is not interpreted as a measure of degree of belief—a person may believe that the probability of a fair coin landing heads is one-half but afford this event a weight of less than one-half in the evaluation of a prospect. Third, unlike expected utility theory, prospect theory explicitly incorporates principles of framing and editing that allow for different descriptions of the same choice to give rise to different decisions.

# 3.1. Characterizing the value and weighting functions

According to prospect theory, the shapes of the value function v(.) and weighting function w(.) reflect the psychophysics of diminishing sensitivity. That is, the marginal impact of a change in outcome or probability diminishes with distance from relevant reference points. For monetary outcomes, the status quo generally serves as the reference point distinguishing losses from gains, so that the function is concave for gains and convex for losses (see Fig. 2A). Concavity for gains contributes to risk aversion for gains as with the standard utility function (Fig. 1). Convexity for losses, on the other hand, contributes to risk seeking for losses. For instance, the disvalue of losing \$50 is more than half the disvalue of losing \$100, which will contribute to a preference for the gamble (lose \$100 with probability .5) over the sure loss (lose \$50 for sure).

The prospect theory value function is also steeper for losses than gains, a property known as *loss aversion*. People typically require more compensation to give up a possession than they would have been willing to pay to obtain it in the first place (e.g., [65]) and the tendency for the relative disadvantages of alternatives to loom larger than the relative advantages supports a bias toward the status quo (e.g., [106]). In the context of decision under risk, loss aversion gives rise to risk aversion for mixed (gain–loss) gambles so that, for example, people typically reject a gamble that offers a .5 chance of gaining \$100 and a .5 chance of losing \$100 (see Table 3b).

<sup>&</sup>lt;sup>1</sup> There are a number of subtle differences between the original formulation of prospect theory advanced in Kahneman and Tversky [61] and the cumulative version advanced in Tversky and Kahneman [123]. In the present paper, we will confine most of our discussion to choices among risky prospects that offer a single positive and/or negative outcome, for which these formulations coincide.

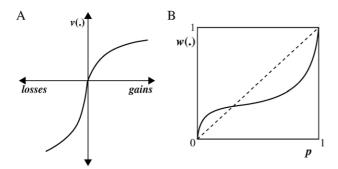


Fig. 2. Value and weighting functions from prospect theory. (A) Value function v as a function of gains and losses. (B) Weighting function w for gains as a function of the probability p of a chance event.

Following Kahneman and Tversky [63], we can parameterize the value function as a power function<sup>2</sup>:

$$v(x) = \begin{cases} x^{\alpha} & x \ge 0 \\ -\lambda(-x)^{\beta} & x < 0 \end{cases} \tag{4}$$

where  $\alpha$ ,  $\beta > 0$  measure the curvature of the value function for gains and losses, respectively, and  $\lambda$  is the coefficient of loss aversion. Thus, the value function for gains (losses) is increasingly concave (convex) for smaller values of  $\alpha(\beta) < 1$ , and loss aversion is more pronounced for larger values of  $\lambda > 1$ . Tversky and Kahneman [123] estimated median values of  $\alpha = .88$ ,  $\beta = .88$ , and  $\lambda = 2.25$  among their sample of college students.

For probability, there are two natural reference points: Impossibility and certainty. Hence, diminishing sensitivity implies an inverse-S-shaped weighting function that is concave near zero and convex near one, as depicted in Fig. 2B. It explains the fourfold pattern of risk attitudes (Table 3a), because low probabilities are overweighted (leading to risk seeking for gains and risk aversion for losses) and high probabilities are underweighted (leading to risk aversion for gains and risk seeking for losses). It also explains the Allais Paradox because the weighting function is steeper between .99 and 1 than it is between .10 and .11 (so that the difference between a 0.99 chance of a prize and a certainty of a prize in Decision 1 looms larger than the difference between a .10 and .11 chance of a prize in Decision 2). This inverse-S-shaped weighting function seems to be consistent with a range of empirical findings (see [1,23,49,96,126,128,129]).

Following Lattimore et al. [74], the weighting function can be parameterized in the following form (which assumes that the relation between w and p is linear in a log-odds metric):

$$w(p) = \frac{\delta p^{\gamma}}{\delta p^{\gamma} + (1 - p)^{\gamma}} \tag{5}$$

where  $\delta > 0$  measures the elevation of the weighting function and  $\gamma > 0$  measures its degree of curvature. The

weighting function is more elevated (exhibiting less overall risk aversion for gains, more overall risk aversion for losses) as  $\delta$  increases and more curved (exhibiting more rapidly diminishing sensitivity to probabilities around the boundaries of 0 and 1) as  $\gamma$  < 1 decreases (the function exhibits an S-shaped pattern that is more pronounced for larger values of  $\gamma > 1$ ). Typically, the decision weights of complementary events sum to less than 1 (w(p) + w(1 - p) < 1), a property known as subcertainty ([61]). This property is satisfied whenever  $\delta < 1$ . For chance prospects entailing possible gains, Tversky and Fox [122] estimated values of  $\delta$  and  $\gamma$ for gains from the median responses of their sample of college students to be .69 and .69, respectively. Tversky and Kahneman [123] found similarly shaped weighting functions for losses and gains when they fitted a single parameter function to their data. A more recent investigation using the two-parameter function above suggests that whereas the curvature parameter  $\gamma$  does not vary significantly between losses and gains, the elevation parameter  $\delta$  tends to be significantly higher for losses than gains [3].

The prospect theory parameters  $\alpha$ ,  $\beta$ ,  $\lambda$ ,  $\gamma$ , and  $\delta$  can all be estimated for individuals using simple choice tasks on computer. Although the typically measured values of these parameters suggest an S-shaped value function  $(0 < \alpha, \beta < 1)$  with loss aversion  $(\lambda > 1)$  and an inverse-S-shaped weighting function  $(0 < \gamma < 1)$  that crosses the identity line below .5  $(0 < \delta < 1)$ , there is considerable heterogeneity between individuals in these measured parameters. For instance, in a sample of ten psychology graduate students evaluating gambles involving only the possibility of gains, Gonzalez and Wu [49] obtained measures of  $\alpha$  ranging from .23 to .68,  $\delta$  ranging from .21 to 1.51, and  $\gamma$  ranging from .15 to .89.

In sum, prospect theory explains attitudes toward risk via distortions in the shapes of the value and weighting functions. The parameters obtained by Tversky and Kahneman [123] and Tversky and Fox [122] suggest that the fourfold pattern of risk attitudes for simple prospects that offer a gain or a loss with low or high probability (Table 3a) is driven primarily by curvature of the weighting function because the value function is not especially curved for the typical participant in those studies (with  $\alpha = \beta =$  .88). Pronounced risk aversion for mixed prospects that offer an equal probability of a gain or loss (Table 3b) is driven almost entirely by loss aversion because the curvature of the value function is similar for losses versus gains and the decision weights are similar for gain versus loss components.

# 3.2. Framing and editing operations

Expected utility theory and most normative models of decision making under risk assume the principle of description invariance: Preferences among prospects should not be affected by how they are described. Decision makers act as if they are assessing the impact of options on

<sup>&</sup>lt;sup>2</sup> The power function implies constant relative risk aversion—as the stakes of a prospect (x,p) are multiplied by a constant k then so is the certainty equivalent of that prospect, C(x,p) so that C(kx,p) = kC(x,p).

final states of wealth. Prospect theory, in contrast, explicitly acknowledges that choices are influenced by how prospects are cognitively represented in terms of losses versus gains and their associated probabilities.

First, this representation can be systematically influenced by the way in which options are described or "framed." Recall that the value function is applied to a reference point that distinguishes between losses and gains. A common default reference point is the status quo. However, by varying the description of options, one can influence how they are perceived. For instance, decisions concerning medical treatments can differ depending on whether possible outcomes are described in terms of survival versus mortality rates [84]. Second, the weighting function is applied to probabilities of risky outcomes that a decision maker happens to identify. The description of gambles can influence whether probabilities are integrated or segregated and, therefore, affect the decisions that people make [62]. For instance, people were more likely to favor a .25 chance of \$32 over a .20 chance of \$40 when this choice was described as a two-stage game in which there was a .25 chance of obtaining a choice between \$32 for sure or an .80 chance of \$40 (in the two-stage game version people are apparently attracted to the pseudo-certainty of receiving \$32). People may also actively reframe prospects, adopting aspirations as reference points [51] or persisting in the adoption of old reference points, viewing recent winnings as "house money" [120].

Third, people may mentally transform or "edit" the description of prospects they have been presented. The original formulation of prospect theory [61] suggested that decision makers edit prospects in forming their subjective representation. Consider prospects of the form ( $x_1, p_1$ ;  $x_2$ ,  $p_2$ ;  $x_3$ ,  $p_3$ ) that offer  $x_i$  with (disjoint) probability  $p_i$  (and nothing otherwise). In particular, decision makers are assumed to (1) combine common outcomes of a prospect—for example, a prospect that offers (\$10, .1; \$10, .1) would be naturally represented as (\$10, .2); (2) segregate sure outcomes from the representation of a prospect—for instance, a prospect that offers (\$20, .5; \$30, .5) would be naturally represented as \$20 for sure plus (\$10, .5); (3) cancel shared components of options that are offered together—for example, a choice between (\$10, .1; \$50, .1) or (\$10, .1; \$20, .2) would be naturally represented as a choice between (\$50, .1) or (\$20, .2); (4) simplify prospects by rounding uneven number or discarding extremely unlikely outcomes—for example, (\$99, .51; \$5, .0001) might be naturally represented as (\$100, .5); (5) reject options without further evaluation if they are obviously dominated by other options—for instance, given a choice between (\$18, .1; \$19, .1; \$20, .1) or (\$20, .3), most people would naturally reject the first option because it is stochastically dominated by the second.

# 3.3. Summarizing the key elements of prospect theory

Prospect theory has been very successful in explaining a wide range of empirical regularities that have been documented outside the laboratory (see [22])—from the premium that equities demand over annuities in the market [16] and the tendency to hold on to losing stocks too long while selling winners too early [90] to the attractiveness of state lotteries (cf. [25]). It also provides a flexible framework for modeling empirical regularities and individual differences that have been observed in laboratory studies.

The key elements of prospect theory may be summarized as follows (see Table 4). The first two elements refer to the valuation of outcomes, the next two refer to the weighting of probabilities, and the last two refer to the representation of prospects.

# 3.3.1. Curvature of the value function

The value function is concave for gains and convex for losses (e.g., [1,2,49]). This has been typically attributed to the psychophysics of diminishing sensitivity. Generally, the curvature of the value function is relatively small and, therefore, may not contribute substantially to measured risk attitudes; Tversky and Kahneman [123] estimated  $\alpha = \beta = .88$  using the median response of participants, which are close to values obtained by several other researchers (however, Gonzalez and Wu [49] estimated  $\alpha = .49$ ). Curvature of the value function plays a greater role in riskless choice (see e.g., [118,119]).

#### 3.3.2. Loss aversion

Losses loom larger than equivalent gains. This is modeled by a value function with a loss limb that is steeper than the gains limb (the parameter  $\lambda > 1$  in Eq. (4) above). In risky choice, this is manifested as strong risk aversion for mixed (gain–loss) gambles. For instance, most people would reject a gamble for which they gain \$100 if a fair coin lands heads and lose \$100 if a fair coin lands tails. Typically, losses have at least twice the impact of equivalent gains (i.e.,  $\lambda \geq 2$ ) so that people would require a 50% chance of gaining at least \$200 to make up for a 50% of losing \$100 ([123], see also [2,64,63] for an explanation of why loss aversion is needed to explain risk aversion for mixed gambles see [97]).

#### 3.3.3. Curvature of the weighting function

The inverse-S-shaped weighting function is characterized by a tendency to overweight low probabilities and underweight moderate to high probabilities (modeled by  $\gamma < 1$  in Eq. (5)). This shape is typically attributed to the psychophysics of diminishing sensitivity [1,19,49,122,123]. The robust fourfold pattern of risk attitudes (Table 3) suggests that distortions in probability weighting are more pronounced than distortions in value: Although the shape of the value function implies risk aversion for gains and risk seeking for losses, this pattern seems to be reversed for low-probability events and reinforced for high-probability events.

<sup>&</sup>lt;sup>3</sup> For examples of framing effect in a riskless context, see Thaler [118,119]).

Table 4
Summary of the major components of prospect theory

Component	Phenomenon	Description	Manifestations in risky choice	Relevant parameters
Value function	Sensitivity to gains and losses	Value function is: - Concave for gains - Convex for losses	Risk aversion for medium probability gains     Risk seeking for medium probability losses	$0 < \alpha < 1$ for gains $0 < \beta < 1$ for losses
	Loss aversion	Value function steeper for losses than gains	Risk aversion for mixed (gain-loss) gambles	λ > 1
Weighting function	Diminishing sensitivity to probability near 0, 1	Weighting function is - Convex near 0 - Concave near 1	Fourfold pattern of risk attitudes	<i>γ</i> < 1
	Subcertainty	w(p) + w(1-p) < 1	Overall tendency toward risk aversion for gains and risk-seeking for losses	$\delta < 1$
Prospect representation	Framing effects	Choices are influenced by perceived reference points and associated probabilities	<ul> <li>Passive framing (e.g., reflection and pseudocertainty effects)</li> <li>Active framing (e.g., house money and aspiration effects)</li> </ul>	N/A
	Editing operations	People spontaneously edit their representations to simplify decision tasks	<ul> <li>Combination of common outcomes</li> <li>Segregation of sure outcomes</li> <li>Cancellation of identical outcomes</li> <li>Simplification and rounding</li> <li>Detections of dominance</li> </ul>	N/A

# 3.3.4. Elevation of the weighting function

The sum of decision weights for complementary probabilities is typically less than one (i.e., w(p) + w(1-p) < 1), a principle known as "subcertainty." This implies a weighting function that crosses the identity line below .5 (modeled by  $\delta < 1$  in Eq. (5)). Loosely speaking, this reflects a more pronounced tendency to underweight probabilities than to overweight them. The overall attractiveness of risky prospects varies from individual to individual, and this is modeled by individual differences in the elevation of the weighting function (see [49]).

#### 3.3.5. Framing effects

Cognitive representations of prospects influence how they are evaluated, in terms of losses and gains relative to some reference point and the association of probabilities with consequences. These representations can be systematically influenced by the way in which options are described so that people make different choices among the same prospects that are characterized in different ways.

# 3.3.6. Editing operations

When subjectively representing prospects, decision makers may actively edit prospects from the way in which they are originally described, usually to simplify the representation.

#### 3.4. Affective substrates of prospect theory

Prospect theory provides a characterization of decision making under risk that emphasizes cognitive operations of representation and the psychophysics of diminishing sensitivity. However, it is becoming increasingly evident that affect plays a prominent role in risky choice (for reviews, see [76,85,105]). In particular, a number of recent studies point to an affective component underlying observed features of the value and weighting functions. This is of particular interest given the involvement of limbic brain regions in decision making, to be discussed further below.

# 3.4.1. Curvature of the value function

The degree of curvature of the value function represents a decision maker's sensitivity to increasing units gained or lost. Although cognitive appraisal of scope (i.e., number of units) surely plays a role in the representation of value for fungible resources such as money, several researchers have argued that people may also rely on their affective response to possible outcomes as a "common currency" for assessing value and making tradeoffs among disparate items (e.g., [93,113] cf. [87]). To the extent that decision makers assess value based on affective reactions, they should be relatively insensitive to the quantity of the item being evaluated (for several examples, see [66]) and the corresponding value function will, therefore, be relatively flat. Indeed, Hsee and Rottenstreich [55] find that the value function exhibits greater curvature (i.e., lower slope above a minimum number of units gained or lost) for consequences that are more "affect-rich." For instance, in one study, participants were asked how much they would be willing to pay to save various numbers of pandas that were each represented either by cute pictures (an "affect-rich" representation) or dots (an "affect-poor" representation). In the affect-poor (dots) conditions, participants were willing to donate about twice as much if they had been

asked about four pandas than if they had been asked about a single panda. However, in the affect-rich condition (photos), participants were willing to pay about the same amount if they had been asked about one panda or four pandas.

#### 3.4.2. Loss aversion

Although the affective sources of loss aversion are poorly understood, loss aversion does appear to be moderated by affect. For example, the affective richness of consumption goods seems to enhance differences in perceived value of gaining versus losing these items. Dhar and Wertenbroch [29] report that loss aversion is more pronounced for "hedonic goods" (goods rated "pleasant and fun, something that appeals to the senses...") than utilitarian goods (goods rated "useful, practical, functional..."). For instance, in one study, participants were about equally likely to choose a \$7 gift certificate for a music CD or audio tape (a hedonic good) over a \$7 gift certificate for computer disks (a functional good), suggesting that these two goods were viewed as equally attractive when considered as potential gains. In contrast, participants who were given both gift certificates were then later asked to give one up were five times as likely to surrender the computer disk certificate as the music certificate, suggesting that loss aversion was more pronounced for the more affect-laden option. In the context of risky choice, ambient affective states seem to moderate loss aversion. Isen et al. [57] report that participants placed in a positive mood (for instance, by giving them an unexpected small bag of candy) tend to exhibit greater risk aversion for mixed (gain-loss) gambles and that this effect appears to be driven by greater sensitivity to possible losses rather than greater appreciation of possible gains.

# 3.4.3. Curvature of the weighting function

Although traditional accounts of the curvature of the weighting function stress the psychophysics of diminishing sensitivity (e.g., [123]), others have speculated that affective responses to gambles, such as hope and fear ([122], p. 282) or anticipated elation versus disappointment [20], may play a role. Indeed, Rottenstreich and Hsee [104] report that the curvature of the weighting function seems to be more pronounced for more "affect-rich" consequences, such as a kiss from a movie star or an electrical shock, than for "affectrich" consequences such as money. In one study, participants were asked to price a .01 and a .99 chance of receiving a hypothetical \$500 gift certificate. For one group, the certificate would go toward payment of university tuition (an affect-poor prize) and for a second group the certificate would go toward a European vacation (an affect-rich prize). For the .01 chance, the median participant in the vacation condition was willing to pay more (\$20) than the median participant in the tuition condition (\$5). However, for the .99 chance, the median participant in the vacation condition was willing to pay less (\$450) than the median participant in the tuition condition (\$478). In a similar vein, Faro and Rottenstreich [37] find that people anticipate that others' decisions

will reflect a less pronounced fourfold pattern of risk attitudes than their own decisions (i.e., more linear weighting of probabilities), but people who score higher on a standard empathy concern scale (and are therefore better able to "appreciate others' emotional reactions") tend to be more accurate.

# 3.4.4. Elevation of the weighting function

There is some evidence that overall risk preferences for pure gain and loss gambles are influenced by affective states, which may be reflected in differences in the elevation of the weighting function (or possibly the degree of curvature of the value function). For instance, Mano [78] finds that participants reporting higher states of arousal were willing to pay more to play lotteries of various probabilities (indicating greater risk seeking, consistent with a more elevated weighting function for gains) and were willing to pay less to insure against possible losses of various probabilities (indicating less risk aversion, consistent with a less elevated weighting function for losses). Lerner and Keltner [75] report that people who score higher on a scale of dispositional fear tend to be more risk-averse whereas people who score higher on a scale of dispositional anger tend to be more risk-seeking.

# 4. The neural basis of risky decision making

Although the study of decision making using cognitive neuroscience techniques is relatively young, a growing body of evidence suggests that decision making under risk is mediated by a network of cortical and limbic structures devoted to processing sensory, cognitive, and affective information, as well as widely-projecting neuromodulatory systems. In the discussion to follow, we will outline a set of preliminary hypotheses regarding the neural systems that may underlie some of the specific features of prospect theory. These hypotheses are summarized in Table 5. We first outline the important distinction between decision utility and experience utility. We then describe the state of current knowledge regarding the representation of utility, the representation of probability, and the processes involved in prospect representation.

It should be noted at the outset that, whereas much of the literature cited here comes from experimental studies of non-human animals, prospect theory has to date only been applied to human decision making. However, because fundamental psychological processes are likely to be at least partially conserved between human and non-human decision making (for example, see Marsh and Kacelnik [80] for a prospect theory-informed study of risky decision making in birds; Real [98] for a discussion of the Allais Paradox relating to the foraging behavior of bumblebees; Weber et al. [127] for a comparison of risk sensitivity in humans versus foraging birds and insects), the appeal to neuroscientific data from animals can provide useful insights

Table 5
Summary of neural systems hypothesized to be involved in the major aspects of prospect theory

Component	Prospect theory feature	Brain areas	Neurotransmitter systems
Value function	Representation of value		
	- Anticipated gains	- Ventral striatum - ACC	• DA (increase)
	- Anticipated losses	- Amygdala	
	- Experienced gains	<ul><li>Dorsal/ventral striatum</li><li>VMPFC</li></ul>	
	- Experienced losses	<ul><li>ACC</li><li>Amygdala</li><li>Dorsal striatum</li></ul>	• DA (decrease)
	• Loss Aversion	• Amygdala	• NA
Weighting function	• Diminishing sensitivity - Overweight low <i>p</i> - Underweight high <i>p</i>	<ul><li>Ventral striatum (hope?)</li><li>Amygdala (fear?)</li></ul>	• DA (hope?)
	• Subcertainty		• 5-HT (impulsivity)
Representation	• Framing	• DLPFC • ACC	
	• Editing	• DLPFC • VLPFC (inhibition)	• DA • 5-HT

Abbreviations: Dopamine (DA), Serotonin (5-HT), Noradrenaline (NA), Dorsolateral prefrontal cortex (DLPFC), Anterior cingulate cortex (ACC), Ventromedial prefrontal cortex (VMPFC).

into the basic neural mechanisms underlying these psychological processes.

# 4.1. Neural representations of utility

Kahneman et al. [65] distinguish between "decision utility," which refers to the weight of an outcome in a decision, and "experience utility," which refers to its hedonic quality. Although it is decision utility that is the primary focus of prospect theory, both forms of utility are important for understanding the neural basis of decision making. Decision utility may be derived from predictions of the experience utility of different options, which in turn may be influenced by retrospective evaluations of similar past experiences. However, Kahneman et al. [65] review a number of contexts in which people's retrospective evaluations and their decisions do not accord with their on-line ratings of experience utility—for instance, retrospective

evaluations are dominated by evaluations of salient moments (the peak and end of an experience) and underweight the duration of experiences (e.g., [59]). Thus, it is important to distinguish the representation of experienced reward and punishment (which may correspond to experience utility) from anticipated reward and punishment (which may correspond to predicted or decision utility). Results from cognitive neuroscience suggest that this distinction may be reflected in the roles of different brain systems in decision making. Of particular relevance, Berridge and Robinson [19] have distinguished between the "wanting" (presumably reflecting decision utility) and "liking" (presumably reflecting experience utility) aspects of motivation. We now review the neural bases of each of these forms of utility in turn.

# 4.1.1. Decision utility

Regions involved in decision utility should exhibit activity related to the anticipation of rewards or the assessment of subjective value of future events. Human and nonhuman animal studies provide evidence for the roles of the dopamine system, ventral striatum, prefrontal cortex, and amygdala in the representation of decision utility.

4.1.1.1. Dopamine system. Dopamine (DA) is a modulatory neurotransmitter that is produced by regions in the midbrain (the substantia nigra pars compacta and the ventral tegmental area) and transmitted broadly to a set of cortical and subcortical regions [26]. The dopaminergic system appears to be a primary substrate for the representation of decision utility. A number of studies (reviewed by [108]) have shown that dopamine neurons increase their firing for unexpected rewards and for stimuli that predict future rewards, whereas they decrease their firing in the absence of an expected reward. However, it is critical to note that DA does not appear to code directly for the hedonic value of rewards, as blockade of DA receptors does not reduce the desirability of rewarding stimuli [56]. Rather, DA blockade results in "liking" without "wanting" [18]; animals will fail to act to obtain rewards but will nonetheless express pleasure at receipt of the reward. One possibility is that DA codes for the incentive value of stimuli, which subsequently guides action selection (e.g., [18,82]).

4.1.1.2. Ventral striatum. The ventral striatum (including the nucleus accumbens or NAc) serves as a locus for signal integration between the prefrontal cortex, amygdala, and hippocampus (for review, see [125]) and a wealth of recent data suggest that it plays a critical role in the representation of anticipated reward magnitude (reviewed by [69]). In one study, Breiter et al. [21] visually represented several gain and loss outcomes using different roulette wheel "spinners". Using fMRI, these authors found modulation of ventral striatal responses to the expectation and experience of monetary gains and losses, and a clear monotonic increase in activity during exposure to a riskless "gains only" stimulus (but see [31]). Similarly, using a monetary incentive delay task,

Knutson et al. [70] demonstrated that NAc activity increases in anticipation of larger rewards. The ventral striatum is a primary target of the DA system, and changes in ventral striatal activity seen during neuroimaging may reflect either DA activity or the intrinsic activity of ventral striatal neurons.

4.1.1.3. Prefrontal cortex. The prefrontal cortex is a large and heterogeneous brain region, and it appears that different regions may play different roles in decision making. The dorsolateral prefrontal cortex (DLPFC) is particularly important for the maintenance and manipulation of cognitive representations in working memory and the planning of future actions based on those representations. One possibility is that this region plays a role in decision making related to the representation of prospects and subsequent decision utility computations. On the Iowa Gambling Task (IGT), a popular neuropsychological test of decision making [12], patients with lesions to the dorsolateral prefrontal cortex show decision making impairments. In this task, subjects are presented with four decks of cards with varying monetary payoff values and must choose among the decks to maximize their total payout. Two of the decks have negative expected value and high risk, whereas the remaining decks are less risky and have positive expected values. Patients with DLPFC lesions do not learn to choose optimally on this task [39,77]. These deficits may reflect an inability to use strategies or rules to control behavior such that DLPFC patients behave in a disorganized manner; for example, patients with DLPFC lesions were able to accurately assess the quality of financial advice on a task involving the management of a simulated business but were unable to actually use the advice in making decisions [48].

The ventromedial prefrontal cortex (VMPFC) also appears to be involved in the development of anticipatory responses to losses. Patients with lesions to the ventromedial prefrontal cortex exhibit normal skin conductance responses (SCR<sup>4</sup>) to experienced losses in the IGT but fail to develop anticipatory SCRs to risky choices as normal subjects do [13]. However, imaging studies have associated VMPFC more strongly with experienced reward than with reward anticipation, as discussed below.

4.1.1.4. Amygdala. The amygdala is a complex subcortical structure that is heavily involved in emotion and learning, particularly for negative outcomes (but also possibly for positive outcomes, see [11]). The amygdala is essential for both the production of fear responses and for the learning of associations between particular stimuli and fear responses (see Fanselow and LeDoux [36] for review). It is also involved in the perception of fearful facial expressions [88]. As discussed in greater detail below, it appears that the amygdala plays a key role in the representation of experience utility for losses. However, the amygdala also appears to be

important for decision utility regarding negative outcomes. In the IGT, patients with amygdala lesions do not learn to choose the less risky, positive expected value decks. Whereas normal (control) subjects develop anticipatory SCRs in response to choices from the risky decks following practice, patients with amygdala lesions do not develop such responses nor do they exhibit normal increases in SCRs to losses [14]. These results suggest that the acquisition of fearful anticipatory SCRs to losses requires the amygdala. Neuroimaging results have shown that the amygdala is active during the anticipation of losses ([21,58]).

# 4.1.2. Experience utility

Regions sensitive to experience utility should exhibit activity during the experience of positive or negative outcomes and show modulation according to the valence and/or magnitude of the outcome. The neural basis of experience utility has been associated with a network of limbic, brainstem, and cortical areas. In particular, neuro-imaging results have implicated the striatum and orbital and ventromedial prefrontal cortices in the processing of experienced rewards and the amygdala in the processing of experienced losses.

4.1.2.1. Striatum. The striatum is a complex structure that can be separated into the dorsal striatum (including the caudate nucleus and dorsal putamen) and the ventral striatum (including the nucleus accumbens and ventral putamen), each of which participates in different corticostriatal loops (e.g., [50]). In particular, the ventral striatum receives inputs primarily from limbic structures such as the hippocampus, amygdala, and VMPFC, whereas the dorsal striatum receives inputs primarily from dorsal and lateral prefrontal cortices. The ventral striatum appears to respond to both anticipated rewards [70] and experienced rewards [21], whereas the dorsal striatum (including the caudate nucleus) appears to play a distinct role in the processing of experienced reward magnitude and valence. For example, Delgado et al. [28] described a direct relationship between reward magnitude and valence, and activity in the dorsal striatum. These authors employed an event-related fMRI procedure in which subjects received monetary rewards and punishments of varying size dependent upon performance in a gambling task. Their findings showed that the degree of activation of the caudate nucleus varied consistently with both the magnitude and valence of the reward; the caudate nucleus responded most for large rewards and least for large punishments. Similarly, Knutson et al. [70] found that dorsal striatal areas respond differentially to the receipt of large gains and losses. As with the DA system, it is thought that the role of the striatum is closely tied to action selection; for example, the response of the striatum to rewards that are contingent upon behavior is greater than for rewards that are not contingent upon behavior ([121,131]. It is also unclear to what degree these striatal responses reflect DA activity versus cortical inputs to the striatum.

<sup>&</sup>lt;sup>4</sup> The SCR is a measure of electrical conductance between 2 points on the skin and is sensitive to physiological arousal, stress, and anxiety.

4.1.2.2. Prefrontal cortex. The ventromedial prefrontal cortex (VMPFC) has been associated with the receipt of rewards [71,91,100] and with the evaluation of desirable stimuli [34]. Furthermore, activity in this region correlates with subjective taste preferences for beverages [83], suggesting that activity in the region is sensitive to the relative subjective desirability of experienced stimuli. Patients with lesions to the VMPFC are impaired at the Iowa Gambling Task [12,15], that is, they never develop a preference for the "safe" decks in the IGT (i.e., those with positive expected value), tending to continue choosing from the "risky" decks (i.e., those with negative expected value). However, these patients do exhibit normal SCR responses to experienced losses [13], suggesting that VMPFC is not necessary for the emotional experience of a loss. Rather, the impairment of VMPFC patients on the IGT appears to reflect an impairment of executive control over behavior rather than one of value representation per se. Fellows and Farah [38] used a shuffled version of the IGT in which the losses associated with each deck were encountered within the first few trials, thereby reducing the reversal learning aspect of the task. Although VMPFC lesion patients were impaired at the standard IGT, they were unimpaired at the shuffled version, suggesting that their impairment is related to the reversal requirement.

The anterior cingulate cortex is also sensitive to the experience of negative outcomes, as reflected in the feedback error-related negativity (ERN) event-related brain potential. The ERN is greater for losses than for gains in a gambling task [45]. Of particular interest in this study is the fact that the ERN occurred even when the actual loss was smaller than an alternative possible loss (i.e., a relatively positive outcome), suggesting that it uniquely reflects the negative aspect of outcome value. One recent proposal suggests that the increased ERN for negative feedback reflects decreases in phasic dopaminergic signals to the anterior cingulate cortex which, in turn, signal negative prediction error [54]. Thus, ERN responses for negative outcomes may be a reflection of dopaminergic activity.

4.1.2.3. Amygdala. The amygdala may be involved specifically in the representation of negative outcomes. The primary evidence in favor of this is that patients with lesions to the amygdala show learning impairments on the IGT. The amygdala appears to play a role in the processing of losses per se, as patients with amygdala lesions do not exhibit normal SCRs to losses in the IGT [14]. This may reflect the amygdala's more general role in the processing of fear-related stimuli, reflected in its mediation of fear conditioning [72,81] and in the processing of fearful facial expressions [88]. Interestingly, there is some evidence to suggest that the amygdala may also encode information concerning gains ([44]; see also [6] for data suggesting that the amygdala's apparent negative bias may result, in part, from the higher average intensity of negative stimuli).

# 4.2. Neural representation of outcome probability

From the standpoint of prospect theory, the important aspects of probability representation are the curvature of the weighting function (reflecting the underweighting of high probabilities and overweighting of low probabilities) and the elevation of the weighting function (representing the overall willingness to entertain risk). Current neuroscientific research does not provide direct evidence regarding the mechanisms underlying these phenomena, but recent work has begun to elucidate the regions that are involved in the representation of outcome probabilities.

A substantial body of recent work examining the cortical representation of outcome probability has examined oculomotor tasks in primates. This work has focused on the lateral intraparietal area (LIP), a region that shows modulated activity during oculomotor tasks [102,109] and that acts to guide saccadic eye movements in a manner believed to reflect motor planning activity [47,114]. The importance of LIP in the representation of reward probability was demonstrated by Platt and Glimcher [94], who trained monkeys to make visual saccades into and out of the receptive fields of individual LIP neurons in exchange for juice rewards of varying magnitude and delivery probability. Significantly greater activation was seen in LIP neurons when saccades were instructed with a reward probability of 80% compared to when equivalent movement was instructed with a reward probability of 20%. That is, the activity of individual LIP neurons changed according to the probability that a particular response would result in a reward. Remarkably, movement amplitude, latency, and velocity did not change with outcome probability and, thus, it seems apparent that LIP neuronal activity is correlated with the probability that a particular (rewarded) response will be required regardless of the movement actually made. Subsequently, Sugrue et al. [117] also affirmed a convincing role for the LIP in the representation of reward probability as assayed through saccades. After training rhesus monkeys in a visual discrimination task involving a fixation, delay, and saccade routine, unit recordings were made in LIP as the animals made choices between stimuli linked to high and low-probability rewards. LIP neurons matched for receptive field properties showed differential activity depending on anticipated reward probability and, moreover, in the presence of low-probability reward the activity of these units became tonic as their discriminability declined. It must be noted that, because these studies did not vary magnitude as well as probability, it is not possible to determine whether LIP is representing probability per se or some function of probability (e.g., expected utility). In addition, it is not clear how these findings extend to other task domains or whether they are specific to eye movements.

Reward probability may also be represented less directly by the dopamine system. In a discrimination learning task, Fiorillo et al. [40] found that dopaminergic neuronal activity

varied monotonically with reward outcome probability. These authors trained monkeys on a visual discrimination task and recorded the activity of single dopaminergic neurons under conditions in which the receipt of a reward was maximally uncertain (50% reward) and maximally certain (0% or 100% reward). These neurons responded to rewards when they were unexpected (i.e., 0% condition) and to cues that predicted reward (i.e., 100% condition). In addition, dopaminergic neurons showed monotonically increasing phasic activation during the delay period for stimuli that were maximally unpredictable (i.e., 50% condition). Similar results were found in humans using fMRI by Aron et al. [9]. In this study, activity in the midbrain (putatively dopaminergic regions) was modulated by the predictability of subsequent cognitive feedback during a probabilistic learning task. That both of these studies find greatest activity during conditions of maximal uncertainty suggests that the dopamine system, rather than directly coding probability, may be coding for the degree of risk associated with a decision.

# 4.3. Prospect theory and the brain

The foregoing review outlines a relatively complex set of neural structures and interactions involved in the representation of decision and experience utility and probability. We now turn to examine how these data might be related to the value and weighting functions of prospect theory.

# 4.3.1. Shape of the value function

Curvature of the value function in prospect theory appears to be similar for gains and losses [2,123]. This suggests that a common process may be involved in the representation of value magnitude regardless of valance (i.e., equally for both gains and losses). Consistent with this hypothesis, there is evidence from neuroscience to suggest that several neural systems involved in value representation may separately represent valence and magnitude, at least for experienced outcomes. Analyzing human event-related potentials, Yeung and Sanfey [130] demonstrated that the well-characterized P300 eventrelated potential is sensitive to reward magnitude but not valence, whereas the subsequent feedback-related ERN showed the reverse pattern. Thus, the neuroscientific data provide at least qualified support for the existence of systems that respond uniquely to magnitude regardless of valence. However, this segregation is not complete, as the striatum appears to be sensitive to both the magnitude and valence of outcomes (e.g., [28]).

#### 4.3.2. Loss and risk aversion

In prospect theory, the value function is typically 2–3 times steeper for losses than for equivalent gains. For mixed (gain/loss) prospects, loss aversion gives rise to pronounced risk aversion. From a neural standpoint, one might surmise that loss aversion arises from the differential influence of

responses in the various systems that code for positive and negative expected values. The ventral striatum may be a central locus for the integration of these signals, as it receives inputs from amygdala, hippocampus, and prefrontal cortex as well as dopaminergic inputs from the midbrain and therefore has access to signals coding for both positive and negative value. For learning tasks involving reward associations (e.g., the IGT), it is clear that lesions to the amygdala and ventromedial prefrontal cortex result in decreased risk aversion. However, no published studies have examined these patients on pure or mixed gambles of the sort discussed above and, thus, it is not known whether these deficits persist when the learning demands are removed. Recent results showing that VMPFC lesion patients can perform the IGT normally under particular circumstances [39] suggest that their deficits reflect learning problems more than they reflect a general modulation of loss aversion. These findings are consistent with those of Rolls and colleagues (e.g., [103]) suggesting that the orbitofrontal cortex may be specifically involved in reversal of reward associations.

Recent evidence also suggests that the noradrenergic system may be important for loss aversion. Noradrenaline is known to mediate anxiety and stress (for reviews, see [46,89]) and has been shown to play a role in posttraumatic stress reactions [115] and the consolidation of fear memories [73]. Rogers et al. [101] examined the effect of central NA blockade on decision making in healthy volunteers through the administration of propranolol (a βadrenergic antagonist). Subjects were presented with mixed gain-loss gambles as well as pure gain and loss gambles. Participants administered a single 80 mg dose of propranolol appeared to be less sensitive to the magnitude of possible losses for mixed (gain-loss) gambles when the probability of loss was high (though not when it was low), whereas their sensitivity toward the magnitude of possible gains was not significantly affected. In contrast, propranolol and control participants displayed roughly equal tendencies toward risk aversion for pure gain gambles and risk seeking for pure loss gambles. Taken together, this pattern is consistent with the hypothesis that the drug affects loss aversion ( $\lambda$  in prospect theory) rather than curvature of the value function ( $\alpha$  and  $\beta$ ). Further studies are necessary to determine whether manipulation of other neurotransmitter systems also affects loss aversion. For example, although the modulatory neurotransmitter serotonin is thought to underlie the response to punishment (e.g., [27]), studies of decision making following tryptophan depletion (which reduces serotonin levels) suggest that loss aversion is not affected [99].

#### 4.3.3. Curvature of the weighting function

The weighting function in prospect theory is inverse-S-shaped, reflecting overweighting of low probabilities and underweighting of high probabilities. A critical question arising from prospect theory is why the probability

weighting function takes this particular shape. The standard explanation for this finding has appealed to the psychophysics of diminishing sensitivity, but other evidence suggests that it may instead (or in addition) reflect emotional aspects of the decision. In particular, the underweighting of high-probability gains and overweighting of low-probability losses may reflect fear, whereas the overweighting of low-probability gains and high-probability losses may reflect hope. The neural bases of these functions are not currently known. However, one might hypothesize that fear would involve the amygdala, whereas hope would involve the ventral striatum. It is also possible that the risk-related DA activity observed by Fiorillo et al. [40] in anticipation of uncertain rewards may reflect "hope", although this is speculative at present.

# 4.3.4. Elevation of the weighting function

The weighting function is generally characterized by "subcertainty" in which decision weights for complementary prospects sum to less than 1. This is manifested as a more pronounced tendency toward risk aversion than risk seeking for simple gambles involving gains (and presumably a more pronounced tendency toward risk seeking than risk aversion for simple gambles involving losses). There is little current evidence regarding the neural substrates for elevation of the weighting function in general, or subcertainty in particular. However, we speculate that elevation of the weighting function may be related to impulsivity, given that the impulsive acceptance of gambles would result in an increase in weighting function elevation (prospect theory parameter  $\delta$ ). This would suggest that elevation may be related to the dopaminergic and serotonergic systems, both of which are associated with impulsivity [24,35]. It is also of great interest that there is a substantial degree of individual variability in weighting function elevation [49]. If a link between DA/5-HT systems and elevation is established, then future genetic association studies focused on these transmitter systems could possibly provide an explanation for some of the individual differences observed in elevation.

# 4.3.5. Framing and editing operations

The representational aspects of prospect theory, encompassing framing effects and editing operations, concern how the representations of prospects affect their utility and how these representations can be manipulated or altered by the decision maker. Although there is little evidence regarding the neural basis of these components, several results provide the basis for preliminary speculations. In particular, recent dual-process models of judgment and choice have distinguished spontaneous, associative, affective processing ("System I") from effortful, rule-based, and cognitive processing ("System II"; see [33,111,116]). Kahneman [60] argues that many judgment and decision processes may be governed by a combination of both forms of processing. For instance, the use of memory accessibility

or similarity judgment to assess likelihood (the availability and representativeness heuristics) or the use of affective responses to make choices (the affect heuristic) may reflect System I processing. On the other hand, the use of higher-order reasoning to detect inconsistencies in judgment or dominance in choice may reflect System II processing. In the context of prospect theory, we surmise that passive framing, valuation, and probability weighting processes may be governed primarily by System I, whereas active framing and editing may be governed primarily by System II. As the foregoing review suggests, System I operations are likely to rely upon limbic and basal ganglia regions. The more controlled processes associated with System II are more likely to rely upon the lateral and dorsomedial prefrontal cortices (e.g., [86]).

Although no neuroscientific studies have directly examined framing effects, there is suggestive evidence that the degree to which an outcome is viewed as a relative gain or loss affects the neural processing of the outcome. Breiter et al. [21] compared the response to a \$0 outcome when it was either the best or worst outcome among three possible outcomes. The response to the outcome in the ventral striatum was greater when it was viewed as a gain than as a loss. Similarly, the response to rewards in ventral striatum and ventromedial prefrontal cortex differs when the reward occurs in the context of a winning streak [30]. Thus, there is suggestive evidence that the processing of reward depends upon the context in which it occurs. There are no current results that address the issue of reframing.

Editing processes, which involve the spontaneous reformulation of prospects, are likely to heavily involve working memory and executive control processes and, thus, may be reliant upon dorsolateral prefrontal cortices. In addition, editing processes likely require inhibition of prepotent (automatic) responses to allow manipulation of the prospect before making a decision. To the degree that editing requires controlled processing, it may be necessary to inhibit a relatively fast and automatic response driven by System I. Such inhibition is likely to involve the right lateral prefrontal cortex [8], as well as the DA and NA systems [7]. Consistent with this proposal is the fact that patients with VMPFC lesions appear to be impaired at suppressing their initial response on the basis of new information in the IGT [39].

# 5. Future directions

As the foregoing review outlines, there is a large body of suggestive evidence regarding the neural basis of decision making, and it is possible to at least weakly associate neural systems with the different components of prospect theory. Further work will be needed to better judge the degree to which this theory provides leverage towards understanding the neural basis of decision making.

Some of the most interesting outstanding questions include:

5.1. How can we extend the present account from decisions under risk to decisions under uncertainty?

In this paper, we have focused on decision making under risk, where the probabilities of possible outcomes are known precisely by the decision maker. Indeed, the probability weighting function from prospect theory applies only to these contexts. It is an important question how to extend the treatment from risk to uncertainty, where decision makers must judge for themselves the probabilities, with some degree of vagueness or imprecision. Cumulative prospect theory [123] provides such an extension and a characterization of decision weights under uncertainty can be found in both Tversky and Fox [122] and Wu and Gonzalez [128]. Subsequent studies have found that decisions under uncertainty adhere reasonably closely to the predictions of a "two-stage model" in which decision makers first assess the probabilities of events themselves, then weight these judged probabilities according to the same inverse-S-shaped function that they use for decisions under risk ([42,43,122,128]; but see [67]).<sup>5</sup>

Recently, Barron and Erev ([10]; see also [53]) examined "small feedback-based" decisions in which small decisions are repeated many times so that the probabilities of relevant outcomes are learned over time from experience rather than provided explicitly to participants. Similarly, Hertwig et al. [53] examined decisions in which participants were allowed to learn the probability distribution of possible outcomes by sampling from a distribution with replacement before making a choice among prospects. In an intriguing set of studies, these authors observed patterns of behavior that on their surface seem to reverse the patterns of over- and underweighting previously documented by Kahneman and Tversky and others. We say "on their surface" because it is important to recognize that these studies entailed uncertainty rather than risk. Although one could, in principle, compare decision weights to the probability distributions from which outcomes were sampled with replacement, such a comparison is not particularly meaningful in prospect theory. For one thing, the sample that a particular participant observes is unlikely to coincide with the process that generated it. Moreover, even if the sample does perfectly reflect the process that generated it, there is

no particular reason to believe that a participant's subjective beliefs will necessarily coincide with the relative frequency of events that they observed. Thus, it appears that these effects are driven primarily by distortions in belief rather than distortions in the weighting of probabilities. Indeed, when Fox and Tversky ([43], Study 2) presented participants with an entire distribution of events, participants subsequently overestimated the probability of drawing low-frequency events and underestimated the probability of drawing high-frequency events. Moreover, decision weights under uncertainty reflected the same over- and underweighting of these judged probabilities as did decision weights under risk in which participants were provided with probabilities.

At the neural level, it is likely that experience-based and description-based decisions may rely upon overlapping but partially separate sets of neural systems. In particular, the dorsal striatum and DA system are important for learning based on trial-by-trial feedback [95,110]. Examination of feedback-based decision making would allow a greater connection between the substantial literature on the cognitive neuroscience of learning. Particularly exciting is the possibility that quantitative models of decision making, such as prospect theory, could be interfaced with computational learning models, providing a compound model of both learning and decision making.

# 5.2. How are affective and cognitive signals integrated in probability weighting?

A substantial body of work cited in this paper suggests that decisions under risk, as modeled by prospect theory, may be driven by both cognitive and affective signals. Future research is needed to tease out the relative contribution of these factors. For instance, Hsee and Rottenstreich [55] distinguish "valuation by calculation" from "valuation by feeling" and observe that the characteristic concave shape of the value function for gains may reflect a weighted average of a linear function derived by cognitive appraisals of quantity and a step function implied by affective assessment of the nature of consequences. Likewise, we surmise that the characteristic inverse-S shape of the weighting function may stem from the combination of a cognitive assessment of probability or expected value and adjustments due to the anticipatory emotions hope (that a small probability gain might be realized) and fear (that a large probability gain may not be realized). These insights suggest that the neural systems involved in probability weighting will likely include convergence zones for emotional and cognitive signals. As noted above, the ventral striatum is a likely candidate for this sort of integration, given its connections and its receipt of substantial DA inputs (cf. [125]). Future work using paradigms that combine objective probability weighting with emotionally laden stimuli could address this issue.

<sup>&</sup>lt;sup>5</sup> Although the two-stage model fits the data quite well, a third stage is needed to accommodate ambiguity aversion [32] and the preference to bet on more familiar domains of uncertainty such as the domestic, rather than a foreign, stock market. This third stage might be modeled as a shift in the elevation of decision weights in situations where the decision maker feels especially knowledgeable or ignorant relative to other domains or people (for more detailed discussions, see [43], pp. 892–893; [42]).

# 5.3. What is the role of inhibition in decision making?

A number of studies have begun to focus on the role of cognitive control processes in decision making, but relatively little attention has been paid to the role of response inhibition (although see [39]). However, there a number of clinical syndromes (e.g., attention deficit disorder, drug abuse, and compulsive gambling) in which impairments of decision making seem to largely reflect the inability to inhibit immediate responses in favor of more optimal delayed responses. The relationship between response inhibition and the temporal discounting of rewards is not currently known, and understanding this issue could provide substantial leverage towards the characterization and treatment of decision making disorders.

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