

Reason, emotion and decision-making: risk and reward computation with feeling

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Many models of judgment and decision-making posit distinct cognitive and emotional contributions to decision-making under uncertainty. Cognitive processes typically involve exact computations according to a costbenefit calculus, whereas emotional processes typically involve approximate, heuristic processes that deliver rapid evaluations without mental effort. However, it remains largely unknown what specific parameters of uncertain decision the brain encodes, the extent to which these parameters correspond to various decision-making frameworks, and their correspondence to emotional and rational processes. Here, I review research suggesting that emotional processes encode in a precise quantitative manner the basic parameters of financial decision theory, indicating a reorientation of emotional and cognitive contributions to risky choice.

Introduction

Most of the decisions we make everyday involve uncertainty. Out at dinner, for example, a new menu item can sound tempting, but might be disappointing. An alternate route around a traffic jam might save time, but might make you even more late. A hot stock tip might strike it rich, but you might lose your entire investment. What processes underlie these decisions? A long tradition of research in judgment and decision making (JDM), stemming from choice or preference theory in microeconomics [1] and decision theory in philosophy [2], suppose that uncertain decisions are based on cognitive processes typically regarded as involving means-end reasoning, logical inference, mental effort and exact computation according to a cost-benefit calculus (Box 1). In the 1990s, however, JDM models increasingly incorporated emotional processes [3– 5], influenced by a reconsideration of emotion in neuroscience [6]. As these models developed, a prevalent emphasis of emotional contributions to JDM was as approximate, heuristic processes that deliver rapid evaluations without mental effort [3,5,7–10]. In addition, JDM researchers increasingly accounted for conflict in decision making as the divergence between cognitive and emotional evaluations [3,8], and pathological decision making as the result of affect heuristics [3,5] (Box 2).

Despite the popularity and commonsense appeal of distinguishing between cognitive and emotional contributions to JDM, many fundamental issues remain unresolved. Theories can be characterized in terms of the representations and the computations over those representations they posit, and it remains unclear in what ways cognitive and emotional contributions to JDM differ along these dimensions. That is, at the level of representation, what specific parameters of uncertain decision contexts are encoded by the brain, to what extent do such representations correspond to the parameters of various decision-making frameworks, and to what extent do putatively distinct cognitive and emotional contributions to JDM correspond to distinct underlying representations of uncertain decision contexts? Addressing these issues poses several challenges, not least that competing theories are not behaviorally distinguishable. This suggests that adjudicating among different theories requires neural studies that use quantitative and parametric frameworks with suitable resolution to distinguish among the main parameters of these various models and disassociating the representation of their basic parameters from other potential components of uncertain choice, including learning, motivation and salience (see Ref. [11] for discussion). Based on recent work using such experimental designs, I suggest that putative distinctions between cognitive and emotional contributions to JDM at the level of representation collapse. In particular, I focus on emerging evidence suggesting that emotional contributions to JDM do not encode approximate, heuristic evaluations. Rather, it suggests that emotional processes encode the precise, mathematically defined parameters of traditionally cognitive accounts of decision-making from economics and related fields, such as finance. On a more general note, such findings indicate that once-considered basic distinctions, such as that between cognition and emotion, do not map seamlessly onto brain functioning. That is, just as studies of the deep interconnectivity among emotional and cognitive structures suggests that assigning cognitive or emotional specialization to structures is deeply problematic [12], proposed functional distinctions, such as complexity differences between emotional and cognitive representations and computations, are likewise problematic.

The minimal parameters of decision-making under uncertainty

To begin, it is necessary to identify the underlying representational schemes, or minimal parameters, that various

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Box 1. Cognitive models of decision-making under uncertainty

Cognitive models of JDM assume individuals integrate information regarding the value and likelihood of possible outcomes on the basis of some expectation-based calculus. The standard formulation of such an expectation-based calculus is expected utility theory (EUT), whereby the value of uncertain choice (or prospect) is determined by the sum of the value of individual outcomes, u(x), weighted by their objective probability, p(x), giving $\sum_x p(x)u(x)$ (Figure 1a). Prospect theory (PT) was developed as a more psychologically realistic alternative to expected utility, and particularly to capture subtleties regarding sensitivity to risk, such as loss aversion, resulting in an S-shaped value function that passes through a reference point rather than the concave utility function of EUT (Figure 1b). According to PT, the value of a prospect is given by $\sum_x \pi(p(x))v(x - r)$, where the value of individual outcomes, v, depend on a reference point and are weighted by a non-linear function of the probabilities [13]. Neither

EUT nor PT explicitly compute risk. Rather, it is implicitly captured by the utility's transformation of reward, resulting in a concave utility function (EUT) or an S-shaped value function (PT). Hence, EUT and PT posit a single-dimensional index for the valuation of prospects. An alternative approach stems from FDT [16], which has been applied widely in behavioral ecology settings [15] (Figure Ic). In this approach, a risky choice is decomposed into its various statistical dimensions, which are then used to evaluate the choice by contrasting its scores along those dimensions or statistical meents. Among the various statistical moments that could be used, there is considerable behavioral evidence that human decisionmaking is sensitive to primarily the first two moments, expectation (expected value) and reward variance (risk), although in some contexts sensitivity to higher moment, such as skewness and kurtosis, is also possible [49].

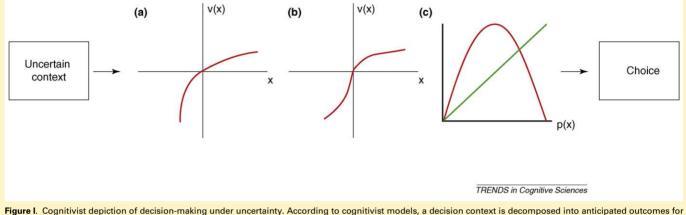


Figure I. Cognitivist depiction of decision-making under uncertainty. According to cognitivist models, a decision context is decomposed into anticipated outcomes for which utilities and probabilities can be assigned. These are then subject to some expectation-based calculus: (a) a typical expect utility function, (b) a typical value function from prospect theory, (c) the first two statistical moments as in FDT (in this case taken from the gambling task discussed in main text). Note that cognitive evaluations might result in emotions, but that such emotions do not enter into the computation of the decision.

JDM theories posit. Theories of decision-making under uncertainty rest on two fundamental representations of a decision context. Informally, a decision maker must represent both an estimate of the predicted value of a prospect (expected value) and how far away from the actual value that estimate might be (risk). This latter representation is essential to capture a pervasive feature of decisionmaking under uncertainty, namely, sensitivity to risk in the form of both risk aversion and risk seeking. We often trade off predicted value for less risk, such as when we put savings into a fixed interest account rather than the stock market, or order an unexciting but predictable menu item over one that might be either superb or horrible. Alternatively, we might seek risk, particularly in the face of losses [13]. Sensitivity to risk is observed in a wide range of animal behavior from non-human primates to fish, birds and bumblebees [14,15], indicating the importance of representing both expectations of reward and risk for all organisms that must confront uncertainty.

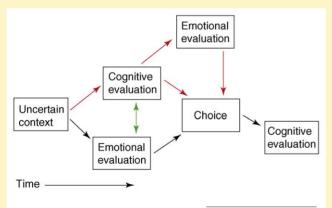
Cognitive theories of JDM formalize these two representations of expected value and risk and posit that these are encoded either as a single-dimensional index according to a utility (expected utility theory [EUT]) or value (prospect theory [PT]) function, or are encoded separately as posited by financial decision theory (FDT) [16] in terms of some of an uncertain context's statistical moments, which could be subsequently integrated to guide choice (Box 1). Where do theories of emotional contributions to JDM stand in relation to these views? For emotional contributions to JDM to be distinct from cognitive ones, the answer must lie at least at the level of representation in terms of some distinct encoding. Indeed, at the level of representation, theories of emotional contributions to JDM typically suppose that emotional processes instantiate some sort of heuristic encoding of reward and risk, in the sense of heuristic as an approximate process (Box 2), typically supposing that positive affective responses represent an approximate evaluation of reward whereas negative affective responses represent an approximate evaluation of risk. For the sake of comparison, cognitive representations in terms of utility functions are continuous, whereas an affect heuristic encodes an uncertain context via a small subset of discontinuous representations. The driving consideration is that such a small subset of discontinuous representations, although approximate, simplifies computation and so can be computed rapidly and without mental effort.

The question of what representations of risky choices are used in human decision-making cannot be adjudicated at the level of behavior alone. This is because the expected utility function of EUT and the value function of PT can both be approximated by FDT as the weighted sum of expected value and variance, resulting in behavioral equivalence despite divergent underlying representations. However, these models make highly constrained predictions regarding the specific functional form brain activity would

Box 2. Emotional contributions to JDM

Although emotional reactions to risky contexts are widely acknowledged, a central controversy in JDM concerns whether emotional reactions are the result of cognitive evaluations, or whether emotional reactions can guide choice independent of cognitive evaluation. In favor of the former, cognitive appraisal theories propose that emotional evaluations are post-cognitive evaluations [50] (red arrows in Figure I). Based on behavioral evidence, early alternative views proposed that emotional processes constitute an evaluative system that can be more rapid than cognitive ones and can lead to choice independent of cognition [51] (black arrows in Figure I). This led to more fully developed JDM models, according to which, emotional reactions constitute an 'affect heuristic' which, like other heuristics, reflect a speed-accuracy tradeoff whereby behavioral options are evaluated only with sufficient resolution to bias behavior in a typically adaptive manner. At the level of representation, then, cognitive and emotional processes differ in terms of encoding risky contexts either in terms of cost-benefit parameters (Box 1) or reduced-complexity, heuristic approximations that are more rapid and automatic in requiring minimal (or no) cognitive load. As a heuristic, emotional processing might also be the source of pathologies of decision-making, in that heuristics by definition introduce misrepresentations of uncertain contexts, which in some cases could be maladaptive (note, however, that cognitive heuristics could, likewise, lead to suboptimal choice).

Although JDM views were originally influenced by behavioral evidence, the rise of affect-based JDM models in the 1990 s was strongly influenced by neurobiological evidence. Among these, the somatic marker hypothesis of Damasio and colleagues [30,52–55] has been extremely influential in reviving interest in the role of emotion in decision-making under uncertainty [30,42,52–55]. Based on clinical studies of patients with ventromedial prefrontal cortex damage, Damasio and colleagues [30,52–55] proposed that their deficits in decision-making were due to their inability to generate emotions, or somatic markers, which encode an appraisal of a situation or choice outcome. A central feature of this view is that somatic markers, like affect heuristics in JDM, involve representations that are distinct from cognitive cost-benefit analyses [30,42].



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Figure I. Models of emotional contributions to uncertain decisions. Red arrows indicate cognitivist models of emotion, in which uncertain contexts trigger cognitive evaluations, which could either directly guide choice or could lead to post-cognitive emotional evaluations that subsequently guide choice. Black arrows indicate heuristic models of emotion, in which rapid emotional evaluations can directly guide choice. Note that on this model post-hoc cognitive evaluations could be generated, which could act as a rationalization of a choice that was in fact guided by emotion. The green arrow represents possible bidirectional influences between cognitive and emotional evaluations. Where these are weak, the result is a dual-process model of choice. Timeline indicates rough temporal relations proposed among these processes.

display to implement their underlying representations and computations of uncertain decision contexts. To what extent, then, is there evidence that the brain encodes these various proposed dimensions of risky decision contexts: the utility function of EUT, the value function of PT or a decomposition of value in terms of expected reward and of reward variance (risk) as in FDT? Furthermore, can such candidate cognitive representations of uncertain contexts be distinguished from affective, heuristic ones corresponding to emotional contributions to decision-making?

Evidence for neural correlates of JDM parameters

Numerous physiological studies have investigated brain responses to uncertainty in non-human primates and functional imaging in human brain responses to uncertainty (reviewed in Refs. [17,18]). To date, however, their emphasis has been on reward-related learning or choice rather than on the more basic question of underlying representations independent of learning, motivation and salience (see Ref. [18] for discussion). Among those examining this latter issue, there is some evidence for a single-dimensional PTlike signal [19]. Here, I focus primarily on whether there is evidence for underlying representations of expected reward and risk, however, in part because it is plausible that the issue of single- versus multi-dimensional value indices will be resolved by regarding EUT- or PT-like signals as integrations of these underlying component representations [20].

Suggestive evidence that the activity of dopamine neurons encodes expected value and risk stem from an important physiological study of non-human primate reinforcement learning [21]. This study reported that phasic responses in dopamine neurons in the ventral tegmental area varied monotonically with reward probability for a given level of reward across four levels of probability (0, 0.25, 0.5, 0.75, 1). In addition, this study reported sustained activity in this population of cells that related to uncertainty, in that it was maximal when uncertainty was highest (0.5). Although this provides suggestive evidence for expected reward and risk encoding in midbrain dopamine neurons, the limited range of probabilities used in the study did not allow for the specific functional form of reward-related encoding beyond monotonicity. Similarly, several uncertainty measures other than variance, such as entropy, are maximal at 0.5. To establish whether this candidate signal encodes expected reward, then, it is necessary to establish that such a signal varies linearly with probability. Likewise, to establish an encoding of risk as variance for this task, it is necessary to establish that such a signal varies quadratically with probability.

Recent human functional imaging studies have found evidence that the parameters of FDT are encoded by the brain in risky decision contexts independent of the influence of learning, motivation and salience [11,22]. To do so, this used a simple gambling task involving a deck of ten cards from which two cards were drawn on every (independent) trial with the bet being whether the second card would be higher or lower than the first (Figure 1). By varying expected reward and risk orthogonally and across the full range of probabilities, the study found immediate bilateral activation in ventral striatum that varied linearly with probability (expected reward), whereas a delayed activation in bilateral midbrain and ventral striatum varied quadratically with probability (risk as variance) (Figure 2). It is striking that both non-human primate

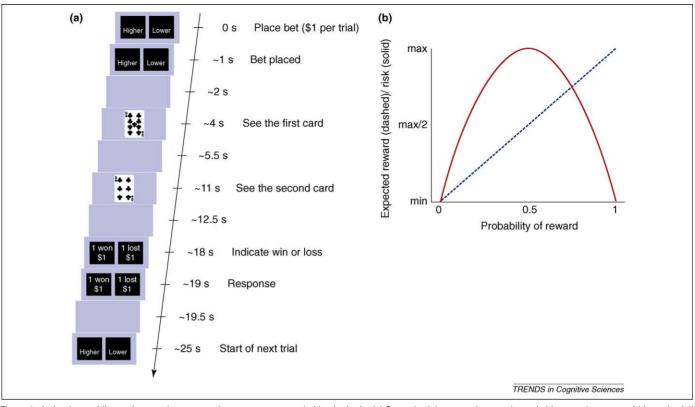


Figure 1. A simple gambling task to test how uncertain contexts are encoded by the brain. (a) On each trial, two cards were drawn (without replacement within each trial) from a deck of ten, numbered 1 to 10. Before seeing either card, subjects first placed a \$1 bet on one of two options, 'second card higher' or 'second card lower' (than first card shown). Subjects could earn \$1 if they guessed the right card and lost \$1 if they were wrong. (b) Expected reward and risk as a function of the probability of reward. Expected reward, measured as mathematical expectation of reward, increases linearly in the probability of reward *p* (dashed line). Expected reward is minimal at p = 0 and maximal at p = 1. Risk, measured as reward variance, is an inversely quadratic function of probability that is minimal at p = 0 and p = 1 and maximal at p = 0.5 (solid line). As such, expected reward and risk are orthogonal over the full range of probabilities, *p* in [0,1]. Reproduced, with permission, from Ref. [11].

physiology and human functional magnetic resonance imaging (fMRI) studies converge on evidence for temporally and spatially distinct encodings of expected reward and risk in dopaminergic midbrain areas. Although dopaminergic midbrain areas have been implicated in many forms of reward-related learning [23], these results suggest a primary role of these structures in encoding the parameters of uncertain choice contexts independent of such learning [11]. This study and a related one found that the insula also encodes risk as variance and found evidence for a novel risk-prediction-error-signal in insula that is roughly analogous to the error signal for reward found in midbrain dopamine areas [22]. The quantification of a reward-prediction-error-signal and its computational role in reinforcement learning dramatically enriched the understanding of midbrain dopamine areas [23]. Less wellknown, however, is the analogous need to update predictions of risk and to use risk prediction error to modulate

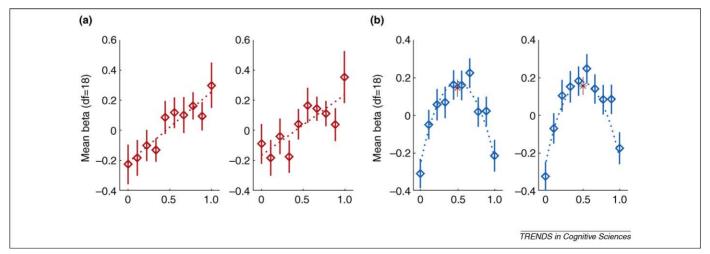


Figure 2. Neural correlates of reward and risk. (a) Immediate neural correlates of expected reward. Mean activations (parameter estimates β with standard error) for ten probabilities. In left and right ventral striatum (vst), neural responses increase with increasing probability of win. Dashed line indicates the best linear fit. (b) Delayed neural correlates of risk. Mean activations (parameter estimates β with standard error) for ten probabilities. Neural responses in left and right ventral striatum increase towards medium probabilities and decrease towards low and high probabilities. Dashed lines indicate best quadratic fit. Reproduced, with permission, from Ref. [11].

Box 3. Outstanding questions

- Why are there multiple representations of risk and reward across the brain, and in what ways do these relate to distinct mechanisms underlying action selection?
- If implicit, emotional representations accurately track the parameters of uncertain contexts, what intervening processes result in sub-optimal decisions?
- What are the neural correlates of individual differences in risk and reward sensitivity, and does the development of these structures correspond to differences in risk taking across psychological development?

reward learning [24]. The discovery of such a signal in insula indicates that its underlying representations encode precise quantitative information about risk and risk prediction errors, corresponding in striking fashion to the parameters of FDT, where such risk updating has a central role.

Reevaluating affective heuristic processing?

These results suggest several potential challenges for the affect heuristics view of emotional contributions to uncertain decisions, including neurobiological versions in terms of somatic markers (Box 3). On the one hand, reward and risk seem to be encoded in many of the brain areas that have been closely identified with emotional processing, including midbrain dopamine areas and insula. Midbrain dopamine areas are centrally implicated in both positive and negative emotion [25], motivated behavior [26], dimensions of personality related to emotionality [27], affective disorders [28] and figures prominently in theories of core affect [29]. The insula has also been centrally implicated in emotion [30], uncertainty [31-33] and risk aversion [34,35]. Given its bidirectional connections with numerous structures implicated in reward and decision-making, including orbitofrontal cortex, amygdala, anterior cingulate and nucleus accumbens [36], the insula is well-positioned to integrate affective value with adaptive behavior. Furthermore, just as emotional processes are often identified with implicit, or System 1, processes in dual-processing accounts [37,38], risk and reward processing in these structures is fast, automatic and implicit, in contrast to the characterization of cognitive processes, such as memory, attention and problem solving, which are typically regarded to be mediated primarily by cortical structures, involve controlled processes and are sequential and rulebased [12,37]. On the other hand, the specific mathematical form of the encoding of reward and risk in these structures is strikingly in accordance with the parameters of FDT, a paradigmatic cost-benefit and cognitive computation. This is suggestive evidence that the most likely candidate structures for encoding a heuristic, approximate representation of uncertain contexts (the insula, in particular, has a central role in the somatic marker hypothesis) do not, in fact, encode such approximate representations. Hence, these results suggest there need be no deep speed-accuracy tradeoff in terms of encoding the basic parameters of uncertain contexts. In this regard, it is worth noting that this supposed tradeoff was developed largely on the basis of non-quantitative treatments of emotional processing, differences in reaction time between

emotional and cognitively mediated processes, and other indirect evidence. However, research in other areas of implicit decision-making, such as sensory integration, in which the brain must decide whether to integrate or segregate sensory information from different modalities such as audition and vision, suggests that fast decision-making need not be approximate in the above sense. Indeed, recent work has shown such integration to be statistically optimal from the perspective of Bayesian causal inference [39]. Therefore, the decisions the brain makes regarding sensory integration are essentially the best ones that could be made, given the sensory information. Although Bayesian causal inference has been typically regarded as limited to conscious, high-level cognition, it is performed continually and effortlessly in perception.

Given the central adaptive problems of both sensory cue integration and uncertain decision contexts, it is not altogether surprising that the brain has developed efficient and computationally complex solutions that are both fast and accurate. The most parsimonious way to reconcile these results could be simply to view emotional processes as the brain's way of encoding the parameters of expectation-based calculi, such as those of FDT and to recognize that there need be no deep tradeoff between speed and accuracy in terms of reward and risk perception. A possible rejoinder to this is to suggest that in the absence of welldefined estimates of such parameters, as in situations of ambiguity, it is necessary to generate such crude or approximate representations. Yet, such situations seem to be precisely when accurate representations of uncertainty are most needed to guide learning in light of new information, and the accuracy of such representations conditional on the available information remains an open issue. The possibility that insula might underlie such computations in the form of risk-prediction-error-signals [22] suggests that the computations underlying risk and reward learning might be substantially more complex than current understanding of these structures indicates.

The finding that emotional systems encode and compute the basic parameters of FDT also raises some questions for somatic-based theories of emotions. According to the view sketched here, the crucial feature of emotional processing for risky choice is their underlying representation of expected reward and risk. This is concordant with theories that characterize emotions in terms of value-stimulus associations, whereby emotions are states elicited by reinforcers [40,41]. Indeed, it extends these associations to additional parameters of value-stimulus associations, such as risk. Whereas somatic theories ground emotions in representations of an organism's homeostatic state, according to these latter accounts, value-stimuli associations might relate to peripheral states, but the peripheral states themselves, or their central representation, do not participate in the computation of a decision. From this perspective, it is not clear what additional role somatic states would confer because the parameters of risky choice would already be represented and computed according to expected reward-risk tradeoffs. It is possible that somatic states are correlates of representations of expected reward and risk, but from this perspective it remains an open question what causal role such states would have

in resolving risky choice. Whether or not the representation of uncertain contexts involves an embodiment in somatic states or their central representation, the findings considered here challenge the notion that somatic markers act as an alternative encoding to the parameters of traditional cognitive JDM theories [30,42].

Conclusions

The investigation of the neural basis of uncertain choice has progressed rapidly in the last few years, progressing from investigating neural responses to basic contrasts such as certainty versus uncertainty, to quantitative parametric frameworks capable of testing the extent to which brain activation reflects the parameters of formal JDM models. Perhaps the most surprising finding to date is that core emotional structures, including the midbrain dopamine system and insula, decompose uncertain choice contexts along the statistical dimensions that are the cornerstone of FDT. Previous accounts of emotion as value-stimulus associations tended to focus on orbitofrontal cortex as the primary structure involved in representing reward expectation and viewed midbrain dopamine areas as involved in reward-related learning rather than in the representation of reward expectation per se [40]. However, recent findings suggest that the encoding of value in midbrain dopamine areas might underlie an early implicit encoding that is signaled to orbitofrontal cortex, where it guides choice. [43] Indeed, an important issue for future research is to work out the relationship between multiple representations of value across the brain. Although there is evidence that cortical areas mediating high-level cognitive processes, such as lateral prefrontal cortex in the case of ambiguity and posterior parietal cortex in the case of risk [44], are also recruited by complex decision problems, it is intriguing that at the level of perception the basic parameters of FDT (and plausibly the component representations of EUT or PT-like value functions [20]) are encoded in the brain's central emotional systems. Another important area of future research is to better understand the subjective nature of valuation. in the sense that value is not merely transduced from the environment, but depends on subjective states and needs. Recent work linking the insula, emotion and craving is particularly intriguing in this regard [45].

Finally, to end on an historical note, although the finding that emotional processes might implement the parameters of formal choice theory is surprising from current characterizations of cognition and emotion, it is not without historical precedent. Indeed, the deep division between emotional and cognitivist models of uncertain choice is puzzling given the historical foundations of utility. As Fishburn [46] notes, the notion of utility changed radically as economics turned away from psychological to axiomatic foundations in the early twentieth century, where the goal increasingly was to use the minimal conception of utility that generates sufficient structure on preference relations [1] independent of psychological considerations. As late as 1918, however, the economist Irving Fisher was still able to debate whether 'utility' should be replaced with a more transparent notion of human want, tracing the notion from Benthem's reduction of utility to

pleasure and pain to consider such affective terms as 'desirability' or 'wantability' [47]. In 1883, the French economist, Charles Gide, put it more colorfully, noting that 'as a shadow follows a butterfly from one flower to another, so utility accompanies desire, and abides only where desire rests' [48]. From this perspective, it is not altogether surprising that investigations of the neural basis of uncertain choice are finding fundamental connections among value, motivation and emotion. What might be more surprising, however, is the degree of correspondence between these connections and the quantitative parameters of formal models of decision-making under uncertainty.

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References

- 1 von Neumann, J. and Morgenstern, O. (1944) Theory of Games and Economic Behavior. Princeton University Press
- 2 Jeffrey, R. (1983) The Logic of Decision. Chicago University Press
- 3 Loewenstein, G.F. et al. (2001) Risk as feelings. Psychol. Bull. 127, 267– 286
- 4 Mellers, B. (1999) Emotion-based choice. J. Exp. Psychol. Gen. 128, 332–345
- 5 Finucane, M.L. et al. (2000) The affect heuristic in judgments of risks and benefits. J. Behav. Decis. Making 13, 1–17
- 6 Dalgleish, T. (2004) The emotional brain. Nat. Rev. Neurosci. 5, 583– 589
- 7 Bohm, G. and Brun, W. (2008) Intuition and affect in risk perception and decision making. *Judgm. Decis. Making* 3, 1–4
- 8 Greene, J.D. et al. (2004) The neural bases of cognitive conflict and control in moral judgment. Neuron 44, 389-400
- 9 Haidt, J. (2001) The emotional dog and its rational tail: a social intuitionist approach to moral judgment. *Psychol. Rev.* 108, 814-834
- 10 Weber, E.U. and Johnson, E.J. (2009) Mindful judgment and decision making. Annu. Rev. Psychol. 60, 53–85
- 11 Preuschoff, K. et al. (2006) Neural differentiation of expected reward and risk in human subcortical structures. Neuron 51, 381–390
- 12 Pessoa, L. (2008) On the relationship between emotion and cognition. Nat. Rev. Neurosci. 9, 148–158
- 13 Kahneman, D. and Tversky, A. (1979) Prospect theory: an analysis of decision under risk. *Econometrica* 4, 263–291
- 14 Stephens, D.W. and Krebs, J.R. (1986) Foraging Theory. Princeton University Press
- 15 Real, L.A. (1991) Animal choice behavior and the evolution of cognitive architecture. *Science* 253, 980–986
- 16 Markowitz, H. (1952) Portfolio selection. J. Finance 7, 77-91
- 17 Platt, M.L. and Huettel, S.A. (2008) Risky business: the neuroeconomics of decision making under uncertainty. Nat. Neurosci. 11, 398–403
- 18 Rangel, A. et al. (2008) A framework for studying the neurobiology of value-based decision making. Nat. Rev. Neurosci. 9, 545–556
- 19 Tom, S.M. et al. (2007) The neural basis of loss aversion in decisionmaking under risk. Science 315, 515–518
- 20 Bruguier, A. et al. (2008) Investigating signal integration with canonical correlation analysis of fMRI brain activation data. Neuroimage 41, 35–44
- 21 Fiorillo, C.D. et al. (2003) Discrete coding of reward probability and uncertainty by dopamine neurons. Science 299, 1898–1902
- 22 Preuschoff, K. et al. (2008) Human insula activation reflects risk prediction errors as well as risk. J. Neurosci. 28, 2745–2752
- 23 Schultz, W. et al. (1997) A neural substrate of prediction and reward. Science 275, 1593–1599
- 24 Preuschoff, K. and Bossaerts, P. (2007) Adding prediction risk to the theory of reward learning. Ann. N. Y. Acad. Sci. 1104, 135–146

Opinion

- 25 Leknes, S. and Tracey, I. (2008) A common neurobiology for pain and pleasure. Nat. Rev. Neurosci. 9, 314–320
- 26 Montague, P.R. et al. (2004) Computational roles for dopamine in behavioural control. Nature 431, 760–767
- 27 Depue, R.A. and Collins, P.F. (1999) Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. *Behav. Brain Sci.* 22, 491–517
- 28 Stein, D.J. (2008) Depression, anhedonia, and psychomotor symptoms: the role of dopaminergic neurocircuitry. CNS Spectr. 13, 561–565
- 29 Duncan, S. and Barrett, L.F. (2007) Affect is a form of cognition: a neurobiological analysis. Cogn. Emotion 21, 1184–1211
- 30 Bechara, A. and Damasio, A.R. (2005) The somatic marker hypothesis: a neural theory of economic decision. *Games Econ. Behav.* 52, 336–372
- 31 Elliott, R. et al. (2000) Dissociable neural responses in human reward systems. J. Neurosci. 20, 6159–6165
- 32 Critchley, H.D. *et al.* (2001) Neural activity in the human brain relating to uncertainty and arousal during anticipation. *Neuron* 29, 537–545
- 33 Paulus, M.P. et al. (2003) Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. Neuroimage 19, 1439–1448
- 34 Kuhnen, C.M. and Knutson, B. (2005) The neural basis of financial risk taking. Neuron 47, 763–770
- 35 Rolls, E.T. *et al.* (2008) Expected value, reward outcome, and temporal difference error representations in a probabilistic decision task. *Cereb. Cortex* 18, 652–663
- 36 Reynolds, S.M. and Zahm, D.S. (2005) Specificity in the projections of prefrontal and insular cortex to ventral striatopallidum and the extended amygdala. J. Neurosci. 25, 11757–11767
- 37 Sanfey, A.G. and Chang, L.G. (2008) Multiple systems in decision making. Ann. N. Y. Acad. Sci. 1128, 53-62
- 38 Evans, J. (2008) Dual-processing accounts of reasoning, judgment, and social cognition. Annu. Rev. Psychol. 59, 255–278
- 39 Körding, K.P. et al. (2007) Causal inference in multisensory perception. PLoS One 2, e943

- 40 Rolls, E. (1998) The Brain and Emotion. Oxford University Press
- 41 Rolls, E. (2005) Emotion Explained. Oxford University Press
- 42 Bechara, A. (2004) The role of emotion in decision-making: evidence from neurological patients with orbitofrontal damage. *Brain Cogn.* 55, 30–40
- 43 Kim, H. et al. (2007) Temporal isolation of neural processes underlying face preference decisions. Proc. Natl. Acad. Sci. U. S. A. 104, 18253– 18258
- 44 Huettel, S.A. et al. (2006) Neural signatures of economic preferences for risk and ambiguity. Neuron 49, 765–775
- 45 Naqvi, N.H. and Bechara, A. (2009) The hidden island of addiction: the insula. *Trends Neurosci.* 32, 56–67
- 46 Fishburn, P. (1989) Retrospective on the utility theory of von Neumann and Morgenstern. J. Risk Uncertain. 2, 127–158
- 47 Fisher, I. (1918) Is "utility" the most suitable term for the concept it is used to denote? Am. Econ. Rev. 8, 335–337
- 48 Gide, C. (1904) Principles of Political Economy. D.C. Heath & Co
- 49 Bossaerts, P. and Plott, C. (2004) Basic principles of asset pricing theory: evidence from large-scale experimental financial markets. *Rev. Finance* 8, 135–169
- 50 Folkman, S. and Lazarus, R.S. (1988) Coping as a mediator of emotion. J. Pers. Soc. Psychol. 54, 466–475
- 51 Zajonc, R.B. (1980) Feeling and thinking preferences need no inferences. Am. Psychol. 35, 151–175
- 52 Damasio, A. (1996) The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 351, 1413–1420
- 53 Damasio, A.R. (1994) Descartes Error: Emotion, Reason and the Human Brain. Avon
- 54 Damasio, A.R. et al. (1991). In Frontal Lobe Function and Dysfunction (Levin, H.S. et al., eds), pp. 217–229, Oxford University Press
- 55 Bechara, A. et al. (2005) The Iowa Gambling Task and the somatic marker hypothesis: some questions and answers. Trends Cogn. Sci. 9, 159–162