

1 **Neuroeconomics of risk sensitive decision making**
2
3

4 Sarah R. Heilbronner^{1,2}, Benjamin Y. Hayden^{2,3}, and Michael L. Platt^{1,2,3,4}
5

6 ¹Center for Cognitive Neuroscience, ²Department of Neurobiology,
7 ³Center for Neuroeconomic Studies,
8 ⁴Department of Biological Anthropology and Anatomy,
9 Duke University
10

11 Figures: 3
12

Corresponding author:
Benjamin Y. Hayden

13 Department of Neurobiology
14 Duke University Medical School
15 Durham, NC 27710
16 Tel: (919) 668-0333
17 FAX: (919) 668-0335
18 E-mail: hayden@neuro.duke.edu
19

19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

ABSTRACT

Risk pervades nearly all the choices we make in daily life. Until recently, the neural mechanisms underlying risk-sensitive decision making were largely unknown. Here we review recent results bearing on this topic. Our review indicates that risk aversion is not as common as is generally believed. Moreover, risk preferences are not stable, but depend strongly on the circumstances in which they are assessed. The brain areas that mediate risky decision making are likewise diverse and heterogeneous and contribute to a variety of component processes. These findings validate a broad neuroeconomic approach emphasizing the importance of multiple convergent investigations into the brain mechanisms underlying decision making.

33

34

INTRODUCTION

35

36 Uncertainty is ubiquitous, and adaptive behavior requires dealing with it in a biologically

37 meaningful fashion. Our goal in this chapter is to describe current evidence concerning the

38 mechanisms that allow decision makers to deal with the uncertainty that characterizes our world.

39 A fundamental premise is that these mechanisms are embodied in neuronal and chemical events

40 in the brain. We therefore advocate a neuroeconomic approach to understanding the mechanisms

41 of risk sensitive decision making (Glimcher, 2002; Sanfey, Loewenstein, McClure, & Cohen,

42 2006). This emphasis distinguishes our goals from those of behavioral psychologists,

43 economists, and evolutionary biologists. Nonetheless, each of these other approaches offers

44 valuable insights, so we will consider evidence from these related fields (Glimcher, 2003).

45 A neuroeconomic approach has several appealing features. First, the brain is the

46 biological basis of cognition and behavior; thus, any model of decision making must ultimately

47 be valid at the neural level. Second, a more detailed understanding of the neural mechanisms

48 underlying decision making will allow us to refine and elaborate upon current models of

49 behavior and cognition. Finally, the neuroeconomic approach brings us closer to developing

50 treatments for mental disorders characterized by risky behavior and impulsivity, including

51 compulsive gambling, addiction, obsessive-compulsive disorder, and attention deficit

52 hyperactivity disorder. Accurate neural models will be crucial for resolving these pressing

53 medical concerns.

54 The specific goal of this chapter is to review current evidence regarding the brain

55 mechanisms supporting decision making under economic risk. To do this, we will discuss other

56 topics related to economic decision making more broadly, focusing on impulsivity and inter-
57 temporal choice. Because risk sensitive decision making and inter-temporal choice share several
58 intuitive properties, there has been much speculation about how the two processes are related
59 (Green & Myerson, 2004; Rachlin, 2000). Although it remains unclear whether these types of
60 decisions share common neuronal mechanisms, we believe that the neuroeconomic approach
61 provides a solid foundation on which a synthesis may be built.

62

63 **Risk sensitivity**

64

65 If decision makers are simply trying to maximize reward, they should be indifferent to
66 risk. That is, they should equally prefer two options offering the same average payoff, but with
67 different probabilities and rewards for any given decision. In practice, however, humans and
68 nonhuman animals reliably avoid or seek risk, often paying large penalties for their choices. For
69 example, vendors of consumer electronics sell extended warranties that are only useful in the
70 unlikely situation that the device breaks within a certain timeframe. Such warranties are known
71 to be poor investments, yet their continuing popularity attests to people's willingness to pay
72 money to reduce uncertainty.

73 In general, humans and other animals are risk averse (Kacelnik & Bateson, 1996;
74 Kahneman & Tversky, 1979; Rabin, 2000); that is, they will reliably pay a premium to reduce
75 risk. Risk sensitivity in humans is typically assessed by examining responses made to
76 hypothetical questions concerning simple choices between two lotteries offering different reward
77 payoffs with different probabilities. In such situations, people typically require a bonus, known
78 as the risk premium, before they will choose the risky option. Studies of nonhuman animals have

79 generally found that they, like humans, are risk averse (Kacelnik & Bateson, 1996). Given the
80 constraints of working with non-linguistic species, risk sensitivity in animals is generally tested
81 by examining responses of individuals trained to choose between two options offering food
82 rewards offered with different probabilities. Such tests have been performed on species as
83 phylogenetically distinct as bees and rhesus macaques (Hayden & Platt, 2007; Shafir,
84 Wiegmann, Smith, & Real, 1999). Despite the large differences between human and animal
85 studies, the reliable observation of risk aversion in humans and animals suggests that it is
86 widespread and divorced from experimental context (Kacelnik & Bateson).

87 A closer investigation, however, reveals that risk aversion is not ubiquitous. In fact, there
88 are a surprisingly large number of situations that promote risk seeking. In general, it appears that
89 risk preferences are highly dependent on context. For example, risk seeking is promoted by small
90 stakes (Prelec & Loewenstein, 1991; Weber & Chapman, 2005), low probabilities (Kacelnik &
91 Bateson, 1996), and framing as a loss (Tversky & Kahneman, 1981). In fact, the list of contexts
92 that promote risk seeking is so extensive that these situations do not seem to be exceptions.
93 Instead, it appears that risk preferences are fundamentally context-dependent (see Table 1).

94

95 *The utility curve*

96 Since the work of Daniel Bernoulli, economists have sought explanations for risk
97 aversion. Bernoulli proposed that risk-sensitivity could be explained by the shape of a
98 hypothetical construct known as the utility curve (also see Von Neumann and Morgenstern
99 1944). The utility curve indicates the subjective value (or utility) derived from a given quantity
100 of a good. Bernoulli knew that the benefit one obtains from any particular good tends to decline
101 as one obtains more of that good (the law of diminishing marginal utility). This law gives the

102 utility curve its characteristic concave shape (see panel A of Figure 1). The utility curve provides
103 a satisfying explanation for risk aversion. With diminishing marginal utility, the utility of the
104 safe outcome (the vertical line labeled “safe” in panel A of Figure 1) is necessarily greater than
105 the average utility of the two “risky” goods shown in the same panel (compare the two horizontal
106 dashed lines). Thus the concavity of the utility curve offers a satisfying, elegant explanation for
107 risk aversion and helps to predict the appeal of a specific gamble to a particular individual.

108 The concave utility curve account of risk sensitivity has faced several major challenges.
109 First, as noted above, risk aversion is not nearly as universal as generally supposed. Second, in
110 practice it is nearly impossible to estimate an individual’s utility function without asking him or
111 her questions about risk, a disturbingly circular approach. The impracticality of validly
112 ascertaining an individual’s utility curve makes it difficult to exploit the predictive power offered
113 by the utility curve account. Another problem arises as a direct consequence of the weak
114 assumption that utility curves are continuous and have monotonically decreasing derivatives.
115 Given these assumptions, observed levels of risk aversion for small stakes necessarily lead to
116 ridiculously large levels of risk aversion for larger stakes (Rabin, 2000; Rabin & Thaler, 2001).
117 However, without these simple assumptions, the utility curve model loses much of its
118 explanatory power. Finally, it is not clear that decisions regarding hypothetical goods accurately
119 reflect true individual preferences (Holt & Laury, 2002), or even whether people hold stable
120 preferences that are expressed in their choice behavior (Ariely, Loewenstein, & Prelec, 2005).
121 Such failures of the basic assumptions of economic theory make it impossible to satisfactorily
122 explain risk sensitivity within the context of axiomatic economic principles such as utility theory.

123

124 *Prospect Theory*

125 Another major challenge to the traditional utility curve account comes from prospect
126 theory (Kahneman & Tversky, 1979, 2000). Prospect theory comprises three specific hypotheses.
127 First, individuals make decisions with respect to changes in current wealth state, rather than with
128 respect to absolute wealth. Second, the utility curve has a characteristic shape that differs from
129 the one proposed by Bernoulli. As shown in panel B of Figure 1, the utility curve is concave for
130 gains and convex for losses, has a steeper slope for losses, and is not continuously differentiable
131 at the zero point. This characteristic shape leads to risk aversion for gains (as in panel A) and risk
132 seeking for losses (the latter occurring because the average of the risky losses is less aversive
133 than the assured loss). Third, as shown in panel C of Figure 1, decision makers transform
134 reported probabilities according to a specific function that over-weights low probabilities and
135 under-weights high probabilities. This property explains why a single person may both play the
136 lottery (over-weighting the low probability of winning the jackpot) and purchase disaster
137 insurance (under-weighting the high probability of avoiding disaster).

138 The aspect of prospect theory that has received the most attention is the asymmetry
139 between the domains of gains and losses (Bernartzi & Thaler, 1995; Kahneman & Tversky,
140 1979; Tversky & Kahneman, 1991), a difference well-illustrated by one of the original scenarios
141 constructed by Kahneman and Tversky. In the Asian Disease Problem, participants make a
142 hypothetical choice between safe and risky medical interventions for an infected population
143 (Tversky & Kahneman, 1981). In one condition, the choices are framed in terms of lives lost; in
144 the other, choices are framed in terms of lives saved. Participants are risk seeking in the loss
145 frame, but risk averse in the gain frame, even though the facts about each intervention program
146 remain identical across conditions. This framing effect has since been extended to a variety of
147 scenarios and frame types; indeed, it has even been reported that some nonhuman animals are

148 risk averse for gains but risk seeking for losses (Harder & Real, 1987). The ubiquity of risk
149 aversion for gains and risk seeking for losses suggests that these behavior patterns reflect the
150 operation of a mechanism that may be adaptive in many common natural environments
151 (Gigerenzer, Todd, & Group, 1999; Kacelnik & Bateson, 1996; McNamara & Houston, 1986).

152 Prospect theory retains a great deal of predictive power, particularly in describing human
153 behavior with regards to money (Kahneman & Tversky, 2000). However, in many ways, it has
154 fallen short as a complete theory of risk sensitivity. Most importantly, it does not fully
155 encapsulate the range of risk sensitive behavior observed in both humans and nonhuman animals.
156 As discussed above and summarized in Table 1, risk seeking in the gains domain has been
157 observed in a wide variety of species across a large array of contexts (Dukas & Real, 1993; Gilby
158 & Wrangham, 2007; Kaminski & Ator, 2001; McCoy & Platt, 2005a). Furthermore, when
159 gambles are framed as losses, nonhuman animals are not reliably risk seeking, further
160 diminishing the predictive value of prospect theory (Kacelnik & Bateson, 1996; Marsh &
161 Kacelnik, 2002).

162

163 *Regret*

164 Acknowledging these weaknesses in both prospect theory and expected utility theory,
165 others have proposed cognitive accounts of risk sensitivity. For example, regret theory recasts
166 risk aversion as regret minimization (Bell, 1982; Loomes & Sugden, 1982). Regret is
167 operationally defined as the difference between the received outcome and the outcome of the
168 foregone option, and is distinct from disappointment, or the difference between the received
169 outcome and the greatest alternative outcome from that option. Regret avoidance can induce both
170 risk aversion (because of the possibility of losing) and risk seeking (because of the possibility of

171 a foregone win), assuming the participant knows outcomes will be revealed after the gamble. In
172 fact, knowledge of the alternative outcome can significantly influence people's choices: for
173 example, people are more risk seeking when they will be forced to learn the outcome of the
174 unchosen option than when they will not (Zeelenberg, 1999), suggesting that regret does regulate
175 decisions (Humphrey, 2004). Recent studies of the neural mechanisms of regret suggest that
176 neural substrates of regret aversion are distinct from those that subserve disappointment aversion
177 (Camille, et al., 2004; Coricelli et al., 2005).

178

179 *Scalar utility theory*

180 Another explanation for risk sensitivity emerged from behavioral ecology. Scalar utility
181 theory explains risk preferences by the observed psychophysical properties of the representation
182 of quantities (Hamm & Shettleworth, 1987; Kacelnik & Brito e Abreu, 1998; Perez &
183 Waddington, 1996; Smallwood, 1996). According to Weber's law, perceptual variance scales
184 with the mean of stimulus intensity. Thus, as the sizes of two different rewards (or delays)
185 increase, they will be more and more difficult to discriminate. This property causes the expected
186 probability distribution of a risky reward, derived from its history, to become positively-skewed
187 around the true mean, whereas the probability distribution of the fixed reward will be at the true
188 mean. If decisions reflect the outcome of a competitive process between two samples randomly
189 selected from the means of two reward distributions, a decision maker obeying Weber's law will
190 sample more often from the smaller end of the x axis, and will thus prefer the safe option to the
191 risky one (Kacelnik & Brito e Abreu). In the case of delays (or, presumably, any other losses or
192 costs), participants seek to minimize the amount of time until food acquisition, so the risky

193 outcome will be preferred. Scalar utility theory therefore predicts both risk aversion toward gains
194 and risk seeking toward losses.

195 Evidence for scalar utility effects on risk sensitivity comes from the finding that humans
196 and other animals typically adhere to Weber's law in perceptual discrimination of time and
197 amount (Gibbon, 1977; Gibbon, Church, Fairhurst, & Kacelnik, 1988; but see Bizo, 2006 for
198 counter-evidence). However, mounting evidence for risk seeking in the gains domain (see Table
199 1) reduces the appeal of this model. Moreover, it is unclear whether proposed failures of memory
200 are large enough to explain patterns of economic decision making for humans or nonhuman
201 animals.

202

203 *State variables and risk sensitivity*

204 Another explanation for risk sensitive behavior derives from consideration of the impact
205 of state variables like energy budgets on decision making. For example, some animals need to
206 find enough food each day in order to survive to make another choice in the future. Thus, risk
207 seeking for gains may be the only option for an organism that is on the brink of starvation
208 (Caraco, 1981). This situation can be generalized to any in which the animal's utility function is
209 convex over the range of possible gains. While Risk Sensitivity Theory, as these ideas are called,
210 elegantly applies ideas drawn from foraging theory to risk sensitive preferences, the required
211 energy state is so narrow that it has proved difficult to reproduce in a laboratory setting or
212 confirm in field studies (Kacelnik, 1997). Furthermore, risk seeking has been reliably observed
213 in situations where animals are far from starvation (Gilby & Wrangham, 2007; Heilbronner et
214 al., 2008). As revealed in Kacelnik and Bateson's (1996) literature review, juncos (*Junco*
215 *hyemalis*) in the original studies of state-dependent risk seeking (e.g., Caraco, 1981) may be

216 more the exception than the rule. In contrast with songbirds, other animals may store excess
217 energy as fat, and so may be able to survive for long periods of time without food. For these
218 reasons, there has been little empirical evidence to support the theory's predictions.

219

220 *Reward salience and risk sensitivity*

221 A final possible explanation for risk sensitivity is the relative salience of the possible
222 outcomes of the gamble (e.g., Bechara, Damasio, Damasio, & Anderson, 1997), an account we
223 will call *biased anchoring*. A salient outcome may be more available to cognitive processes
224 (memory, value representation, attention, etc), and thus bias decisions (Tversky & Kahneman,
225 1973). Risk aversion may reflect the use of the loss (from a gamble) as an anchor by which to
226 judge the expected utility of a given option. Likewise, risk seeking could result from using the
227 win as an anchor, effectively over-weighting the large payoff from a risky choice. For example,
228 it is known that humans in a positive mood are more risk averse than controls (Isen & Geva,
229 1987). Despite their good mood, they exhibit a tendency to think more about the possibility of
230 losing than do controls (Isen & Geva 1987). These participants' tendency to avoid risk may
231 reflect a biased focus on the possibility of losing.

232

233 *Summary*

234 Though decision makers are risk averse in many circumstances, there are many other
235 contexts in which decision makers are reliably risk seeking. We have summarized a few of the
236 major models designed to explain the full range of risk sensitive behaviors. Although each
237 account explains risk sensitive behavior in certain contexts, a single general account of risk

238 sensitivity remains elusive. It is likely that a richer understanding of the neuronal mechanisms
239 underlying risk sensitivity can lead to a greater understanding of behavior toward risk.

240

241 **Neural signatures of economic risk**

242

243 *Representations of expected value and risk*

244 Neuroscience offers the opportunity to carve decision making into component processes
245 (Romo & Salinas, 2003; Schall, 2004). One central goal of the neuroeconomic study of risk-
246 sensitive decision making is to determine where and how these processes are instantiated in the
247 brain (Glimcher, 2002; Sanfey et al., 2006). In any risky decision, at least two options must be
248 represented, and for at least one of them, the associated uncertainty will have to be represented as
249 well.

250 Several studies have probed the representation of uncertainty in the brain (reviewed in
251 Knutson & Bossaerts, 2007; Platt and Huettel 2008). One neural substrate that has recently been
252 implicated in this process is the dopamine system, which is generally linked to the representation
253 of reward (Schultz, 2006). Dopamine neurons in the substantia nigra pars compacta (SNc) and
254 the ventral tegmental area (VTA) project to the striatum and to the cortex (Schultz). Reward-
255 predicting cues and unpredicted rewards generally elicit phasic (i.e. brief) responses from
256 dopamine neurons, while failures to receive predicted rewards phasically suppress their activity
257 (Bayer, Handel, & Glimcher, 2004; Schultz, Dayan, & Montague, 1997; Tobler, Fiorillo, &
258 Schultz, 2005). Such responses are thought to encode a reward prediction error, or the difference
259 between the expected and obtained reward (Montague, Dayan, & Sejnowski, 1996; Schultz et al.,
260 1997), information that is particularly useful for learning in uncertain environments (Sutton &

261 Barto, 1998). (For discussion of dissenting views on dopamine function see Redgrave & Gurney,
262 2006; Ungless, 2004).

263 Explicit representations of expected and obtained rewards have obvious benefits to the
264 decision maker. Dopamine's role in representing uncertain outcomes was examined directly in a
265 study of the responses of dopaminergic neurons to conditioned stimuli associated with either
266 fixed or risky rewards (Fiorillo, Tobler, & Schultz, 2003). Monkeys observed one of five visual
267 stimuli, each associated with a specific likelihood of reinforcement (0%, 25%, 50%, 75%, and
268 100%). Then, following a delay, the reward was either given or withheld. The authors found that
269 the population of dopamine neurons, as well as some single dopamine neurons, encoded both the
270 expected value of the information and its uncertainty (which is maximized at a reward
271 probability of 50%) in distinct ways. Brief phasic responses signaled the expected value of the
272 reward, while subsequent tonic changes in activity represented the uncertainty associated with
273 the stimulus.

274 These results suggest that dopamine neurons may contribute to the representation of both
275 reward uncertainty and predicted reward value, an idea that was tested in a recent neuroimaging
276 study (Preusschoff, Bossaerts, & Quartz, 2006). On each trial, human participants placed a bet on
277 which of two playing cards ranging from 1 to 10 would have a higher numeric value. One card
278 was then revealed, informing the participant of how likely they were to win (e.g., revealing a low
279 number signals a high probability of winning if the subject guessed that the second card would
280 be the larger of the two). The authors found that blood flow in the dorsal and ventral striatum
281 (the primary target of dopamine neurons) was correlated with expected value of the gamble (i.e.,
282 the signaled probability of a win), while blood flow in the ventral striatum, the midbrain, and the
283 mediodorsal thalamus was correlated with risk (which was highest when the first card provided

284 no information about the likelihood of a win). Notably, these two signals had different temporal
285 dynamics: expected value was encoded in the early part of the hemodynamic response, whereas
286 risk was encoded in the late part of the response. Despite the large difference in the timescales
287 between the firing rates of single neurons (milliseconds) and the hemodynamic response
288 (seconds), these results are roughly consistent with the idea that dopamine neurons encode
289 different forms of reward-related information in early and late portions of their responses.

290 To fully understand risk sensitive decision making, we will need to dissociate the neural
291 correlates of risk and expected value. To do so, Knutson and colleagues (2005) used a version of
292 the monetary incentive delay task (MID). Each participant was presented with a cue indicating
293 whether money would be won or lost, what the expected value of a win or loss was, and what the
294 approximate probability of a win or loss would be. Then the participant had to press a button as
295 fast as possible. If the participant responded quickly enough, the indicated amount was given (or
296 taken away in the case of losses). Here, expected value was encoded by the nucleus accumbens
297 (NAcc, a structure that largely overlaps with the ventral striatum), whereas probability was
298 represented by the medial prefrontal cortex (MPFC). The authors inferred that emotional
299 information is maintained within subcortical circuits that include the NAcc, and then is
300 transmitted to cortical circuits including MPFC, where it is combined with probability and can
301 ultimately influence the decision.

302

303 *Competing systems for losses and gains*

304 How is the gamble actually evaluated in a risky decision? For a risky option, multiple
305 possible rewards must be combined into a single representation of value. One proposal is that
306 this combined signal reflects the outcome of a competition between systems representing the

307 possibilities of winning and of losing. Given the importance of dopamine neurons for signaling
308 reward prediction error, this system is a reasonable place to begin looking for a neural basis of
309 this posited competition. However, at present, it remains unclear whether dopamine neurons are
310 capable of representing negative reward predictions or outcomes (Bayer et al., 2004; Schultz,
311 2006). Neurons that represent negative reward prediction errors *have* been located within the
312 lateral habenula, a structure within the diencephalon (Matsumoto & Hikosaka, 2007); such
313 neurons may provide a functional complement to dopamine neurons. In addition, several cortical
314 regions, including the dorsolateral prefrontal cortex (DLPFC)(Kobayashi et al., 2006), the
315 amygdala (Gottfried, O'Doherty, & Dolan, 2003; Paton, Belova, Morrison, & Salzman, 2006),
316 the posterior cingulate cortex (McCoy, Crowley, Haghghian, Dean, & Platt, 2003), and the
317 orbitofrontal cortex (Gottfried, O'Doherty, & Dolan, 2002; Zald, Hagen & Pardo, 2002) contain
318 heterogeneous populations of neurons whose responses code for both gains and losses (or for
319 larger and smaller than expected wins).

320 Given that different structures may encode winning and losing, the valuation of a risky
321 option could reflect the outcome of a compromise between signals carried by separate brain
322 regions. This hypothesis has been tested in several neuroimaging studies. In one, participants
323 made investments in a simulated stock market (Kuhnen & Knutson, 2005). The experimenters
324 found that risk seeking decisions were preceded by activation in the ventral striatum. Because the
325 ventral striatum is a primary target of dopamine neurons (discussed above), activation there is
326 likely correlated with dopamine release. In contrast, risk averse and risk neutral decisions were
327 preceded by activation in the insula. In prior studies, the insula has been most reliably activated
328 by aversive or unpleasant stimuli. The authors hypothesized that risk seeking in this task is
329 mediated by a brief positive affect associated with the gamble, while risk aversion is mediated by

330 a brief negative affect. These ideas imply that the decision to gamble reflects the outcome of
331 competition between distinct areas representing the possibility of winning and the possibility of
332 losing.

333 A recent study has challenged the notion that separate anatomical areas mediate the
334 representation of winning versus losing (Tom, Fox, Trepel, & Poldrack, 2007). Participants on
335 each trial indicated their level of preference for a gamble offering equal probabilities of winning
336 or losing money. To tempt the generally risk averse participants into gambling, the average size
337 of the gain was set to about twice the average size of the loss. To specifically isolate decision
338 utility, the authors did not resolve the gambles until after a delay. Surprisingly, although the
339 authors found a standard set of areas exhibiting positive correlation with the size of the potential
340 win, they did not find any brain region whose responses were positively correlated with possible
341 losses. One explanation for this discrepancy reflects the difference between decision utility (the
342 amount of utility expected at the time of the decision) and experienced utility (the amount of
343 utility actually gained). The authors argue that their focus on decision utility, as opposed to
344 experienced utility, allowed them to eliminate confounding factors such as prediction error. They
345 suggest that earlier studies that found discrete brain regions activated for potential gains and
346 losses may in fact reflect a combination of these confounding factors. These results indicate that
347 the pre-decision competition between representations of the possibility of winning and losing
348 may take place within single brain areas rather than between different brain areas.

349 Whether the possibilities of winning and losing are represented in the same or different
350 brain areas, it is clear that seemingly extraneous factors, such as the way a gamble is framed, can
351 bias the relative influence of potential outcomes. One recent study has identified a neural
352 substrate for the effects of framing on risk-sensitive decision making (De Martino, Kumaran,

353 Seymour, & Dolan, 2006). The authors asked participants to make decisions in a series of
354 gambles, some of which were framed as gains and others of which were frames as losses. The
355 extent to which framing biased choices varied across individuals. The authors showed that
356 individual susceptibility to framing was reflected in activation in the amygdala. Because the
357 amygdala is associated with emotional information processing, they concluded that framing is
358 fundamentally an emotional process. In contrast, they found that activation in the orbitofrontal
359 and mediofrontal cortices was correlated with reduced susceptibility to framing.

360

361 *Neurophysiological correlates of risky decision making*

362 The neural mechanisms of calculating and storing evaluative information remain
363 unknown. Previous studies have shown that the firing rates of single neurons in the lateral
364 intraparietal area (LIP) of primate parietal cortex are positively correlated with the expected
365 value of visual orienting movements (Platt & Glimcher, 1999). Monkeys in these types of studies
366 are typically rewarded with a small squirt of juice for correct performance. When the likelihood
367 of receiving the reward was instead set at 50%, the authors found that the expected value of the
368 movement and the firing rate of the neurons decreased in concert. LIP neurons also encode
369 expected value when it is determined by information gathered from recent trials (Sugrue,
370 Corrado, & Newsome, 2004) or by the Nash equilibrium optimal strategy in a competitive game
371 (Dorris & Glimcher, 2004).

372 The next obvious step in understanding this circuitry is to find the source of the reward
373 information that modulates neuronal activity in LIP. Several studies from our lab support the
374 hypothesis that one source of this information is the posterior cingulate cortex (CGp) (Dean,
375 Crowley, & Platt, 2004; Dean & Platt, 2006; McCoy et al., 2003; McCoy & Platt 2005a). CGp is

376 a cortical structure that receives direct and indirect projections from several reward-related
377 structures, including the orbitofrontal cortex, the anterior cingulate cortex, and the striatum (Vogt
378 & Gabriel, 1993). CGp projects to the parietal cortex (Kobayashi & Amaral 2003; Vogt &
379 Gabriel, 1993), as well as other areas contributing to action-based decision making (Dorris &
380 Glimcher, 2004; Platt & Glimcher, 1999; Shadlen & Newsome, 2001; Sugrue et al., 2004; Yang
381 & Shadlen 2007).

382 Our studies (Dean et al., 2004; McCoy et al., 2003) indicate that individual CGp neurons
383 respond with relatively long-lasting changes in activity following movements toward a target that
384 predicts a reward (Figure 2C). Many of these neurons signal the value of the reward expected or
385 experienced for executing the movement. This information appears to be encoded in positive or
386 negative terms by separate populations of CGp neurons. In other words, CGp neurons are
387 monotonically tuned for reward size, in the same way that neurons in other parts of the brain are
388 tuned for orientation, brightness, or motion direction. Notably, some CGp neurons are positively
389 tuned (higher firing for larger rewards and lower firing for smaller rewards) while others are
390 negatively tuned. This heterogeneity means that the aggregate neuronal signals from positively
391 and negatively tuned neurons may average out, and that the greater neuronal population may not
392 encode reward size. This fact in turn means that CGp neuronal populations should project onto
393 different downstream or readout neurons. Another interesting feature of this area is that many
394 CGp neurons exhibit enhanced responses to unexpected omissions of rewards (McCoy et al.,
395 2003). This response property is reminiscent of dopamine neurons (see above), and suggests that
396 CGp monitors the consequences of actions to guide changes in behavior. In any case, the
397 heterogeneity in reward encoding links CGp with other brain areas, including the amygdala,
398 DLPFC, and OFC, in which the activity of individual neurons is both positively and negatively

399 correlated with reward size (Gottfried et al., 2002; 2003; Kobayashi et al., 2006; Paton et al.,
400 2006; Zald et al., 2002).

401 These prior observations suggested that CGp might contribute to the computations
402 underlying risk-sensitive decision making. To examine the contribution of CGp to risky decision
403 making, we recorded the activity of single CGp neurons during a gambling task (McCoy & Platt,
404 2005b). In this task, monkeys chose between two targets: the safe target reliably offered a
405 middle-sized reward; the risky target stochastically offered either a larger or smaller reward.
406 Monkeys strongly preferred the risky target even though the risky and safe options were matched
407 for expected value. In fact, as risk level (defined as the variance of the two possible outcomes of
408 the risky option: CV in Figure 2D) increased, the monkeys' tendency to choose the risky option
409 rose from 55% to 80%. As can be seen in Figure 2D, we found long-lasting (200ms to 2 sec)
410 changes in the responses of these neurons that were correlated with risk. In addition, CGp
411 neurons fired more vigorously after monkeys chose the risky option than after monkeys chose
412 the safe option. These results suggest that CGp maintains representations of the value of
413 uncertain options for use by downstream decision structures in the parietal lobe and elsewhere.

414

415 *Expected and unexpected forms of uncertainty*

416 Most studies of risk-sensitive decision making focus on tasks in which the level of risk is
417 well-defined to both the experimenter and to the participant. That is, all parties are assumed to
418 know that the outcome of any risky choice is fully stochastic, and that no information can be
419 gathered that will reduce the amount of uncertainty associated with the risky option. However,
420 there is evidence that the brain deals with different forms of uncertainty in different ways.

421 Several authors have found it useful to divide uncertainty into measurable and un-
422 measurable forms (Ellsberg, 1961; Knight, 1921), two forms of uncertainty that are sometimes
423 called knowable and unknowable, or expected and unexpected. Whereas measurable uncertainty
424 is characterized by a precise numerical description of the possible outcomes, un-measurable
425 uncertainty is characterized by probabilities that are not known or that cannot be known. Un-
426 measurable uncertainty sometimes includes the uncertainty associated with a single event drawn
427 from a stochastic distribution (Knight, 1921). The terms *un-measurable uncertainty*, *unexpected*
428 *uncertainty*, and *ambiguity*, while perhaps used in subtly different ways, probably represent
429 states along a continuum of uncertainty, and we will not strongly distinguish among them here.

430 In most studies of decision making in humans, participants are presented with precise
431 numerical descriptions of the different probabilities associated with different outcomes; this form
432 of uncertainty is known. Likewise, in most animal studies, subjects are so well-trained that the
433 animal can be assumed to have a stable internal representation of the likelihood of outcomes, so
434 risk is thought to be known. However, many situations, especially those outside the laboratory,
435 present un-measurable uncertainty (Knight, 1921). In such situations, decision makers need to
436 pay more attention, learn more quickly, and search for sources of information that will allow
437 them to gain information about contingencies in their environment (Yu & Dayan, 2005).

438 Measurable and un-measurable forms of uncertainty have some intuitive linkage with
439 expected and unexpected forms of uncertainty discussed in neuroscience. Separate neuronal
440 systems may mediate expected and unexpected forms of uncertainty (Yu & Dayan, 2005).
441 Specifically, it has been speculated that the acetylcholine system (ACh) signals the expected
442 uncertainty in a given situation (Yu & Dayan, 2002) while the norepinephrine system (NE)
443 signals unexpected uncertainty (Aston-Jones & Cohen, 2005; Dayan & Yu, 2006). These two

444 neuromodulators are thus thought to have complementary roles in decision making.
445 Acetylcholine and norepinephrine both act by biasing cortical processing from feedback-driven
446 (top-down) to stimulus-driven (bottom-up) responses by suppressing the activity of intracortical
447 neurons (Aston-Jones & Cohen, 2005; Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-
448 Jones, 1999), thereby facilitating responsiveness to changes in the environment and stimulating
449 learning (Yu & Dayan, 2005). The precise mechanisms by which these transmitters act may
450 allow them to specifically potentiate the differential responses to unexpected and expected forms
451 of uncertainty (Yu & Dayan, 2005).

452 In economics, the distinction between risk and ambiguity is exemplified by the Ellsberg
453 paradox (Ellsberg, 1961). Consider two bags full of red and blue balls. Bag 1 holds 50 red and 50
454 blue balls. Bag 2 contains n red and $100-n$ blue balls, where n is randomly chosen between 0 and
455 100. One ball will be chosen at random from one of the bags, and a payoff of \$10 will be given
456 for the red and \$1 for the blue. Although the expected value of the two bags is identical, most
457 participants will prefer the first (risky) bag to the second (ambiguous) bag. This predilection for
458 choosing the option with a known uncertainty is referred to as ambiguity aversion.

459 In a recent study, the neural correlates of ambiguity aversion were assessed using three
460 complementary methods (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005). In one, participants
461 chose between a risky and an ambiguous decision using cards. In another, participants gambled
462 on topics about which they felt that they had more or less background information (“Was the
463 temperature in New York/Bishkek greater than 60 degrees on October 15th last year at 5 pm?”).
464 In the third condition, they competed against players with more information than they had in a
465 gambling game. The authors found that, across the three conditions, the level of ambiguity was
466 positively correlated with the level of activation in the orbitofrontal cortex (OFC) and the

467 amygdala, and negatively correlated with the level of activity in the striatum. In addition,
468 participants with OFC lesions were insensitive to the level of ambiguity in a gamble. These
469 convergent results suggest that the OFC contributes directly to ambiguity aversion.

470 Ambiguity preferences were also studied in a second recent neuroimaging study (Huettel,
471 Stowe, Gordon, Warner, & Platt, 2006). On each trial, participants chose between two gambles,
472 each identified by a circle on a screen. Gambles were either certain (a full circle), risky (with
473 circle portions corresponding to the probabilities of the two outcomes), or ambiguous (empty
474 circle). Behavioral data for each participant was fit with separate parameters for risk and
475 ambiguity preference levels. Each individual's ambiguity seeking was most strongly predicted by
476 activation in the lateral prefrontal cortex. Because activation in this region is associated with
477 cognitive control, it was inferred that ambiguity preference reflects successful control of the
478 prepotent urge to avoid ambiguity. Furthermore, activation in this area was negatively correlated
479 with a clinical measure of impulsivity. In contrast, risk preference correlated with activity in the
480 parietal cortex, a finding that is reminiscent of findings from other physiological studies that the
481 parietal cortex represents quantitative information in contexts with low uncertainty (Platt &
482 Glimcher, 1999; Roitman, Brannon & Platt, 2007; Sugrue et al., 2004).

483

484 *Summary*

485 Researchers are in the early stages of identifying the neural substrates responsible for
486 integrating information about current needs and reward history and using this information to
487 select appropriate behaviors. Such areas appear to be critical for decision making in risky
488 contexts, because they estimate and represent the likelihood of different outcomes and participate
489 in selecting specific options. Critical brain regions include the striatum, the orbitofrontal cortex,

490 and the cingulate cortex. Dopamine, which signals expected reward, is a particularly important
491 neuromodulator regulating both risky and certain decisions. Future studies will focus on
492 identifying the specific roles of these areas and brain chemicals in different aspects of risky
493 decision making.

494

495 **Functional manipulation of risk preferences**

496

497 Manipulating decision making processes directly tests theories about their underlying
498 neural mechanisms, permitting us to distinguish effects correlated with behavior from those that
499 cause behavior. Moreover, manipulation represents one of the ultimate goals of this research:
500 given the ubiquity of failures to accurately deal with uncertainty in several psychiatric disorders,
501 treatments for suboptimal risky decision making are a potential target for therapies.

502 Affect influences one's propensity to gamble. Positive affect is a cognitive state
503 characterized by a positive outlook, greater engagement in the environment, and a general
504 tendency to experience good moods. It can be induced via participant gifts, winning at
505 competitive games, or even autobiographical recall of positive events. Participants in a positive
506 state typically exhibit a greater optimism about their prospects in a gambling situation (Nygren,
507 Isen, Taylor, & Dulin, 1996). They overestimate the likelihood of rare positive events and
508 underestimate the likelihood of rare negative events. Paradoxically, these participants have a
509 reduced tendency to accept any gamble. Consistent with this observation, they require a greater
510 probability of winning than control participants to induce risk seeking behavior (Isen & Geva,
511 1987).

512 Risk aversion among participants with positive affect is certainly puzzling. These
513 participants showed reduced utility for gains and increased disutility for losses (Isen, Nygren, &
514 Ashby, 1988). Although participants with positive affect are reliably more optimistic than control
515 participants and focus more on positive thoughts and memories (Mischel, Ebbesen, & Zeiss,
516 1973), they show a greater tendency to list thoughts about loss, suggesting that their decisions
517 are anchored to the possibility of losing (Isen & Geva, 1987). These results suggest that
518 participants with positive affect enjoy their state, are aware of its lability, and will adopt
519 cognitive and behavioral strategies designed to maintain their affect.

520 Negative affect is a cognitive state characterized by a negative orientation towards the
521 present situation and life in general, by recurring negative and pessimistic thoughts that often
522 cause distress, and by a tendency towards bad moods. Participants in whom negative affect has
523 been induced exhibit greater pessimism about their likelihood of winning gambles but are more
524 risk-seeking. This tendency is especially pronounced in situations with low probabilities of
525 winning (lotteries), and in situations in which one possible outcome (such as a loud annoying
526 sound) is aversive (Leith & Baumeister, 1996). In general, the behavioral consequences of
527 negative affect and depression tend to overlap. Even though they are thought to be generated by
528 different processes (Hartlage, Alloy, Vazquez, & Dykman, 1993), understanding negatively
529 motivated risk sensitivity may help us treat depression.

530 Another method of inducing risk sensitivity is direct manipulation or activation of neural
531 tissue. The simplest way to do this is to provide transcranial magnetic stimulation (TMS) to the
532 scalp, which, depending on the stimulation conditions, can activate or inactivate underlying
533 populations of neurons. Two studies of this kind examined the role of the dorsolateral prefrontal
534 cortex in risk-sensitive decision making. TMS-induced de-activation of right DLPFC promoted

535 risk seeking, even when it was financially disadvantageous (Knoch et al., 2006). Although this
536 effect may be explained by a transient induction of negative affect (Gershon, Dannon, &
537 Grunhaus, 2003), the authors argue that the rDLPFC normally suppresses the tendency to choose
538 the more seductive risky option, and disruption of this brain area leads to a release from
539 suppression of this risk averse tendency. Notably, this hypothesis provides a nice link between
540 the concepts of self-control and risk. Consistent with this idea, activation of the DLPFC through
541 transcranial direct current stimulation (tDCS) promotes risk aversion (Fecteau et al., 2007). Such
542 results are especially interesting given the observed activation of these areas in decision making
543 under ambiguity (Huettel et al., 2006).

544

545 *Summary*

546 Risk preferences are not static. Instead, they are highly labile, and depend on a variety of
547 circumstances. Experimenters can manipulate these circumstances to predictably alter risk
548 preferences. Such manipulations provide strong tests of the validity of neural models of risky
549 decision making.

550

551 **Impulsivity and risk sensitivity**

552

553 Just as decisions deviate from normative ideals when options are uncertain, so do
554 decisions deviate when options are delayed. Humans and other animals generally exhibit a
555 preference for immediacy, preferring sooner rewards to later ones, and seeking to defer
556 unpleasant outcomes (but see Frederick, Loewenstein, & O'Donoghue, 2002). Such behavioral
557 impulsiveness has long been associated with risk sensitivity. Nonetheless, the precise

558 relationship between these two behavioral patterns and the relationships between their
559 underlying neural mechanisms remain obscure.

560 Two distinct ideas about the relationship between impulsivity and risk sensitivity have
561 emerged. In one view, “general impulsivity” is a personality trait that encompasses a suite of
562 potentially maladaptive behaviors, including both risk seeking and high devaluation of future
563 rewards (see Myerson, Green, Hanson, Holt, & Estle, 2003). Impulsive individuals are risk
564 seeking, fail to fully consider the consequences of decisions, and do not accurately weigh costs
565 and benefits. General impulsivity has been implicated in a variety of psychiatric disorders,
566 including drug and gambling addiction (e.g. Mitchell, 1999) the manic phase of bipolar disorder,
567 schizophrenia, attention deficit hyperactivity disorder, and even some personality disorders
568 (Henry et al., 2001; Oades, Slusarek, Velling, & Bondy, 2002).

569 Performance on a temporal discounting task, a measure of impulsivity, can also predict
570 academic performance, social competence, and successful handling of stressful situations
571 (Mischel, Shoda, & Rodriguez, 1989), suggesting that general impulsivity influences all of these
572 behavioral tendencies. Thus, short time horizons and risk seeking behavior (to the point of
573 obsessive gambling) may be comorbid, implying a common underlying cause. Studies of human
574 pathologies have provided some empirical support for this linkage. For example, addicted
575 smokers are more impulsive than non-smokers on a temporal discounting task (Mitchell, 1999),
576 and they are also more likely to be problem gamblers (Pettry & Oncken, 2002).

577 In contrast to the idea of general impulsivity, the relationship between impulsivity and
578 risk sensitivity may be explained by the concept of interruption risk. The future is inherently
579 uncertain: a delayed reward is riskier than its more immediate counterpart. Any number of events
580 may devalue a delayed reward— food could rot, a giver could renege on his or her offer, the

581 chooser's energy or monetary demands may change, etc. (McNamara & Houston, 1986). One
582 simple prediction of the idea that risk mediates impulsivity is that devaluation of future rewards
583 should be consistent across time spans, since the possible risk is, on average, the same across
584 periods. However, humans and nonhuman animals do not exhibit such behavior (e.g. Ainslie &
585 Haslam, 1992; Madden, Begotka, Raiff, & Kastern, 2003; Mazur, 1987). Instead, they generally
586 show a *preference reversal*: in a choice between \$5 now and \$6 in a month, participants may
587 prefer the \$5, but if the choice is between \$5 in 12 months and \$6 in 13 months, they are likely to
588 prefer the \$6. This behavioral inconsistency demonstrates that impulsivity must reflect more than
589 just interruption risk. Nevertheless, uncertainty is probably still a major force behind impulsivity
590 in inter-temporal choice (Rachlin, 2000). This perspective offers the counterintuitive prediction
591 that individuals who are more willing to wait for delayed rewards should be more risk seeking.
592 Interestingly, in a straightforward questionnaire, human participants were slightly more likely to
593 take a risk if they were relatively patient in a temporal discounting task (Myerson et al., 2003).

594 Additionally, participants may perceive choices between engaging in risk seeking and
595 risk averse strategies as ones that they will follow for several trials. If participants construe the
596 risky option to be virtually certain to pay off at some point, then their attitudes about the relative
597 appeal of sooner and later rewards become important (Rachlin, 2000; Rachlin, Raineri, & Cross,
598 1991). Our lab recently found that by varying the time between choices (the inter-trial interval or
599 ITI), we could influence the likelihood that monkeys would gamble in a sequential choice task
600 (Figure 3, Hayden & Platt, 2007). Specifically, monkeys were risk seeking with short ITIs and
601 risk neutral with long ITIs (Figure 3C). Moreover, the precise level of risk seeking was predicted
602 by the hyperbolic discount function inferred from inter-temporal choice data. Such results are
603 predicted by Rachlin's String Theory (2000), which argues that gambles may be construed as a

604 series of outcomes in the future (Figure 3A and B). If the possibility of winning is more salient
605 than the possibility of losing, then future outcomes may be grouped into strings of losses
606 followed by a win. Such a construal biases the subjective likelihood of winning. These results
607 imply that choices about risky options have an important temporal component, and that
608 preferences and perceptions about reward rates help to shape preferences.

609 While a comprehensive review of the mechanisms supporting impulsive decision making
610 is beyond the scope of this chapter (see chapters 4 and 5 of this volume), we will highlight just
611 two of the important areas of convergence between studies of the neural mechanisms of risk and
612 impulsivity. We can ask first whether there are patients with brain damage who show abnormal
613 risk preferences or temporal discounting rates. Likely candidates are those with damage to the
614 ventromedial prefrontal cortex (VMPFC). Although such patients typically lie within a normal
615 range of performance on most cognitive tasks, they exhibit deviant decision making patterns. For
616 example, on the Iowa Gambling Task (IGT), participants repeatedly choose among decks of
617 cards with different reward and probability parameters. VMPFC patients will continue to pick a
618 deck that is disadvantageous in the long-term but offers occasional large payoffs (Bechara et al.,
619 1997). These failures have been attributed to myopia for future rewards (Bechara, Damasio,
620 Damasio, & Anderson, 1994; Bechara, Tranel, & Damasio, 2000). Although VMPFC patients do
621 not exhibit deviant patterns of temporal discounting, they do show shorter time perspectives (a
622 measure of how far into the future one regularly considers) than control participants (Fellows &
623 Farah, 2005). Furthermore, in addition to being future myopic, the patients' behavior on the IGT
624 could be interpreted as risk seeking, perhaps attributable to hyper-sensitivity to wins (but see
625 Bechara et al., 2000). Indeed, in a traditional gambling task, VMPFC patients are relatively risk

626 seeking (Sanfey, Hastie, Colvin, & Grafman, 2003). The co-occurrence of abnormal time
627 perspectives and risk seeking suggests that the VMPFC may subserve both types of decisions.

628 Future studies of the relationship between impulsivity and risk sensitivity may focus on
629 dopamine. Although no study has investigated the idea that dopamine mediates both impulsivity
630 and risk sensitivity, the evidence is tantalizing. Dopamine agonists used to treat Parkinson's
631 Disease may induce pathological gambling (Dodd et al., 2005), and abnormal dopamine
632 functioning may produce impulsivity (Cardinal, Pennicott, Sugathapala, Robbins, & Everitt,
633 2001). Dopamine may mediate both processes by activating cortex, both directly through the
634 mesocortical pathway and indirectly through striatal projections. Such activations may induce
635 general approach behavior, both to risky options and to immediate options (Schultz, 2006).

636 The common role of dopamine in both risk seeking and impulsivity is consistent with the
637 idea that dopamine serves as a general reward signaling molecule. Dopamine may in fact
638 participate in hypothesized domain-general reward decisions. Economic theories elegantly unite
639 ideas about different types of valuation into a single common framework. Such theories allow
640 the direct comparison of possible outcomes that differ along different dimensions, such as
641 expected value, risk level, and delay.

642

643 *Summary*

644 Many authors have noted that responses to probabilistic rewards and delayed rewards
645 have much in common. The fact that both risky options and delayed options tend to be
646 discounted provides a second impetus to develop a common framework to explain the effects of
647 both factors on decision making. Determining the mechanistic bases of these types of decisions
648 remains a central goal of neuroeconomics.

649

REFERENCES

- 649
650
- 651 Ainslie G., & Haslam N. (1992). Hyperbolic Discounting. In: *Choice Over Time*. G. Loewenstein
652 & J. Elster (Eds.), New York: Russell Sage.
- 653 Ariely D, Loewenstein G, and Prelec D. Tom Sawyer and the construction of value. *Journal of*
654 *Economic Behavior & Organization* 60: 1-10, 2005.
- 655 Aston-Jones G, and Cohen JD. An integrative theory of locus coeruleus-norepinephrine function:
656 adaptive gain and optimal performance. *Annu Rev Neurosci* 28: 403-450, 2005.
- 657 Bayer HM, Handel A, and Glimcher PW. Eye position and memory saccade related responses in
658 substantia nigra pars reticulata. *Exp Brain Res* 154: 428-441, 2004.
- 659 Bechara A, Damasio AR, Damasio H, and Anderson SW. Insensitivity to future consequences
660 following damage to human prefrontal cortex. *Cognition* 50: 7-15, 1994.
- 661 Bechara A, Damasio H, Tranel D, and Damasio AR. Deciding advantageously before knowing
662 the advantageous strategy. *Science* 275: 1293-1295, 1997.
- 663 Bechara A, Tranel D, and Damasio H. Characterization of the decision-making deficit of patients
664 with ventromedial prefrontal cortex lesions. *Brain* 123 (Pt 11): 2189-2202, 2000.
- 665 Bell DE. Regret in decision making under uncertainty. *Operations Research* 30: 961-981, 1982.
- 666 Benartzi S, and Thaler R. Myopic loss aversion and the equity premium puzzle. *The Quarterly*
667 *Journal of Economics* 110: 73-92, 1995.
- 668 Bizo LA, Chu JY, Sanabria F, and Killeen PR. The failure of Weber's law in time perception and
669 production. *Behav Processes* 71: 201-210, 2006.
- 670 Camille N, Coricelli G, Sallet J, Pradat-Diehl P, Duhamel JR, and Sirigu A. The involvement of
671 the orbitofrontal cortex in the experience of regret. *Science* 304: 1167-1170, 2004.
- 672 Caraco T. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*).
673 *Behavioral Ecology and Sociobiology* 8: 213-217, 1981.
- 674 Cardinal RN, Pennicott DR, Sugathapala CL, Robbins TW, and Everitt BJ. Impulsive choice
675 induced in rats by lesions of the nucleus accumbens core. *Science* 292: 2499-2501, 2001.
- 676 Coolidge JL. The Gambler's Ruin. *The Annals of Mathematics* 10: 181-192, 1909.
- 677 Coricelli G, Critchley HD, Joffily M, O'Doherty JP, Sirigu A, and Dolan RJ. Regret and its
678 avoidance: a neuroimaging study of choice behavior. *Nat Neurosci* 8: 1255-1262, 2005.
- 679 Dayan P, and Yu AJ. Phasic norepinephrine: a neural interrupt signal for unexpected events.
680 *Network* 17: 335-350, 2006.
- 681 De Martino B, Kumaran D, Seymour B, and Dolan RJ. Frames, biases, and rational decision-
682 making in the human brain. *Science* 313: 684-687, 2006.
- 683 Dean HL, Crowley JC, and Platt ML. Visual and saccade-related activity in macaque posterior
684 cingulate cortex. *J Neurophysiol* 92: 3056-3068, 2004.
- 685 Dean HL, and Platt ML. Allocentric spatial referencing of neuronal activity in macaque posterior
686 cingulate cortex. *J Neurosci* 26: 1117-1127, 2006.
- 687 Dodd ML, Klos KJ, Bower JH, Geda YE, Josephs KA, and Ahlskog JE. Pathological gambling
688 caused by drugs used to treat Parkinson disease. *Arch Neurol* 62: 1377-1381, 2005.
- 689 Dorris MC, and Glimcher PW. Activity in posterior parietal cortex is correlated with the relative
690 subjective desirability of action. *Neuron* 44: 365-378, 2004.
- 691 Dukas R, and Real LA. Effects of recent experience on foraging decisions by bumble bees.
692 *Oecologia* 94: 244-246, 1993.
- 693 Ellsberg D. Risk, Ambiguity, and the Savage Axioms. *The Quarterly Journal of Economics* 75:
694 643-669, 1961.

- 695 Fecteau S, Pascual-Leone A, Zald DH, Liguori P, Theoret H, Boggio PS, and Fregni F.
 696 Activation of prefrontal cortex by transcranial direct current stimulation reduces appetite
 697 for risk during ambiguous decision making. *J Neurosci* 27: 6212-6218, 2007.
- 698 Fellows LK, and Farah MJ. Dissociable elements of human foresight: a role for the ventromedial
 699 frontal lobes in framing the future, but not in discounting future rewards.
 700 *Neuropsychologia* 43: 1214-1221, 2005.
- 701 Fiorillo CD, Tobler PN, and Schultz W. Discrete coding of reward probability and uncertainty by
 702 dopamine neurons. *Science* 299: 1898-1902, 2003.
- 703 Frederick S, Loewenstein G, and O'Donoghue T. Time Discounting and Time Preference: A
 704 Critical Review. *Journal of Economic Literature* 40: 351-401, 2002.
- 705 Gershon AA, Dannon PN, and Grunhaus L. Transcranial magnetic stimulation in the treatment of
 706 depression. *Am J Psychiatry* 160: 835-845, 2003.
- 707 Gibbon J. Scalar Expectancy Theory and Weber's Law in animal timing *Psychological Review*
 708 84: 279-325, 1977.
- 709 Gibbon J, Church RM, Fairhurst S, and Kacelnik A. Scalar expectancy theory and choice
 710 between delayed rewards. *Psychol Rev* 95: 102-114, 1988.
- 711 Gigerenzer G, Todd PM, and Group A. *Simple heuristics that make us smart*. Oxford: Oxford
 712 University Press, 1999.
- 713 Gilby IC, and Wrangham RW. Risk-prone hunting by chimpanzees (*Pan troglodytes*
 714 *schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and*
 715 *Sociobiology* 61: 1771-1779, 2007.
- 716 Glimcher P. Decisions, decisions, decisions: choosing a biological science of choice. *Neuron* 36:
 717 323-332, 2002.
- 718 Glimcher PW. The neurobiology of visual-saccadic decision making. *Annu Rev Neurosci* 26:
 719 133-179, 2003.
- 720 Gottfried JA, O'Doherty J, and Dolan RJ. Appetitive and aversive olfactory learning in humans
 721 studied using event-related functional magnetic resonance imaging. *J Neurosci* 22:
 722 10829-10837, 2002.
- 723 Gottfried JA, O'Doherty J, and Dolan RJ. Encoding predictive reward value in human amygdala
 724 and orbitofrontal cortex. *Science* 301: 1104-1107, 2003.
- 725 Green L, and Myerson J. A discounting framework for choice with delayed and probabilistic
 726 rewards. *Psychol Bull* 130: 769-792, 2004.
- 727 Hamm SL, and Shettleworth SJ. Risk aversion in pigeons. *Journal of Experimental Psychology*
 728 13: 376-383, 1987.
- 729 Harder LD, and Real LA. Why are bumble bees risk averse? *Ecology* 68: 1104-1108, 1987.
- 730 Hartlage S, Alloy LB, Vazquez C, and Dykman B. Automatic and effortful processing in
 731 depression. *Psychol Bull* 113: 247-278, 1993.
- 732 Hayden BY, and Platt ML. Temporal discounting predicts risk sensitivity in rhesus macaques.
 733 *Curr Biol* 17: 49-53, 2007.
- 734 Heilbronner, SR, Rosati, AG, Stevens, JR, Hare, B, Hauser, MD. A fruit in the hand or two in the
 735 bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*. *In press*.
- 736 Henrich J, and McElreath R. Are peasants risk-averse decision makers? *Current Anthropology*
 737 43: 178-181, 2002.
- 738 Henry C, Mitropoulou V, New AS, Koenigsberg HW, Silverman J, and Siever LJ. Affective
 739 instability and impulsivity in borderline personality and bipolar II disorders: similarities
 740 and differences. *J Psychiatr Res* 35: 307-312, 2001.

- 741 Hertwig R, Barron G, Weber EU, and Erev I. Decisions from experience and the effect of rare
742 events in risky choice. *Psychol Sci* 15: 534-539, 2004.
- 743 Holt CA, and Laury SK. Risk Aversion and Incentive Effects. *The American Economic Review*
744 92: 1644-1655, 2002.
- 745 Holt DD, Green L, and Myerson J. Is discounting impulsive?. Evidence from temporal and
746 probability discounting in gambling and non-gambling college students. *Behav Processes*
747 64: 355-367, 2003.
- 748 Hsu M, Bhatt M, Adolphs R, Tranel D, and Camerer CF. Neural systems responding to degrees
749 of uncertainty in human decision-making. *Science* 310: 1680-1683, 2005.
- 750 Huettel SA, Stowe CJ, Gordon EM, Warner BT, and Platt ML. Neural signatures of economic
751 preferences for risk and ambiguity. *Neuron* 49: 765-775, 2006.
- 752 Humphrey SJ. Feedback-conditional regret theory and testing regret-aversion in risky choice.
753 *Journal of Economic Psychology* 25: 839-857, 2004.
- 754 Isen AM, and Geva N. The influence of positive affect on acceptable level of risk:the person
755 with a large canoe has a large worry. *Organizational behavior and human decision*
756 *processes* 39: 145-154, 1987.
- 757 Isen AM, Nygren TE, and Ashby FG. Influence of positive affect on the subjective utility of
758 gains and losses: it is just not worth the risk. *J Pers Soc Psychol* 55: 710-717, 1988.
- 759 Isen AM, and Patrick R. The effect of positive feelings on risk taking: When the chips are down.
760 *Organizational behavior and human performance* 31: 194-202, 1983.
- 761 Kacelnik A. Normative and descriptive models of decision making: time discounting and risk
762 sensitivity. *Ciba Found Symp* 208: 51-67; discussion 67-70, 1997.
- 763 Kacelnik A, and Bateson M. Risky Theories - The Effects of Variance on Foraging Decisions.
764 *American Zoologist* 36: 402-434, 1996.
- 765 Kacelnik A, and Brito e Abreu F. Risky choice and Weber's Law. *J Theor Biol* 194: 289-298,
766 1998.
- 767 Kahneman D, and Tversky A. *Choices, Values, and Frames*. Cambridge, England: Cambridge
768 University Press, 2000.
- 769 Kahneman D, and Tversky A. Prospect Theory: an analysis of decision under risk. *Econometrica*
770 47: 263-291, 1979.
- 771 Kaminski BJ, and Ator NA. Behavioral and pharmacological variables affecting risky choice in
772 rats. *J Exp Anal Behav* 75: 275-297, 2001.
- 773 Knight FH. *Risk, Uncertainty, and Profit*. Boston, MA: Houghton Mifflin, 1921.
- 774 Knoch D, Gianotti LR, Pascual-Leone A, Treyer V, Regard M, Hohmann M, and Brugger P.
775 Disruption of right prefrontal cortex by low-frequency repetitive transcranial magnetic
776 stimulation induces risk-taking behavior. *J Neurosci* 26: 6469-6472, 2006.
- 777 Knutson B, and Bossaerts P. Neural antecedents of financial decisions. *J Neurosci* 27: 8174-
778 8177, 2007.
- 779 Knutson B, Taylor J, Kaufman M, Peterson R, and Glover G. Distributed neural representation
780 of expected value. *J Neurosci* 25: 4806-4812, 2005.
- 781 Kobayashi S, Nomoto K, Watanabe M, Hikosaka O, Schultz W, and Sakagami M. Influences of
782 rewarding and aversive outcomes on activity in macaque lateral prefrontal cortex. *Neuron*
783 51: 861-870, 2006.
- 784 Kobayashi Y, and Amaral DG. Macaque monkey retrosplenial cortex: II. Cortical afferents. *J*
785 *Comp Neurol* 466: 48-79, 2003.

- 786 Kuhnen CM, and Knutson B. The neural basis of financial risk taking. *Neuron* 47: 763-770,
787 2005.
- 788 Leith KP, and Baumeister RF. Why do bad moods increase self-defeating behavior? Emotion,
789 risk taking, and self-regulation. *J Pers Soc Psychol* 71: 1250-1267, 1996.
- 790 Lerner JS, and Keltner D. Fear, anger, and risk. *J Pers Soc Psychol* 81: 146-159, 2001.
- 791 Loomes G, and Sugden R. Regret Theory: An Alternative Theory of Rationality Under
792 Uncertainty. *The Economic Journal* 92: 1982.
- 793 Madden GJ, Begotka AM, Raiff BR, and Kastern LL. Delay discounting of real and hypothetical
794 rewards. *Exp Clin Psychopharmacol* 11: 139-145, 2003.
- 795 Marsh B, and Kacelnik A. Framing effects and risky decisions in starlings. *Proc Natl Acad Sci U*
796 *S A* 99: 3352-3355, 2002.
- 797 Matsumoto M, and Hikosaka O. Lateral habenula as a source of negative reward signals in
798 dopamine neurons. *Nature* 447: 1111-1115, 2007.
- 799 Mazur JE. An adjusting procedure for studying delayed reinforcement. In: *Quantitative analyses*
800 *of behavior, vol 5 The effect of delay and intervening events on reinforcement value*,
801 edited by Commons ML, Mazur JE, Nevin JA, and Rachlin H. Mahway, NJ: Erlbaum,
802 1987.
- 803 McCoy AN, Crowley JC, Haghghian G, Dean HL, and Platt ML. Saccade reward signals in
804 posterior cingulate cortex. *Neuron* 40: 1031-1040, 2003.
- 805 McCoy AN, and Platt ML. Expectations and outcomes: decision-making in the primate brain. *J*
806 *Comp Physiol A Neuroethol Sens Neural Behav Physiol* 191: 201-211, 2005a.
- 807 McCoy AN, and Platt ML. Risk-sensitive neurons in macaque posterior cingulate cortex. *Nature*
808 *Neuroscience* 8: 1220-1227, 2005b.
- 809 McNamara JM, and Houston AI. The Common Currency for Behavioral Decisions. *The*
810 *American Naturalist* 127: 358-378, 1986.
- 811 Mischel W, Ebbsen EB, and Zeiss AR. Selective attention to the self: Situational and
812 dispositional determinants. *Journal of Personality and Social Psychology* 1973.
- 813 Mischel W, Shoda Y, and Rodriguez MI. Delay of gratification in children. *Science* 244: 933-
814 938, 1989.
- 815 Mitchell SH. Measures of impulsivity in cigarette smokers and non-smokers.
816 *Psychopharmacology (Berl)* 146: 455-464, 1999.
- 817 Montague PR, Dayan P, and Sejnowski TJ. A framework for mesencephalic dopamine systems
818 based on predictive Hebbian learning. *J Neurosci* 16: 1936-1947, 1996.
- 819 Myerson J, Green L, Hanson JS, Holt DD, and Estle SJ. Discounting delayed and probabilistic
820 rewards: processes and traits. *Journal of Economic Psychology* 24: 619-635, 2003.
- 821 Nygren TE, Isen AM, Taylor PJ, and Dulin J. The influence of positive affect on the decision
822 rule in risk situations: focus on outcome (and especially avoidance of loss) rather than
823 probability. *Organizational Behavior and Human Decision Processes* 66: 59-72, 1996.
- 824 Oades RD, Slusarek M, Velling S, and Bondy B. Serotonin platelet-transporter measures in
825 childhood attention-deficit/hyperactivity disorder (ADHD): clinical versus experimental
826 measures of impulsivity. *World J Biol Psychiatry* 3: 96-100, 2002.
- 827 Paton JJ, Belova MA, Morrison SE, and Salzman CD. The primate amygdala represents the
828 positive and negative value of visual stimuli during learning. *Nature* 439: 865-870, 2006.
- 829 Perez SM, and Waddington KD. Carpenter bee (*Xylocopa micans*) risk indifference and a review
830 of nectarivore risk-sensitivity studies. *American Zoologist* 36: 435-446, 1996.

- 831 Petry NM, and Oncken C. Cigarette smoking is associated with increased severity of gambling
832 problems in treatment-seeking gamblers. *Addiction* 97: 745-753, 2002.
- 833 Platt ML, and Glimcher PW. Neural correlates of decision variables in parietal cortex. *Nature*
834 400: 233-238, 1999.
- 835 Platt, ML, and Huettel, SA. Risky business: the neuroeconomics of decision-making under
836 uncertainty. *Nature Neuroscience*. *In press*.
- 837 Prelec D, and Loewenstein G. Decision Making over Time and under Uncertainty: A Common
838 Approach. *Management Science* 37: 770-786, 1991.
- 839 Preusschoff K, Bossaerts P, and Quartz SR. Neural differentiation of expected reward and risk in
840 human subcortical structures. *Neuron* 51: 381-390, 2006.
- 841 Rabin M. Risk Aversion and Expected-Utility Theory: A Calibration Theorem. *Econometrica*
842 68: 1281-1292, 2000.
- 843 Rabin M, and Thaler RH. Risk Aversion. *Journal of Economic Perspectives* 15: 219-232, 2001.
- 844 Rachlin H. *The Science of Self-Control*. Cambridge, MA: Harvard University Press, 2000.
- 845 Rachlin H, Raineri A, and Cross D. Subjective probability and delay. *J Exp Anal Behav* 55: 233-
846 244, 1991.
- 847 Redgrave P, and Gurney K. The short-latency dopamine signal: a role in discovering novel
848 actions? *Nat Rev Neurosci* 7: 967-975, 2006.
- 849 Roitman JD, Brannon EM, and Platt ML. Monotonic coding of numerosity in macaque lateral
850 intraparietal area. *PLoS Biol* 5: e208, 2007.
- 851 Romo R, and Salinas E. Flutter discrimination: neural codes, perception, memory and decision
852 making. *Nat Rev Neurosci* 4: 203-218, 2003.
- 853 Sanfey AG, Hastie R, Colvin MK, and Grafman J. Phineas gauged: decision-making and the
854 human prefrontal cortex. *Neuropsychologia* 41: 1218-1229, 2003.
- 855 Sanfey AG, Loewenstein G, McClure SM, and Cohen JD. Neuroeconomics: cross-currents in
856 research on decision-making. *Trends Cogn Sci* 10: 108-116, 2006.
- 857 Schall JD. On building a bridge between brain and behavior. *Annu Rev Psychol* 55: 23-50, 2004.
- 858 Schultz W. Behavioral theories and the neurophysiology of reward. *Annu Rev Psychol* 57: 87-
859 115, 2006.
- 860 Schultz W, Dayan P, and Montague PR. A neural substrate of prediction and reward. *Science*
861 275: 1593-1599, 1997.
- 862 Shadlen MN, and Newsome WT. Neural basis of a perceptual decision in the parietal cortex
863 (area LIP) of the rhesus monkey. *J Neurophysiol* 86: 1916-1936, 2001.
- 864 Shafir S, Wiegmann DD, Smith BH, and Real LA. Risk-sensitive foraging: choice behaviour of
865 honeybees in response to variability in volume of reward. *Anim Behav* 57: 1055-1061,
866 1999.
- 867 Silberberg A, Murray P, Christensen J, and Asano T. Choice in the repeated-gambles
868 experiment. *J Exp Anal Behav* 50: 187-195, 1988.
- 869 Smallwood P. An Introduction to Risk Sensitivity: The Use of Jensen's Inequality to Clarify
870 Evolutionary Arguments of Adaptation and Constraint. *American Zoologist* 36: 392-401,
871 1996.
- 872 Sugrue LP, Corrado GS, and Newsome WT. Matching behavior and the representation of value
873 in the parietal cortex. *Science* 304: 1782-1787, 2004.
- 874 Sutton RS, and Barto AG. *Reinforcement Learning: An Introduction*. Cambridge, MA: MIT
875 Press, 1998.

- 876 Tobler PN, Fiorillo CD, and Schultz W. Adaptive coding of reward value by dopamine neurons.
877 *Science* 307: 1642-1645, 2005.
- 878 Tom SM, Fox CR, Trepel C, and Poldrack RA. The neural basis of loss aversion in decision-
879 making under risk. *Science* 315: 515-518, 2007.
- 880 Tversky A, and Kahneman D. Advances in prospect theory: Cumulative representation of
881 uncertainty. *Journal of Risk and Uncertainty* 5: 297-323, 1992.
- 882 Tversky A, and Kahneman D. Availability: a heuristic for judging frequency and probability.
883 *Cognitive Psychology* 5: 207-232, 1973.
- 884 Tversky A, and Kahneman D. Loss aversion in riskless choice: a reference-dependent model.
885 *The Quarterly Journal of Economics* 106: 1039-1061, 1991.
- 886 Tversky A, and Kahneman D. The framing of decisions and the psychology of choice. *Science*
887 211: 453-458, 1981.
- 888 Ungless MA. Dopamine: the salient issue. *Trends Neurosci* 27: 702-706, 2004.
- 889 Usher M, Cohen JD, Servan-Schreiber D, Rajkowski J, and Aston-Jones G. The role of locus
890 coeruleus in the regulation of cognitive performance. *Science* 283: 549-554, 1999.
- 891 Vogt, B. A., & Gabriel M. *Neurobiology of Cingulate Cortex and Limbic Thalamus*. Boston:
892 Birkhauser, 1993.
- 893 Von Neumann JV, and Morganstern O. *Theory of Games and Economic Behavior*. Princeton,
894 NJ: Princeton University Press, 1944.
- 895 Weber BJ, and Chapman GB. Playing for peanuts: Why is risk seeking behavior more common
896 for low-stakes gambles? *Organizational Behavior and Human Decision Processes* 97:
897 31-46, 2005.
- 898 Yang T, and Shadlen MN. Probabilistic reasoning by neurons. *Nature* 447: 1075-1080, 2007.
- 899 Yu AJ, and Dayan P. Acetylcholine in cortical inference. *Neural Netw* 15: 719-730, 2002.
- 900 Yu AJ, and Dayan P. Uncertainty, neuromodulation, and attention. *Neuron* 46: 681-692, 2005.
- 901 Zald DH, Hagen MC, and Pardo JV. Neural correlates of tasting concentrated quinine and sugar
902 solutions. *J Neurophysiol* 87: 1068-1075, 2002.
- 903 Zeelenberg M. Anticipated regret, expected feedback and behavioral decision making. *Journal of*
904 *Behavioral Decision Making* 12: 93, 1999.
- 905
- 906
- 907

FIGURE CAPTIONS

907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946
947
948
949
950
951
952
953

FIGURE 1. Utility-based models of risk

A. A hypothetical utility curve. Participants are assumed to value rewards in a way that differs systematically from the associated numerical values. Typically, the value of a reward rises more slowly than its numerical value. The distinction between a value and utility can explain some forms of risk aversion. Although the expected value (abscissa) of the safe and risky reward (i.e., the average of the two risky rewards) may be the same, the expected utility (ordinate) of these options may differ systematically. For a concave utility curve (such as that shown here), the expected utility of a gamble is smaller than the expected utility of a safe option.

B. Utility curve and probability transform function according to prospect theory. Prospect theory hypothesizes a concave utility function for gains and a steeper convex utility function for losses.

C. Prospect theory also hypothesizes that probabilities are weighted non-linearly. High probabilities are underweighted while low probabilities are over-weighted.

FIGURE 2. Neurophysiological correlates of reward and risk.

A. Responses of a hypothetical positive reward prediction error neuron. When an unexpected reward occurs, firing rate increases phasically. When a reward is expected but no reward occurs, firing rate drops phasically. Responses of dopamine neurons are similar to these hypothetical neurons, although the extent to which they encode expected reward omissions remains unclear.

B. Responses of hypothetical negative reward prediction error neurons. When an unexpected reward occurs, firing rate falls phasically. When a reward is expected but no reward occurs, firing rate rises phasically. Responses of habenula neurons may instantiate negative reward prediction error signals.

C. Responses of posterior cingulate cortex neurons vary with reward size. These neurons respond differentially to reward size both before and after the occurrence of the reward. Across the population of neurons, some neurons are positively tuned for reward size while others are negatively tuned for reward size. After McCoy et al. 2003.

D. Responses of posterior cingulate cortex neurons vary with risk. These neurons respond more strongly to choices of the risky option than choices of the safe option. In addition, these neurons respond with higher tonic firing rates for higher risk levels (CV). After McCoy and Platt 2005.

FIGURE 3. Risk and impulsivity: one model

A. According to Rachlin's String Theory, repeated gambles may be construed as a series of outcomes in the future. If the possibility of winning is more salient than the possibility of losing, then future outcomes may be grouped into strings of losses followed by a win. Such a conception biases the subjective likelihood of winning.

B. Future outcomes are discounted according to a hyperbolic decay function. Strings of losses followed by a win may not be evaluated until the end of the string. By this process, the delay between sequential trials may influence the utility of the prospect of a gamble.

C. One way to test this possibility is to examine the influence of the delay between trials on risky behavior. We have recently shown that monkeys' propensity to gamble is a decreasing function of the delay between trials in a sequence. These results link together the concepts of risk and impulsivity. After Hayden and Platt 2007.

953
954
955

TABLES

Table 1: Situations that promote risk-seeking behavior

Short inter-trial intervals	Hayden & Platt (2007); McCoy & Platt (2005b)
Long inter-trial intervals	Kaminski & Ator (2001)
Negative energy states	Caraco (1981)
Rich foraging environments	Gilby & Wrangham (2007)
Severe memory constraints	Dukas & Real (1993)
Lack of cultural norms concerning money	Henrich & McElreath (2002)
Decisions from experience	Hertwig, Barron, Weber, & Erev (2004)
Loss frames	Tversky & Kahneman (1981)
Losses	Kahneman & Tversky (1979)
Hypothetical payouts	Holt & Laury (2002)
Small rewards	Prelec & Loewenstein (1991); Weber & Chapman (2005)
Negative affect	Leith & Baumeister (1996)
Positive affect	Isen & Patrick (1983)
Anger	Lerner & Keltner (2001)
Variable delays	Kacelnik & Bateson (1996)
Low probability of gain	Tversky & Kahneman (1992)

956
957
958
959
960

Table 1: Although risk aversion is generally assumed to be universal for both humans and animals, the list of situations promoting risk seeking is surprisingly long. The length and heterogeneity of this list provides a challenge to general theories of risk, most of which assume that risk aversion is universal.