

Neuroeconomics: making risky choices in the brain

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Choosing to accept enough risk, but not too much, is an important survival skill, and depending on the circumstances, animals may either seek or avoid risk. Given the choice between a sure bet and a larger but uncertain reward, a paper in this issue reports macaques consistently take the riskier option, and posterior cingulate cortex neurons represent the riskiness of those choices.

You are diagnosed with a disease for which the only available treatment is surgery. Without the surgery, you may survive for six months. If successful, the surgery will cure the disease, but there is a 50% chance that you may die of surgical complications. This is a tragic and extreme example of decision-making involving risk, but our daily lives are full of such choices with uncertain outcomes. Economists and psychologists have long studied how people and animals deal with uncertainty in making decisions. More recently, neurobiologists have begun to study the brain processes involved in decision-making¹, but the cellular mechanisms underlying risky choices have not been systematically explored. Now McCoy and Platt² report in this issue that individual neurons in posterior cingulate cortex respond according to the riskiness of the animal's choice. This is an excellent example of how neurobiological studies can enrich the formal economic theories of decision-making.

In economics, the numerical measure of an individual's preference or subjective value for an object is referred to as utility. Although it may be difficult to compare apples and oranges, utilities of any items should incorporate the preferences of an individual. This way, his or her choices can be summarized by a parsimonious principle, such as utility maximization. In situations where the outcome of a decision is uncertain, risk can be formally defined as a spread from the mean in the objective values of possible outcomes (variance). For example, a lottery that pays either \$10 or \$20 is riskier than the one paying \$14 or \$16, although they have the same mean payoffs. By definition, risk is zero for a choice that has a fixed outcome. Expected utility theory provides a solution to the problem

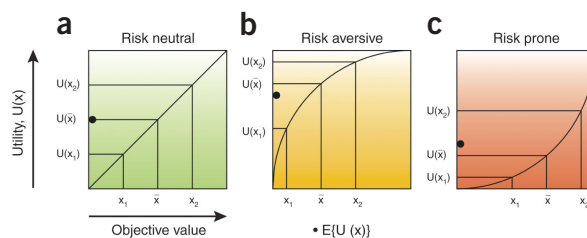


Figure 1 Utility theory's account of risk preference based on the comparison between the utility of the average outcome or reward, $U(\bar{x})$, and the expected utility, $E\{U(x)$ (black disk). (a) When a small (x_1) and large (x_2) reward are expected with the same probability ($P = 0.5$), the expected utility and the utility of the average reward are equal for a risk-neutral individual. (b,c) The expected utility is smaller and larger for a risk-averse (b) and risk-prone (c) individual, respectively, than the utility of the average reward.

of decision-making involving risk. In this theory, the utility of a choice is determined by summing the utility of each possible outcome weighted by its probability³. In other words, the utility of a choice with uncertain outcomes is its expected utility. For example, imagine that you are trying to choose between a piece of chocolate that is known to have a cherry filling and another one with a filling that is equally likely to be whiskey or pineapple. Let us also assume that you enjoy the one with a whiskey filling four times as much, and the one with cherry twice as much as the one with pineapple (4 units of utility, or 'utils'), and the one with cherry twice as much (2 utils) than the one with pineapple (1 util). According to the expected utility theory, then, the utility of the chocolate with an unknown filling would be the average of utility for whiskey-filled chocolate and utility for pineapple-filled chocolate (2.5 utils), and thus you should prefer this risky chocolate to the cherry-filled one.

The amount of risk involved in choosing a piece of chocolate might be difficult to quantify, but this can be done when different options are identified according to an objective measure (such as money). For example, imagine that the utility of money is proportional to its amount (Fig. 1a). In this case, the expected utility is

equivalent to the utility of the average outcome. For example, the utility of a lottery that is equally likely to pay 10 or 20 dollars would correspond to the utility of the average payoff of \$15. In other words, uncertainty in the outcome (risk) does not affect utility when utility of a choice is proportional to its objective value. In this situation, the decision-maker is said to be 'risk-neutral', and is indifferent to any combination of possible outcomes as long as their mean remains the same.

However, such linear utility functions often do not fit actual behavior, because people and animals can and do seek or avoid risk. In his celebrated paper³ published in 1738, Daniel Bernoulli recognized the link between the risk preference and the shape of the utility function. He proposed that the utility function should be logarithmic rather than linear, consistent with the common intuition that a small amount of money should mean more (constitute a larger increase in utility) to a beggar than to a millionaire. An individual with such a concave utility function would tend to avoid a risky choice, because risk decreases expected utility (Fig. 1b). In contrast, an individual with a convex utility function would tend to prefer a risky choice (Fig. 1c). In reality, people show both of these tendencies. For

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example, an individual might insure a car used to drive to the casino. Such observations have led to more complex shapes of utility functions⁴ and other elaborations of utility theory⁵. People and animals tend to be risk-prone when the choice involves potential losses^{5,6}, but risk-averse when they face potential gains or when the animal's energy intake is sufficient for its daily metabolic requirement⁷.

Economic and psychological theories of decision-making can successfully account for a broad range of human and animal choice behaviors, but the neural basis for this fundamental aspect of life is only beginning to be understood. Given the central role of utility in formal theories of decision-making, it is not surprising that much effort has been devoted to identifying neural signals related to the utility of choices made by the animal. Indeed, signals resembling utility have been found in many brain areas, including the posterior cingulate cortex⁸ targeted in McCoy and Platt's new study². However, it has not been possible to determine whether such signals are actually related to utility (subjective value) or to the objective value of reward (such as its size). This can be accomplished by presenting a decision-maker with the task of choosing between two alternatives with the same mean outcome, one of which has a fixed outcome and the other of which has an uncertain outcome. This is precisely the approach used in McCoy and Platt's study.

Monkeys were trained to choose between two targets, indicating their choice with an eye movement. Choosing one of the targets delivered a fixed amount of juice reward, but the amount of juice available from the other target was uncertain. By choosing the risky target, the animal had a 50:50 chance of receiving a larger or smaller reward than the mean, although the average reward was always the same for both targets. There were no other differences between the tar-

gets, so only the riskiness of the animal's choice differentiated the two. Risk was systematically manipulated by changing the difference between the smaller reward and the larger reward available from the risky target. The monkeys tested in McCoy and Platt's experiment systematically preferred the risky target, and the riskier the target, the more likely the animals were to choose it. Remarkably, the animals continued to show a bias for risky choices even when the probability of obtaining a larger reward from the risky target was reduced so that the risky choice led to a smaller average reward.

McCoy and Platt also recorded the activity of individual neurons in the posterior cingulate cortex while the animals were making their choices, and found that more than half of the neurons signaled not only the animal's choice but also the riskiness of that choice. Because the animals were risk-prone in this experiment, the utility of the risky target must be larger than the utility of the average reward. Therefore, neurons responding more strongly to a risky target might have been signaling its utility, rather than merely the size of the expected reward. This is indeed what McCoy and Platt found. They reasoned that such quantities as utility or expected reward size must be estimated from the animal's recent experience^{9–12}. However, they found that the activity in the posterior parietal cortex did not encode the size of reward in the previous trial. They then estimated the utility of each target on a trial-by-trial basis according to the sum of reward size and risk, and found that this was more reliably reflected in the neural activity.

The study of McCoy and Platt raises several exciting questions for future studies. First, by providing quantitative data regarding the risk preference of monkeys, it lays the foundation for further neurobiological studies of risk preference in primate brains. It would be interesting, for example, to determine whether monkeys are

intrinsically risk-prone, or whether their risk preference can be manipulated by any environmental or cognitive factors^{6,7}. Second, this study will stimulate similar future studies in other brain regions, as an animal's ability to make adaptive decisions depends on cooperation among multiple cortical and subcortical areas^{11–15}. For example, are risk-related signals found in the present study first generated in the posterior cingulate cortex? If not, what is the function of risk-related signals represented in this particular brain area? How do signals related to risk or utility ultimately influence the choice of the animal? As McCoy and Platt demonstrated, answers to many of these questions may be within reach now. As with any other choice in our stochastic environment, the decision to study the neural basis of risky choices might be risky, but such studies will be surely rewarding.

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Wnts send axons up and down the spinal cord

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Certain Wnts attract ascending somatosensory axons up the spinal cord toward the brain. A study in this issue shows that other Wnts guide corticospinal axons down the spinal cord, not by an attractive mechanism but by repulsion through the receptor Ryk.

The developing spinal cord is a major highway for growing axons. Axons enter and exit the highway at specific points, and, when appro-

appropriate, cross over to the other side. But the main traffic flow, as on any highway, is in both directions along the longitudinal axis—up to or down from the brain. What are the guidance cues that send these axons up or down the spinal cord? Over the past decade, researchers have uncovered many of the molecular signposts that regulate axon entry, exit and cross-

ing over. Yet, until recently, the signals that direct axons up and down the spinal cord had been elusive. The first breakthrough came a couple of years ago, when the Zou group demonstrated that Wnt proteins are important in directing axon growth toward the brain¹. Now, further work from the same group, by Liu *et al.* in this issue², suggests that other Wnt

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