

DECISION MAKING UNDER UNCERTAINTY: PREFERENCES, BIASES, AND CHOICE

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Imagine a choice between two potential jobs: a position that is stable but intellectually mundane, or one that is more exciting but offers only short contract with some chance of renewal. These kinds of decisions can be agonizing because they involve uncertainty. Although the first job option is a known quantity, the second job offers the possibility of being more fulfilling, but also the possibility of being let go in the near future. This uncertainty means that it is not possible to know the exact consequences of the decision in advance, making it difficult to judge the best course of action. Many important decisions involve this same sort of uncertainty—such as whether to invest in a new business, commit to a partner, or pursue a medical treatment. Yet uncertainty is not something only humans experience: It is pervasive in the natural world, and all animals must sometimes make decisions without complete information about the consequences of their actions. For example, foraging animals have to decide which patch of food to exploit, but will likely not know precisely how much food they will extract from different patches. Rather, this forager will have to decide where to go on the basis of some estimation of how much food different patches might provide, as well as the likelihood of that amount.

Uncertainty is a ubiquitous feature of animal and human lives. Consequently, illuminating how decision makers respond to uncertainty is a problem of interest across the social and biological sciences. Economists aim to predict patterns of choice in economic markets, where decisions often

involve tradeoffs between the value earned and the risks incurred. Psychologists and neurobiologists aim to tease apart the mechanisms that humans and other species use to encode and evaluate uncertainty. Finally, biologists aim to understand the evolution of different behavioral strategies (often accounting for how psychological mechanisms may constrain possible behaviors), as uncertainty may influence the biological consequences that animals accrue from their decisions, including fitness benefits. This review will integrate theory across these fields to understand the psychological mechanisms that animals use to make decisions under uncertainty, as well as what biological function these mechanisms might have. I further argue that comparative research is a powerful tool for understanding the nature of economic decision making. Discovering that a particular decision making pattern is widely shared across humans and other species—or conversely, unique to humans alone—can provide important insights about the types of experiences that engender these psychological processes. For example, if many other animals also exhibit some human-like bias when faced with uncertainty, this would suggest that experience with economic markets or human culture is not necessary for this bias to emerge (see also Santos & Rosati, 2015).

This review is divided into three major sections. The first part examines different models of decision making under uncertainty from economics, psychology, and biology. This section will provide theoretical benchmarks for conceptualizing how

and why decision makers account for uncertainty when they are making decisions. The second section will focus on empirical evidence concerning whether other species are sensitive to uncertainty, as well as what preferences they exhibit when making decisions. This section will focus on the psychological mechanisms that influence decision making: how animals detect variance in possible payoffs, learn about different potential courses of action, and ultimately evaluate options to settle on their preferred response. The final section will examine how these psychological mechanisms for thinking about uncertainty play out in the real world. This section will examine how an individual's state, the larger social context, or even differences in species-typical environment can influence the expression of risk preferences.

MODELS OF CHOICE UNDER UNCERTAINTY

Economics, psychology, and biology have all developed formal models of choice that reveal how decision makers can maximize their value (see Chapters 14 and 15, this volume). Such models can provide powerful tests of whether decision makers are acting in an optimal fashion—and can further help in revising our notions of optimality when actual behavior does not agree with the models. However, different fields often have quite different assumptions about what the optimal response to uncertainty is, as these disciplines diverge in terms of what value individuals are trying to maximize. Whereas economics and psychology often assume decision makers want to maximize some (internal or subjective) measure of “goodness” such as utility, biological models assume behaviors are designed to maximize long-term fitness benefits. These different expectations can lead to different predictions about decision-making strategies. Furthermore, whereas some models predict what an ideal decision maker should do (prescriptive models), other models rather aim to accurately describe what real-world decision makers actually do (descriptive models)—and different disciplines may have different focus in this sense as well. This section will therefore cover several diverse models of choice under uncertainty from across economics,

psychology, and biology—which will guide later examinations of empirical evidence for patterns of animal decision making.

Classical Economics and Expected Utility

The challenge of deciding the best course of action when outcomes are uncertain was recognized even by early philosophers, predating modern economics as a field. Blaise Pascal (1670/1995) proposed his famous theological “wager,” contrasting two possible courses of action: either living as if God exists, or living as if God does not exist. In Pascal's analysis—dated to the 1660s—acting as though God exists produces an infinitely high “payoff” if correct, but a small cost if incorrect. In contrast, acting as though God does not exist produces a small benefit if correct, but an infinitely high cost if incorrect. Pascal's treatment of this philosophical problem introduced several concepts that are now foundational to decision science. In particular, Pascal suggested that decisions involving uncertain outcomes should be based on the value of each outcome weighted by its likelihood. Whichever action results in the greatest expected value is thus the best course of action. In the case of this wager, the payoffs resulting from a belief in God are infinite—so even a very small possibility of being correct means that behaving as though God exists is the course of action with the highest expected value.

Pascal's wager highlights an important prediction of expected value theory: People should be willing to gamble on an infinitesimally small chance of winning an infinitely large amount reward. However, most people actually will not take this kind of extreme risk, suggesting that expected value approaches do not fully capture how people make decisions. Daniel Bernoulli (1738) formalized this violation as the St Petersburg paradox, arguing that the true currency of decisions under risk is not expected value. People do not decide only on the basis of probability of different outcomes alone, but rather weight the utility or goodness of those outcomes. The trick is that utility and value do not have a one-to-one relationship, because utility offers diminishing marginal returns. Consequently, a one-unit increase in a larger reward produces less utility to a decision maker than the same increase relative

to a smaller initial reward. Bernoulli specifically conceptualized expected utility theory in terms of how the relative impact of some amount of money depends on the decision maker's wealth. That is, he suggested that winning some amount of money has less utility for a comparatively wealthy person than it does for a poorer person.

In the 20th century, Von Neumann and Morgenstern (1947) formalized this general approach with a set of four axioms describing the behavior of a rational decision maker. First, their hypothetical decision maker should have well-defined preferences (the *completeness axiom*): For any two options (e.g., apples and oranges), either one is preferred or they are equivalent. Second, these preferences should exhibit a consistent rank (the *transitivity axiom*): If apples are preferred to oranges, and oranges are preferred to bananas, then apples should be preferred to bananas. Third, these preferences exist on a common comparative scale (the *continuity axiom*): If apples are better than oranges, but oranges are better than bananas, then there should be probability where receiving an orange is thought to be equivalent to gambling on the likelihood of either winning the desired apple, or losing out and receiving only a banana. Finally, these preferences should not be impacted by irrelevant alternatives (the *independence axiom*): If someone prefers apples to oranges, apples should still out-rank oranges even if there is some broccoli lying around too. Von Neumann and Morgenstern showed that by following these principles, a decision maker would act to maximize his or her own personal utility function.

Behavioral Economics and Psychological Realism

The power of rational choice theory is that a few reasonable-sounding first principles can generate a wide-ranging set of predictions about how individuals should act. However, subsequent empirical research has revealed that humans (and other animals) often violate many of these predictions. Accumulating evidence of such anomalies led economists and psychologists to develop new theories that are more firmly grounded in the psychological processes supporting choice. These newer models aim to accurately capture real-world behavior,

rather than reason about optimal behavior from first principles like rational choice theory. As there has been a subsequent explosion of models about decision making under uncertainty (Starmer, 2000), this section will address several broad developments in risky choice theory.

The first major attempt to synthesize several decision making anomalies came from prospect theory, developed by Daniel Kahneman and Amos Tversky. Prospect theory also assumes that decision makers act to maximize their utility, but proposes several major changes as to how utility is determined by real-life decision makers (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). First of all, people are not assumed to judge outcomes on the basis of their impact on total wealth (an assumption of classical theory). Rather, decision makers assess whether their choice results in a positive or negative change relative to a more local reference point. Second, this theory proposes that positive changes relative to the status quo (gains) are treated differently from negative changes (losses). In particular, people dislike a negative change much more than they like an equivalent positive change, a phenomenon called *loss aversion*. This means that the magnitude of how bad people feel about losing \$10 from their pocket exceeds the positive feeling that results from finding \$10 on the street. Third, people exhibit diminishing sensitivity to changes: The difference between winning \$10 and winning \$20 does not feel equivalent to the difference between \$110 and \$120, even though the absolute difference is the same. This results in a utility curve that is concave for gains, but convex for losses. More recent additions to prospect theory have further suggested that probabilities themselves might be weighted, not treated as equivalent to their actual magnitude as in previous work. In particular, people may overweigh the importance of outcomes that occur rarely, but underweigh the likelihood of outcomes that have a high probability (Kahneman & Tversky, 2000).

Overall, prospect theory successfully accounts for several major deviations between actual decision patterns and rational choice theory. One important example is the framing effect: People tend to be risk-averse for gains—trying to avoid variance in outcomes—but are actually risk-seeking for losses.

A classic study by Tversky and Kahneman (1981) illustrated this phenomenon by contrasting possible strategies to fight a disease outbreak. One strategy would certainly help a set number of people, whereas the other strategy was riskier: It might help everyone, or it might help no one. The twist was that people heard about these strategies either in terms of the number of people who would live, or the number of people who would die. The consequences of each strategy across situations were identical, except in whether the researchers described the outcome in terms of lives saved or lives lost. In fact, participants who made decisions about number of lives saved (the gain frame) were averse to taking risks. In contrast, participants who had to make decisions about the number of deaths (the loss frame) preferred the riskier option. That is, they gambled on the possibility of no deaths, rather than accept a certain number of deaths would definitely occur. Prospect theory accounts for this preference flip—called *the reflection effect*—because the utility curves for gains and losses have different shapes.

Broadly speaking, prospect theory and its descendants use expected utility theory as a general framework, but modify the utility computations involved to better align with real behavior (Barberis, 2013). More recent models of decision making from psychology have further deviated from expected utility theory by focusing on other types of psychological substrates that are not obviously involved in such utility calculations. For example, people have mental states (e.g., knowledge) that can impact how they make decisions. Such knowledge states play an important role in how people respond to distinct types of uncertainty: *risk*, where the likelihoods of potential outcomes are known; and *ambiguity*, where even the likelihood of different outcomes is not known in advance. Rational choice theory expects that people make decisions on the basis of expected value, regardless of their confidence in their knowledge (Savage, 1954). However, empirical research shows that decision makers' knowledge and confidence in their judgments can have a profound impact on preferences, such that people actually respond very differently to risk and ambiguity. The Ellsberg paradox is one illustration of this distinction. Imagine a decision maker faced with a choice between

one urn known to contain 50% red balls and 50% blue balls, and another urn with an unknown distribution—there could be anywhere between 0% and 100% red balls. Which urn is more likely to produce a red ball? The expected value of these urns is actually identical, because the average chance of pulling a red ball out of the ambiguous urn (that could vary from 0% to 100% red balls) is also 50%, the same as the risky urn with the known distribution. However, people overwhelmingly prefer to bet on the risky option (Ellsberg, 1961). Although many situations conflate variation in known probability with ambiguity, studies that carefully tease them apart show that people strongly dislike choosing ambiguous options (Camerer & Weber, 1992). That is, people are biased against choosing the unknown.

Other models focus on other diverse aspects of psychological experience, such as emotional states. One prominent example is the risk-as-feelings model, developed by George Loewenstein and colleagues (Loewenstein, Weber, Hsee, & Welch, 2001). This theory proposes that people process risks at two psychological levels: by computing the costs and benefits provided by different options (as in expected utility approaches) and by evaluating their emotional responses to the available options. Such emotions may influence decision making via several complex pathways (Loewenstein & Lerner, 2003). For example, people may experience negative emotions after taking a risk and losing, including disappointment that they did not win, or regret that they did not choose differently (Coricelli, Dolan, & Sirigu, 2007). The mere anticipation of feeling such potent emotions can also shape decisions. For example, people may make choices that minimize the chance they will regret what they did—showing *regret aversion* even if their strategy reduces their total payoffs in the long run (Zeelenberg, 1999).

Finally, recent work in neuroeconomics aims to bridge economics and neurobiology by developing theories of how decision making is actually implemented in the brain (Loewenstein, Rick, & Cohen, 2008; Sanfey, Loewenstein, McClure, & Cohen, 2006). Research on decision making under uncertainty in particular has aimed to identify neural signals of value and probability, as well as to understand the interactions between neurobiological

systems that influence choices (Platt & Huettel, 2008). In contrast to many theories from economics aiming to identify some unitary construct of value (e.g., utility), many neurobiological models of decision making suggest that more than one fundamentally different process can influence choices. Although there are several flavors of dual-process models, they often propose two distinct processes shaping choice: a more analytical system that is effortful and slow, as well as a more intuitive system that is automatic and fast (Kahneman, 2011). For example, the risk-as-feelings model discussed previously proposes that decisions about risk result from interactions between an analytical system that considers the rewards and probabilities in play, and an emotional system that reacts to this information (Loewenstein et al., 2001). These neuroeconomics models therefore try to decompose fairly complex decision-making behaviors into the underlying neural processes that represent or influence choice.

Behavioral Ecology and Biological Function

Theories from economics and psychology generally treat decision making as a process where individuals attempt to maximize their personal index of utility (see Chapter 15, this volume). Biological models also assume that individuals attempt to maximize some measure of value, but the “currency” in question is not utility, but rather biological fitness (Hammerstein & Hagen, 2005; Kacelnik, 2006; Krebs & Davies, 1978). Furthermore, biological models focus on a different type of prototypical decision-making situation: choices about food or caloric value that an animal obtains while foraging (see Chapter 14, this volume). Biological models therefore involve normative reasoning from first principles, much like classical economic theories. However, this approach has different assumptions about what decision makers aim to maximize.

The prevalent biological theory for decision making under uncertainty, called risk sensitivity theory, emphasizes that animals do not simply maximize mean foraging returns. Rather, animals also account for the potential variance in their payoffs—and the reason is because uncertainty in foraging returns can directly impact fitness above and beyond the mean

returns. The key to understanding how variance in foraging returns can impact fitness is to consider an animal trying to acquire one additional unit of food. Although this additional amount of food clearly seems related to the decision maker’s fitness, it does not have a one-to-one correspondence: The marginal gain from a given piece of food depends on how much food the animal has already acquired. This idea therefore parallels approaches from economics and psychology arguing that the relationship between one additional unit of reward and one additional unit of subjective utility is not linear. However, risk sensitivity theory specifically proposes that the relationship between foraging returns and fitness depends on the animals’ energetic state when they make their choice (Caraco, 1981; Caraco, Martindale, & Whittam, 1980; Stephens, 1981). Imagine one bird who is currently satiated, and one who is on the verge of starvation. The starving bird needs a greater payoff than the satiated animal to survive, because winning big is its only chance to meet its energetic needs. This type of analysis suggests that animals should shift their risk strategies across contexts: exhibiting risk-seeking behavior when energetic requirements exceed expected payoffs, but exhibiting more risk-averse behavior if the average expected payoffs will already meet these requirements.

Risk sensitivity theory therefore predicts that animals will generally be sensitive to variance in payoffs, but their particular preferences can flip across situations. This theory has been extremely influential, and the importance of variance is now a lynchpin of much work in behavioral ecology. However, the explanatory power of the specific predictions of this theory is currently unclear. Some early studies examining how animals respond to risk in different energetic states provided support for risk sensitivity theory. For example, when birds make decisions under conditions of relative food deprivation or when being maintained at cooler temperatures (i.e., birds needed more calories to meet their energetic requirements), they are more risk-prone than when making choices under better conditions (Caraco et al., 1980, 1990). However, a recent review pointed out that there have been few direct tests of the specific predictions of risk sensitivity theory,

and suggested that current evidence provides at best weak support (Kacelnik & El Mouden, 2013). Indeed, some research shows that animals may broadly account for risk, but nonetheless violate the specific predictions of risk sensitivity theory. In particular, energetic state may have different influences on risk preferences depending on the species in question. Although smaller animals may face a significant risk of starvation, larger-bodied animals do not face such a serious starvation threat and may respond differently to risk. In line with this idea, chimpanzees (*Pan troglodytes*) actually engage in riskier foraging behaviors resulting in more variable payoffs (such as hunting) when they are in a better state and therefore have the necessary energetic reserves to take risks (Gilby & Wrangham, 2007).

Regardless of support for the specific predictions of risk sensitivity theory, research examining the relationship between energetic state and risk preferences highlights another fundamental difference between economic and biological theory. Rational choice theory is premised on the idea that decision makers are internally consistent in their preferences, exhibiting the same preferences across contexts (Kacelnik, 2006). This is why situations where people act inconsistently across contexts, such as in response to framing, represent violations of rational choice theory. Biological models, in contrast, focus on how choices influence an animal's reproductive success, and natural selection does not necessarily prioritize consistency in preferences. Context may even provide important information about the fitness value of a behavioral strategy, so inconsistent preferences can maximize fitness in some situations (Fawcett et al., 2014; Houston, 1997). Therefore, context-sensitive decision making may be biologically optimal. The putative rationality of such context-dependent shifts in decision-making strategies therefore represent a major divergence between biological and economic theories of decision making under uncertainty.

PSYCHOLOGICAL MECHANISMS FOR UNCERTAINTY IN ANIMALS

Foundational theories from economics, psychology, and biology predict that decision makers will

be sensitive to risk (although the reasons for this prediction are not necessarily the same). Research on human decision making shows that humans are sensitive to risk, and generally exhibit a strong aversion to options with variable payoffs. Do other animals exhibit similar responses? This section will address the empirical evidence that animals are indeed sensitive to uncertainty, as well as explore the psychological processes that shape their responses. Some mechanisms for decision making under risk seem to be widely shared, including basic capacities to encode and detect differences in reward distributions. Yet many models of human decision making involve complex reasoning and emotional processes. Nonhuman studies can therefore address whether other species share these capacities, as well as help constrain interpretations of the psychological mechanisms that influence human choice (Santos & Rosati, 2015).

Methods for Probing Animal Decision Making

Human decision-making studies typically present linguistic descriptions of hypothetical one-shot choices, often concerning different payouts of money (Hertwig & Erev, 2009). For example, people might be asked, "Would you prefer a 50% chance of winning \$20, or \$10 for sure?" Animals, however, cannot answer such hypothetical questions (and are not particularly motivated to seek out money). Consequently, most animal decision making tasks measure behavioral responses to real choices, typically involving a series of iterated decisions about consumable rewards such as food or juice. Within this general methodological approach—iterated, experience-based decisions for real rewards—researchers have developed several paradigms to probe nonhumans' sensitivity to and preferences for uncertainty.

The most commonly used setup to probe animal decision making under risk involves decisions about quantitative uncertainty: distributions that provide different amounts of the same type of reward (much like human studies involving different monetary payouts). A typical experimental setup using this approach might contrast options that differ in the average payoff they provide, or the spread of

possible outcomes that can occur. Importantly, in these paradigms, animals generally must initially learn that some cue (such as a color or location) signals the differences in reward distributions. For example, pigeons (*Columba livia*), starlings (*Sturnis vulgaris*), or rats (*Rattus norvegicus*) might learn that different rewards are associated with pecking different buttons or making nose pokes in different locations (see B. Marsh & Kacelnik, 2002; Paglieri et al., 2014; Zentall & Stagner, 2011). Similarly, rhesus macaques (*Macaca mulatta*) might learn that saccading their eyes to different visual targets will produce different volumes of juice rewards (McCoy & Platt, 2002). In other cases, primates such as chimpanzees, bonobos (*Pan paniscus*), or capuchins (*Cebus apella*) might learn that they can point at differently-colored containers, which reveal different reward distributions across trials (see De Petrillo, Ventricelli, Ponsi, & Addessi, 2015; Heilbronner, Stevens, Rosati, Hare, & Hauser, 2008). Finally, nectar- or pollen-feeding species such as rufous hummingbirds (*Selasphorus rufus*) or bumblebees (*Bombus* sp.) might learn that different artificial flowers vary in the volume or concentrations of nectar they contain (Hurly & Oseen, 1999; Real, 1991). Although these setups vary in terms of the cues that signal reward distributions, as well as the particular way that animals respond to make choices, they all share a commonality of presenting animals with decisions about options that vary in terms how much rewards they provide. Such studies of quantitative risk, therefore, provide a fairly equivalent metric to examine how difference species respond to payoff variation, and comprise the strongest comparative data of risk sensitivity in nonhumans.

However, by their nature these paradigms often require extensive training periods for animals to learn the predictive cues signaling reward distributions. Animals may have to complete hundreds or thousands of trials, including forced-choice or exposure trials (where only one option is available for the animal to choose, thereby ensuring they experience it) as well as trials that involve actual choices between different distributions. Even fairly simple tasks involving just one dyadic contrast between two options that provide the same average payoff but differ in variation across trials (e.g., a choice

between a safe option that always provides four pieces of food and risky option that provides one or seven pieces with equal probability) may involve animals acquiring risk preferences over hundreds of trials (see Heilbronner et al., 2008, for such learning effects in apes). It is therefore important to note that differences in the training animals receive when initially learning payoff contingencies, as well as the number of trials and subsequent feedback that is experienced, can all shape how a given individual will respond to risk in the long run.

Given the long period of experience or learning that are typical of these risk tasks, some recent work has examined animals' more spontaneous reactions to uncertainty. The common premise of these sorts of paradigms is that animals can infer their chance of winning on a given trial (rather than learn some association between a given response and a given payoff distribution). Moreover, these setups also allow the rewards in play to vary on a trial-by-trial basis without training each new set of contingencies. One example of a risk paradigm using this approach tested how chimpanzees and bonobos make decisions when the risk involved variance in the type of food they received (Rosati & Hare, 2011, 2012, 2013). Apes saw an intermediately preferred food type (such as peanuts) placed under one container, whereas either a highly desirable (banana) or less-desirable (cucumber) type of food was placed under another container—the trick was that apes did not know which was there. In one study using this task (Rosati & Hare, 2013), apes were first introduced to the setup on one day, and then completed less than 20 choice trials on a second. In another inferential paradigm, chimpanzees, bonobos, gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*) could infer the hiding locations of rewards that were distributed under different containers (Haun, Nawroth, & Call, 2011; see also Pelé, Broihanne, Thierry, Call, & Dufour, 2014). In this setup, a smaller reward would be placed under one known container, whereas a larger reward would be placed under one container from a larger set. Because the apes did not know which container in that set had the big piece of food, a selection of one of these containers represented a risky choice. This type of setup allowed the relative value and probability of

winning to vary parametrically across trials, without new training on each decision contrast. Although these setups are more difficult to fit into traditional economic approaches focused on relative expected value of (quantitative) gambles, they do provide important information about how different species react to uncertainty in matched situations without such extensive training and experience.

Sensitivity to Expected Value, Variance, and Skew

Economic and psychological research shows that humans can use information about the distribution of payoffs when making decisions under uncertainty, responding to three aspects of a payoff distribution (see Figure 16.1): (a) the expected value, or mean payoff; (b) the variance, or spread of potential outcomes; and finally, (c) the distribution's skew, or asymmetry around the mean. These three characteristics of a statistical distribution can all vary independently, so some tasks will even pit them against each other to see which gets priority in the decision making process. For example, one piece of evidence that humans show an aversion to risk is that they are even willing to sacrifice some expected value to avoid variability in payoffs. Although most studies of risk involve gambles where payoff variance is distributed normally around the mean, another defining characteristic of a distribution is its skew. Current evidence indicates people do detect distribution skew, and are more risk-seeking when variance is negatively skewed such that better outcomes are more likely, with a small chance of very bad outcomes (Symmonds, Wright, Bach, & Dolan, 2011;

Wright, Symmonds, Morris, & Dolan, 2013). That is, humans seem to prefer a gamble where choices generally result in a better-than-average outcome, but occasionally result in a much more undesirable one.

Can other animals detect uncertainty, and if so do they show the same sorts of preferences for risk that humans do? A wide body of research shows many diverse nonhuman species do detect variance in payoffs, and also tends to show an aversion to risk much like humans (see Kacelnik & Bateson, 1996, for a large review of comparative work). Species that exhibit some level of risk aversion include insects, such as bumblebees (Harder & Real, 1987; Real, 1991) and honeybees (*Apis mellifera*; Shafir, Wiegmann, Smith, & Real, 1999); birds, such as blue jays (*Cyanocitta cristata*; Clements, 1990), white-crowned sparrows (*Zonotrichia leucophrys*; Caraco, 1983), juncos (*Junco phaeonotus*; Caraco et al., 1980), hummingbirds (Hurly & Oseen, 1999; Waser & McRobert, 1998), starlings (Bateson & Kacelnik, 1995), and pigeons (Hamm & Shettleworth, 1987); rodents, such as rats (Logan, 1965); and primates, such as bonobos (Heilbronner et al., 2008), ringtailed lemurs, mongoose lemurs, and red ruffed lemurs (*Lemur catta*, *Eulemur mongoz*, *Varecia rubra*; MacLean, Mandalaywala, & Brannon, 2012). These results show that at least mild aversion to risk is a strategy spanning wide phylogenetic spaces, suggesting that risk aversion is a deeply conserved behavioral response. Consequently, human risk preferences in economic decision-making contexts are likely shaped by psychological mechanisms with deep biological origins.

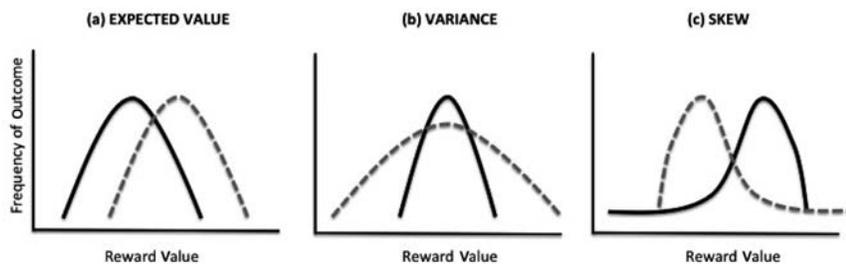


FIGURE 16.1. Payoff distributions in choice under uncertainty. Distributions that vary in (a) expected value, or mean; (b) variance, or deviation; and (c) skew, or asymmetry.

However, there are important exceptions to this general pattern. For example, although many bird species appear risk-averse in foraging tasks involving quantitative risk, grey jays (*Perisoreus canadensis*) are relatively risk-prone when tested in similar contexts (Ha, Lehner, & Farley, 1990). Several primate species also appear risk-seeking when faced with numerical variation in payoffs, including chimpanzees (Heilbrunner et al., 2008), rhesus macaques (McCoy & Platt, 2002; Platt & Huettel, 2008), and capuchins (De Petrillo et al., 2015). Similarly, inferential paradigms (involving inferences about the location of different rewards) have also identified species differences in response to risk. For example, when faced with options that vary in the quality of reward type they provide, chimpanzees tend to gamble on winning the preferred food type, whereas bonobos prefer the reliable but intermediate-value reward (Rosati & Hare, 2012, 2013). Similarly, when larger or smaller rewards are hidden under different numbers of containers, chimpanzees and orangutans played the odds that they would find the larger reward, whereas bonobos and gorillas were more likely to go with the smaller reward in a known location (Haun et al., 2011). These species are therefore sensitive to risk—in that they discriminate between constant and variable options—but show a different pattern of preferences than humans and many other species.

Furthermore, current comparative research suggests that although animals can detect skew, they may show different preferences for asymmetrical variance than do humans. For example, white-crowned sparrows (Caraco & Chasin, 1984) and rhesus monkeys (Strait & Hayden, 2013) tended to prefer positively skewed risk. In this situation, smaller rewards are more likely, but there is a small chance of a very good outcome. One possibility is that this bias results from the differential salience of high-value and low-value payoffs for the animals. However, this is not the whole story, as rhesus monkeys' patterns of preferences for skew were actually fairly complicated: In addition to their preference for positive over negative skew, they generally preferred gambles with strong skew over weak skew or no skew, but also preferred normally distributed gambles over weak skew. This highlights that skew

can have complex effects on risk preferences, and therefore that it is necessary to account for skew to characterize the computations that underlie decision making.

In all, current comparative evidence suggests that risk-aversion is generally a widely shared strategy, but that there are also some striking disparities given that some species may actually seek out risky gambles. When considering this sort of comparative data, it is important to note that payoff contingencies and task design can clearly influence risk preferences (see Heilbrunner & Hayden, 2013, for a review). Moreover, the ways in which animals initially learn about payoff distributions can shape their responses to risk in fundamental ways, as explored in the next section. These sorts of contextual factors are critical considerations when comparing the performance of species tested in different setups (or setups that are designed to be analogous, but involve different learning acquisition periods). Moreover, these sorts of context-dependent shifts in risk preferences indicate that a given individual or species is unlikely to have a static strategy for dealing with uncertainty, such that they always avoid or always prefer risk regardless of context. Yet even given these caveats, some species seem to respond differently to variation in payoffs compared to other species—even when tested in broadly comparable or directly matched situations. The origins of such species differences in risk preferences is therefore an important issue for biological theories of decision making.

Learning About Payoffs

In many of the paradigms discussed previously, animals must first gain extensive experience with potential options, learning about the different reward distributions in play to make informed decision. For example, animals might sample all available options in an initial exposure phase involving forced choice or exposure trials, where only one option is available at a time to ensure that the individual has tried it out (see Zentall & Stagner, 2011). In other cases, animals might complete many hundreds or thousands of choice trials to learn about the distributions—with the main focus being on how animals perform after their patterns of choices

have stabilized (see McCoy & Platt, 2002). Learning mechanisms can therefore have a big impact on how animals perform in decision making tasks. Moreover, foraging animals must often learn about payoff distributions by sampling different courses of action over time, for example by feeding on different patches (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), so these learning mechanisms shape behavior in the real world as well. Consequently, illuminating the psychological mechanisms that animals use to learn about uncertainty and update their responses is critical to understanding how different species respond to risk.

What processes drive animal learning, and are there parallels between the psychology of humans and nonhumans? In fact, it is clear that experience-based learning can play an important role in the construction of risk preferences in humans (Hertwig & Erev, 2009), and in some contexts these same sorts of learning mechanisms shape other species as well. For example, when humans and pigeons are presented with structurally identical decisions and learn about their options through direct experience, they exhibit similar risk preferences (Ludvig, Madan, Pisklak, & Spetch, 2014; see also Weber, Shafir, & Blais, 2004). These kinds of direct comparisons between humans and nonhumans provide strong evidence for shared learning substrates across human and other species. However, animals and humans may show important differences in how they learn about more complicated distributions.

One example of a more complex task that had been implemented across species is the Iowa Gambling Task. In the original version of this task developed for humans (Bechara, Damasio, Tranel, & Damasio, 1997), individuals could choose between four decks containing cards, with each representing either a win or a loss of money. These decks differ in their average payoffs as well as their variance: Two decks produced losses on average over trials but occasionally result in a big payoffs, whereas the other decks did not have as much risk—and did not include very high-value cards—but resulted in average gains over time. Although people have no initial knowledge about the payoffs provided about these decks, most learn to prefer the higher-value,

lower-risk decks as they sample the different options. Comparative adaptations of this paradigm, however, suggest that other species may not always be as sophisticated as humans at detecting the optimal response. For example, one study compared the responses of humans, chimpanzees, and capuchins to a simplified version of this task involving only two decks (Proctor, Williamson, Latzman, de Waal, & Brosnan, 2014). Across several conditions that differed in the relative variance and mean payoffs of the two decks, capuchins generally showed less evidence of learning the optimal response compared to humans or chimpanzees. Furthermore, several rodent adaptations of this setup involving operant tasks suggest that rodents may also fail to converge on the optimal response (see de Visser et al., 2011 for a review). For example, one adaption replaced the original monetary losses with time-out penalties, where choices could no longer be made. Although some rats could succeed at detecting the optimal option in this task, a significant portion persisted in choosing the option that provided a bigger immediate food reward but then imposed a longer, unpredictable time-out (Rivalan, Ahmed, & Dellu-Hagedorn, 2009). These results suggest that although other species can learn about reward variance by sampling unknown options, they may differ in how fast they learn or what aspects of the payoffs are most salient compared to humans.

The ability to flexibly update reward representations during learning may hold the key to a related question: Why do individuals sometimes make errors and choose suboptimally? Some evidence suggests that these seemingly maladaptive responses can stem from the mechanisms animals use to initially learn about rewards. One well-studied example involves a gambling paradigm with a choice between pecking two keys that differ in the variability and mean value of the rewards they provide (Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2011). In this situation, pigeons can develop a preference for an option associated with lower average payoffs, but which sometimes provides a low-probability, high-value payoff. Indeed, humans tested in an analogous associative learning situation may show the same preference (Molet et al., 2012). What accounts for this counterintuitive selection of an

option with lower expected value than the alternative? The trick is that this task involved two phases. Pigeons first choose between two key locations that differed in their reward distributions—but after their choice they then saw a discriminative stimulus (such as color) that differed in how well they predicted specific rewards. The initial associations that pigeons learned between color and rewards seem to drive their later risk preferences. For example, in one version of this task (Zentall & Stagner, 2011), pigeons chose between a risky option that provided an average of two pieces of food, and alternative that provided a constant three pieces of food. If the pigeons selected the risky-payoff key, there were two possible outcomes: On 20% of trials pigeons saw a red stimulus that was always followed by 10 food pellets, whereas on the other 80% of trials they saw a green stimulus that never produced a reward. That is, the red and green colors perfectly predicted their payoff on that trial and were highly discriminable given the big difference in reinforcement they produced. In contrast, the alternative option resulted in either a blue or a yellow stimulus, which both produced three pieces of food. Consequently, these color stimuli did not differentially predict subsequent reinforcement. A second experiment (Zentall & Stagner, 2011) showed that pigeons correctly preferred the higher-value option if the riskier option no longer produced a color cue that perfectly signaled a very large payoff. These findings suggest that the particular ways that animals (or humans) learn about reward distributions can impact the preferences they later show for different distributions—an important consideration when comparing decision making preferences across individuals or species that face different experimental setups.

Feedback and Outcomes

The previous examples dealt with situations in which animals receive extensive initial experience to learn about payoff distributions—that is, how animals acquire global information about their available options and develop a preference for a particular course of action. In most cases, however, animals show some stochastic variation in responses, rather than blindly choosing one option all of the time. For example, in situations where animals exhibit

a strong preference (e.g., when rhesus macaques gamble for juice; McCoy & Platt, 2002), they still choose the alternative on some trials. Indeed, even tasks involving more inferential paradigms necessarily involve a series of iterated choices, during which time animals might adjust their strategies on a trial-by-trial basis. What information do animals use when choosing whether to play the odds on a given trial?

One important type of information that animals seem to use is what happened on their previous choice. In particular, many species exhibit a win-stay/lose-shift strategy across trials, showing a greater propensity to gamble again after a previous choice where they gambled and won, compared to those trials where they previously gambled and lost. Evidence for these sorts of trial-by-trial adjustments comes from diverse species, including monkeys (Barraclough, Conroy, & Lee, 2004; Hayden, Nair, McCoy, & Platt, 2008; McCoy & Platt, 2002), apes (Rosati & Hare, 2013), rodents (Stopper & Floresco, 2011), and humans in similar iterated tasks (Hayden & Platt, 2009; Worthy, Hawthorne, & Otto, 2013). However, it is important to note that not all species respond to feedback in the same way. For example, bonobos use a win-stay/lose-shift strategy like the previously mentioned species, adjusting their strategies depending on the outcome of their previous choice, but chimpanzees rather prefer to gamble regardless of their previous payoffs when faced with the same problem (Rosati & Hare, 2013). This suggests that even very basic mechanisms for adjusting responses on the basis of feedback can vary across species.

In more complex decision making paradigms, animals can use information beyond whether they simply won or lost. Imagine gambling at a slot machine. The goal is to match a set of outcomes, and on each trial it is possible to definitely win (all reels match), definitely lose (no reels match), or experience a near miss (some subset of the reels match, but not quite all of them). In fact, whereas clear losses in this situation reduce risk-taking behavior, these kinds of near misses actually seem to increase it. That is, the experience of almost winning makes people even more inclined to gamble again (Griffiths, 1991), possibly because people

seem treat such near-misses as more like a true win than a true loss (Clark, Lawrence, Astley-Jones, & Gray, 2009). Do animals respond to this kind of feedback in the same way? In fact, some evidence suggests that feedback about near misses can also increase risk-seeking in rodents, much like in humans. In one study, rats could gamble in an adaptation of a slot machine game (Cocker, Le Foll, Rogers, & Winstanley, 2014; Winstanley, Cocker, & Rogers, 2011). They first learned about a series of three flashing lights that were designed to be similar to slot machine reels, such that a winning outcome was produced if all three lights were illuminated. On each trial, rats could decide whether to try to collect payoffs (a risky strategy, as they faced a time-out penalty if they lost), or start a new trial instead. Rats were more likely to try to gamble and collect the reward when three lights turned on (a win), but also showed increased risk-taking if only two lights were turned on—a near miss. This indicates that other species also respond to feedback about near misses, much like humans.

Finally, decision makers can consider not just feedback about their previous decision, but also integrate feedback about whole sequences of decisions over time to form expectations about future outcomes. In particular, humans seem to expect that winning will come in streaks—a phenomenon called the hot-hand bias, after the belief that sports players who have had success will continue to do so (Ayton & Fischer, 2004; Nickerson, 2002). More generally, people tend to perceive (illusory) streaks in sequences of random outcomes, and even form the expectation that they will continue to win big at a random event if they have won several times in a row. Indeed, people with a higher propensity to perceive such streaks are more likely to take risks in gambling contexts (Wilke, Scheibehenne, Gaissmaier, McCannet, & Barrett, 2014). Do other animals integrate information about sequences in this way, or even form expectations about their future winnings on the basis of such sequences? One study examined this question by presenting monkeys with sequences of visual stimuli (Blanchard, Wilke, & Hayden, 2014). To win, the monkeys had to correctly guess what symbol would occur next. In fact, monkeys tended to guess that the next symbol

would match the previous one—and consequently fared worse at guessing the next image when faced with sequences specifically designed so that the outcomes did not occur in streaks. An open question, however, is whether animals merely predict that sequences of outcomes will match, or whether they form the expectations that their own behavior plays a critical role in shaping these outcomes, like humans.

Counterfactual Reasoning and Regret

There is robust evidence that many animals use feedback about the outcome of their previous choice to adjust what they do next. But humans do not only learn from what happened previously—we also account for what would have happened in the past had we acted differently (Bell, 1982; Loomes & Sugden, 1982). That is, in addition to learning the actual outcomes of their actions, people can also reason about hypothetical (or counterfactual) events that did not actually occur. This type of reasoning seems especially common when people receive a bad outcome (Byrne, 2002): Thinking about alternative courses of action may help people to learn to adjust their future behaviors appropriately. In terms of decision making under risk, this means that people tend to adjust their choices when they are given feedback about their forgone option, and discover that they could have won big if they had chosen differently (Coricelli et al., 2007). The critical difference from the examples of feedback explored in the previous section is that when people use information about counterfactual outcomes, they learn from events that they did not directly experience.

Can animals also consider what would have happened if they had chosen differently? Some recent evidence indicates that such learning mechanisms may be shared at least with other primates. For example, rhesus macaques played a computerized version of the game rock-paper-scissors in one set of studies (Abe & Lee, 2011; Lee, McGreevy, & Barraclough, 2005). On each trial, the monkey could choose one of three visual targets on the screen. They then found out whether they had won a juice reward by beating their computer opponent on that round. The trick was that the monkeys found out not only if they had made a winning move, but also

whether they would have won if they chose a different target: The color of all three targets changed after the monkeys' choice to indicate how much juice they would have provided to the monkey, given the computer's choice on that round. The key question was whether the monkeys accounted only for the payoffs from the juice rewards they actually received, or whether they also learned about the alternative courses of action they did not take. In fact, the monkeys' choice strategies revealed that they accounted for realized payoffs and hypothetical payoffs. When monkeys lost on a given trial, they were subsequently more likely to choose what would have been the winning option—but they were not more likely to choose the second forgone target, indicating they specifically switched to the (counterfactual) winning target, as opposed to simply avoiding the losing target they had directly experienced. That is, the monkeys learned about the value of their decision, as well as the value of a hypothetical alternative course of action.

Monkeys exhibit a similar sensitivity to counterfactual outcomes when making decisions in a more typical risky decision making context. In one example, rhesus monkeys played a computerized game where they could choose between eight possible options (Hayden, Pearson, & Platt, 2009). Seven consistently provided small juice rewards, whereas the final one sometimes provided a much larger reward, but sometimes provided a much smaller reward. The monkeys were given feedback about what the risky option would have provided, regardless of whether they had chosen it. As in the rock-paper-scissors task, modeling of the monkeys' behaviors showed that the monkeys adjusted their future strategies on the basis of what they would have received. If the risky option would have provided the high-value outcome, they were especially likely to seek this option out in future trials, rather than simply learning about the outcomes they had directly experienced because of their own choices.

In humans, counterfactual reasoning is often driven by a particular emotional experience: the feeling of regret. People feel regret when they realize that things would have turned out better had they acted differently, and this experience can cause people to shift their patterns of choice (Coricelli

et al., 2007; Zeelenberg, Beattie, van der Pligt, & de Vries, 1996). Do nonhumans attend to hypothetical outcomes because they experience emotions like regret? Some evidence suggests that emotional responses may play some role in nonhuman decision making as well. When chimpanzees and bonobos could choose a risky gamble that delivered either a desirable food type or an undesirable food type, they were more likely to exhibit behavioral markers of negative emotions—including negative vocalizations, tantrum-like banging, and scratching (an arousal or stress response in primates) when they gambled and lost. These responses are analogous to disappointment at receiving the bad option. Furthermore, the apes seemed to realize they should have chosen differently: Both species spontaneously attempted to switch their choice after the fact after they gambled and lost. Importantly, apes rarely tried to switch their choice after choosing the safe alternative, even though it was also possible in this situation that a better outcome was available. Rather, apes made a selective attempt to correct their choice only after losing. Overall, these results from monkeys and apes suggest that at least some primates may consider counterfactual events when making decisions, and in some cases may even show some behavioral signatures of emotional experience.

Magnitude Biases

Most studies reviewed thus far have assumed that although decision makers might differ in their particular preferences for risk, they are generally accurate at detecting differences between reward distributions. However, there are good reasons to suspect that this is not the case. In fact, decision makers might find some forms of uncertainty to be easier to detect or more salient than others. These kinds of biases therefore have a potent impact of risk preferences because they shape the way information about risk is encoded. One such fundamental psychological biases shaping sensitivity to risk in humans are magnitude effects on perceptual judgments of numerical size. In fact, a long tradition of research in psychophysics suggests that animals and humans alike exhibit a fundamental bias in detecting differences between stimuli: The overall magnitude of the stimulus can change how easy it is

to discriminate values. For example, it is relatively easy to glance at two items and tell they are a different amount than three items. However, it is more difficult to discriminate 102 items from 103 items. The absolute difference in amount is identical, but the overall higher magnitude makes the one-unit difference less salient in the second case. Known as Weber's law, this magnitude effect has been influential in understanding how a wide variety of species make perceptual, temporal, and numerical judgments (Brannon, 2006; Gibbon, 1977; see also Chapters 1, 14, and 25, this volume).

These same constraints may also apply to how decision makers detect differences in payoff distributions. Imagine a choice between taking \$10 for sure, versus a gamble with an equal chance of winning either \$20 or nothing. Now imagine a choice between taking \$110 for sure, or a gamble resulting in either \$100 or \$120. The risk posed by the gamble in the first decision seems to loom larger than the risk posed in the second. Yet sensitivity to variance alone cannot account for this difference, because the risky option presents the same variance (or standard deviation) in both situations. One proposal suggests that this is because overall magnitude influences decisions under risk much like it does numerical judgments. Rather than being sensitive to variance alone, decision makers may be sensitive to the variance in outcomes divided by their mean, known as the coefficient of variance (Weber et al., 2004). As in the previous example, the coefficient of variance predicts that individuals will be more sensitive to changes in risk at lower reward magnitudes than at higher reward magnitudes.

This magnitude effect can have a potent effect on human risk-taking. Meta-analyses of studies involving different magnitudes of variance, as well as explicit empirical tests of this idea, have shown that humans are more likely to choose risky options when their coefficient of variation was low even when variance is held constant (Hertwig, Barron, Weber, & Erev, 2004; Weber et al., 2004). Do animals also exhibit this bias in encoding risk? Much like with humans, meta-analyses of animal data from a wide range of species indicate that nonhuman decision making under risk can differ across magnitudes in the same fashion (Shafir, 2000).

Indeed, when humans and pigeons were presented with equivalent choices between a safe and risky option across two reward magnitudes, they showed similar increases in risk-seeking responses for choices at higher magnitudes, even when variation between potential options was held constant (Ludvig et al., 2014). This suggests that magnitude effects in decision making influence a wide variety of species, much like the finding that humans and animals alike follow Weber's law when making numerical comparisons—suggesting that this bias reflects deep-seated characteristics of the way organisms make such judgments.

These types of magnitude biases may have pervasive influences across many components of risk decision making. For example, there is some evidence that magnitude can impact animals' accuracy at detecting different probability distributions in the first place. In one study, chimpanzees faced a choice between two trays of containers (Hanus & Call, 2014). The trays differed in their number of containers, as well as how many cups within the array had been baited with a food reward: One tray might have two cups where only one was baited, whereas the alternative tray might have six cups where two were baited. They question was how well the chimpanzees could select a container from the tray with a higher likelihood of getting a reward. In fact, the apes were more successful at choosing a cup from the higher-probability tray when the difference in relative probability was bigger (e.g., 50% of cups were baited in one tray, versus 25% in the other) than when it was smaller (e.g., 50% versus 33%). This suggests that the same analog representational system that drives differences in sensitivity to magnitudes can also influence animals' sensitivity to probabilistic variation in outcomes.

Framing Effects

These perceptual biases impact how numerical differences in risk shape decision making preferences at a fairly basic level. But this kind of perceptual bias is not the only such bias shaping preferences for uncertainty. As reviewed previously, another potent bias with wide-ranging effects on human economic decision making concerns how options are presented, or 'framed.' In particular, humans

treat decisions that appear to involve gains in resources as distinct from those that involve losses—even if the outcomes of these decisions are actually equivalent. As humans also psychologically overweight losses compared to gains, the result is that people respond quite differently to identical choices depending on whether they perceive them to improve or worsen the status quo. Do animals also evaluate their choices in this reference-dependent, loss-averse fashion?

One of the first studies to address whether animals judge options differently depending on whether they are perceived as a loss or a gain focused on how capuchin monkeys exchange tokens to receive treats (Chen, Lakshminarayanan, & Santos, 2006). In particular, monkeys received some allocation of tokens, and then could decide whether to trade those tokens with different experimenters who were offering food rewards. One experimenter initially showed the monkey one piece of fruit, but sometimes gave the monkey a bonus piece if the monkey chose to trade their token with them. A second experimenter always showed two pieces of fruit, but sometimes removed one if they were chosen. The average rewards provided by both experimenters was therefore identical, but the experimenters differed in whether they appeared to offer a relative gain or a relative loss compared to the initially presented amount. Despite the equivalent average payoffs, monkeys preferred to trade with the gain experimenter over the loss experimenter. Chimpanzees and bonobos also seem to evaluate equivalent options as more desirable when they are framed as a gain rather than a loss (Krupenye, Rosati, & Hare, 2015). This suggests that these evaluation mechanisms may be shared across several primate species.

Animals can therefore show a human-like bias in evaluating the desirability of losses versus gains. An important second question is whether this bias then shapes their preferences for risk: Are animals risk-averse for gains, but risk-seeking to avoid certain losses? Initial attempts to answer this question compared responses to variability in rewards with responses to variability in the delays to receive rewards. Here the rewards themselves are conceptualized as gains, whereas temporal delays to receive those rewards function as a cost or penalty and are

therefore analogous to losses. One representative study compared starlings' responses to these two situations (Reboreda & Kacelnik, 1991). In the gain frame, they could choose between a safe food option that provided a constant amount of food, and a risky option that provided variable amounts, with the delays to receive the food always held constant. In the loss frame, they chose between a safe option that always provided food after a fixed delay, and a risky option that provided food after variable delays, with amounts held constant. As predicted by human framing results, the birds chose the safe option more often when the amount of food varied, but the risky option when the delay to receive food varied. Indeed, a variety of species show these patterns: mild risk-aversion for food rewards, but more risk-seeking responses toward the delays to receive those rewards (see Kacelnik & Bateson, 1996, for a review).

Of course, rewards and temporal delays are quite different, and the original demonstrations of framing effects on human risky choice involve responses to rewards that are themselves perceived as gains or losses. Thus, a stronger demonstration of human-like framing effects in nonhumans would use a more comparable situation. Several studies have developed novel paradigms to test just that. In the first such test, starlings were initially acclimated to receiving either a smaller or larger amount of food (B. Marsh & Kacelnik, 2002). Birds were then confronted with a decision about risk. In both situations this risky decision was identical, but the framing of the choice differed depending on the amount of rewards the birds were used to receiving: All of the potential outcomes represented a relative gain in payoffs if birds were acclimated to the smaller initial amount, but were relative losses for those acclimated to the larger amount. In fact, birds preferred to gamble on the risky option when they were used to receiving more food, whereas they favored the safe option when previously acclimated to the smaller amount. Capuchins show similar responses to risk in the token-trading paradigm described earlier (Lakshminarayanan, Chen, & Santos, 2011). Here, the monkeys preferred a safe experimenter who provided the same amount across trials when contrasted with a risky experimenter who varied the

rewards they provided—but only when both experimenters tended to augment their initially proffered amount of food (gain frame). When both decreased their initial amount (loss frame), monkeys rather preferred the risky experimenter. Together, these comparative results indicate that several taxonomically diverse groups of animals exhibit human-like framing effects, suggesting that this bias is driven by widely-shared psychological processes.

Ambiguity and Information Seeking

The previous sections examined how animals encode and evaluate differences in known payoff distributions (i.e., risk). But what happens when animals do not have good knowledge about those distributions (i.e., ambiguity)? As discussed earlier, humans do not treat these situations as equivalent: We do not like choosing options where the potential range of consequences is unclear, showing a robust aversion to ambiguity. But the psychological underpinnings of this effect are not entirely clear—and several explanations for ambiguity aversion invoke complex forms of reasoning that seem unlikely to play a role in nonhuman choice. For example, people might avoid ambiguous options because they feel they cannot justify this choice to others (Curley, Yates, & Abrams, 1986), or people may actively try to assess their own competence or expertise (Heath & Tversky, 1991). More generally, ambiguity aversion involves some sensitivity to one's own knowledge, and the degree of metacognitive abilities possessed by nonhumans is a matter of current debate (Terrace & Son, 2009; see also Chapter 31, this volume). If these capacities are in fact necessary for the emergence of ambiguity aversion, nonhumans might not show this bias. Yet it is also the case that wild animals face decisions involving incomplete or unknown information (Dall et al., 2005), so perhaps the psychological tools for acting appropriately in this situation are widely shared. Comparative studies are therefore critical to understand not only how other species respond to ambiguity, but also to illuminate the mechanisms underlying human choices.

Current evidence suggests that at least some primates also distinguish between known and unknown probabilities, exhibiting a human-like

aversion to ambiguity. For example, one computer-based task presented rhesus monkeys with a choice between a gamble with known probability of winning a high-value reward, and an ambiguous option with an unknown probability of winning (Hayden, Heilbronner, & Platt, 2010). Both options were visually represented as a bar with the probability of winning shown as a shaded portion, but part of the ambiguous bar was blocked from view such that the monkeys could not properly estimate the probability of winning on any given trial. Although these options were mathematically equivalent in terms of the payoffs they provided across trials, monkeys highly preferred the risky option with known probability—and even showed similar patterns of responses to human participants tested in an equivalent setup. These results suggest that exhibiting a human-like bias against ambiguity may not require the more complex forms of reasoning that have been proposed to underlie human behavior.

Other primate species also share this bias, and further highlight the importance of learning in shaping how individuals respond to ambiguity. Although most human studies of choice under ambiguity involve one-shot decisions (as is the case for human studies of risk preferences), animal work can provide insights into the learning mechanisms that influence responses to ambiguity under more real-world situations where decision maker must sample their available options. For example, one study examined chimpanzees' and bonobos' responses to four different types of choices (Rosati & Hare, 2011). In three types of choices, apes always saw the set of possible outcomes in advance, and therefore knew the probability of winning the high-value payoff: a 100% chance, a 0% chance, or a 50% chance. In the fourth type of choice, the apes' view of the potential outcomes was blocked, so they did not know the likelihood of winning. Although the average payoff from this ambiguous option was identical to the average payoff of the risky option (50% chance of winning), the apes were less likely to gamble on the ambiguous option. Importantly, the apes' initial bias against ambiguity later dissipated: Across trials, apes learned that the ambiguous and risky options were equivalent. Thus apes' experience with the ambiguous option shifted their strategies over time.

A final question is whether animals will take action to remedy their lack of knowledge when faced with incomplete information. That is, will animals seek out new information before making a choice if it is possible to acquire it? Most comparative research focuses on situations where animals learn by sampling and updating the knowledge about reward payoffs by simply participating in the task. In this kind of situation, it is not necessary to do anything special to gain information about the available options—animals simply acquire information by virtue of making a series of choices. However, humans will also actively seek out information to improve decision making (Loewenstein, 1994); indeed, gaining knowledge may even be pleasurable for humans (Loewenstein, 2006). In this way, a sense of curiosity may allow humans to resolve ambiguity before making decisions.

There is some suggestive evidence that some other species can also actively adjust their behavior so that they are also more likely to learn relevant information before making decisions. For example, apes engage in information-seeking behaviors (such as changing their perspective) when they lack knowledge about the location of a reward (Call & Carpenter, 2001). One study extended this metacognition paradigm to examine how apes respond to risky decisions (H. L. Marsh & MacDonald, 2012). Using a basic procedure similar to some previous decision making work (Haun et al., 2011), a treat was hidden under one of several containers out of the ape's sight, but they had to select just one. The trick was that in this setup, the ape could actually seek out more information about their likelihood of winning by peering under the containers from a different perspective to see which was baited. In fact, they were more likely to peer into the containers when their likelihood of selecting a baited container was low because more containers were present, than when it was higher because fewer containers were present. Importantly, there are species differences in the basic propensity to engage information seeking: whereas apes and rhesus monkeys (Hampton, Zivin, & Murray, 2004; Rosati & Santos, 2016) seem to engage in these targeted searching behaviors when they lack knowledge, capuchins do not (Paukner, Anderson, & Fujita, 2006). Thus, there

may also be important differences in how animals seek information when faced with uncertainty as well (see Chapter 31, this volume).

UNCERTAINTY IN THE REAL WORLD

Nonhuman decision making is supported by a set of complex mechanisms that shape how animals encode, evaluate, and learn about uncertainty in their environment. As the previous sections showed, in many cases there are strong parallels between the cognitive mechanisms that humans and nonhumans use to make such decisions in many contexts. A critical issue is therefore how these strategies play out in more real-world situations where hungry animals must seek out food, sometimes in the company of others, and may even be pursuing different ecological “goals” in their foraging strategies depending on the particular environment with which they are faced. This final section will address how a decision maker's physiological state, their broader social context, and finally more persistent differences in cognition across individuals or populations can impact how animals think about and respond to uncertainty (see Figure 16.2).

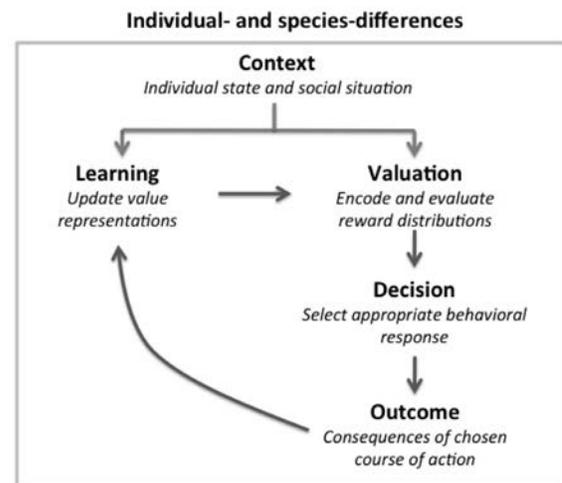


FIGURE 16.2. Psychological processes shaping choice under uncertainty. Context can flexibly influence how animals assign value to different options, as well as how they learn about payoff distributions in the first place. Individuals and species may also show more fundamental biases in how they generally respond to uncertainty.

Individual State

Risk sensitivity theory predicts that preferences for uncertainty should depend on a decision maker's state—in particular, their energetic status (see Chapter 14, this volume). This is a major difference between biological approaches to risk decision making and rational choice theory in economics, as classical economic theory assumes that individuals should exhibit consistent preferences across contexts. Indeed, human economic studies tend to use monetary rewards where these sorts of physiological considerations are less salient. In contrast, comparative studies of decision making typically involve foraging situations where animals seek out food rewards, so decision maker's energetic state or level of satiation is consequently of prime importance.

How does an individual's state interact with the psychological processes animals use to think about uncertainty? Although most work examining the influence of energetic state on decision making does not delve into the specific mental capacities in play, there are some hints concerning how physiology influences decision making from a mechanistic perspective. In particular, animals may encode the value of options differently depending on their energetic state when they encounter them. For example, some species treat rewards as having higher value if they initially experience them with lower energetic reserves, compared to when they encounter identical rewards in a higher energetic state (B. Marsh, Schuck-Paim, & Kacelnik, 2004; Pompilio, Kacelnik, & Behmer, 2006). That is, an animal's energy budget can influence how they encode the relative value of different options. The psychological mechanisms that animals use to encode value may therefore function as a rough heuristic for a reward's marginal benefit: higher when the reward is encountered in a low energetic state than a high state. Once the value of the reward is encoded, it can have an enduring impact on choices even if the individual is no longer in that low state.

These sorts of state-dependent learning mechanism can result in preferences that seem suboptimal. One such example is the sunk-cost fallacy, or valuing something more on the basis of past investment, even if it currently makes no sense to do so (see Chapter 15, this volume). This bias has been

extensively explored in humans (Arkes & Ayton, 1999), and there is now compelling evidence that animals also overvalue options previously associated with greater effort or temporal costs to acquire (Pattison, Zentall, & Watanabe, 2012; Pompilio & Kacelnik, 2005). For example, in one study starlings could first experience two ways to acquire food: a high-cost route that required a lot of effort before the birds could peck an associated key to get food, and a lower-cost route that required less effort to access the associated key (Kacelnik & Marsh, 2002). Although both keys actually produced the same amount of food, when the birds were later given a choice between the keys (without having to do any work) they actually preferred the one associated with more effort. That is, the starlings assigned more value to the cue that (previously) involved greater cost. One possibility is that when the birds were initially exposed to the two routes of obtaining rewards, their learning hinged on the marginal value provided by each key: Given that they had to initially expend more energy to obtain a piece of food from the higher-cost route, that key was then associated with a larger relative increase in value than the alternative key.

These results suggest that energetic state can have potent effects on individual's decision-making preferences. The psychology of self-control suggests another pathway by which physiological state can impact decision making. Self-control is an important component of executive functions, allowing individuals to flexibly regulate their behavior and override undesirable responses. In fact, some evidence suggests that self-control is a limited resource that can be used up, so that it is more difficult to exert self-control in another situation (Baumeister, Vohs, & Tice, 2007). This phenomenon, called *ego-depletion*, may in fact be related to the physiological consequences of exerting self-control. For example, some argue that ego-depletion actually reduces metabolic stores of energy (Gailliot et al., 2007), or at least alter neurobiological systems influencing reward-processing and motivation (Molden et al., 2012). These same types of processes can play an important role in decision making under uncertainty. For example, suppressing unwanted emotional responses is effortful, and can make it more

difficult to exert cognitive control in subsequent situations (Muraven, Tice, & Baumeister, 1998). Being placed in a situation where it is necessary to control emotional reactions—such as recollecting an embarrassing or anger-provoking episode from one’s past—may subsequently increase risk-taking because self-regulation capacities are impaired (Leith & Baumeister, 1996).

This result highlights that energetic state and psychological state can be intimately connected. And although human economic decision-making research has focused less on energetic effects on risk task, there is strong evidence that mood states can shift responses to uncertainty in humans. For example, people experience negative states such as disappointment or regret as a consequence of unfavorable outcomes when making decisions under risk (Coricelli et al., 2007; Loewenstein & Lerner, 2003). Furthermore, altering psychological states such as anger, anxiety, or stress has a causal impact on human risk preferences (Isen & Patrick, 1983; Porcelli & Delgado, 2009; Raghunathan & Pham, 1999). It is currently unclear whether moods shift risky decision making in animals as well. However, many other species also show clear behavioral, physiological, and neurobiological signs of emotional processes (LeDoux, 2000; Panksepp, 1998; Phelps & LeDoux, 2005), and some primates even show human-like emotional responses specifically in risky decision making contexts (Rosati & Hare, 2013). Consequently, it is an important question for future research whether experimentally manipulating animals’ psychological state can also shift their risk strategies, as in humans.

Social Context

Nonhuman risk preferences depend on context: Individuals make different decisions depending on their own physiological or psychological state. But no decision maker is an island. In fact, social-living species (including humans) must constantly make value-based decisions in the company of others. Mechanistically, there is increasing evidence that social context can shift a decision maker’s goals or emotional state, influencing many of the psychological processes discussed in previous sections. For example, people are more likely to make risky choices if it improves their status relative to

a hypothetical competitor (Ermer, Cosmides, & Tooby, 2008; Hill & Buss, 2010). Mechanistically, competitive social contexts may shift people’s mood states (such as anger) and thereby facilitate risk-prone decision making (Fessler, Pillsworth, & Flamson, 2004). Competition may even impact the subjective utility people derive from payoffs: people weigh potential losses more heavily when alone, but focus on the possibility of winning more than others in social contexts (Bault, Coricelli, & Rustichini, 2008). Competition is an important component of social interactions in other animals as well, and there is some evidence that competition can shift other species’ preferences in similar ways. For example, chimpanzees and bonobos both become more risk-seeking following a competitive interaction with a human, compared to a neutral context (Rosati & Hare, 2012). Importantly, this effect seems fairly specific to competitive interactions, as a more positive play interaction had no effect on their choices. More generally, these types of studies indicate that social context can influence economic decisions that involve individual-level strategies—possibly because social context can be an important cue as to the value of various resources in the current environment.

These studies show that social context can influence economic decisions unrelated to social interactions per se. But it is important to point out that many social interactions inherently pose problems involving risk, as decision makers must choose between courses of action where the variability in payoffs stems from another individual’s behavior. For example, in situations involving competition between conspecifics that differ in their visual access to resources, animals can choose between relatively risky piece of food (that another individual can also see and therefore might approach) or relatively safe piece that the other individual cannot see and is therefore unlikely to pursue. This sort of sensitivity to “social risk” has been demonstrated in multiple primate species, including chimpanzees, rhesus macaques, and ringtailed lemurs (Flombaum, Santos, & Hauser, 2002; Hare, Call, Agnetta, & Tomasello, 2000; Sandel, MacLean, & Hare, 2011). Thus, animals seem equipped to respond to social risk when competing with group-mates for food.

Many cooperative interactions similarly involve payoffs that can vary depending on the partners' chosen action (see Volume 1, Chapter 44, this handbook). Nonhumans' responses to a variety of prototypical cooperative situations have been extensively studied, including the prisoner's dilemma (Stephens, McLinn, & Stevens, 2002), the stag-hunt game (Bullinger, Wyman, Melis, & Tomasello, 2011), the ultimatum and other negotiation games (Jensen, Call, & Tomasello, 2007; Melis, Hare, & Tomasello, 2009), the trust game (Engelmann, Herrmann, & Tomasello, 2015), as well as mutualistic interactions that involve simultaneous coordination of behaviors (Melis, Hare, & Tomasello, 2006). To take one example, in the stag-hunt game individuals can choose between pursuing a low-value resource (the hare) that can be acquired individually, or a high-value resource (the stag) that requires cooperation—but choosing to pursue the stag without anyone else joining results in a complete loss. In fact, chimpanzees seem quite risk-prone in this kind of situation, preferring to gamble on the possibility that their partner will also choose the high-value item (Bullinger et al., 2011). Similarly, chimpanzees in a modified version of the trust game tend to invest effort in giving their partner a high value resource—a risky strategy given that the partner might choose to keep all the food for himself (Engelmann et al., 2015). Importantly, humans not only respond to risk in social contexts, but also treat decisions involving social risks as distinct from equivalent nonsocial choices. For example, people are less willing to invest in their partner in the trust game, but more willing to gamble in a matched nonsocial risky decision with identical stakes (Bohnet & Zeckhauser, 2004). This phenomenon, called betrayal aversion, indicates people can be more averse to social risk where others may take taken advantage of them. Although animals clearly account for risk when making social decisions, it is currently unclear whether they also distinguish between social risk and nonsocial risk in this way.

Variation Across Individuals and Populations

The previous sections examined whether the same individual can flexibly shift their strategies when

confronted with risky choices across different contexts. This evidence shows that humans and animals alike have flexible risk preferences that can be adjusted according to the particular situation at hand. However, despite the context-sensitivity of decision strategies, humans and animals may also exhibit relatively stable or trait differences in their responses. For example, one person may be generally more risk-prone than most others across contexts, even if their particular degree of risk-seeking behavior can be modulated. This final section will examine the possibility that there are also more stable differences in nonhuman risk preferences: Do some individuals or some populations generally exhibit different preferences than others?

One approach to answering this question is to examine individual variation in risk preferences within a species. In fact, there is significant individual variation in human responses to risk, and that propensity to take risks has an underlying genetic component. For example, twin studies indicate that degree of risk aversion is heritable, as monozygotic twins show more similar responses on economic risk tasks than do dizygotic twins (Cesarini, Dawes, Johannesson, Lichtenstein, & Wallace, 2009). Furthermore, some specific genetic variants in the serotonergic and dopaminergic neurotransmitter pathways can predict an individual's propensity to gamble on risky prospects (Carpenter, Garcia, & Lum, 2011; Frydman, Camerer, Bossaerts, & Rangel, 2011; Kuhnen & Chiao, 2009; Zhong, Israel, Xue, Ebstein, & Chew, 2009). However, most nonhuman research examining the genetics risk-taking have focused not on economic decision making per se, but rather on related behaviors such as novelty seeking or physical risk taking (Kreek, Nielsen, Butelman, & LaForge, 2005; van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005; Watson et al., 2015). For example, variation in the D4 dopamine receptor predicts whether great tits (*Parus major*; Fidler et al., 2007), vervet monkeys (*Cercopithecus aethiops*; Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007), and horses (*Equus caballus*; Momozawa, Takeuchi, Kusunose, Kikusui, & Mori, 2005) engage in novelty-seeking (see Chapter 28, this volume). Although these results are therefore suggestive of shared genetic substrates

underlying risk-taking in humans and other species, it is currently unclear if these results extend to value-based decision making contexts.

However, genetic variation is just one type of stable influence on individual differences in risky decision making. Humans also exhibit persistent gender differences in willingness to take risks: Men tend to be more willing to do so than women (Byrnes, Miller, & Schafer, 1999; Croson & Gneezy, 2009). This gender difference likely stems from a myriad of sources, including cultural norms of behavior, but there is some evidence that biological influences play a role as well. For example, risk taking can vary with levels of sex hormones such as testosterone (Apicella et al., 2008; Stanton, Lienen, & Schultheiss, 2011; Stanton, Mullette-Gillman, et al., 2011). There are some hints that animals may exhibit similar variation in risk preferences. For example, one study examined framing effects in a large sample of chimpanzees and bonobos, finding that male apes were more susceptible to framing biases than were females (Krupenye et al., 2015). Given that nonhumans do not face the same norms of social behavior as humans do, these kinds of comparative studies can provide important insights into the contributions of social experiences and biological influences on the emergence of individual variation in human decision making.

For comparative psychologists, a final important question is whether there are stable differences in patterns of decision making across species. As discussed previously, risk preferences in animals generally seem to be strongly conserved, as the majority of species tested thus far exhibit at least mildly risk-averse for gains—a pattern that holds across many diverse insects, mammals, and birds (Kacelnik & Bateson, 1996, 1997). However, most research to date focuses on only one species in a given study, and there may be important differences in methodology across studies. Thus, the broad-strokes pattern of risk-aversion seen across many taxa may hide subtler differences in risk preferences between species. Indeed, there are some known deviations from this pattern. For example, rhesus macaques (McCoy & Platt, 2002; Platt & Huettel, 2008), capuchins (De Petrillo et al., 2015), and chimpanzees (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2012, 2013) have all been

shown to be fairly risk seeking. Although preferences in any given study are clearly dependent on contextual variables, these species nonetheless are notable given that several other species show more risk-averse patterns of choice in similar or identical contexts.

What is the origin of these kinds of species differences in decision making? One possibility is that different species' cognitive capacities have a recognizable "psychological signature" of their typical socioecological environment—much like morphological characters such as body form or dentition can vary depending on different species' niche. That is, species with differences in their natural history might exhibit systematic differences in the cognitive skills that are central to decision making. Indeed, the use of the comparative method to relate differences in species' traits to differences in socioecological variables of interest is one of the most powerful tools in evolutionary biology (Mayr, 1982). This approach is therefore important for illuminating the origins of variation in cognitive abilities (MacLean, Matthews, et al., 2012).

Although there have been few studies comparing closely related species on matched tasks examining risk preferences, there are some hints that species facing different species-typical environments in the wild may show targeted differences in their decision making strategies. For example, chimpanzees and bonobos show such divergences in their risk preferences. Although these species only diverged from each other less than one million years ago (Won & Hey, 2004), they exhibit important differences in their socioecology (Hare, Wobber, & Wrangham, 2012; Kano, 1992). In particular, chimpanzees are thought to live in environments that display more seasonal variation in production, and chimpanzees also exhibit greater dependence on risky hunting than do bonobos (Boesch, Hohmann, & Marchant, 2002; Malenky & Wrangham, 1994). These differences in natural history therefore predict that chimpanzees may be more willing to accept risk compared to bonobos—and in fact, chimpanzees are more risk seeking than bonobos across populations and across several different experimental paradigms (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2012, 2013). These results provide

some initial evidence that strategies for dealing with risk may be shaped by a species' ecological niche, such that variation in preferences for uncertainty across species reflect biologically rational responses to species-typical environments.

CONCLUSION

Humans and animals alike face uncertainty in their daily lives. Humans use complex, context-sensitive psychological mechanisms when making decisions about risk, and current comparative research suggests that many of these same mechanisms support animal choice behavior as well. Much like humans, various nonhuman species are sensitive to variation in their payoffs—and use similar psychological processes to encode payoffs, learn and update information, and evaluate the desirability of different options. Indeed, several species exhibit human-like economic biases, such as framing effects and the hot-hand effect. Some species also show human-like responses to decision problems often thought to recruit fairly sophisticated capacities in humans—capacities that are likely unique to our species. For example, several primates species show human-like aversion to ambiguity or incomplete knowledge—a bias previously attributed to high-level cognitive processes such as being able to justify one's choices to others. Given that animals show similar responses to ambiguity, this suggests that such processes may not be necessary. Overall, these comparative findings indicate that many of the psychological processes driving human economic behavior build on mechanisms that are widely shared with other taxonomic groups, in some cases ranging from primates to insects.

This is not to say that there are not important differences in how individuals or even species respond to uncertainty. Indeed, comparative evidence also shows that although many species may show human-like patterns of decision making under uncertainty, there are almost always important exceptions. Increasing evidence suggests that some species are more risk seeking (or risk averse) than are others, even when facing well-matched problems. Biologically minded approaches to decision making are therefore uniquely positioned to address

questions about why these different decision making mechanisms emerged in the first place—that is, to illuminate the ultimate biological function of these psychological processes. In particular, comparisons of decision making across species that vary in socioecological characteristics can shed light on the evolutionary origins of different choice strategies. Moreover, comparative research has highlighted important facets of decision making that have not been the focus of human research, especially the importance of energetic state on decision making preferences and the learning mechanisms that drive these preferences.

Over the past four decades, behavioral economists and psychologists have developed new—and more nuanced—theories about how humans respond to uncertainty. In many cases comparative research has drawn on theoretical advances from these fields to examine if other species also exhibit the defining characteristics of human economic behavior. But this collaborative borrowing goes both ways, as comparative research can inform and drive advances in psychology and economics as well. Indeed, some of the most pressing questions in the social sciences concern the origins of human economic biases: do they reflect human nature, are they learned, and if so what experiences engender their emergence? Comparative research with nonhumans is critical to address these questions precisely because animal lives have both continuity and discontinuity with our own. Evolutionary theory therefore provides a path to understand why this variation emerges in the natural world.

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