

Feature Review

Efficiently irrational: deciphering the riddle of human choice

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For the past half-century, cognitive and social scientists have struggled with the irrationalities of human choice behavior; people consistently make choices that are logically inconsistent. Is human choice behavior evolutionarily adaptive or is it an inefficient patchwork of competing mechanisms? In this review, I present an interdisciplinary synthesis arguing for a novel interpretation: choice is efficiently irrational. Connecting findings across disciplines suggests that observed choice behavior reflects a precise optimization of the trade-off between the costs of increasing the precision of the choice mechanism and the declining benefits that come as precision increases. Under these constraints, a rationally imprecise strategy emerges that works toward optimal efficiency rather than toward optimal rationality. This approach rationalizes many of the puzzling inconsistencies of human choice behavior, explaining why these inconsistencies arise as an optimizing solution in biological choosers.

The riddle of human choice

Nicholas William Leeson was a trader at London's Barings' Bank, leading a unit at the Singapore Stock Exchange. By the end of 1992, Nick's group accounted for 10% of Barings' annual worldwide profit. That year, however, one of Nick's traders sold when she was instructed to buy, accidentally losing £20 000. Facing this administrative loss, Nick began to make secret trades, some riskier than usual, to cover his deficit before it was discovered. These riskier-than-usual trades sometimes worked out, but sometimes led to greater losses. As his losses (and presumably his anxiety) grew, Nick became increasingly willing to accept risky trades with lower and lower probabilities of success. By late 1993, Nick had clandestine losses of £23 million, by 1994 his hidden losses had grown to £208 million.

To cover these losses, on January 16, 1995, Nick agreed to a particularly risky trade, betting a huge amount on the overnight stability of the Tokyo Stock Market. At 05:46 h that morning, a major earthquake struck Japan, decimating the Tokyo markets and Nick's accounts. Now facing truly massive losses, Nick bet more and more each day that the Nikkei average would suddenly recover. By the morning of February 23, Nick had lost £827 million, bankrupting the oldest merchant bank in the UK [1].

Scholars and philosophers (e.g., [2,3]) have generally assumed that people are trying to maximize, sometimes money, sometimes love, and sometimes something else, with their choices. For example, Pascal hypothesized that, in the long run, we strive to maximize the accumulation of these articles, referred to as **expected value** (see [Glossary](#)). Unfortunately, the observation that humans often sacrifice higher expected value to avoid risk largely disproved this conjecture in the 18th century [4]. This led mathematicians to hypothesize instead that human choice in all

Highlights

A central question for decision-making scholars is: why are humans and animals so predictably inconsistent in their choices? In the language of economics, why are they irrational?

Data suggest that this reflects an optimal trade-off between the precision with which the brain represents the values of choices and the biological costs of that precision. Increasing representational precision may improve choice consistency, but the metabolic cost of increased precision is significant.

Given the cost of precision, the brain might use efficient value-encoding mechanisms that maximize informational content. Mathematical analyses suggest that a mechanism called divisive normalization approximates maximal efficiency per action potential in decision systems.

Behavioral studies appear to validate this claim. Inconsistencies produced by decision-makers can be well modeled as the byproduct of efficient divisive normalization mechanisms that maximize information while minimizing metabolic costs.

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its complexity aims to maximize a more subjective notion of accumulation, referred to as **expected utility**. The first half of the 20th century saw a general effort to narrow down the set of all reasonable algorithms for maximization under this assumption by focusing on the notion that well-organized patterns of choice must be transitive: if a human prefers feeling loved to owning cars, and owning cars to pastrami sandwiches, then they simply cannot also prefer pastrami sandwiches to love (Box 1). If they do then it can be proven that their choices cannot achieve any goal. No stable maximization (or **utility**) function can ever be used to describe (or justify) intransitive choice (e.g., [5,6]). This critical insight led economists to refine definitions of the behavioral signatures of goal-directed decision-making, focusing on the notion that choices can be

Box 1. Inconsistent patterns of choices

Inconsistent patterns of choices are those in which the decisions of a chooser cannot be construed as pursuing a meaningful goal. A classic example would be a chooser who prefers apples to oranges and oranges to pears, but also prefers pears to apples (Figure 1A). Such a chooser who had a pear should reasonably be expected to trade their pear plus US\$0.01 for an orange. Having gained the orange, we might reasonably expect them to trade that orange plus US\$0.01 for an apple. What makes this pattern inconsistent is that such a chooser should then also be willing to trade their apple plus US\$0.01 for their original pear. At this stage, they have spent money and time but gained nothing, a classic definition of an inconsistent choice.

Broadly speaking, patterns of inconsistency can be separated into two classes: random and structured. Random inconsistency arises when subjective value varies randomly from moment to moment. A decision-maker who, on average, values apples only a tiny bit more than oranges would occasionally make an intransitive choice just due to these uniformly distributed random fluctuations (Figure 1B). These kinds of inconsistencies have been well characterized by random utility models [59,86]. The key feature of this class of model is that intransitive errors are expected to be distributed uniformly across the whole range of subjective values.

Of greater relevance to this article are patterns of inconsistencies that suggest a non-uniform distribution of intransitive errors. A chooser who prefers US\$3 for sure over a 50% chance of winning US\$10 when in the presence of 50% chance of winning US\$3, but prefers the risky 50% chance of winning US\$10 when the unselected lottery is removed, shows a more structured pattern of inconsistency. Structured inconsistencies of this kind generally arise from context effects; changing the context in which an offer is made systematically changes the decision-maker's preferences in a systematic and repeatable way.

The best understood of these context effects are those mediated by the reference point. One of Kahneman and Tversky's [9] central observations was that whether a chooser was risk-seeking or risk-averse depends not only on the specific outcome they are considering, but also on a hidden internal reference point (originally called the status quo). Systematically shifting the hidden reference point can even lead to choice cycles of the kind described in the preceding text.

In general, inconsistencies associated with random utility theory and the more complex inconsistencies associated with behavioral economics have been seen as distinct. One central goal of rational imprecision theory [24] has been to provide a framework that unites these two classes of inconsistency by defining non-uniform random utility models that can capture both classes of inconsistent behavior. The main text of this article suggests a resolution to many classes of inconsistent choice in this way.

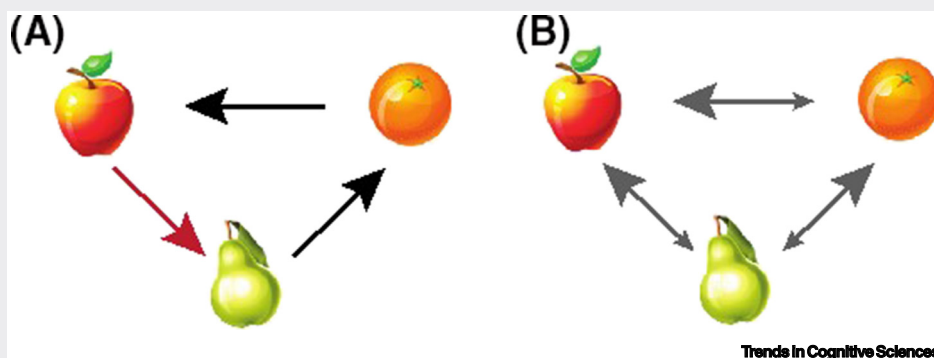


Figure 1. Patterns of intransitive choice.

Glossary

Efficient coding hypothesis:

proposal that neural codes are structured to carry as much information per action potential as possible.

Expected utility: average long-run subjective value of an option or offer.

It is calculated by first transforming the gains and losses associated with each possible outcome into a subjective form, for example, by taking the logarithm of the amount and multiplying them by the associated probabilities.

Expected value: average long-run objective value of an option or offer. It is calculated by multiplying the probability of each possible outcome by the gain or loss associated with that outcome. A fair coinflip that pays US\$2 on heads and US\$0 on tails has an expected value of US\$1.

Intertemporal choice: choices in which a decision-maker must select between a smaller sooner reward and a larger delayed reward.

Intransitivity: formally, this is a violation of the transitive relationship between choice objects. If one prefers dogs to cats and cats to birds, it would be intransitive to also prefer birds to dogs. This is the most fundamental form of an irrational choice.

Likelihood: knowledge about how likely an outcome is that a decision-maker gathers during the decision-making process.

Loss aversion: empirical observation that, for many decision-makers, losses loom larger than equivalent gains.

Moral value: the original name for 'Utility' proposed by Daniel Bernoulli in the 18th century.

Multiple-selves: hypothesis that human decision-makers comprise two or more independent internal decision-making modules that compete for control of behavior. Under this hypothesis, intransitive choices arise when the modules in control of behavior switch.

Neuroeconomics: relatively young interdisciplinary field that unites neuroscientists, psychologists, and economists who seek to understand choice behavior.

Objective function: formal mathematical specification of what it is that the decision-maker is trying to accomplish with their choices. Maximizing caloric intake is an example of a simple objective function.

meaningful only if they maximize a subjective utility function, a pattern now referred to technically by economists as **rational choice** (Box 2).

The extension of this approach to the domain of risky choice [7,8] reveals that Nick Leeson's decisions were technically 'irrational' in just this sense. It is reasonable for a decision-maker to choose to tolerate or abjure risk. Either preference can lead to coherent, logically consistent, and transitive choice behavior, maximizing a subjective notion of value that is rational in the technical sense. However, what Nick Leeson did falls outside that category. When Leeson was earning money, he was not risk seeking, but, as he lost money that he had earned, in an effort to earn that same amount a second time, he became newly risk seeking. His decision criteria, whether driven by emotions or logic, were changing dynamically in a destructive feedback loop that induced a risk-related **intransitivity**. As his account balances dropped lower and lower below his **reference point**, Nick changed his decision-making process. What he had rejected previously as too risky, he now preferred, driven not by the absolute number of pounds in his accounts, but rather by the widening gap between his balances and his hidden internal reference point. This fundamental inconsistency, the neoclassical economists showed, meant that Nick's behavior could not be seen as maximizing or goal directed. No coherent hidden agenda or (continuous monotonic and stable) subjective function was being pursued.

Over the past 50 years, it has become abundantly clear that this kind of intransitivity, an intransitivity mathematically associated with an internally or externally held reference point, is a key feature of human decision-making [9–12]. This is not the only form of inconsistency that is widely observed. Human decision-makers systematically treat losses relative to the dynamic reference point differently than they treat gains, and they distort their representations of outcome probabilities [9,13,14]. Both of these lead to dynamic instabilities in choice behavior, such as the one shown by Leeson.

Until recently, the standard explanation for these puzzling failures to maximize rested on the notion that human choosers behaved intransitively because decision-makers were built from several independent modules (**multiple-selves**), some emotional and others coldly logical. While

Prior (probability): knowledge about how likely an outcome is that a decision-maker has in advance of the decision-making process.

Rational choice: economic term-of-art often confused with the lay expression 'to choose rationally'. It identifies patterns of choice behavior that efficiently maximize some objective or subjective quantity. In this sense, patterns of inconsistent or circular choices are defined technically as irrational.

Reference point: hidden internal benchmark against which decision-makers define an outcome as a gain or a loss.

Utility: subjective value to the decision-maker of any gain or loss.

Box 2. Rational choice

The word 'rationality,' as used by economists, has a highly technical meaning and this has generated endless confusion among non-economists. At its heart, the notion captured by the phrase 'rational choice' is the idea that 'rational choices' are those that show logical consistency. This idea was first developed during the 1920s in an effort to identify patterns of choice that were objectively wasteful.

What can be said about a chooser who strictly prefers apples to oranges, but also strictly prefers oranges to apples? Samuelson [5] showed that there is no possible mathematical transformation of value (or anything related to value) that can be maximized by such a pattern of behavior. Such a chooser is defined by an economist as 'irrational' because their choices are not directed at any kind of maximization: their choices cannot be said to be goal-directed.

The 1940s saw an expanded mathematical definition of rationality that was somewhat more positivist. Houthakker [6] examined the logical properties of a chooser who is both transitive in their choices (they prefer apples to oranges to pears) and who is monotonic in their preferences, that is, they never see more of a good thing as worse than less of a good thing. He proved that such a chooser can always be described as maximizing some monotonic transformation of value; they are always, by definition, technically rational. Thus, a decision-maker who has a consistent plan to maximize utility by purchasing drugs rather than food would be identified by an economist as 'rational' in the technical sense [87]. By contrast, someone who switches back and forth between maximizing their drug consumption and maximizing their food consumption would be technically defined as irrational.

The important thing to remember when thinking about the economic notion of rationality is that it is entirely neutral with regard to morality, ethics, and perhaps even to some intuitive notions of well-being. It is perfectly reasonable to say that someone is rational in their pursuit of heroin, suicide, or world domination. All that rationality defines is the internal consistency, the goal directedness, of the choices they use to pursue those goals.

each module (even the emotional ones) might be fully transitive when operating on its own, when control shifted dynamically between these multiple-selves, inconsistencies arose as the mechanisms traded off control between one another (e.g., [15,16]). According to this view, having different and potentially incompatible risk attitudes for losses and gains emerged from the fact that different, and slightly incompatible, neurobiological or psychological modules are assumed to be dynamically interacting as we make choices over gains and choices over losses, a dynamic trade-off that leads to inconsistency.

However, over the past two decades, a revisionist interdisciplinary approach has begun to suggest that humans are not as irrationally intransitive as they at first appeared [17–21]. Some data suggest that the structural features of the human brain [22] impose resource constraints that are the targets of rational optimization. Other work suggests a more fundamental information-theoretical constraint [23–26]. Taken together, these data are beginning to suggest that humans, emotions and all, are not only much more goal directed in their maximization than implied by behavioral economics, but are also much closer to the objective optimizers that Pascal imagined than the neoclassical economists imagined.

Building on Herb Simon's insight that biological constraints are critical to understanding human choice [27,28] and Duncan Luce's [29] insight that maximization by human choice is constrained by stochasticity in the human brain (see also [30]), this **neuroeconomic** [31] approach has suggested that economists may have misspecified the problem human decision-makers face. The neoclassical economists treated humans as abstract computational machines that could represent (and store) the subjective utilities of every option with infinite precision. They assumed choosers could perfectly weigh these precise representations against one another. They assumed that the human decision-making machinery was insensitive to the real biological costs of storing information, representing value, and computing choice.

Nevertheless, we know that precision in neural computation is metabolically costly and that increasing the precision of representation, storage, and computation necessarily increases costs. This notion, that at an evolutionary timescale the benefits of precision must trade off against the costs of representational accuracy, suggests that the imprecision in our choices, our intransitivities, is a precisely calibrated feature. The finite precision of our decision-making architecture may be efficient in the sense that reducing intransitivity any further might incur more metabolic cost than it yields benefit. In fact, many of the technical irrationalities cataloged at the end of the 20th century now appear to reflect an evolutionary trade-off that efficiently balances the costs of computational precision against the costs of intransitivity [22,24,32]. Configurations of choice that at first appear problematic or puzzling, begin to look like they maximize the efficient trade-off of costs and benefits. Such systems may be seen as rationally imprecise, resting on a razors-edge balance that regulates inconsistency to achieve efficiency.

From multiple-selves to subjective value

The reigning supposition that human decision-makers are inconsistent because of an internal conflict is at least as old as literature. In the *Phaedrus*, Plato [33] explains that we are like a charioteer with two horses, one 'good' and one 'emotional.' Freud's system of id, ego, and superego [34] follows this script closely, and its adoption by Paul Maclean in his Triune Brain Theory [35] firmly established the notion that multiple neural modules compete to control behavior. However, data gathered over the past two decades challenge this conclusion. Neurobiological searches for these competing modules have repeatedly identified instead a single representation of value. Although puzzling, the source of our intransitivities appears to be something more fundamental than an internal competition between our emotional and logical selves.

The contemporary notion that value, subjective or objective, is represented neurobiologically in the form of a single common currency, has its origins in the first efforts to search for subjective value representations in the brain (Figure 1A; e.g., [36,37]). Those studies identified what looked like a decision variable, but it was not until 2004 that it was definitively shown that firing rates could be observed in the parietal cortex that tightly correlated with the economic notion of expected utility, but not at all with choice probability (Figure 1B; see also [38]). However, this evidence (Figure 1C) was silent about how these representations behaved when choosers became inconsistent. To search for conflict in the utility representation, one needed a reliably inconsistent behavior. For that, several labs turned to choices in which decision-makers are conflicted between taking less now or waiting patiently for more later, that is, **intertemporal choices**.

Decision-makers prefer to receive rewards sooner rather than later. For economists, there is nothing inconsistent about such a preference [39]. As long as the decision-maker decrements the subjective value of a reward consistently, one can prove that perfect transitivity can be maintained [40]. Unfortunately, neither humans nor animals appear to decrement reward value in this way. Instead, discount rates are higher for rewards offered at short delays and lower for rewards offered at longer delays (e.g., [41–43]). This creates yet another inconsistency when choosers view the first day or week of a delay as much more aversive or costly compared with many subsequent days or weeks of additional delays.

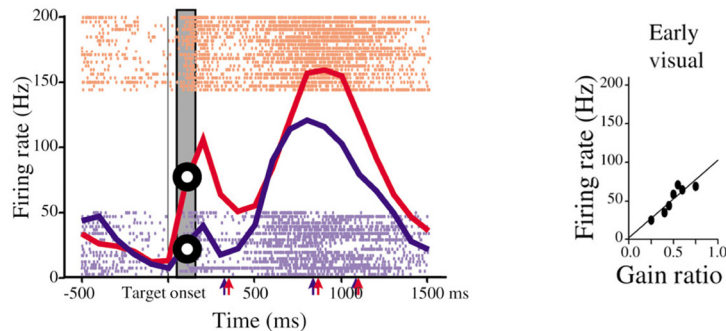
How can one make sense of such inconsistent behavior? One answer [16] drawn from the multiple-selves model is that our brains have two independent modules: an ‘impulsive’ chooser, which only values immediately available rewards; and a ‘rational’ patient chooser, which values all rewards as a function of the delay-to-reward duration. In this conception, human behavior represents the combined action of these two modules, each internally consistent when acting alone, but yielding strongly intransitive behavior when combined.

In a landmark fMRI study designed to test this hypothesis [44], human decision-makers made real choices between rewards offered at different delays. When rewards were offered immediately, a single value-related signal was identified at two locations: the ventral striatum (VS) and the ventromedial prefrontal cortex (vmPFC). When rewards were offered at longer delays, no value-related signal was observed (Figure 2A). This was either because immediately available rewards are simply worth more and, thus, easier to detect with fMRI or it was because a specific impulsive module had been identified. To resolve this question, the authors set out to identify a signature of the patient chooser: isolating the trials in which subjects took the longest to respond, they looked for particularly active brain areas. They found evidence of such activation in the dorsolateral prefrontal cortex (dlPFC) and the posterior parietal cortex (PPC) and hypothesized that this reflects the activity of the independent patient module predicted by theory.

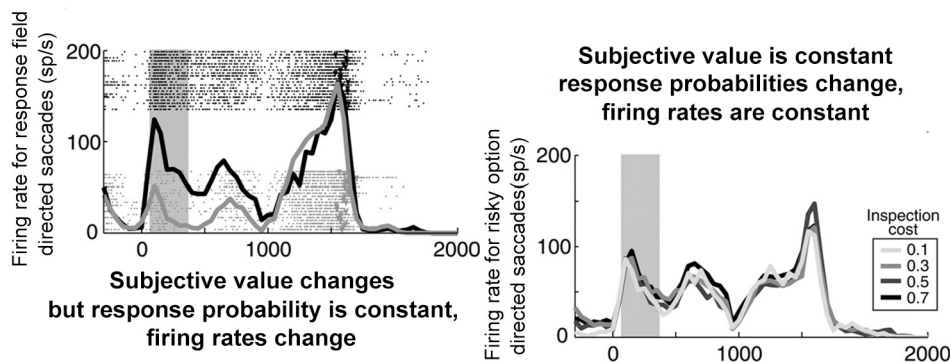
However, the finding was unavoidably ambiguous. Was the VS signal so strong for immediately available rewards because it only encoded immediate rewards, or was it also encoding the subjective value of long-delayed rewards, but at a level so low that it was undetectable to early fMRI scanners? To answer this, one would need to examine activity in the VS and the vmPFC when the magnitude of the delayed reward was suddenly increased [45]. This manipulation revealed that, as soon as the delayed reward was large enough to yield a subjective value signal detectable by fMRI, its representation was clear in both of these brain areas. It turned out that this was not an area that specifically represented the preferences of an emotional-impulsive self; instead, it was an area that represented all rewards, at a magnitude modulated by delay. A detailed characterization of the vmPFC and VS activity revealed that the signal precisely captured, at a within-subject level, both the impulsive early high valuation and the more gradual later decline in

Value representation in parietal cortex

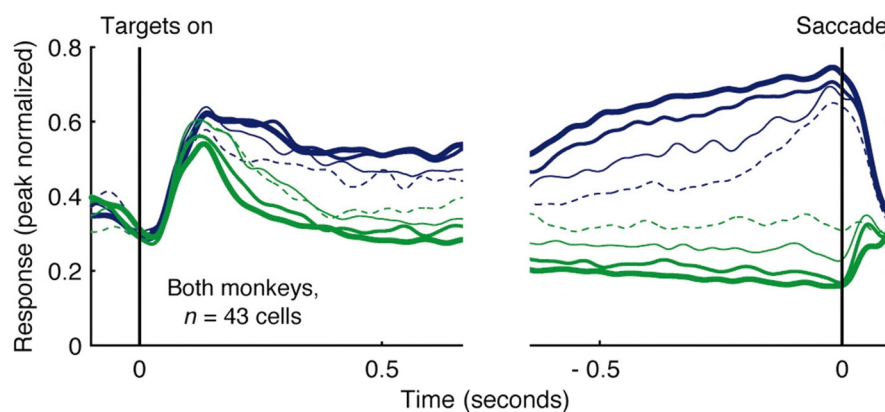
(A) Firing rate correlates with value and reward likelihood



(B) Not with response probability



(C) Firing rate tracks dynamically changing subjective value



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Figure 1. Parietal neurons carry an abstract representation of subjective value. (A) When awake behaving monkeys are presented with potential rewards, the activity of single neurons encodes the value of those rewards. Parallel experiments (not shown) indicate that, when the likelihood of reward is varied, these same neurons also encode reward probability in exactly the manner predicted by economic theory [36]. (B) These changes in neuronal activity specifically encode an abstract representation of reward value and not the likelihood that a decision-maker will select the reward. Using a strategic game, it is possible to show that, when an abstract notion of subjective value varies, but the directly observable probability that the subject will make a particular behavioral response (the choice probability) is held constant (left), these neuronal firing rates change. When abstract subjective value is held constant but choice probabilities are systematically

(Figure legend continued at the bottom of the next page.)

value with time. Across subjects, the data revealed that brain activations were just as intransitive as the subjects. An individual subject's degree of inconsistency, if significant, could be derived from the neural measurement [45,46]. Thus, even when decision-makers were behaving inconsistently, there was a unitary neural representation of a single hidden decision variable (Figure 2B). Subsequent replication of these experiments in monkeys (Figure 2C) showed that, if anything, the match between the neural firing rates in the PPC and the irrational subjective value curves was even better at the higher resolution of single neuron recordings. Could it be that there is a unitary representation of a single utility-like signal, rather than the many competing signals predicted by multiple-selves theory?

At the same time, a similar examination of another behavioral pattern sometimes seen as an inconsistency, **loss aversion**, yielded similar results [47]. Humans often treat losses relative to the reference point as more consequential than equivalent gains, presumably because losses are more anxiety-provoking. In this study, brain activity was examined as decision-makers evaluated financial lotteries that involved varying levels of gains and losses. As in intertemporal choice, these data revealed that human choosers were inconsistent, but that this inconsistency did not appear to arise from multiple modules, one only anxious and one only logical. Instead, the study revealed that several brain areas irrationally encoded losses and gains asymmetrically, but not by using multiple independent modules (but see [48] for one counter-example).

A series of three subsequent meta-studies strongly support this conclusion that a single decision-variable is represented neurally and that emotional and rational evaluations are fully integrated [49–51]. All three of these metastudies, together aggregating data from hundreds of studies, tell the same story. Value representations in the brain do not reflect multiple competing agents. Instead, these data suggest that the irrationalities we observe in behavior reflect a fundamental irrationality in the neural representation of subjective value, in humans, nonhuman primates [52], rodents [53], and perhaps even insects [54]. The representation of subjective value appears fundamentally imperfect, but imperfect in similar ways, in animals separated by hundreds of millions of years of evolution.

From irrational subjective value to efficient subjective value

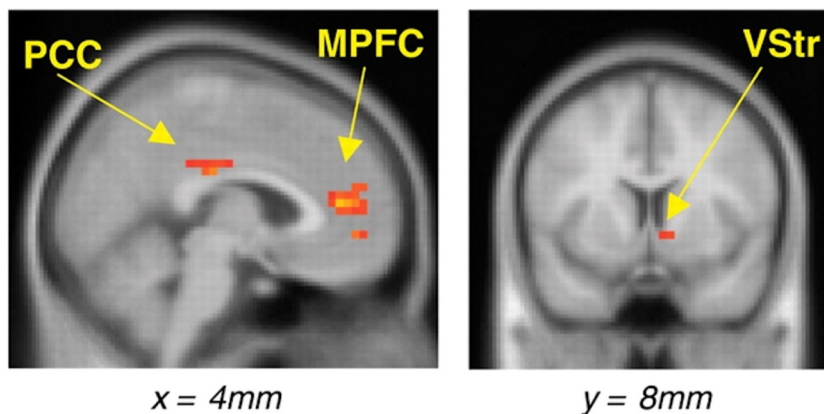
What neural features underlie these imperfect or technically irrational representations of subjective value? One widely accepted answer is that these imperfections arise from 'unavoidable' limits to neural computation: inconsistent behavior reveals an imprecision in the neurobiological representation that evolution has failed to eliminate for some reason (e.g., [55,56]).

Consider thinking about this process another way: the human brain consumes 10 watts of power. To provide that power, humans ingest ~2000 kcal of food a day, 20% of which (400 kcal) drives the brain [57]. Imagine a brain with ten times the precision and capacity, hence ten times the metabolic demand. That brain would require an additional 3600 kcal, requiring that we triple our daily intake to support this ten-times increase in precision.

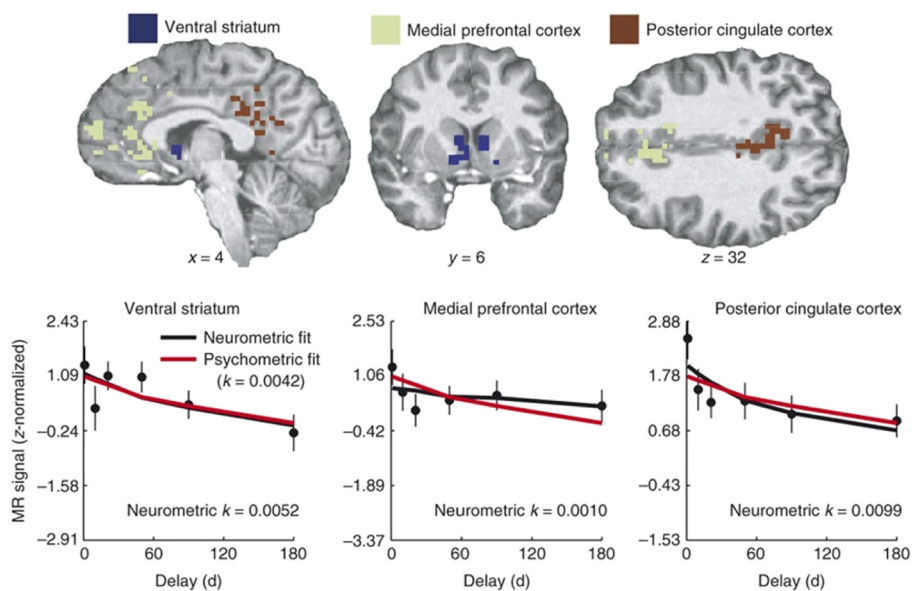
Should natural selection push against costly irrationalities toward a more precise brain even if that added precision comes at such a high cost? Natural selection does not aspire to perfection. It pushes organisms toward greater fitness (e.g., [58]). Building a brain that always picks the best candy bar is better than building a brain that occasionally picks second-best, but perhaps not if

varied (right), the neuronal firing rate is constant [84]. (C) When reward rates are dynamically changed and the decision-maker must decide how to best allocate its choices to maximize reward, neuronal firing rates depend on the average rate of reward. Stacked green and blue lines accurately rank rates of reward obtained by freely choosing monkeys [37].

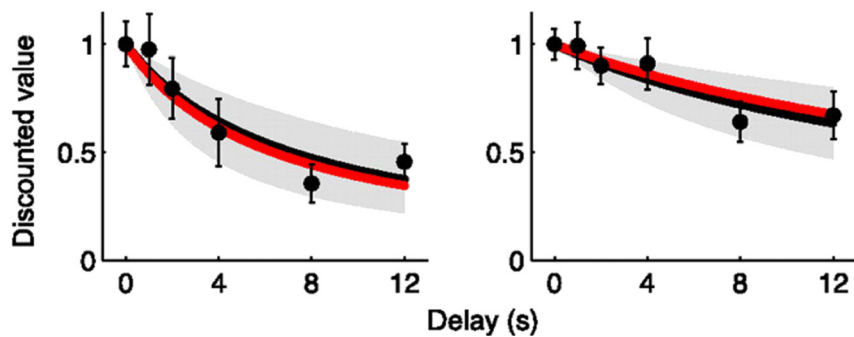
(A) BOLD responds strongly for immediate rewards



(B) BOLD tracks subjective value at all delays



(C) Neuronal activity tracks subjective value at all delays



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you have to buy three times as many candy bars to survive. Formally, it is known that precision is monotonically costly and increasing precision must, by the laws of thermodynamics, increase metabolic costs [24]. Once we incorporate these costs into our thinking, it becomes clear that intransitivities might simply be desirable economies. Rather than modeling neural decision-variables as Platonic signals corrupted by noise, one might see in them an optimized trade-off between informational density and representational costs. Once we acknowledge that it is efficiency, not rationality as the neoclassicists proposed, that the brain should maximize, this significantly changes how we need to model choice [23,32].

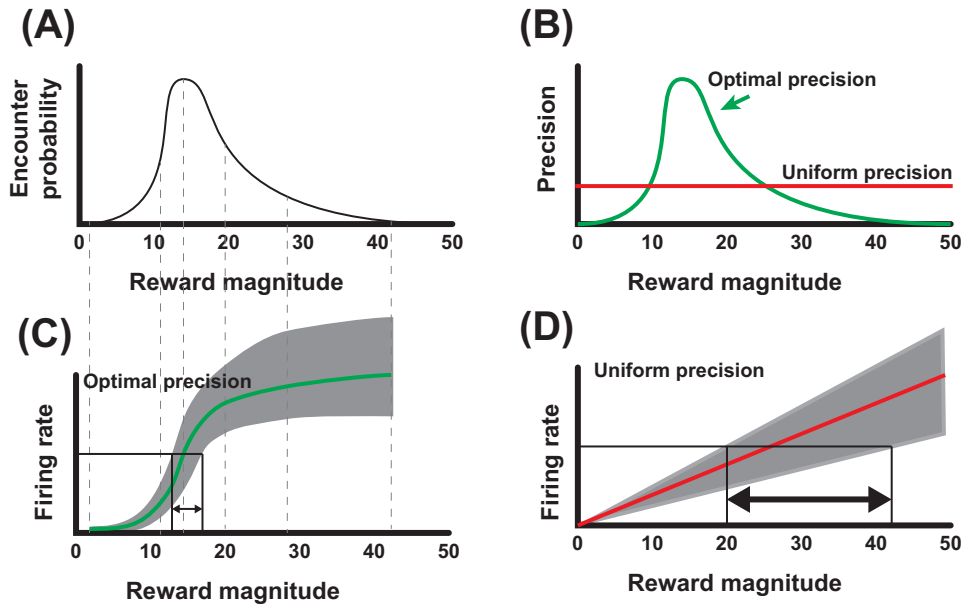
When are irrationalities efficient?

Random Utility Theory [59] pioneered our understanding of the irrationalities expected from a chooser with limited precision. As precision declines, decision-makers make more and more errors, sometimes picking the second-best option rather than the best, or even occasionally picking the third-best option. The theory predicts that these errors are more common when the options being compared are close in value, regardless of the values of those options. Thus, Classical Random Utility theory presumes that people are imperfect choosers, but hypothesizes that there is no real pattern to their errors, certainly not patterns like the systematic irrationalities that we observe in human and animal choice behavior.

Could a biological system do better than Random Utility Theory predicts? Consider an idealized chooser who knows they have limited precision to encode subjective value, but also knows with certainty that they are much more likely to encounter a subjective value in a particular range, for example, something around the value of a candy bar rather than the value of a car (Figure 3A). Such a chooser would maximize their efficiency by dedicating more precision to the likely range of subjective values and less to the unlikely ranges; efficiently adapting their precision to maximize accuracy where it is most important and to minimize accuracy where it is less valuable (Figure 3B). This **efficient coding hypothesis** (Box 3), the idea that neural codes could be efficient, not simply accurate, was first studied during the 1950s and 1960s [60,61] and has been broadly impactful in the study of perceptual systems [62].

Consider a chooser who must represent the nutritional value of food choices to maximize the expected nutritional outcomes. We can think of Figure 3A as plotting a histogram of the many options that our chooser might encounter in a particular environment [63]. For this 1D case, the optimal encoding strategy for a system of limited precision, the provably efficient solution, is for the neuronal firing rate function to be the integral of the frequency histogram (Figure 3C). For contrast, consider Figure 3D, which plots a linear firing rate function. Of course, like all neurons, these two hypothetical neurons are imprecise. Their mean firing rate is marked by the black line, but moment-by-moment firing rates lie randomly within the gray bands. When the efficient neuron is firing at half its maximal rate, we know that reward magnitude lies between 13 and 17. By contrast, when the linear neuron is at its half-maximal rate, the reward magnitude lies between 20 and 43. This reveals that, by tuning the firing rate function correctly, either by sculpting

Figure 2. Human subjective value signals predict both impulsive and patient choices. Value-related brain activity tracks subjectively measured reward magnitude in an intertemporal task, even when that subjective value declines hyperbolically in a way characteristic of inconsistent choices. (A) Activity in the medial prefrontal cortex (mPFC), posterior cingulate cortex (PPC), and ventral striatum (VStr) is much stronger for immediately available rewards than it is for delayed rewards [44]. (B) For a single representative subject, activity in these areas declines smoothly (dots), but hyperbolically (black curves), as the delay to reward increases. This decline precisely matches the same subject's behaviorally estimated subjective value curve, which is also hyperbolic (red) [45]. (C) More precise measures of single neuron activity made in monkeys making intertemporal choices yield even more precise matches between behavioral estimates and neuronal estimates (same colors as in B) [38]. Both behavioral and neural estimates are clearly hyperbolic. Abbreviation: BOLD, blood oxygen-level dependent.



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Figure 3. Noisy neural systems must adopt nonlinear firing rates to be efficient. The goal of efficient coding in decision-making is to maximize information about the objective values of rewards in the spike rates used to compare options. This maximizes the likelihood of selecting the best possible option. (A) Hypothetical distribution describing the objective probability that a chooser operating in an example environment will encounter rewards of any given magnitude. (B) To maximize information, precision should be greatest at reward magnitudes that are likely to be encountered. Allocating precision uniformly erroneously dedicates neuronal bandwidth to options that are rarely encountered. (C) Taking the integral of the encounter probability curve yields (under 1D conditions) a firing rate function that maximizes accuracy at the expectation point. The half-maximal firing rate (black horizontal line) then indicates the actual reward magnitude with higher precision. (D) By contrast, a uniform firing rate yields estimates of reward magnitude that are less accurate at expectation (and more accurate off expectation).

the curvature of the function optimally or rescaling the function linearly (e.g., [64]), we can increase precision where it is most valuable at the cost of decreasing precision where it is least valuable. Of course, this would also impose a structure on our errors and intransitivities would be more common in some cases than in others.

The theory of efficient representation

A significant amount of work during the 1990s [65–67] examined efficient coding in the visual system using the divisive normalization equation (Equation 1):

$$FR_1 = \frac{Input_1^\alpha}{M + \sum_i \omega_i Input_i^\alpha}, \quad [1]$$

where the firing rate of neuron 1 is equal to the primary input to that neuron (e.g., the brightness of a particular pixel) raised to an exponent divided by the mode (or center) of the input distribution plus a weighted sum of all current inputs to the other neurons, each raised to the same power. Using numerical methods [68], it has been shown that, if this divisive normalization equation is used to represent a set of visual images pixel-by-pixel, one can find values for α , M , and ω that do, in fact, minimize the total number of errors (or equivalently maximize the amount of information) in the representation of the image. This class of function re-encodes visual images in a maximally efficient way, putting the most information in the fewest action potentials.

Box 3. The efficient coding hypothesis

Attneave and Barlow [60,61], building on Claude Shannon's *Theory of Information* [88], proposed that neural codes in sensory systems were driven by evolution toward maximization of the amount of information carried by each action potential. This information maximization can be viewed as a two-stage process. First, eliminate redundancy in the incoming information. Second, adjust the firing rate function so more of the available range is dedicated to encoding likely inputs. This prevents one from wasting bandwidth on improbable events that are never observed. If encoding visual images, for example, the overall brightness of the image changes over the day in a way that induces both redundancy and local correlations. Changes in pupil size both reduce this redundancy and adapt to the range of brightness that impinges on the retina.

Neurobiological functions that achieve this same kind of information maximization when encoding visual images have now been widely studied (e.g., [66,68]). Neurons in the visual cortex, for example, encode something along the lines of Equation 1:

$$FR_1 = \frac{X_1^2}{\sigma^2 + \sum_i (\omega_i X_i)^2}, \quad [1]$$

where FR_1 is the firing rate of the neuron encoding the objective intensity of pixel 1, σ is the expected mean intensity level, and ω_i are weights that capture the correlations between pixels. The denominator removes from the firing rate of neuron 1 information already carried by other neurons, maximizing information per action potential. This model, known as divisive normalization, has subsequently been observed in many sensory systems and it has even been proposed that this mechanism is a canonical neural computation [89].

It has also been proposed [18] that a similar process might be operating in the neural representation of subjective value, a hypothesis that has been confirmed in several experiments (e.g., [90]). While this is an active area of research, it is not yet clear exactly how efficiently either sensory or decisional variables are represented in the nervous system. Over the next decade or so, it should become clear whether neural computations, such as divisive normalization, provide an accurate approximation widely used by the nervous system or whether more complex models will be required to understand the underlying neural architecture.

Over the past few years, this work has been extended to the domain of subjective value [24] and has yielded a clear view of how an efficient decision-making system would encode subjective value and, thus, what kinds of intransitivity it would be expected to produce. Treating the efficient encoding problem as a problem in thermodynamics, it was possible to derive the class of functions that achieves an optimal trade-off between maximizing information and minimizing costs. Interestingly, the class of functions derived in this way is formally equivalent to the divisive normalization class of representations used in the study of the visual system. Perhaps even more surprising, a large class of behaviorally observed 'irrational' choice behaviors are mathematically equivalent to both divisive normalization and information maximization. Divisive normalization class functions are optimally efficient representations for subjective value, and they unavoidably yield irrational choice behavior specifically because they efficiently trade off the costs and benefits of precision.

So what exact firing rate functions (or equivalently subjective value functions) should we expect to see in an efficient system? Several groups [20,23,32] have examined how a neural system might be designed to optimally encode specific inputs. The basic answer is that an optimal system must select a transformation function that maximizes a specific quantity (e.g., calories obtained) for a specific class of inputs. The firing rate function needs to be tuned to the inputs, as in Figure 3A. This work is critical because it refocuses us on two properties that are the subject of intense current investigation: what is the input distribution the chooser should seek to represent and what is the actual object (expected information, expected value, or expected sample recovery) being maximized. However, all of this work points to the notion that, to maximize fitness, organisms require economical transformations of value that yield some irrationalities because eliminating those irrationalities would be inefficient.

Divisive normalization in choice

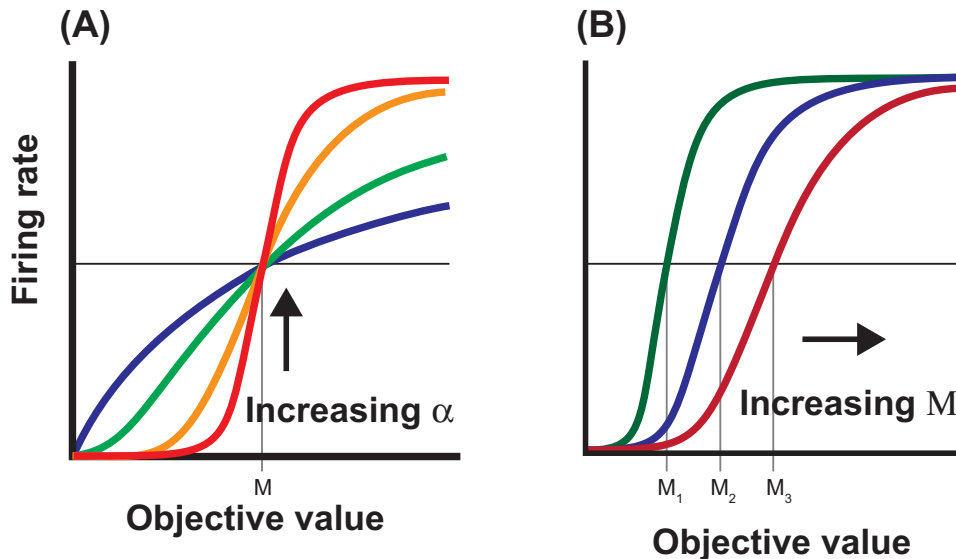
The classic divisive normalization equations achieve efficiency by devoting more firing rate range to more likely inputs; when the likely inputs are tightly clustered, then a sigmoidal firing rate

function centered on these likely values is efficient. When the likely inputs are more broadly distributed, then an efficient encoding function would use a more gradually sloped form. The divisive normalization functions achieve this flexibility with two key parameters, M and α . As Figure 4 shows for a simple example with a single choice option, M centers the transformation on the most likely input and α controls the overall shape of the function. At $\alpha = 1$, the function looks very much like a classical utility function [4]. As α increases, that function takes on the characteristically sigmoidal shape of the Kahneman and Tversky [9] value function. This suggests that the shift from a classically concave function to a sigmoid observed behaviorally is driven by changes in the distribution of the options under consideration.

In situations with more than one option, as in Equation 1, M serves as a kind of a temporal average, an estimate of what future input is most likely. By contrast, the weighted sum that aggregates information about the current options is a kind of spatial average that, because of the exponent, controls the shape of the function based on the specific values of each of the current inputs. These temporal and spatial averages can be thought of as a kind of **prior** and **likelihood** estimation, maximizing information in the posterior firing rate distribution [24]. In fact, some current research suggests that the relative contributions of temporal and spatial components are under dynamic control to better align the firing rate function with the best estimate of the input distribution [69].

Efficient representation of the most common input

If M reflects a tool for centering the encoding function on the median or mode of the distribution of possible rewards, then what happens if we change the size of the median (or modal) reward size?



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Figure 4. Divisive normalization firing rate functions are highly flexible. Functions that relate firing rate to objective reward magnitude for a system using divisive normalization (Equation 1 in the main text; note that, in this functional form derived from [85], the exponent α is embedded in the constant M , rather than being written separately for clarity in expressing the lateral shift of the function.). (A) Adjusting the exponent in Equation 1 steepens the function around the expectation, or reference, point. This corresponds to adjusting the firing rate function to encode narrower or wider input distributions. However, these functional shapes also tile the set of previously described utility and value functions. When $\alpha = 1$ (blue), the function mimics the shape of the classical utility function proposed by Bernoulli. As the exponent increases (red, $\alpha = 3$), the function comes to resemble the value function of Kahneman and Tversky. (B) As the expectation point M is increased, the center of the function shifts to the right. This corresponds to a strategy that centers the firing rate function on the modal value of the input distribution.

In 2005, this experiment was conducted while recording from midbrain dopamine neurons [70]. As predicted, dopamine neurons indeed re-centered their firing rate functions in response to changes in the input distribution. More recently, similar results have been observed in the orbitofrontal cortex [71] and the PPC [72]. The neural firing rate functions adapt to changes in the input distribution as expected in an efficient system. However, what kind of irrationalities would such a system yield at the behavioral level (see also [73])?

In one experiment designed to search for such irrationalities [74] (Figure 5), hungry subjects were asked to indicate the maximum amount they would pay for each of 30 different snacks. Ten high-value (and ten low-value) snacks were then identified for each individual, and subjects made repeated bids on these high (or low) value items during a 300-trial adaptation block. Without warning, the input set was suddenly changed to include all 30 snack foods. After the change, subjects transiently shifted their bids downward (or upward after low-value adaptation), and this shift decayed over the course of about 45 trials, exactly the effect that would be expected if an efficient coding system using a divisive normalized representation was re-centering the mode of its representation. The critical feature is that the subjects showed inconsistent pricing behavior when the mean of the input distribution changed. However, that inconsistency reflected a provably efficient encoding scheme that makes the most of a limited informational capacity (see also [25]).

Efficient representation of the current offerings

The role of the weighted sum in the denominator is to adapt the firing rate function to the current choice set. Consider a situation in which all of the options in the current choice set are suddenly high valued. In a system without divisive normalization, this can result in all of the firing rates being close to the maximum rate and, thus, hard to distinguish, a loss of information created by the bounded and limited precision firing rate. An efficient system solves this problem by reducing the overall firing rates (much like M , but instantaneously), more accurately centering the firing rates for each option within the available firing rate range. To put all of this more formally: ω reduces informational redundancy induced by input covariance and α captures distributional shape. The summing operation with the reference point term M adjusts the slope and lateral position of the function by combining all of these terms.

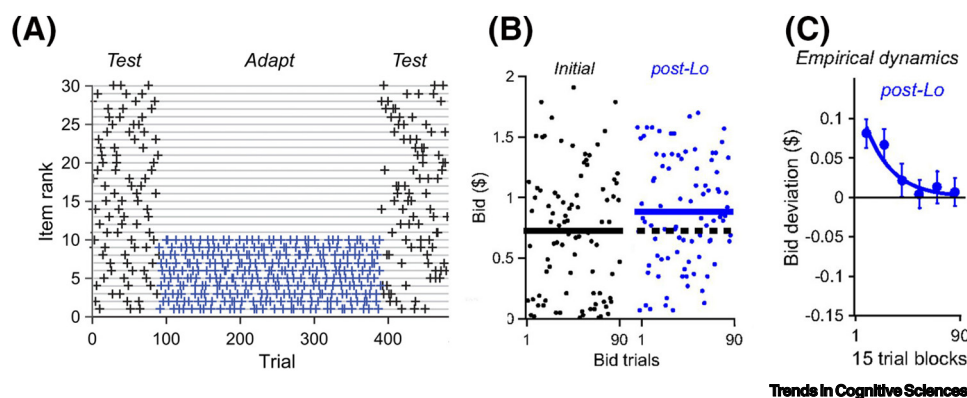


Figure 5. Human choice anomalies show evidence of divisive normalization. Effect of adapting the reference point on choice behavior. (A) Task design from [74]. Subjects state the maximum amount they would pay for different foods in an incentive-compatible manner. First, they encounter a range of values (black). Subjects are then adapted to a low-value subset, shifting the expectation downward (blue). Finally, valuations are remeasured immediately after adaptation (black). (B) Initial bids made during the first test period show an average value of about US\$0.70 (black). Measurements during the second test period indicate that subjective values are initially shifted upward by adaptation by about 10% (blue). (C) The effect of this adaptation of the reference point declines over 90 trials with a roughly exponential time course.

Choice set size effects

However, such a system would be highly sensitive to the number of options under consideration. As the number of elements in the denominator grows, so does the aggregate value of the denominator, shifting overall firing rates lower and lower. As choice sets grow in size, error rates (irrationalities) should increase in a characteristic fashion, a pattern very different from the class of errors predicted by the Random Utility Theory [75]. This arises because, as the number of options increases, the amount of information we put into the system also increases. Performance decays efficiently as the informational demand on the network increases.

It has been known for some time (e.g., [76]) that, as choice sets increase in size, performance decreases. However, a precise examination of the form of performance decrease observed under these conditions reveals that the divisive normalization model significantly outperforms traditional random utility models in accounting for the irrational features of decision-making in the face of large choice sets. While humans do choose irrationally when faced with large choice sets, it appears they do so in a way that maximizes accuracy in the face of increasing informational demands [75].

Three option irrationalities

A more subtle class of irrationalities that one might expect in an efficient system are so-called ‘three option errors,’ errors that arise when a subject must identify the best of three possible options (e.g., [72,77]). Consider the problem faced by a divisively normalized system when it must choose between two options very close in value to one another, both in the presence, and in the absence, of a low-valued third option. The insertion of the third option, even if it is never chosen, adds information to the system and should degrade performance. Worse, as the value of the unchosen third option increases, performance (and neuronal firing rates) should degrade further. Parietal neurons [72] turn out to show patterns of firing rates that also align well with the prediction of the divisive normalization model under these conditions. Subsequent work [77] aimed at understanding the role of gain adaptation more generally on encoding accuracy has yielded a similar result. A generally efficient representation could account for systematic errors as efficiencies, in this case under a broader range of conditions than those captured in the original experiment.

However, this class of three-option irrationalities has been somewhat more controversial than some of the other features of an efficient representation, which have been more widely observed. One important paper [78] yielded similar results, but not with complete consistency. Another study [79] initially reported a failure to observe this particular irrationality in human choosers when measuring reaction times rather than choices, although a reanalysis of that data [80] suggests that most of their subjects do show this effect, if somewhat more weakly than might have been expected. While much work remains, it does seem clear that richer forms of divisive normalization [81] will be important and may be able to effectively capture even these more heterogeneous results.

To summarize, efficient coding systems should show very characteristic irrationalities, and there is growing evidence that the neural architecture is well tuned to provide just this kind of efficiency (Box 4). Choice errors should show a strong dependency on a kind of reference point, and they do both neurally and behaviorally. Subjects should be risk-averse above this reference point and risk-seeking below it, as has been observed. Sudden shifts in the mean of the input distribution should cause systematic intransitivities (like the ones Nick Leeson showed) while the reference point is adapting, again as observed. Increases in the number of options should lead to inconsistencies, as should direct manipulation of the structure of the choice set, a phenomenon that has

Box 4. Computing subjective value with neurons

One important test of any neurobiological theory is whether real neurons can perform the computations the theory requires. Growing evidence suggests that simple networks can perform divisive normalization-like computations [91]. In such a network (Figure I), neuron R_1 receives a direct excitatory input (V_1), a baseline rate of activation that it shares with all other R neurons, and a single inhibitory interneuron input, G_1 , which divisively regulates the activity of R_1 . Each gain control neuron receives inputs from all other output neurons, thus computing a (weighted) sum of those inputs and using that as the divisive input to the output neurons exactly as required by the efficient equations. Although such broad connectivity appears counterintuitive, it has been documented in the rodent visual system [92].

Essentially all networks of this kind have a single equilibrium state [91]. When inputs are applied to the network, the network eventually settles to represent the input divided by a weighted sum of the outputs of all of the output neurons. If the inputs change faster than the time constant of the network, the output signal represents a time-weighted average of the sequence of inputs. One cannot help but notice that this means that any broadly integrating gain control network converges to something almost like, but not completely identical to, the divisive normalization equations described in the main text.

At full equilibrium, the output of the network shown in Figure I closely approximates Equation 1:

$$FR_1 = \frac{x_1}{M + \sum_i \omega_i FR_i} \quad [1]$$

How might M be represented in a real network? One possibility is that a long time-constant version of this network might compute M and pass it on to a faster network optimized to compute the weighted sum of current options. When two such networks are cascaded, one with rapid dynamics and one with slow dynamics, the network with slow dynamics effectively computes the M term and then injects it into the faster network [69].

At least in the parietal cortex, both the dynamics predicted by these models and the dependence of firing rate on output (rather than input, as in the original divisive normalization equations) have now been observed [90]. Parietal neurons do, indeed, receive both excitatory and inhibitory inputs and those inputs are, over at least a limited range, interacting roughly divisively in nature as required by the models.

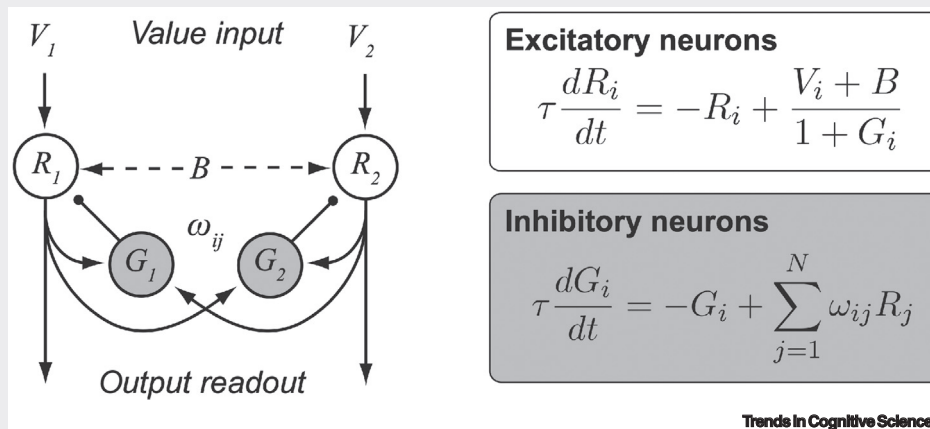


Figure I. A divisive normalization network. The proposed network of LoFaro and colleagues [91] computes a divisive normalization-like transformation. Individual pyramidal cells receive an objective value input. The output of each R-neuron is divisively reduced by a nearby inhibitory interneuron, which aggregates information about all inputs to the R-neuron layer. Thus, the G-neurons capture all available information about the choice set and remove that information from the R-neuron, effectively maximizing information about how the V-input of that neuron differs from other V-inputs. LoFaro and colleagues showed that models of this class must have a single equilibrium state that closely approximates standard divisive normalization.

now been well documented. What should stand out here is that many of the inconsistencies that motivated Simon, Luce, Kahneman, and Tversky emerge as efficient responses from an informationally constrained system.

From expected value theory to rational imprecision

In the mid-17th century, Pascal proposed that what humans were doing when they made choices was to objectively maximize the expected value. The goal of choice should be defined by a simple **objective function**: compare options by multiplying the probability of each outcome with the magnitude of gain and then select the option that objectively maximizes the long-run average value one accumulates from all of one's decisions. It seems as if Nick Leeson was not doing that when he bet his bank on riskier and riskier options each day.

As it became clear during the 18th century that human choosers often fail to maximize the expected value, mathematicians abandoned the notion of an objective maximization function. Instead, they concluded that humans maximize a hidden subjective transformation of value, which today we call the utility function. The virtue of this approach is that it appears to explain both why and how humans are risk averse.

The neoclassical economists of the late 19th and early 20th centuries shifted their emphasis away from the specification of a particular utility function and toward a more general notion of what constituted utility maximization. Developing the notion of rationality, they defined axiomatic rules that any kind of perfect maximizing behavior would have to follow. If humans followed these rules, humans were choosing in a goal-directed fashion even if we could not be certain exactly what goal or goals they were pursuing.

Accepting that logic, empirical economists and psychologists working at the end of the 20th century noted a range of conditions under which humans behaved intransitively. While a few economists and psychologists sought to explain that this behavior might be related to the physical limitations of human brains, there was an overwhelming shift toward seeing human choosers as accumulations of small mechanisms that were troublingly inefficient when working in aggregate. Instead of trying to define why humans chose the way that they did, these scholars tended to accept that humans were disordered.

However, interdisciplinary work conducted over the past two decades offers a very different interpretation. These data appear to suggest that, as Pascal might have suggested if he had been a neurobiologist, humans really do use a representation of the expected value of each option, but a representation distorted by the needs of a limited precision neural representation. What these data appear to show is that our biological objective function really is, as Pascal hoped, to maximize long-run average value. However, this is a maximization we wisely perform with a level of precision driven by the constraints of efficiency. While many questions remain (see [Outstanding questions](#)), in this view the structure of the transform from value to subjective value is specified not by a need for risk aversion, as the classical economists of the 19th century imagined (e.g., [82]), but by a need for efficiency. We can conclude instead that the observed subjective value function reflects a trade-off between the rising cost of precision, the diminishing returns from increasing precision, and the distributional properties of the world in which we make choices.

What is perhaps most ironic about that notion is that Pascal may have been less wrong than we have thought for the past 350 years. The utility function may not be so much a **moral value** as Bernoulli proposed in the 18th century, but rather a mechanistic tool that tunes our behavior for maximal efficiency in the face of limited precision.

Concluding remarks

The framework we use to make sense of human choice behavior impacts how we think about ourselves and the predictions we make about how people will choose in novel situations. This

Outstanding questions

How efficient is divisive normalization? Theoretically, the class of functions in which divisive normalization sits are optimal encoding functions. Exactly which function is most efficient depends on the distribution of possible inputs. Future work will have to: (i) relate specific patterns of inputs to perfectly efficient encoding systems; (ii) gather data that define what distributions real-world choices take; and (iii) identify the exact divisive cost functions used by the brain.

Can all classes of inconsistent behavior be modeled using divisive normalization? The basic model cannot account for situations in which a contextual element causes a clear reversal of preferences. Divisive normalization models that operate in two successive stages or that encode attributes of the choice objects separately can achieve these kinds of preference reversal. Future work will have to establish the plausibility of these extensions of the basic model.

How is divisive normalization computed in the brain? Simple models that use simulated neurons compute very close approximations of divisive normalization. The development of these models is in its infancy. Opportunities for new discoveries abound.

Divisive normalization focuses on the magnitudes of rewards or punishments. How are probabilities represented in the brain and how do they influence these representations? The representation of probabilities is probably one of the most difficult aspects of the theory and one in which little progress has been made. Importantly, we can identify two kinds of probabilistic representation in the brain. In the first, humans or animals make repeated samples of an action or reward that is variable, and by averaging derive a value estimate which has probability bundled into it. The dopaminergic reward prediction error system is an example. The other kind of probability, in which a truly mathematical representation of the probability of an event is encoded and manipulated, is more poorly understood. Understanding how humans construct these probabilistic representations will be critical.

influences not only research, but also social policy. As our understanding of human behavior has changed, the policies we consider fair or desirable also change. During the 1950s, humans were thought of as perfectly rational. People accurately maximized their personal preferences, or utility functions. To limit an individual's choices, or to force a particular choice, was unthinkable (as long as no one else was being harmed). During the 1970s and 1980s, however, it became clear that humans are often irrational, apparently beset by unresolvable internal conflict between their multiple-selves. Policymakers could help such a decision-maker by restricting their options so as to minimize destructive internal conflict. This logic, that irrationalities arise from an internal conflict and that policymakers should structure the choice environment to eliminate these conflicts, has recently taken a dominant role in policy circles [83]. Designing the choice environment to limit conflict inside the decision-maker is now a standard recipe for improving the well-being of decision-makers.

However, the neuroeconomic data presented here appear to indicate that humans are not intransitive because of internal conflict. Instead, these data suggest that human intransitivities arise from the limits of human computational precision and how the brain distributes that precision in representing subjective value. If true, that conclusion calls for policy interventions that may be different from the ones prescribed by contemporary behavioral economists. In an efficiently irrational chooser, eliminating irrationality ultimately comes down to finding ways to reduce either the costs, or the need for, precision. Consider this example: human choosers are intransitive [74] when they rapidly shift from choosing at a low-value range to a high-value range (Figure 5). This reflects not a conflict between two modules, but rather the slow adaptation of the divisive normalization mechanism as it shifts to maximize precision in a new range. In this case, minimizing irrationalities is simply a matter of waiting for the mechanism to align with the new value range.

All of this suggests that our new understanding of the limits of the choice mechanism reveals a surprisingly simple structure that admits new approaches to old irrationalities. Understanding that irrationalities emerge from the limits of our precision will suggest new classes of policy intervention that specifically target our representational limits while exploiting our irrational efficiencies.

Declaration of interests

None declared by author.

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What about efficiency in computation? These models all appear to be about efficiencies in the representation of subjective value, but should we also be looking for efficiencies in neural computation? Almost no work has examined the efficiency of neural computations and transformations. Gaining insight into computational efficiency will be essential if we want to make complete sense of the decision-making mechanism.

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