

trade may be preferable to free trade, and the optimal level of regulation “stringency” (a trade ban, sale of ivory stockpiles, or regulated sale of ivory harvested from wild populations) depends on factors that are as yet poorly researched or understood. Furthermore, net revenues from ivory sales often are only part of the income generated from elephants. Such income may also include photo tourism and sports hunting, although this depends on local circumstances (8). Bioeconomic models of the ivory trade should be augmented to capture these complex issues.

Current economic models are ecologically simplistic because they are underpinned by the convenient though often false idea of “equilibrium.” Until recently, deterministic single-species models, which do not consider the interactions between a particular species and a variable multispecies environment, have dominated the field. Most economic analyses of the ivory trade are based on a simple logistic model (4, 9), which assumes that the population growth rate for elephants will decline until it reaches zero when elephant numbers reach the “carrying capacity” of the environment. At the “carrying capacity,” the size of a population will, in theory, remain constant, because birthrate and death rate are equal and environmental resources (such as forage) are consumed at the same rate as they are produced. Such models do not recognize that elephant habitat may not be at equilibrium with climate, and that rainfall and forage abundance vary on time scales that range from years to decades (10). This variability in turn affects reproductive and mortality rates, the age structure of elephant populations, and hence the supply of ivory over time. Moreover, the “quality” of habitat, or the ability of land to support wildlife, is also affected by other factors—elephant density, fire, and economic activities at the margins of protected areas. Rather than sitting at a single idealized “carrying capacity,” ecosystems may occupy one of several “multiple stable states” at any given point in time or may be in transition from one state to another (11).

Although some economists have attempted to focus on multispecies models (12) and models that incorporate temporal variability (13) and spatial scale (14), there remains a gap between stylized economic models and recent ecological thinking. There is a strong need to bridge the gap between ecological theory and the economics of natural resources by incorporating variability, complexity, scale, and uncertainty into current economic models.

Space is now widely considered to be the new frontier in environmental and resource economics. Economists are already using theories from the dynamics of fragmented populations (“metapopulations”) to analyze the spatial pattern of dispersal and harvesting in

marine environments (14). Yet when considering terrestrial ecosystems, economists have yet to realize that these are a mosaic of potential interacting sites whose populations cannot be described by simple logistic economic models. Important conservation concerns, currently undervalued by economists, ensure ecological integrity and the maintenance of ecosystems. Dealing with these concerns requires attention to the interactions between the ecological variability of habitat and the economic (opportunity) costs of protecting interconnected habitat patches. Managing and conserving ecosystems in flux differs from older approaches aimed at maintaining stability (15). In an ecosystem in flux, population sizes and the distribution of animals and plants vary over time and space. This variability has implications for conservation strategies and management of natural resources, because a constant supply of goods like ivory cannot be guaranteed. Furthermore, the land surrounding the periphery of a protected area should be viewed as equal in importance to the core, because potentially it can accommodate changing distributions of plants and animals. Such a view would help to maintain viable metapopulations across a landscape, preventing animal reserves from becoming isolated and possibly overcrowded or impoverished.

Incorporating the spatial dimension of ecology into economic models permits a more accurate evaluation of the ecological impact and economic costs of alternative policies. Currently, however, there is a mis-

match between state-of-the-art economic and ecological theory on the one hand, and the contributions of economists to the debate on the ivory trade on the other. The way forward in the immediate future may be for ecologists to identify the scales at which equilibrium models provide an approximation of reality, and for economists to build this spatial scale into their models. A future goal for economists when analyzing the exploitation of flora and fauna will be to develop models that capture the nonequilibrium nature of ecological systems.

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BEHAVIOR

A Marketplace in the Brain?

George Ainslie and John Monterosso

There are a number of studies that investigate violations of rationality in human decision making. One important violation that is repeatedly observed is a tendency to discount expected outcomes proportionate to their delay. This results in a systematic inconsistency of preference over time. On page 503 of this issue, McClure *et al.* (1) present an elegant functional magnetic resonance imaging (fMRI) study that measures changes in neural activity as human volunteers are presented with the possibility of delayed rewards. This work is an important step toward direct observation of the decision-making process, although its findings are open to different interpretations.

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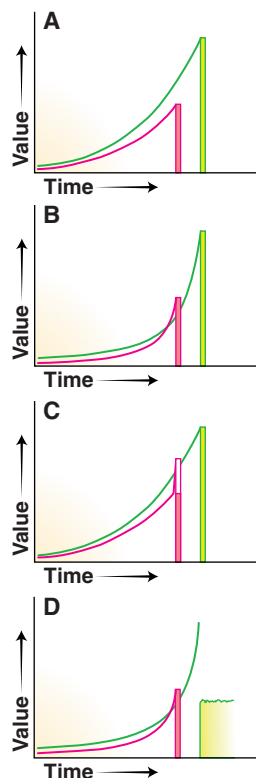
The dominant theory in the behavioral sciences has been that normal people discount the option of a delayed reward according to an exponential curve, that is, by a constant percentage per unit time. This exponential curve is similar to that used by financial markets: current value = nondelayed value \times (1 – discount rate)^{delay}. Exponential discounting implies a stability of preference over time. Individuals who exhibit exponential discounting behavior when faced with a choice between a smaller/sooner reward or a larger/later reward do not change their preference as the smaller reward becomes imminent. Rather, such individuals continually choose options that maximize their long-range prospects with allowances for the reduced value of the delayed goods. But despite its simplifying appeal, exponential discounting and the implied consistency of preference is not a tenable description of the way that either humans or nonhumans tend to evaluate the future. On the contrary,

there are conditions under which most subjects reverse their initial preference for larger/late rewards when smaller/sooner alternatives are near at hand. Furthermore, when given the opportunity, both human and nonhuman subjects choose to lock in their larger/late preference while this is still the most appealing (dominant) option (2–4). Thus, behavioral discounting data followed over time look systematically nonexponential. Consistently, such data are better explained by a function in which value varies proportionally with delay, although opinions differ as to the precise form of this function. Statistical methods of fitting the curve to data strongly favor a hyperbolic function as follows: $\text{Value} = \text{nondelayed value} / [1 + (\text{discount rate} \times \text{delay})]$ (5). The steepness of the proportional curve of value as a function of the time delay varies over a narrow range in nonhuman species but widely in humans (6, 7). Yet the same proportionality of discount rate with delay has been observed over a time period that ranges from seconds to decades, suggesting that the form of this curve may reflect a basic mechanism for perceiving value (8). David Laibson, an economist studying this problem and a co-author of the new study, has pointed out that a two-factor discount function, which he calls hyperboloid, can explain preference reversal and choice of prior commitments while retaining an exponential shape for most of the length of the curve (4). Laibson's formula is a conventional exponential discount function $\delta[\delta = (1 - \text{discount rate}); \delta \text{ factor value} = \delta^{\text{delay}}]$ multiplied by a delay penalty factor $\beta [0 < \beta < 1 \text{ for all delays} > 0; \text{thus, value} = \text{value if immediate} \times \beta \times \delta^{\text{delay}}]$.

Either form of nonexponential discounting, with its implied conflict between the current preference and the predictable preference of future selves, opens the study of inconsistent choice to bargaining theory. Thus, the whole self can be seen as a series of choice-makers, each influenced differently by the range of future options and each in partial conflict with the others. In the choice situation depicted by panels B, C, and D of the figure, an individual at an early time prefers the larger/late reward, but will need to influence or forestall the future self who prefers the smaller/sooner reward as this reward becomes imminent. The commonsense solution—to use willpower—has always lacked a scientific explanation, and exponential discounting theory does not recognize a reason for why willpower should even be needed. However, with nonexponential discounting, bargaining theory predicts that a person's mere identification of these smaller/sooner versus larger/late choices will bundle the expected rewards into a greater aggregate incentive to pick the larger/late option. In simple terms, individual pieces of chocolate may be irresistible unless the credibility of one's diet is staked against each

piece. This sounds like commonsense, but exponential discount curves predict no such bundling effect. Because delay-proportional discount curves decline more slowly as the delay in reward becomes longer and longer, adding them together for a series of rewards should increase differentially the value of larger/late rewards. In fact, this has been observed in experiments with both human (9) and nonhuman subjects (10). Delay-proportional discounting also predicts temporary preferences at shorter time scales in which the period of dominance of smaller/sooner rewards is too brief to support changes in motor behavior, but is long enough to support shifts in attention. It has been argued (11) that these mechanisms provide an instrumental (reward-based) account of phenomena traditionally considered noninstrumental, such as the sudden development of craving induced by an evocative stimulus.

In the new work, McClure *et al.* conduct an fMRI study of neural activity in response to a series of rewards of different values and offered with different time delays. Princeton undergraduates were given a series of choices between smaller/sooner and larger/late rewards: The rewards were gift certificates for Amazon.com, ranging from \$5 to \$40 in value. The smaller/sooner option could be received the same day (“today”) or with a 2- or 4-week delay; the larger/late option could be received either 2 or 4 weeks after the smaller/sooner option. The order of presentation was randomized. Subjects did actually receive one of their certificates for the delay chosen, but did not find out which one until after the end of the test. When these subjects were given a choice in which the smaller/sooner option would be delivered the same day, greater activity was observed in corticolimbic regions (ventral striatum and medial orbitofrontal cortex) compared with baseline or with choices not involving a “today” option. The limbic area is known to be active as rewards are anticipated or delivered (12–14) and in response to emotion-evoking events (15). In contrast, relative to baseline, all choices recruited observable activity within the lateral prefrontal cortex and within the parietal cortex in areas associated with future planning (16, 17). When subjects chose a larger/late alternative, there was also greater activity in the lateral prefrontal



Choosing between immediate and delayed rewards. (A) Exponential curves depicting the value of two alternative expected rewards given at discrete time points (the usual set up of behavioral experiments). Smaller/sooner rewards are depicted in pink, larger/late rewards in yellow. (B) Hyperbolic curves of the value of two alternative expected rewards showing a temporary preference for the smaller/sooner reward as it draws close. (C) β - δ curves of value: The immediacy factor adds a spike to the smaller/sooner curve in (A) to produce a temporary preference. (D) Hyperbolic curves of value, with the larger/late curve summed from an extended reward, which is likely to be the case in ordinary life.

and parietal areas than when they chose the alternative smaller/sooner reward.

The investigators interpret these findings as evidence for Laibson's β - δ dual discount function, with corticolimbic activity furnishing the β component and the lateral prefrontal activity the δ component. They propose that humans share with nonhumans a lower automatic process governed by the limbic system that motivates impatient emotional choices. This process competes with a uniquely human capacity for general reasoning and future planning that is governed by the lateral prefrontal cortex. The authors argue that sudden elicitation of limbic activity by near-term opportunities or other factors creates the spike in the discount curve that makes it seem hyperboloid and is responsible for temporary reversals of preference. They further suggest that limbic-based cue-conditioned appetites—which Loewenstein has described as “visceral factors” (18)—can impose reward contingencies similar to those of reward immediacy. A conditioned stimulus that elicits limbic activation, such as the sight of a tempting dessert or an addict's drug paraphernalia, would presumably remove the β penalty factor at that moment. However, the McClure model does not make it clear whether reward would be discounted for any remaining delay by the rational δ factor or how nonhumans (which are said to lack the δ factor) would discount delayed rewards, much less protect them by observed commitments when these commitments are offered (2, 3).

The differential activation of limbic structures could cause a spike in an otherwise exponential discount curve, but it is the hyperbolic pattern that has been observed in extensive research (5). Something about suggesting the possibility of having the

Amazon.com certificate “today” was clearly evocative to the students, but it is not possible to say whether the differential effect of “today” was caused by a surge in anticipated enjoyment of the Amazon books or by the suggestion of winning a more or less immediate prize *per se*. Nor would it be possible without a series of shorter time delays, ideal of visceral rewards (not money or certificates for later exchange as in the McClure *et al.* study), to tell whether the “ β ” (limbic) activity is best described as an either/or phenomenon (immediate-yes versus delayed-no) as the authors suggest, or as part of a smooth discount curve that cannot be detected by current fMRI methods for delays of 2 weeks. Although the increased activity of “ δ brain areas” (the lateral prefrontal cortex and associated structures) in response to larger/later selections is an important finding, to accord these areas status as a separate decision-making mechanism would add a complicating factor that would have to be reintegrated with motivation. As the behavioral neurobiologists Montague and Berns point out, all organisms need “an internal currency that can be used as a common scale to value di-

verse behavioral acts and sensory stimuli” (19). It may be that the δ brain areas reported by McClure *et al.*, in effect, only broker limbic-based rewards. Such a limitation of δ areas was anticipated by the British empiricist David Hume who wrote: “[Reason alone] is incapable of preventing volition. . . . Reason is and ought only to be the slave of the passions” (20).

As for cue conditioning, it is at first glance a simpler explanation for sudden craving than is a change in the prospects of the success of a reward-governed appetite. The notion of the β factor certainly has intuitive appeal. But conditioning is now thought to associate stimuli only with other stimuli, not responses (21), and thus cannot be the means of transferring reflexive responses from one stimulus to another as was originally thought (22). Cue conditioning and the dual β - δ motivational model are largely compatible with the predictions of hyperbolic discounting theory, but they represent additional mechanisms that are probably not needed to fit the data, including the data that McClure *et al.* report. The study discussed here is the first step in an important direc-

tion, but is not yet enough to specify the mechanism of preference reversal.

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PHYSICS

The Environment Matters— Even on the Atomic Scale

Matthias Bode

A detailed understanding of magnetic excitations is essential for the future progress of magnetic data storage technologies. On page 466 of this issue, Heinrich *et al.* (1) use a scanning tunneling microscope (STM) to elucidate one such excitation, namely the spin-flip of individual magnetic atoms that are dispersed on a non-magnetic matrix and exposed to an external magnetic field. Such excitations can degrade the performance of high-density memories. Extensions of the new method may allow other magnetic excitations to be studied.

When highly diluted magnetic atoms in a nonmagnetic host matrix are exposed to an external magnetic field B , the electron potentials of spin-up and spin-down atoms become slightly different. The energy required to overcome the resulting energy gap in a spin-flip process amounts to twice the Zeeman energy $E_Z = g\mu_B B$. Because B is an adjustable experimental parameter and the Bohr magne-

ton μ_B is a fundamental constant, this relation can be used to measure the Landé g factor, which determines the spin and orbital contributions to the total magnetic moment.

Traditionally, the Zeeman energy is measured with electron spin resonance (ESR), which—due to sensitivity limitations—requires at least 10^7 electron spins. Therefore, a g value determined by ESR is averaged over a large number of supposedly identical magnetic atoms (2). However, the individual properties of the magnetic atoms may be rather different, because their local environment differs structurally, chemically, or both. Heinrich *et al.* (1) now use STM to determine the g values of individual Mn atoms on Al_2O_3 by measuring single-atom spin-flip processes.

How can spin flips and other inelastic processes be measured with an STM? The tunneling current between the tip and the sample is carried by elastic and inelastic “channels.” In an elastic tunneling process, the energy of the electron is conserved when it hops out of an occupied state of the negatively biased electrode into an empty state of the positive one. In contrast, an inelastic tun-

neling process requires energy to be transferred between the tunneling electron and the sample. Because this energy is quantized, inelastic channels cannot contribute to the total tunneling current if the bias potential is lower than the quantization energy. Above this threshold, there will be a sudden conductance jump between tip and sample. This effect is the basis of inelastic scanning tunneling spectroscopy (STS), which has provided profound insights into vibrational resonances of single molecules (3).

The method used by Heinrich *et al.* is an extension of inelastic STS. The authors exploit the fact that magnetic excitations, such as spin-flip excitations, are sensitive to an external magnetic field. The threshold energy for magnetic excitations increases with increasing field strength, but this effect is extremely small (typically <1 meV/tesla). To measure such tiny energy shifts with sufficient sensitivity, Heinrich *et al.* used a home-built STM, which operates at 0.6 K (reducing thermal broadening) and is mounted inside a superconducting magnet that supplies up to 7 tesla. They find that the g value of Mn atoms depends on their adsorption site: A Mn atom close to an Al_2O_3 step edge has a higher g value than a Mn atom far away from a step edge.

A detailed understanding of magnetic excitations is not only of academic interest, but is essential for future increases in the storage density of magnetic memories. The exponential increase in storage density achieved over the past 50 years (4) was mainly based

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