Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright



Available online at www.sciencedirect.com





Economic cognition in humans and animals: the search for core mechanisms

Laurie R Santos¹ and Kelly D Hughes²

Over the past few decades, research in judgment and decisionmaking has revealed that decision-makers, though not always rational, are often quite predictable. Here, we attempt to explore the nature of this systematicity with a different approach to decision-making. Specifically, we propose that some of the systematicity of human decision-making may result from the operation of core knowledge mechanisms, domain-specific learning mechanisms with characteristic processing limitations. In this review, we describe the core knowledge approach and argue that at least some aspects of human decision-making have the signature characteristics of a core knowledge system, namely, such strategies develop early in ontogeny and are shared with closely related primate relatives.

Address

¹Department of Psychology, Yale University, New Haven, CT 06510, USA

²Department of Anthropology, Yale University, New Haven, CT 06510, USA

Corresponding author: Santos, Laurie R (laurie.santos@yale.edu)

Current Opinion in Neurobiology 2009, 19:63-66

This review comes from a themed issue on Cognitive neuroscience Edited by Michael Platt and Elizabeth Spelke

0959-4388/\$ - see front matter © 2009 Elsevier Ltd. All rights reserved.

DOI 10.1016/j.conb.2009.05.005

You can't repeal the laws of economics. Even if they are inconvenient.

- Larry Summers

Although modern humans are unique in their worries about interest rates, 401k plans, and economic bailouts, we are not alone when it comes to our economic concerns. Like humans, all non-human animals struggle with economic problems that they must resolve in order to successfully survive and reproduce. The natural world contains many of the classic problems that pack economic textbooks: individuals evaluate risk and uncertainty when foraging, tackle supply and demand when searching for mates, assess the opportunity costs of reproductive tradeoffs, and so on. Indeed, almost any decision an animal makes can be modeled as an economic choice. Faced with the ubiquity of economic problems, it is hardly surprising that several academic fields have devoted considerable effort to understanding how humans and other animals navigate these complex choices. For example, classical economics has aspired to develop a normative model of economic decisionmaking that would formally capture all human choice with a simple set of axioms (see [1] for review). In a similar way, behavioral ecologists studying non-humans developed optimal models of behavior that describe how a perfectly adapted individual might maximize reproductive success [2,3]. Until recently, comparatively less theoretical work described how animals actually make decisions and the mechanisms that they use to do so. Thankfully, over the past few decades, the field of behavioral economics [4-6] (and more recently neuroeconomics, see [2]) has begun this descriptive enterprise. Surprisingly, this approach has revealed that organisms do not always make decisions in an ideal, rational way (see reviews in [4-6]). Instead, both human [4-6] and nonhuman [7] decision-makers behave in a number of ways that are systematically irrational, violating the predictions of optimal decision-making models.

Why do humans and animals appear to adopt strategies that systematically deviate from the optimal behaviors one might expect? Here, we attempt to address this disconnect by applying a new theoretical approach. Specifically, we propose that organisms make decisions that are systematically non-optimal because they result from the operation of a set of core knowledge mechanisms that are developmentally prior, evolutionarily ancient, and encapsulated in ways that lead to systematic errors $[8^{\circ},9]$. We first introduce the core knowledge approach and then discuss two recent empirical examples of human and non-human economic irrationalities that could be modeled as a result of such mechanisms.

The core-knowledge approach: a quick introduction

The core knowledge approach was originally advanced by Elizabeth Spelke and her colleagues [8 $^{\circ}$,9] as a theoretical approach to the question of how individuals develop the kinds of elaborated knowledge systems that are found cross-culturally in our species. Traditionally, theorists took one of two opposing views of the human mind: either human cognition results from the operation of domain-general learning mechanisms or it instead results from the operation of numerous highly specialized modules. Spelke and colleagues developed the core

knowledge thesis as an intermediate position. Basing their work on empirical evidence from human infants and closely related primate species, they proposed that human cognition results from a foundation of a small number of specialized mechanisms upon which general learning and cognition build [8[•],9,10].

Core knowledge mechanisms are typically thought to have a number of signature characters and properties (see [10]). First, such mechanisms are thought to be developmentally prior (i.e. they tend to emerge without much experience and are thus present in early infancy) and evolutionarily ancient (i.e. they are shared with extant closely related nonhuman primates). Second, core knowledge systems are domain-specific; they attend to and operate only within a particular problem domain. Additionally, these domains are thought to represent the most basic and important cognitive problems necessary for survival and reproductive success (e.g. spatial navigation [11]). Third, core systems are relatively informationally-encapsulated. Rather than taking input from all available perceptual systems, they often focus on a subset of available information. For example, in the spatial domain, researchers have observed that both humans and animals seem to use only a single cue—geometric layout—when reorienting ([11-15], but see [16]). Our core spatial reasoning system is therefore encapsulated to the extent that it ignores other relevant perceptually available properties of the surface layout (e.g. color, odor). This encapsulation leads to the final, crucial signature of core systems-they tend to exhibit systematic processing limitations [8[•]]. In the case of spatial navigation, participants exhibit systematic reorientation limitations because they fail to incorporate relevant landmark and surface information.

The core knowledge approach has lead to considerable empirical headway in understanding the development of a number of domains [8[•],9–16], but to date, theorists have not applied the core knowledge approach to understanding the mechanisms underlying economic decision-making. One reason for this might be that economists and other researchers have thought of adult human economic decision-making as domain-general strategies applied to any task, context, or type of decision. Unfortunately, the domain-general approach fails to capture some features of human and animal decision-making. First, many human (and non-human) decision-making strategies seem to be context specific [4-6]; both populations appear to switch strategies and preferences depending on context or framing. Second, both populations exhibit systematic errors and processing limitations that are consistent with a core knowledge view (e.g. [4-7]). For these reasons, we explore the hypothesis that some economic decisionmaking strategies might stem from core cognitive mechanisms. We now turn to two kinds of deviations from optimal decisions that, we believe, have several of the signatures of core domains.

Relative, not absolute, value

To successfully navigate economic decisions, individuals need to wisely make choices. Economists advise computing the absolute expected value of each decision and selecting the one with the highest payoff [1], but people rarely do this. Instead people often determine the value of different outcomes not on an absolute scale but relative to the current status quo, a feature of decision-making known as reference-dependence [5,6,17-20]. People see outcomes as 'less than' or 'more than' an expectation, and base their valuations on that assessment rather than absolutes. Furthermore, people are also loss averse, meaning that the direction of deviation from an expectation also affects value. People tend to dislike a loss more than they like an equally sized gain [18]. Together, these tendencies lead to systematic errors in decisions that can be observed both in the lab [5-6,17-19] and in the real world [4-6,21-24]. People think of an object as more valuable when they consider losing or selling it than when they consider gaining or buying it [25,26] and switch to riskier behavior when confronting gambles involving losses rather than gains [18]. In one famous real world example, taxicab drivers continue working till they reach a target earning amount each day, which serves as a reference point. On days where drivers earn less than their target, they often continue working longer to make up the difference. Unfortunately, this leads drivers to work more on non-profitable days and less on profitable days, the very opposite of what one should do to maximize profit [24]. In this way, reference dependence and loss aversion can lead to systematic processing errors-deviations from optimality that fall out of the operation of these strategies-much like those observed through the operation of other core reasoning systems.

The possibility that reference-dependence and loss aversion are a part of a core knowledge system is bolstered by the fact that some characteristics of these relative strategies can be observed in young children and non-human animals [7,27–33]. For example, five-year-old children exhibit behaviors characteristic of loss aversion, such as a reluctance to trade or lose a possessed object in order to gain a novel item of absolute equal worth [31]. Researchers have observed a similar reluctance to lose owned objects in primates; both chimpanzees [32-33] and capuchin monkeys [29] appear to think of an object as more valuable when they consider losing or selling it than when they consider gaining or buying it. In addition, recent work from our own laboratory suggests that capuchins appear to share human-like relative-reasoning strategies on economic gambles much like those presented to human subjects [27,28]. Capuchins learned to trade metal tokens for pieces of food in a 'market' involving two potential human traders. Monkeys then chose between a trader who offered one piece of apple but half the time gave two pieces, and an experimenter who offered two pieces of apple but half the time gave only one piece [27]. The payoff from either trader was, on average, the same, but capuchins preferred the trader, who in offering one piece of food, appeared to give a gain half the time. This suggests that capuchins tag the initial offer as a reference point and use the reference point to assign value. Similarly, capuchins become riskier when confronting gambles involving losses rather than gains ([28], for a similar finding in starlings see [30]). Taken together, these studies suggest that relative reasoning strategies like reference dependence and loss aversion possess several features of core mechanisms: they appear to emerge early in development, are shared across species, and lead to systematic processing errors in certain contexts.

Nice, not selfish, preferences

A second prescription of ideal optimized economic behavior is to act out of complete self-interest. For better or worse, people often fail to do this. Humans can be generous with non-kin and even strangers [34] and such generosity may be expressed in fairly complex ways, such as gains relinquished in order to promote an equal distribution of goods [34,35] or wealth donated to punish non-cooperators [34,36]. In fact, many human deviations from self-interested behavior occur in situations in which equity norms are violated. Consider, for example, the Dictator Game [37], in which a proposer gets to present a receiver with a one-time anonymous offer of a portion of a monetary sum. A self-interested agent would keep the entire pot, but people typically give equitable offers, often between 40-50% of the original sum [37]. Although there is currently some controversy concerning how such equity norms could be selected over evolutionary time (e.g. [34,38]), there is growing evidence that such behaviors are cross-culturally widespread [35,39] and emerge relatively early in human development [40,41,42**]. Such features of human equity norms suggest the possibility that these strategies may also result from a set of core mechanisms devoted to sociallyrelevant distribution decisions.

The hypothesis that human equity constraints emerge through core knowledge mechanisms is supported by growing work suggesting that similar equity norms may operate in at least some non-human primates. There is, for example, growing evidence that some non-human primate species detect inequitable situations and react negatively to them ([41,43,44,45-48], but see [46,49,50^{••}] for different results). Capuchins, for example, will reject an otherwise desired food reward if they have previously observed another monkey obtaining a better reward for the same amount of work [47] and spontaneously share their allotment of food with another monkey who helped them obtain it [48]. In addition, some [43,44[•],45] but not all [46,49,50^{••}], primates selectively act in ways that deliver prosocial payoffs to others. Although more work is needed to determine the exact contexts in which primates do and do not exhibit equity norms, the current results raise the possibility that at least

some human-like equity-norms may be shared broadly across the primate order, as one might expect based on the operation of core mechanisms.

Core mechanisms for decision-making?

The goal of this review was to consider the possibility that some aspects of economic decision-making arise through the operation of domain-specific core mechanisms, ones that emerge early in development and are shared broadly across the animal kingdom. To get at this possibility, we considered two cases in which human decision-making behaviors systematically deviate from what is often considered optimal from a classic economic approach. We have argued that such systematic deviations are akin to the processing errors that are hallmarks of encapsulated core knowledge mechanisms and thus suggest the possibility that core mechanisms may govern decision-making behavior in these two contexts. In support of this view, we have gathered evidence suggesting that young children and nonhuman primates exhibit similar decision-making biases to adult humans; these two populations exhibit signatures of reference dependence and loss aversion and exhibit fairness norms in some contexts. Taken together, this evidence provides preliminary support for the claim that some aspects of human decision-making emerge through the operation of core knowledge mechanisms. Though the work reviewed here is not as extensive as the research on core knowledge reasoning in other domains (e.g. [10-12]), we hope that this speculative review will open some new theoretical debates concerning the nature of the kinds of mechanisms that could give rise to human-like decisionmaking strategies and biases. Moreover, we hope that our short review of the existing work on decision-making strategies in comparative-developmental populations will generate even more empirical interest in the strategies and errors exhibited in these subject populations.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- •• of outstanding interest
- 1. Hastie R, Dawes RM: *Rational Choice in an Uncertain World*. Thousand Oaks, CA: Sage; 2001.
- 2. Glimcher PW: Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics Cambridge: MIT Press; 2003.
- Krebs JR, Davies NB: An Introduction to Behavioural Ecology. Blackwell Scientific Publications; 1993. p. 57.
- Camerer, Colin F: Bounded rationality in individual decision making. Experimental Economics 1998, 1(2):163-183.
- Kahneman D, Slovic P, Tversky A (Eds): Judgment Under Uncertainty: Heuristics and Biases. Cambridge, England: Cambridge University Press; 1982.
- Kahneman D, Tversky A: Choices, Values, and Frames. Cambridge: Cambridge University; 2000.
- Santos LR, Lakshminarayanan: Innate constraints on judgment and decision-making? Insights from children and non-human primates. In *The Innate Mind: Foundations and the Future*. Edited

66 Cognitive neuroscience

by Carruthers P, Laurence S, Stich S. Oxford: Oxford University Press; 2008:293-310.

8. Kinzler KD, Spelke ES: Core systems in human cognition.

• Progress in Brain Research 2007, **164**:257-264. This paper is a recent review that provides a nice introduction to the core knowledge approach.

- 9. Spelke ES: Core knowledge. American Psychologist 2000, 55:1233-1243.
- Hauser MD, Spelke ES: Evolutionary and developmental foundations of human knowledge: a case study of mathematics. In *The Cognitive Neurosciences*, vol. 3. Edited by Gazzaniga M. Cambridge: MIT Press; 2004.
- Spelke ES: Developing knowledge of space: core systems and new combinations. In Languages of the Brain. Edited by Kosslyn SM, Galaburda A. Cambridge, MA: Harvard Univ. Press; 2003.
- Dehaene S, Izard V, Pica P, Spelke ES: Core knowledge of geometry in an Amazonian indigene group. *Science* 2006, 311:381-384.
- Hermer-Vasquez L, Spelke ES, Katsnelson AS: Sources of flexibility in human cognition: dual-task studies of space and language. *Cognitive Psychology* 1999, 39:3-36.
- Wang RF, Spelke ES: Human spatial representation: insights from animals. Trends in Cognitive Sciences 2002, 6(9):376-382.
- Doeller C, King J, Burgess N: Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. In Proceedings of the National Academy of Sciences of the United States of America 2008, 105:5909-5914.
- Cheng K: Whither geometry? Troubles of the geometric module. Trends in Cognitive Sciences 2008, 12(9):355-361.
- Kahneman D, Tversky A: Prospect theory: an analysis of decision under risk. *Econometrica* 1979, 47:263-292.
- 18. Tversky A, Kahneman D: The framing of decisions and the psychology of choice. *Science* 1981, **211**:453-458.
- Tversky A, Kahneman D: Rational choice and the framing of decisions. *Journal of Business* 1986, 59:251-278.
- Tversky A, Kahneman D: Loss aversion in riskless choice: a reference-dependent model. Quarterly Journal of Economics 1991, 106:1039-1061.
- Odean T: Are investors reluctant to realize their losses? Journal of Finance 1998, 5:1775-1798.
- Genesove D, Mayer C: Loss aversion and seller behavior: evidence from the housing market. Quarterly Journal of Economics 2001, 116:1233-1260.
- Hardie BGS, Johnson EJ, Fader PS: Modeling loss aversion and reference dependence effects on brand choice. *Marketing Science* 1993, 12:378-394.
- Camerer C, Babcock L, Loewenstein G, Thaler R: Labor supply of New York City cabdrivers: one day at a time. The Quarterly Journal of Economics 1997, 112:407-441.
- Kahneman D, Knetsch JL, Thaler RH: Experimental tests of the endowment effect and the coase theorem. *Journal of Political Economy* 1990, 98:1325-1348.
- Thaler RH: Toward a positive theory of consumer choice. Journal of Economic Behavior and Organization 1980, 1:39-60.
- Chen MK, Lakshminarayanan V, Santos LR: The evolution of our preferences: evidence from capuchin monkey trading behavior. Journal of Political Economy 2006, 114(3):517-537.
- Lakshminaryanan V, Santos LR, Chen MK: The evolution of risky choices: framing effects in non-human economic behavior. *PLOS One*, in preparation.
- Lakshminaryanan V, Chen MK, Santos LR: Endowment effect in capuchin monkeys (Cebus apella). Philosophical Transactions of the Royal Society B: Biological Sciences 2008, 363:3837-3844.

- Marsh B, Kacelnik A: Framing effects and risky decisions in starlings. In Proceedings from the National Academy of Sciences of the United States of America 2002, 99:3353-3355.
- Harbaugh WT, Krause K, Vesterlund L: Are adults better behaved than children? Age, experience, and the endowment effect. *Economics Letters* 2001, 70:175-181.
- 32. Brosnan SF, Grady M, Lambeth SP, Schapiro SJ, Beran MJ: Chimpanzee Autarky. *PLoS ONE* 2008, **3(1)**:1518.
- Brosnan SF, Jones OD, Lambeth SP, Mareno MC, Richardson AS, Schapiro SJ: Endowment effects in chimpanzees. *Current Biology* 2007, 17(19):1704-1707.
- Fehr E, Fischbacher U: The nature of human altruism. Nature 2003, 425:785-791.
- Henrich J, Boyd R, Bowles S, Camerer C, Fehr E, Gintis H, McElreath R: In search of Homo Economicus: behavioral experiments in 15 small-scale societies. *The American Economic Review* 2001, 91:73-78.
- Fehr E, Gachter S: Altruistic punishment in humans. Nature 2002, 415:137-140.
- Camerer C: Behavioral Game Theory—Experiments in Strategic Interaction. Princeton, NJ: Princeton Univ. Press; 2003.
- Nowak MA: Five rules for the evolution of cooperation. Science 2006, 314:1560-1563.
- Henrich J, Boyd R, Bowles S, Camerer C, Fehr E, Gintis H: Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies Oxford: Oxford University Press; 2004.
- Zahn-Waxler C, Radke-Yarrow M, Wagner E, Chapman M: Development of concern for others. *Developmental Psychology* 1992, 28:126-136.
- Warneken F, Tomasello M: Altruistic helping in human infants and young chimpanzees. Science 2006, 311:1301-1302.
- 42. Olson K, Spelke E: Foundations of cooperation in young
- children. Cognition 2008, **108**:222-231.

This paper provides an important demonstration of reciprocity in three year old children, suggesting that the roots of human cooperation emerge relatively early in human development.

- Lakshminarayananan V, Santos L: Capuchin monkeys are sensitive to others' welfare. Current Biology 2008, 18:999-1000.
- 44. Burkart J, Fehr E, Efferson C, van Schaik C: Other-regarding
 preferences in a non-human primate: common marmosets

provision food altruistically. PNAS 2007, **104**:19762-19766. This paper represents the first successful demonstration of other-regarding preferences in a nonhuman primate. Unlike chimpanzees [49], marmoset monkeys prosocially provide food to other individuals.

- de Waal FBM, Leimgruber K, Greenberg AR: Giving is selfrewarding for monkeys. PNAS 2008, 105:13685-13689.
- Cronin KA, Schroeder K, Rothwell E, Silk J, Snowdon CT: Cooperatively breeding tamarins (Saguinus oedipus) do not donate rewards to their long-term mates. Journal of Comparative Psychology, in press.
- 47. Brosnan SF, de Waal FBM: Monkeys reject unequal pay. Nature 2003, 425:297-299.
- de Waal FBM, Berger ML: Payment for labour in monkeys. Nature 2000, 404:563-1563.
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaro J, Schapiro SJ: Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 2005, 437:357-1359.
- 50. Jensen K, Call J, Tomasello M: Chimpanzees are rational
 maximizers in an ultimatum game. Science 2007, 318:107-109.
 This elegant study adapted the Ultimatum Game for chimpanzees. In contrast to humans, chimpanzees accepted any offer from a conspecific and do not punish individuals that give unfair offers.