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Neuroeconomics

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Annu. Rev. Psychol. 2008. 59:647–72

First published online as a Review in Advance on September 17, 2007

The *Annual Review of Psychology* is online at <http://psych.annualreviews.org>

This article's doi:
10.1146/annurev.psych.59.103006.093710

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0066-4308/08/0203-0647\$20.00

Key Words

decision making, emotions, dual-process theories, neuroscience, behavioral economics

Abstract

Neuroeconomics has further bridged the once disparate fields of economics and psychology. Such convergence is almost exclusively attributable to changes within economics. Neuroeconomics has inspired more change within economics than within psychology because the most important findings in neuroeconomics have posed more of a challenge to the standard economic perspective. Neuroeconomics has primarily challenged the standard economic assumption that decision making is a unitary process—a simple matter of integrated and coherent utility maximization—suggesting instead that it is driven by the interaction between automatic and controlled processes. This article reviews neuroeconomic research in three domains of interest to both economists and psychologists: decision making under risk and uncertainty, intertemporal choice, and social decision making. In addition to reviewing new economic models inspired by this research, we also discuss how neuroeconomics may influence future work in psychology.

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Man is equipped with the psychical and physical make-up of his first human ancestors; he is the sort of being who functions best in the exhilarations and the fatigues of the hunt, of primitive warfare, and in the precarious life of nomadism. He rose superbly to the crises of these existences. Strangely and suddenly he now finds himself transported into a different milieu, keeping, however, as he must, the equipment for the old life. Fortunately his power of reflecting (there seems to be an innate tendency to reflect and learn which is a distinguishing characteristic of our species) has enabled him to persist under the new conditions by modifying his responses to stimuli.

Rexford G. Tugwell,
Journal of Political Economy, 1922

INTRODUCTION

Rexford Tugwell's brilliant analysis of human behavior represents one of the last gasps of a sophisticated psychological account of economic behavior that was once integral to economics (cf. Ashraf et al. 2005), but was lost to the field for almost a century. This psychological perspective took account of the different cognitive and motivational processes driving

human behavior—the “equipment for the old life” and the human “power of reflecting”—and of the problems caused by using equipment adapted to the old life to solve problems in “a different milieu”—a human civilization that is dramatically different from that which prevailed when the equipment for the old life evolved.

Even by the time the passage reproduced above was published, the field of economics had rejected the theoretical perspective that can be gleaned from it in favor of a far simpler “rational choice” perspective that treated the power of reflecting, which Tugwell viewed as “the distinguishing characteristic of our species,” as the lone force driving human behavior.¹ Indeed, the *Journal of Political Economy*, where Tugwell's paper appeared, was to become the standard-bearer of this perspective. Coupled with a belief in the efficiency of markets, economists' embracing of the rational choice perspective gave them a worldview very different from that of psychologists. Whereas psychologists tend to view humans as fallible and sometimes even self-destructive, economists tend to view people as efficient maximizers of self-interest who make mistakes only when imperfectly informed about the consequences of their actions.

Despite the divergent worldviews of contemporary psychologists and economists, the two disciplines are essentially siblings separated at birth. Both have a fundamental interest in understanding human behavior. Psychology chose early on to focus on empirical questions, largely deferring attempts to formalize the resulting insights until there were sufficient data to constrain theory. By contrast, economics chose to build a foundation of formal theory, at the expense of adopting highly simplified and, ultimately, unrealistic

¹The rational choice perspective may therefore be a manifestation of the “isolation effect,” a general tendency to “disregard components that the alternatives share, and focus on the components that distinguish them” (Kahneman & Tversky 1979).

assumptions about the processes governing human behavior.² Thus, while psychology became a predominantly empirical discipline, economics became a predominantly theoretical one. This may be one reason why the first journal devoted exclusively to experimental research in psychology, known then as the *Journal of Experimental Psychology*, predates the first analogous journal in economics, *Experimental Economics*, by 82 years (1916 versus 1998).

This is unfortunate, as success in science relies on the interconnection of theory and data. However, there have been attempts to bridge the disciplines. Beginning with the publication of Richard Thaler's (1980) remarkable article, "Toward a Positive Theory of Consumer Choice," a number of economists drew on the nascent field of behavioral decision research for clues about the limitations of the rational choice perspective and insights into alternative assumptions that could better explain real-world human economic behavior. Behavioral decision research arrived, in a sense, custom-made for application to economics, because much of its focus was already on the limitations of the rational choice perspective. Behavioral economics, so named in part because it drew on behavioral decision research, has been a great success story due in part to the strength of the psychological research upon which it drew [for details of these developments, see Angner & Loewenstein (2007)].

Inevitably and fortunately, however, behavioral economics has now moved beyond an exclusive reliance on behavioral decision research; indeed, part of its dynamism has been its willingness to draw upon other lines of

research in psychology, including social psychology and cognitive psychology. And, given the increasing prominence of neuroscience within the field of psychology and the openness of behavioral economics to new methods and ideas, it was only a matter of time before behavioral economics would embrace neuroscience. When that happened, in the late 1990s, the new field of neuroeconomics was born.

Neuroeconomics, we argue, has further bridged the once disparate fields of economics and psychology. However, this convergence is almost exclusively attributable to changes within economics. Neuroeconomics has inspired more change within economics than within psychology because the most important findings in neuroeconomics have posed more of a challenge to the standard economic perspective than to dominant perspectives within psychology. For example, much of the research in neuroscience and more recently in neuroeconomics challenges the bedrock assumption within economics that decision making is a unitary process—a simple matter of integrated and coherent utility maximization. One of the most important insights of neuroscience is that the brain is not a homogeneous processor, but rather involves a melding of diverse specialized processes that are integrated in different ways when the brain faces different types of problems. More specifically, some economists have come to appreciate a distinction between automatic processes, which roughly correspond to what Tugwell called the "equipment for the old life," and controlled processes, which correspond to what Tugwell referred to as the "power of reflecting."

Indeed, neuroeconomics has already inspired a spate of economic models that attempt to formalize the idea that judgment and behavior are the result of the interaction between multiple, often conflicting, processes. For example, Bernheim & Rangel (2004) model the brain as operating in either a "cold" mode or a "hot" mode. Which mode is triggered depends (stochastically) on

Behavioral economics: a subdiscipline of economics that incorporates more psychologically realistic assumptions to increase the explanatory and predictive power of economic theory

²Kenneth Binmore (1988, p. 421), an economist, once described the contrast between psychology and economics more bluntly: "Psychologists accuse economists of having 'no respect for the data', and they are right to do so. It is a disgrace that so little experimental work has been done on the basic tenets on which economic theory is founded. . . . But if economists 'have no respect for the data', it is at least as true that psychologists 'have no respect for theory'."

situational factors, which are partly a function of previous behavior (e.g., whether or not one chooses to enter into a situation that is likely to trigger craving). Loewenstein & O'Donoghue (2004) similarly assume that behavior is the result of the interaction between "deliberative" and "affective" systems. However, rather than assuming that the determination of which system is in control is a stochastic process, they assume that the affective system is normally in control of behavior, and that the deliberative system can influence the affective system's preference by exerting costly cognitive effort or "willpower." Fudenberg & Levine (2006) model choice as the outcome of a struggle between a long-run player and a short-run player (cf. Thaler & Shefrin's 1981 planner-doer model). Benhabib & Bisin (2005) propose that controlled, executive processes "constrain" automatic processes; they monitor the decisions of automatic processes, intervening only when those decisions become excessively suboptimal. Brocas & Carrillo (2006) propose that controlled processes constrain emotional processes that display limited rationality because they are imperfectly informed.

These models represent a shift within economics toward a view that, according to one review of dual processes (Evans 2008), is widely accepted by both cognitive (Posner & Snyder 1975, Shiffrin & Schneider 1977) and social psychologists (Chaiken 1980, Petty & Cacioppo 1981). As the assumptions underlying economic models become increasingly consistent with psychological intuition and empirical reality, psychologists will likely find the techniques and insights offered by these models more readily importable, leading to disciplinary cross-fertilization in the opposite direction of what has mainly occurred until now.

The resulting fresh predictions need not be limited to domains typically studied by psychologists. Economics is centrally focused on tracing out the aggregate implications of individual behavior. Indeed, as Edward Glaeser (2003, p. 10), an economist, notes, "[T]he

great achievement of economics is understanding aggregation." Economic models informed by neuroeconomics may offer new insight to psychologists interested in large-scale phenomena.

Another possible avenue for importation of ideas from economics to psychology and neuroscience involves the coordination and orchestration of neural systems. Most neuroscientists tend to be, at least by economic standards, rather microscopic in their focus—typically focusing on a single information-processing task and a very limited range of neural regions. Economics, in contrast, has developed both analytical and simulation methods for modeling the coordination of diverse resources in pursuit of specific goals. The brain is, in fact, much like a modern economy. Like an economy, which consists of diverse specialized units, such as firms, the brain consists of diverse subsystems adapted for various functions (Cohen 2005). And, much as the economy changes when there is a new development such as a war (the famous problem of a transition from "butter" to "guns") or a new technology such as the Internet, the brain is constantly adapting itself to new types of tasks (e.g., using computers, playing video games, functioning in a new job). Neuroscience research has begun to identify some of the mechanisms that are involved in such learning of new tasks (see Hill & Schneider 2006 for a review), but has only recently begun to address how the brain solves the complex problem of allocating scarce processing resources to competing tasks (e.g., Botvinick et al. 2001, Braver & Cohen 2000, Cohen et al. 2007). Given its central focus on the allocation of scarce resources, economics may ultimately provide an analytic framework for addressing this issue.

As suggested above, neuroeconomics has great potential to contribute to psychology, both directly and through its influence on economics. However, these contributions mainly lie in the future. This review focuses on neuroeconomics research that has primarily influenced economics. Specifically, we focus

our review on three domains of behavior of interest to both economists and psychologists: decision making under risk and uncertainty, intertemporal choice, and social decision making.

DECISION MAKING UNDER RISK AND UNCERTAINTY

When choosing between alternative courses of action, people rarely know with certainty what consequences those actions will produce; most decisions are made under conditions of risk. The still dominant theory of how they do so is the expected utility (EU) model, which was first proposed by Daniel Bernoulli in 1738. According to EU, people choose between alternative courses of action by assessing the desirability or “utility” of each action’s possible outcomes, weighing those utilities by their probability of occurring, and selecting the course of action that yields the greatest sum—i.e., “expected utility.”

Although the model seems superficially plausible and can be derived from a set of seemingly sensible axioms (von Neumann & Morgenstern 1944), researchers have uncovered a wide range of expected utility anomalies—common patterns of behavior that are inconsistent with EU (see Starmer 2000 for a review). Initial attempts by behavioral economists to explain these anomalies adhered to the unitary decision-making perspective, but modified it in the direction of greater psychological realism. For example, EU assumes that the utility of a particular outcome is not simply based on that outcome, but rather on the integration of that outcome with all assets accumulated to that point. Consider, for example, a gamble that offers a 50% chance of winning \$20 and a 50% chance of losing \$10. If your current wealth totals \$1 million, then EU assumes that you view the gamble as offering a 50% chance of experiencing the utility of \$1,000,020 and a 50% chance of experiencing the utility of \$999,990. However, as originally noted by Markowitz (1952) and developed more fully

by Kahneman & Tversky (1979), people typically make decisions with a more local focus; they “bracket” their decisions more narrowly (Read et al. 1999). Most people would, for example, not view the gamble just discussed in terms of different final levels of wealth, but would instead process it as presented—as a 50% chance of winning \$20 and a 50% chance of losing \$10. Moreover, people tend to dislike losses more than they like gains, a phenomenon known as loss aversion (Tversky & Kahneman 1991). Combined with narrow bracketing, loss aversion can help to explain a wide range of phenomena, from the almost universal tendency to reject symmetric bets—e.g., a 50-50 chance to gain or lose \$100—to the preference for investing in bonds over stocks (Benartzi & Thaler 1995, Gneezy & Potters 1997), to the tendency to hold on to stocks and houses that fall in value (Genesove & Mayer 2001).

Other behavioral research has focused not only on the utility or “value” function, but also on probability weighting. Whereas EU assumes that people weigh outcomes according to their raw probability of occurring, behavioral modifications to EU have assumed instead that people overweight small probabilities and underweight large ones (Kahneman & Tversky 1979) or that they tend to place disproportionate attention on the worst and best outcomes that could occur (e.g., Quiggin 1982), either of which can help to make sense of why people often play the lottery *and* buy insurance. In combination, these modifications to EU’s standard assumptions can explain a wide range of risky decision-making phenomena while adhering to a unitary decision-making framework.

There is, however, a range of decision-making phenomena that do not appear to be well explained by any existing unitary models of risky decision making. For example, at an experiential level, people often seem to be of two minds when it comes to risks: they fear outcomes that they know are not objectively serious but experience little trepidation toward outcomes that they know to be

EU: expected utility

Immediate emotions: emotions experienced at the moment of choice. Standard economic theory assumes decision-makers are influenced by anticipated, rather than immediate, emotions

MPFC: medial prefrontal cortex

NAcc: nucleus accumbens

seriously threatening. The former is well illustrated by the behavior of phobics who are typically aware that the object of their fear is objectively nonthreatening, but are prevented by their emotional reactions from acting on this judgment (Barlow 1988, Epstein 1994). Such conflicts are not limited to phobics; many people greatly fear outcomes they cognitively recognize as highly unlikely (e.g., airplane crashes).

To account for regularities of this type, Loewenstein et al. (2001) proposed the “risk as feelings” (RAF) hypothesis, which postulated that people react to risks at two levels—by evaluating them in the dispassionate fashion posited by unitary models, but also at an emotional level; that is, different evaluative mechanisms using different cost functions may each respond differently to the same circumstances. For example, emotional responses to risks tend to be strongly related to newness; we overreact emotionally to new risks (often low-probability events) and underreact to those that are familiar (though they may be much more likely to occur). This can explain why, for instance, people seemed to initially overreact to the risk of terrorism in the years immediately following 9/11 but tend to underreact to the much more familiar risk of driving—eating, drinking, and talking on the cell phone while driving and failing to take full advantage of seatbelts and child seats.

Neuroeconomic research on decision making under risk and uncertainty has thus far focused on examining the extent to which EU anomalies can be attributed to emotions experienced at the moment of choice. Although many studies have found a relationship between immediate emotions and risky decision making, the evidence for multiple systems is mixed. Below, we review some of the major findings.

LITERATURE REVIEW

Risk Aversion and Loss Aversion

Several early studies in neuroeconomics focused on understanding why people are sen-

sitive to differences between outcomes and reference points, rather than to absolute end-states. Knutson et al. (2003), for example, found that activation in medial prefrontal cortex (MPFC; a target of dopaminergic projections) was lower after failing to receive an anticipated reward than after anticipating, and then receiving, no reward (cf. Abler et al. 2005). Similarly, several studies have found that activation in another dopaminergic target, nucleus accumbens (NAcc), was greater following the unanticipated delivery of juice and water than after the anticipated delivery of juice and water (Berns et al. 2001, McClure et al. 2003). This is consistent with earlier animal research, which has found that dopamine neurons within the ventral striatum of monkeys are sensitive to new information about anticipated rewards, which can be viewed as changes relative to the reference point of expectations (e.g., Montague et al. 1996). This research suggests that the tendency to encode gambles as gains and losses rather than as final levels of wealth may not simply be due to the greater simplicity of the former, but rather to a hardwired tendency for specific neural circuits to respond to deviations from expectations.

Other neuroeconomic research has examined whether the prospect of risky outcomes elicits anticipatory emotions. For instance, Kahn et al. (2002) conducted an experiment in which participants played a game that required occasional bluffing, which exposed them to the risk of being caught and suffering a loss. When a choice had been made but the outcome remained unknown, activation in amygdala was greater following bluffs than following honest play. The amygdala is closely associated with the processing of fear (LeDoux 1996), though it is often more generally associated with maintaining vigilance (e.g., Phelps et al. 2000). Knutson et al. (2001) found that self-reported happiness and NAcc activation increased as anticipated (probabilistic) gains increased (cf. Breiter et al. 2001). These studies support the RAF hypothesis that salient risky outcomes elicit emotional

reactions, but note that they did not focus on the key RAF prediction, namely whether emotion actually influenced decision making.

Damasio (1994) and Bechara et al. (1997) have proposed, consistent with RAF, that decision makers encode the consequences of alternative courses of action affectively and that such “somatic markers” serve as an important input to decision making. As a consequence, individuals with damage to regions that affectively encode information should be disadvantaged relative to individuals without such damage in situations in which emotions lead to better decision making. Damasio (1994) originally argued that the ventromedial prefrontal cortex (VMPFC) plays a critical role in this affective encoding process, and Bechara et al. (1997) therefore compared the behavior of individuals with and without VMPFC damage in a gambling task. On any given turn, players could draw cards from one of four decks, two of which included \$100 gains and two of which contained \$50 gains. The high-paying decks also included a small number of substantial losses, resulting in a net negative expected value for these decks. Bechara et al. (1997) found that both nonpatients and those with VMPFC damage avoided the high-paying decks immediately after incurring substantial losses. However, individuals with VMPFC damage resumed sampling from the high-paying decks more quickly than nonpatients did after encountering a substantial loss. Bechara et al. (1997) argued that nonpatients’ ability to generate somatic markers allowed them to play advantageously before consciously understanding the advantageous strategy.

The Bechara et al. (1997) study stimulated much interest and subsequent research (901 citations according to Google Scholar when this review went to press), but it has not been immune to criticism (see Dunn et al. 2005 for a review). Maia & McClelland (2004), for example, propose that the questionnaires Bechara et al. (1997) used were insufficiently powerful to uncover all the knowledge consciously

held by participants. Maia & McClelland (2004) created a more sensitive measure and found that verbal reports (among nonpatients only) indicated knowledge of the advantageous strategy more reliably than did actual behavior and that participants were rarely able to play advantageously without being able to report the advantageous strategy.

Although subsequent critiques have further challenged the findings of Bechara et al. (1997), the somatic marker hypothesis has remained intuitively appealing and has received renewed support. Recently, Bechara and colleagues (Shiv et al. 2005) compared the behavior of individuals with and without damage to the amygdala, the orbitofrontal cortex, the right insular cortex, or the somatosensory cortex (regions critical for the processing of emotions; e.g., Davidson et al. 2000, Dolan 2002) in a new gambling task. Participants were given a chance to bet on a series of coin flips that would each result in winning \$2.50 or losing \$1. Because each gamble has a positive expected value, participants who are fearful of risk are at a disadvantage. Consistent with the hypothesis that the regions of interest in this study are critical for the processing of emotions, participants with damage to those regions earned more money than did participants without such damage. The results are consistent with the somatic marker hypothesis, but they also suggest that the extent to which emotional deficits lead to poor decision making depends critically on the specific decision context.

Negative affect has also been proposed as an explanation for loss aversion in other contexts. One phenomenon that is typically attributed to loss aversion is the “endowment effect” (Thaler 1980), which refers to the tendency for people to value an object more highly if they possess it than they would value the same object if they did not. Kahneman et al. (1990), for example, demonstrated the effect by endowing one group of participants (sellers) with an object and giving them the option of selling it for various amounts of cash. They did not endow another group of

VMPFC:
ventromedial
prefrontal cortex

participants (choosers) and then gave them a series of choices between receiving the object and receiving various amounts of cash. Although sellers and choosers are in identical wealth positions, and face identical choices (leave with money or object), sellers hold out for significantly more money than choosers are willing to forgo to obtain the object.

Weber et al. (2007) attempted to examine the neural underpinnings of the endowment effect in an experiment in which participants had the opportunity to buy and sell digital copies of songs. Specifically, participants were endowed with 32 songs and asked to state how much money they would require to sell the songs. They were also asked to state how much money they would be willing to pay to buy another 32 songs. Weber et al. (2007) found that amygdala activation was greater in the selling condition than in the buying condition. Caution is required when interpreting the results of this study, however. Note that the endowment effect is not the difference between how much people demand to sell a good and how much they are willing to pay to acquire it. Both selling and buying involve one loss and one gain (selling involves losing the good and getting money; buying involves losing money and getting the good). A more natural comparison is between selling and choosing (getting the good or getting money), which holds the money side constant but varies whether one is obtaining or giving up the good. This limitation of the study makes it difficult to interpret the significance of the difference in amygdala activation across the selling and buying conditions, and in particular to identify it as the source of loss aversion.

Indeed, conflicting with the conclusion of Weber et al. (2007) that losses bring qualitatively different processes into play is a study by Tom et al. (2007) that more directly investigated the neural underpinnings of loss aversion. Participants in the experiment were given a series of options to accept or reject a series of gambles that offered a 50% chance of winning money and a 50% chance of los-

ing money. The authors found that no brain regions, including those associated with experiencing fear, showed significantly increasing activation as the size of the potential loss increased. Rather, activation in dorsal and ventral striatum and VMPFC, dopaminergic targets previously shown to be associated with the anticipation and receipt of monetary rewards (e.g., Knutson et al. 2001), showed increasing activation as gains increased and decreasing activation as losses increased (with the latter effect about twice the magnitude of the former). Their conclusion is that loss aversion appears to be driven by an asymmetric response to gains and losses within regions targeted by dopamine projections.

Loss aversion can explain the great dislike of playing “mixed” gambles, which offer a chance of gaining or losing money. However, in and of itself, loss aversion makes no prediction about whether and how risk-taking will change when it comes to gambles that involve all gains (e.g., \$10 versus a 10% chance of \$100) or all losses. In fact, there is good evidence that people generally tend to be risk-averse when it comes to gambles involving gains (as long as probabilities are in the mid-range) and to be risk-seeking for gambles involving all losses. In a canonical demonstration of this phenomenon, Tversky & Kahneman (1981) asked participants to imagine that the United States is preparing for the outbreak of an unusual Asian disease that is expected to kill 600 people. Participants are then asked to choose between two pairs of programs to combat the problem. In the gain condition, participants are told, “If program A is adopted, 200 people will be saved. If program B is adopted, there is a 1/3 probability that 600 people will be saved and a 2/3 probability that no one will be saved.” In the loss condition, participants are told, “If program C is adopted, 400 people will die. If program D is adopted, there is a 1/3 probability that nobody will die and a 2/3 probability that 600 people will die.” Most people presented with these decisions prefer A to B and D to C, which

is surprising because program A is identical to program C, and B to D.

Naturally, such a pattern of choices is anomalous from the rational choice perspective, which assumes that decisions are based on the likelihood and desirability of final outcomes. Kahneman & Tversky (1979) account for this “reflection effect” by proposing that the marginal value of both gains and losses generally decreases with their magnitude. Such diminishing sensitivity produces risk-aversion in the domain of gains (i.e., a preference for a certain gain of x over a gamble with an expected value of x), and risk-seeking in the domain of losses (i.e., a preference for a gamble with an expected value of $-x$ over a certain $-x$), which explains why people like a program that will save 200 lives with certainty but not an (equivalent) program that will lose 400 lives with certainty.

Recent neuroeconomic research suggests, however, that fear may also play a role in producing the reflection effect. De Martino et al. (2006) asked participants to choose between certain and risky gains and losses while having their brains scanned with fMRI. The authors found that amygdala activation was greater when participants chose certain gains over risky gains as well as when participants chose risky losses over certain losses. Moreover, De Martino et al. (2006) found that activity in anterior cingulate cortex (ACC) was greater when participants made choices that ran counter to the reflection effect (i.e., risky gains over certain gains, certain losses over risky losses). The ACC has been hypothesized to detect and signal the occurrence of conflicts in information processing (Botvinick et al. 2001, Carter et al. 1998). Accordingly, the results suggest that greater conflict must be resolved before expressing preferences inconsistent with the reflection effect than before expressing preferences consistent with the effect. Contrary to Tom et al. (2007), the results of De Martino et al. (2006) are consistent with the operation of qualitatively different systems within the brain (Kahneman & Frederick 2006).

Ambiguity Aversion

Thus far we have focused on situations in which probabilities are known and presented in numerical form to subjects. However, in the real world, people often make decisions without explicit knowledge of probabilities—under conditions of “ambiguity.” Some decision-researchers have argued that there is no meaningful difference between uncertain (probabilistic) and ambiguous events. Savage (1954), among others, argued that, even when people cannot articulate the probability of a particular event, they still behave as if the event has a specific “subjective probability.” However, Daniel Ellsberg (1961), in a famous paper, argued that people treat ambiguous probabilities differently from unambiguous ones. In one illustration of this point, Ellsberg presents the reader with two hypothetical urns, each containing red and/or black balls. Urn I contains 100 red and black balls, but in an unknown ratio. Urn II contains exactly 50 red and 50 black balls. Drawing a ball of a designated color from an urn wins \$100.

People tend to be indifferent between betting on red or black from Urn I, which in subjective probability terms can be taken to imply that they believe that each has a 50% chance of occurring. Similarly, people are indifferent to betting on red or black from Urn II, which has the equivalent interpretation. However, most people prefer betting on red from Urn II to betting on red from Urn I *and* betting on black from Urn II to betting on black from Urn I, which is impossible to make sense of if one believes that people are behaving as if they hold coherent probabilities for the different events.

Although ambiguity aversion has received much attention since Ellsberg’s seminal work in 1961, the explanation for the anomaly has itself remained ambiguous. Many explanations have been proposed (Curley et al. 1986), and they can be divided into three major classes. One type of explanation assumes that people react pessimistically to ambiguous

fMRI: functional magnetic resonance imaging

ACC: anterior cingulate cortex

OFC: orbitofrontal cortex

probabilities, as if they assume that when the odds are unknown they will be stacked against the decision maker. Ellsberg himself offered such an account. A second class of explanation assumes that people treat probabilities as if they were outcomes and, much as they tend to be risk-averse with respect to outcomes (e.g., they prefer a sure \$500 over a 50-50 chance to gain zero or \$1000), they are also risk-averse with respect to probabilities (e.g., they prefer a “sure” 50% chance of winning over a 50-50 chance of having either a 0% or 100% chance of winning). Finally, a third explanation assumes that ambiguity aversion involves the overapplication of a heuristic that often makes sense: Avoid betting when other people possess information that you lack, or when you lack information that would be helpful in making a decision.

Curley et al. (1986) tested several proposed explanations behaviorally. They found that participants who said the ambiguous urn could not be biased against them were still ambiguity-averse, suggesting ambiguity aversion is not driven by pessimism about a “hostile” generation of outcomes. The authors also found that ambiguity aversion was uncorrelated with risk aversion, casting doubt on the second class of explanations discussed above. Finally, Curley et al. (1986) found that participants were significantly more ambiguity-averse when they were told that the chosen gamble would be played and the urn’s contents revealed in front of other participants than when the gamble was resolved privately. The authors thus surmised that ambiguity aversion is due to social presentation concerns. However, their findings essentially reveal a situational moderator rather than an explanation for why people are generally ambiguity-averse. Subsequent studies have revealed other interesting moderators (e.g., Fox & Tversky 1995, Heath & Tversky 1991, Kühberger & Perner 2003), but a general explanation for ambiguity aversion has remained somewhat elusive.

Hsu et al. (2005) investigated the neural underpinnings of ambiguity aversion by ask-

ing participants to make choices between certain outcomes and risky gambles and between certain outcomes and ambiguous gambles. In a Card-Deck condition, gambles offer either clear probabilities (e.g., a 50% chance of winning \$10) or ambiguous probabilities (e.g., an unknown chance of winning \$10). In a Knowledge condition, gambles are based on either events participants have some knowledge about (e.g., win \$10 by correctly guessing whether the high temperature in New York City on November 7, 2003 was above 50°F) or events participants likely have far less knowledge about (e.g., win \$10 by correctly guessing whether the high temperature in Dushanbe, Tajikistan on November 7, 2003 was above 50°F). Finally, in an Informed Opponent condition, participants are presented with a deck that contains 20 red and blue cards, but in an unknown ratio. In the ambiguous condition, the opponent is allowed to sample three cards from the deck; in the risk condition, the opponent is not allowed to sample from the deck. Both participants then choose a color. Finally, a card is drawn from the deck, and participants win if they chose the realized color and their opponent chose the opposite color.

Across all conditions, Hsu et al. (2005) found that activation in amygdala as well as orbitofrontal cortex (OFC; a region thought to integrate cognitive and emotional inputs, e.g., Critchley et al. 2001) was significantly greater in the ambiguity condition than in the risk condition.³ The findings appear most consistent with the first and last accounts of ambiguity aversion discussed above. Interestingly, an analysis of the time course of activity within the amygdala and OFC revealed no strong differences between the Informed Opponent condition and the Card-Deck or Knowledge conditions, suggesting that ambiguity-induced negative affect was no greater when others had information the

³The same paper reported that a sample of people with OFC lesions were both risk- and ambiguity-neutral, whereas people without OFC lesions were both risk- and ambiguity-averse.

participant lacked. Though the results do not explicitly favor any one particular explanation for ambiguity aversion, what is clear is that people appear to have an immediate negative emotional reaction to ambiguity.

SUMMARY

The neuroeconomic research on decision making under risk and uncertainty has yielded some provocative findings, but remains largely unintegrated. Consistent with the somatic marker hypothesis, Shiv et al. (2005) find evidence suggesting that mild emotions play an advisory role in the decision-making process. Weber et al. (2007) claim that amygdala activation underlies the endowment effect, but unfortunately, their experimental design (comparing selling prices to buying prices) does not permit such an inference. And while De Martino et al.'s (2006) work on the reflection effect is readily interpreted as evidence for multiple systems (Kahneman & Frederick 2006), Tom et al. (2007) explicitly interpret their results regarding loss aversion as evidence against dual-systems accounts. Finally, the results of Hsu et al. (2005) suggest that negative affect plays a role in ambiguity aversion. Thus, while some of the reviewed research has provided fairly compelling support for the proposed role of emotion in risky decision making, the extent to which such results generally support a dual-system account of behavior is still unclear. Stronger evidence for the multiple systems perspective comes from neuroeconomic research on intertemporal choice. We turn to that work below.

INTERTEMPORAL CHOICE

Another central topic in economics is intertemporal choice—decisions involving alternatives whose costs and benefits are distributed over time. The discounted utility (DU) model is the dominant model of intertemporal choice in economics (Samuelson 1937). Although the DU model, like the EU

model, can be derived from a set of primitive, intuitively compelling axioms (Koopmans 1960), several anomalies have been identified that call the model's descriptive validity into question (see Frederick et al. 2002 for a review).

One of the most important, and frequently criticized, assumptions of DU is the assumption of exponential discounting, which implies that a given time delay leads to the same amount of discounting regardless of when it occurs. Delaying the delivery of a good by one day, for example, presumably leads to the same degree of time discounting whether that delay makes the difference between consuming the good tomorrow rather than today or in a year and a day rather than in a year. However, there is strong evidence that people (as well as animals) do not discount the future exponentially (Kirby & Herrnstein 1995, Rachlin & Raineri 1992). Rather, people care more about the same time delay if it is proximal rather than distal, a general pattern that has been referred to as "hyperbolic time discounting" (Ainslie 1975). For instance, delaying consumption of a pleasurable good from today to tomorrow is more distressing than delaying consumption from a year from now to a year and a day from now.

Several hypotheses have been advanced to explain why people discount the future hyperbolically. The most common has been to simply assume that hyperbolic time discounting is, in effect, hardwired into our evolutionary apparatus. Advocates of this approach often draw attention to the observation that all animals in whom discounting has been measured also discount the future hyperbolically. However, despite the superficial similarity, there is an enormous discontinuity between humans and other animals. Even after long periods of training, our nearest evolutionary relatives have measured discount functions that fall in value nearly to zero after a delay of about one minute. For example, Stevens et al. (2005) report that cotton-top tamarin monkeys are unable to wait more than eight seconds to triple the value of an immediately available

DU: discounted utility

food reward. Although it is possible that the same mechanism could produce functions that differ so dramatically in magnitude of discounting, it seems unlikely. Moreover, much as people often feel of two minds when it comes to decision making under risk, such intrapersonal conflicts are even more prevalent and dramatic when it comes to intertemporal choice (e.g., the choice between a piece of chocolate cake on the dessert cart and adhering to one's diet).

Neuroeconomic research on intertemporal choice has largely focused on whether behavior can be better explained by the interaction of multiple systems. The central debate in this domain of research has focused on the role of the limbic system in intertemporal choice. The limbic system, which commonly refers to the medial and orbital regions of frontal cortex (along the inner surfaces and base of the frontal lobes, respectively), the amygdala (along the inner surface of the temporal lobes), the insular cortex (at the junction of the frontal and temporal lobes), and their subcortical counterparts, is thought to be critical to emotional processing (Dalglish 2004). Some evidence suggests that these structures preferentially respond to immediately available rewards (McClure et al. 2004b, 2007), but recent research argues that these structures respond to rewards at all delays (Glimcher et al. 2007). Below we examine the competing claims as well as related neuroeconomic research on intertemporal choice.

LITERATURE REVIEW

Instead of assuming that hyperbolic discounting is hardwired into our evolutionary apparatus, some researchers have proposed that hyperbolic discounting reflects the operation of two fundamentally different systems, one that heavily values the present and cares little about the future, and the other deliberative, which discounts outcomes more consistently across time (e.g., Loewenstein 1996, Shefrin & Thaler 1988).

McClure et al. (2004b) tested the hypothesis by measuring the brain activity of participants while they made a series of intertemporal choices between small proximal rewards ($\$R$ available at delay d) and larger delayed rewards ($\$R'$ available at delay d'), where $\$R < \R' and $d < d'$. Rewards ranged from \$5 to \$40 Amazon.com gift certificates, and the delay ranged from the day of the experiment to six weeks later. The purpose of the study was to examine whether there were brain regions that show elevated activation (relative to a resting-state benchmark) only when immediacy is an option (i.e., activation when $d = 0$, but no activation when $d > 0$) and whether there were regions that show elevated activation when making any intertemporal decision. McClure et al. (2004b) found that time discounting results from the combined influence of two neural systems. Limbic and paralimbic cortical structures, which are known to be rich in dopaminergic innervation, are preferentially recruited for choices involving immediately available rewards. In contrast, fronto-parietal regions, which support higher cognitive functions, are recruited for all intertemporal choices (as contrasted with rest periods). Moreover, the authors find that when choices involved an opportunity for immediate reward, thus engaging both systems, greater activity in fronto-parietal regions than in limbic regions is associated with choosing larger delayed rewards, whereas greater activity in limbic regions than in fronto-parietal regions is associated with choosing smaller immediate rewards. Other research arriving at the same conclusion with different methods found that people with greater activation in these limbic reward regions in response to gaining or losing money also place greater weight on immediate rewards relative to delayed rewards (Hariri et al. 2006).

Note, however, that since the rewards were gift certificates, the consumption they afforded was not immediate in any conventional sense. To address this limitation,

McClure et al. (2007) ran an experiment in which the brains of thirsty participants were scanned with fMRI while they made a series of choices between receiving a small amount of juice or water immediately (by having it squirted into their mouth) and receiving a larger amount of juice or water up to 20 minutes later. Like McClure et al. (2004b), McClure et al. (2007) found that limbic regions were preferentially recruited for choices involving immediately available juice or water, whereas fronto-parietal regions were recruited for all choices.

The extent to which such findings actually support a two-system account of intertemporal choice is not uncontroversial, however (see, e.g., Ainslie & Monterosso's 2004 commentary on McClure et al. 2004b). Glimcher et al. (2007; Experiment 2) recently conducted a study in which participants made two types of choices. In the Immediate-Option condition, participants chose between small proximal rewards and larger delayed rewards. In the Delayed-Option condition, participants chose between small rewards available at a delay of 60 days and larger rewards available at a delay of more than 60 days. Glimcher et al. (2007) found that limbic and paralimbic structures such as MPFC, ventral striatum, and posterior cingulate were not preferentially recruited for choices involving immediately available rewards. However, this may be due to a counterintuitive finding in the Delayed-Option condition. Inconsistent with previous behavioral research on intertemporal "preference reversals" (Green et al. 1994, Kirby & Herrnstein 1995, Millar & Navarick 1984, Solnick et al. 1980), Glimcher et al. (2007) found that participants adopted an "as soon as possible" strategy in the Delayed-Option condition. Specifically, participants tended to prefer the small reward in both the Immediate-Option and Delayed-Option conditions. Evidence against multiple systems would be more compelling if it were obtained in an experiment that

replicated the behavioral regularity under investigation.

While the above studies examined how people choose between well-defined immediate and delayed rewards, note that consumers rarely face such explicit choices. Although the standard economic perspective assumes that the price of a good represents how much future pleasure must be forgone to finance immediate consumption, it is not at all clear that people spontaneously consider such "opportunity costs" in their purchasing decisions. Consider, for instance, a study by Frederick et al. (2006) in which participants were asked if they would (hypothetically) be willing to purchase a desirable video for \$14.99. The researchers simply varied whether the decision not to buy it was framed as "not buy this entertaining video" or "keep the \$14.99 for other purchases." Although the two phrases represent equivalent actions, the latter highlights the pleasure that is forgone by purchasing the video. Frederick et al. (2006) found that drawing attention to opportunity costs significantly reduced the proportion of participants willing to purchase the video, suggesting that some participants are not spontaneously considering opportunity costs.

If prices do not always deter spending through a deliberative consideration of opportunity costs, then what role do prices play in spending decisions? Knutson et al. (2007) investigated this question in an experiment in which participants chose whether or not to purchase a series of discounted consumer goods while having their brains scanned with fMRI. Participants were given \$20 to spend and were told that one of their decisions would ultimately be randomly selected to count for real. At the conclusion of the experiment, participants indicated how much they liked each product and how much they would be willing to pay for it.

Knutson et al. (2007) found that the extent to which participants reported liking the products correlated positively with NAcc

activation, which itself positively correlated with actual purchasing decisions. However, Knutson et al. (2007) also found that activation in insula during the period when subjects first saw the price correlated negatively with purchasing decisions. Insula activation has previously been observed in connection with aversive stimuli such as disgusting odors (Wicker et al. 2003), unfairness (Sanfey et al. 2003), and social exclusion (Eisenberger et al. 2003). Thus, when delayed rewards are not explicitly represented (as in, e.g., McClure et al. 2004b), but rather implicitly captured by prices, participants appear to rely on an anticipatory "pain of paying" (Prelec & Loewenstein 1998) to deter their spending, rather than an exclusively deliberative consideration of pleasures forgone by consuming immediately.

Subsequent research by Rick et al. (2007) suggests that the pain of paying produces a divergence between desired and typical spending behavior. The authors developed a Spendthrift-Tightwad scale to measure individual differences in the pain of paying. Tightwads report experiencing the pain of paying intensely and also report that they typically spend less than they would ideally like to spend. Spendthrifts report experiencing minimal pain of paying and also report that they typically spend more than they would ideally like to spend. In both cases, emotional reactions to the prospect of spending appear to prevent the implementation of more deliberative goals.

Other evidence suggestive of dual systems in the domain of consumer choice comes from a study of soft drink preferences. McClure et al. (2004a) first asked participants whether they preferred Coke or Pepsi. Participants were then asked to drink unlabeled cups of Coke and Pepsi and indicate which they preferred. Finally, participants had their brains scanned with fMRI while receiving squirts of Coke and Pepsi, and they were again not told which soda they were receiving. The correlation between stated and behavioral (i.e., taste-test) preferences failed to reach signif-

icance. Unlabeled cups of Coke were about as well liked by self-proclaimed Coke-lovers as they were by self-proclaimed Pepsi-lovers. However, while participants were drinking Coke and Pepsi, the difference in activation in VMPFC (a region often associated with the experience of reward; Bechara et al. 1994, Knutson et al. 2001, McClure et al. 2007, O'Doherty et al. 2003) strongly correlated with behavioral preferences. Why did experienced pleasure correlate with behavioral preferences, but not stated preferences?⁴ To begin to answer this question, McClure et al. (2004a) ran another study in which participants were either told that they were about to receive Coke or that they were about to receive either Coke or Pepsi; after both signals, participants received Coke. Activation in several regions (e.g., hippocampus, dorsolateral prefrontal cortex) was significantly greater when participants knew they were about to receive Coke than when they did not know what was coming. However, activation in VMPFC, and other regions commonly implicated in the experience of pleasure, did not vary across conditions.⁵ The authors concluded that structures associated with the experience of pleasure and structures that retain cultural information (e.g., about brands) may function separately to influence stated preferences.

SUMMARY

The extent to which intertemporal choice is generated by multiple systems with conflicting priorities is a hotly debated issue within neuroeconomics. McClure et al. (2004b, 2007) found that limbic and paralimbic cortical structures, which are known

⁴Note that in the real world, "stated preferences" would manifest themselves behaviorally, as supermarkets typically do not allow customers to choose between Coke and Pepsi by taking blind taste-tests.

⁵Analogous results were not found in another study in which participants were told that they were about to receive Pepsi or that they were about to receive either Coke or Pepsi. Activation in no brain regions varied significantly across conditions.

to be rich in dopaminergic innervation, are preferentially recruited for choices involving immediately available rewards, whereas fronto-parietal regions, which support higher cognitive functions, are recruited for all intertemporal choices. Knutson et al. (2007) found evidence consistent with the hypothesis that pain, rather than attention to opportunity costs, acts to deter the desire to consume immediately. Subsequent behavioral research by Rick et al. (2007) suggests that the pain of paying can produce a divergence between desired and typical spending behavior. McClure et al. (2004a) suggested that separable systems are involved in generating brand preferences. Glimcher and colleagues (2007), however, have argued against a dual-system interpretation of intertemporal choice. However, as noted above, their study failed to observe many intertemporal “preference reversals,” a regularity commonly found in purely behavioral studies and other neuroimaging experiments. Although the majority of the evidence therefore supports a multiple systems account of intertemporal choice, the debate will undoubtedly continue.

SOCIAL DECISION MAKING

Although there are widely accepted normative benchmarks for risky decision making and intertemporal choice, no such benchmarks exist for how people should behave toward others. Some hard-line economists have assumed that pure self-interest is, or should be, the norm, but this is almost surely a minority position. To adhere to the belief that people are purely selfish would not only require that one ignores wide-ranging experimental results showing the contrary, but would also clash with commonplace observations of behavior. The experimental research on “other-regarding” behavior not only demonstrates that people care about the welfare of others, but also challenges the validity of some of the more primitive models of social preferences—e.g., those that assume that social preferences can be captured by a function that puts a fixed

weight on the welfare of other persons. Although in some cases (e.g., parents toward children) there may be an element of altruism that could potentially be modeled in this fashion, more generally people tend to care about their own payoff and either the difference between their own payoff and others’ payoffs or the difference between their own payoff and what they view as a fair payoff (Andreoni & Miller 2002, Bolton 1991, Bolton & Ockenfels 2000, Charness & Rabin 2002, Fehr & Schmidt 1999, Loewenstein et al. 1989, Rabin 1993).⁶

Although models of this type take major strides in the direction of providing a more realistic account of other-regarding preferences, once again they leave out important dimensions of the phenomenon. Specifically, as is true for risky decision making and intertemporal choice, people often react to other people at both an emotional and a more intellectual/deliberative level. In some cases, such as crying in a movie, we can be deeply moved by people who do not warrant sympathy—even fictional movie characters who do not actually exist. Other cases, such as mass calamities, if they occur in distant parts of the world to people with whom we are not familiar, can barely touch our heartstrings, even if we realize at an intellectual level that those victims are highly deserving of our sympathy and aid. To capture these phenomena, as well as a variety of experimental findings, Loewenstein & Small (2007) have proposed a dual-process model of helping behavior in which a sympathetic but highly immature emotional system interacts with a more mature but uncaring deliberative system.

The neuroeconomics literature is, in this case, highly supportive of such a perspective overall, although, as discussed below,

⁶Distaste for inequality is not an exclusively human property. Brosnan & de Waal (2003) find that capuchin monkeys will forgo consuming cucumbers when similar monkeys are given grapes, a more desirable reward. Rather than exchanging their tokens for the inferior reward, the deprived monkeys sometimes threw their token out of the test chamber or at the experimenter.

Welfare:

well-being; neuroeconomists and standard economists debate whether welfare is synonymous with objective happiness or (behaviorally) revealed preferences

some of the major findings seem somewhat contradictory. For example, some research has suggested that self-interest sometimes relies on deliberate (and possibly even deliberative) suppression of a more emotional desire for fairness (Sanfey et al. 2003), whereas other work has suggested that self-interest is the more evolutionarily primitive desire that is sometimes suppressed by fairness concerns (Knoch et al. 2006). Below we examine the relevant evidence as well as other neuroeconomic research on social preferences.

LITERATURE REVIEW

Some recent research has suggested that conflicts between affect and deliberation are particularly likely when people face certain moral dilemmas. Consider, for example, one of the classic “trolley” dilemmas (Thomson 1986), in which a runaway trolley is headed for five people who will be killed if it continues its present course. The only way to save them is to hit a switch that will turn the trolley onto an alternate set of tracks where it will kill one person instead of five. Most people say it is morally acceptable to hit the switch (Greene et al. 2001). In an objectively equivalent “footbridge” dilemma (Thomson 1986), a trolley again threatens to kill five people. This time there is a large stranger on a footbridge spanning the tracks, between the oncoming trolley and the would-be victims. The only way to save them is to push the stranger off the bridge and onto the tracks below, which would kill him but save the others. Most people say it is morally unacceptable to push the stranger (Greene et al. 2001).

Why is it only sometimes morally acceptable to kill one to save five? To test this hypothesis, Greene et al. (2001) proposed that the thought of pushing someone to his death is more emotionally distressing than the thought of flipping a switch that would cause a trolley to inflict identical damage. To investigate whether “personal” moral dilemmas that require the direct infliction of harm to achieve

a greater utilitarian good elicit more intense emotional responses than “impersonal” moral dilemmas that require a less direct infliction of harm, they confronted participants with several versions of each dilemma while scanning their brains with fMRI. Participants also faced several nonmoral dilemmas that required a similar degree of mental effort, as judged by reaction times (e.g., deciding between traveling by bus or train given certain time constraints).

As predicted, brain regions consistently associated with emotional processing, such as medial frontal and posterior paracingulate cortex, were more active when participants considered personal moral dilemmas than when participants considered impersonal moral or nonmoral dilemmas. Supporting the notion that emotions play a causal role in personal moral dilemmas, Greene et al. (2001; see also Greene et al. 2004) found that participants took significantly longer to make utilitarian judgments that went against the emotional response in the personal moral dilemmas (e.g., judging that it is appropriate to push the stranger to his death) than to make emotionally congruent judgments, but that reaction times did not differ by judgment in the other two conditions. The results suggest that the personal moral dilemmas elicit a strong prepotent emotional response that must be cognitively overcome in order to respond in a manner inconsistent with the emotion.

Koenigs et al. (2007) also found that emotions play a causal role in personal moral judgments. Participants either had lesions to VMPFC, lesions to brain regions not directly associated with emotional processing, or no brain lesions, and were confronted with a series of moral and nonmoral dilemmas. Given that patients with VMPFC lesions typically show diminished emotional responsivity in general and severely reduced social emotions (e.g., shame) in particular (e.g., Anderson et al. 1999), these participants were predicted to find utilitarian judgments more palatable in the personal moral dilemmas as compared

with normal and lesion control participants. Indeed, Koenigs et al. (2007) found that the frequency of utilitarian judgments did not differ by participant type in the nonmoral and impersonal moral conditions, but that participants with VMPFC lesions were most likely to make utilitarian judgments in the personal moral condition.

In combination, the results of Greene et al. (2001, 2004) and Koenigs et al. (2007) lend strong support to a dual-process perspective. People seem to evaluate these types of moral dilemmas deliberatively (e.g., which choice will lead to fewer people dying) and affectively (which choice would feel worse). Since the deliberative element is intentionally kept constant across the dilemmas, whereas the affective element differs, people with emotion deficiencies (who evaluate all of the dilemmas deliberatively) make decisions that are more consistent.

Another context in which affect and deliberation appear to conflict is that of the “ultimatum game” (Guth et al. 1982). In the typical ultimatum game, a “proposer” offers some portion of an endowment to a “responder” who can either accept the offer or reject it. If the responder accepts the offer, the money is divided according to the proposed split. If the responder rejects the offer, both players leave with nothing. Since purely self-interested responders should accept any positive offer, self-interested proposers should offer no more than the smallest positive amount possible. However, average offers typically exceed 30% of the pie, and offers of less than 20% are frequently rejected (see Camerer 2003). These results are typically obtained in one-shot games, meaning responders’ unwillingness to accept small offers cannot be interpreted as an attempt to elicit larger offers in the future. Also, participants typically play the game anonymously, so the results cannot be attributed to immediate reputational or self-presentation concerns.

Several behavioral economic models have emerged to account for such findings.

Reciprocity-based theories of fairness (e.g., Dufwenberg & Kirchsteiger 2004, Rabin 1993), for example, propose that people enjoy reciprocating intentional kindness with kindness, and intentional unkindness with unkindness. Inequality-aversion models (Bolton & Ockenfels 2000, Fehr & Schmidt 1999) propose that people are averse to outcomes that deviate from equality, whether that inequality is advantageous or disadvantageous. Thus, according to the former account, responders reject low offers because they enjoy reciprocating unkindness with unkindness, whereas the latter account proposes that responders reject low offers because they find the proposed inequality painful.

Sanfey et al. (2003) studied ultimatum game behavior using fMRI to better understand why responders reject positive offers. Participants in their study, all responders, were told they would play the ultimatum game with 10 different human proposers (though offers were actually predetermined by the experimenters). Responders received five “fair” offers (\$5 for proposer, \$5 for respondent), and five unfair offers. In ten other trials, responders received the same offer, but this time from a computer (although what it means to receive an offer from a computer is somewhat ambiguous, given that the computer cannot literally keep the residual money). Consistent with intention-based theories of reciprocity and behavioral work by Blount (1995), participants were more willing to accept low offers from computer proposers than from human proposers. Moreover, activation in the anterior insula, an emotional region of the cortical pain matrix, was greater in response to unfair offers from human proposers than in response to unfair offers from computer proposers. In fact, whether players reject unfair offers from human proposers can be predicted reliably by the level of their insula activity. The insula findings thus appear to support the inequality-aversion models: Responders appear to be rejecting offers not because they enjoy reciprocating unkindness with unkindness, but rather

DLPFC:

dorsolateral prefrontal cortex

rTMS: repetitive transcranial magnetic stimulation

because the prospect of inequality pains them (cf. Pillutla & Murnighan 1996).

A second finding from Sanfey et al. (2003), and follow-up work inspired by it, raises the question of whether self-interest or a desire for fairness is more evolutionarily ancient. Specifically, Sanfey et al. (2003) found that activation in the right dorsolateral prefrontal cortex (DLPFC), a region involved in executive control, goal maintenance, and overriding prepotent responses (e.g., Miller & Cohen 2001), was greater than activation in the insula when responders accepted unfair offers. By contrast, insula activation was greater than right DLPFC activation when responders rejected unfair offers. Sanfey et al. (2003) interpreted this pattern as evidence that the prepotent, emotional response was to reject unfair offers, and that regions associated with higher-level cognition had to override that impulse in order to accept such offers.

Knoch et al. (2006) devised a way to test this hypothesis experimentally. Participants in this experiment played ultimatum games, and proposers could offer anywhere between none and half of their endowment. In the period before making their decisions, some responders received repetitive transcranial magnetic stimulation (rTMS), a method that uses pulsed magnetic fields to temporarily disrupt brain function in specific regions. Some responders received rTMS to the right DLPFC, some received rTMS to the left DLPFC, and others received “sham” (placebo) rTMS to the right or left DLPFC.⁷ By experimentally

⁷van't Wout et al. (2005) were actually the first to conduct such an experiment. Specifically, van't Wout et al. (2005) varied, *within-subject*, whether seven ultimatum game responders received rTMS to right DLPFC or sham rTMS to right DLPFC. Given that participants who experience both real rTMS and sham rTMS are likely to detect a difference between the procedures, demand effects are clearly a concern in this study. Moreover, van't Wout et al. (2005) did not include an active rTMS control, unlike Knoch et al. (2006), who include a condition in which responders receive rTMS to left DLPFC. Taken together, the design of van't Wout et al. (2005) makes it difficult to attribute any observed treatment difference in behavior to the disruption

manipulating activation in the DLPFC, the authors were equipped to make causal conclusions about its role in responder behavior. Knoch et al. (2006) found that responders who had rTMS to the right DLPFC were significantly more likely to accept unfair offers than were responders who had rTMS to the left DLPFC or responders who had sham rTMS. Note that the effect was not mediated by perceptions of fairness: Participants who had rTMS to the right DLPFC were no less likely than other participants to rate low offers as very unfair. Thus, the right DLPFC appears to influence what one is willing to accept, rather than what one considers fair. Contrary to Sanfey et al. (2003), these results suggest that the right DLPFC plays a key role in overriding or weakening self-interested impulses, allowing people to implement their taste for fairness.⁸

Of course, the results need to be interpreted with caution, as we still have a relatively limited understanding of the effects of rTMS, with respect to both where it has its effects (at the targeted site or on distal components of connected circuits) and its influence on neural function. For example, although it is believed that rTMS disrupts activation in regions thought to be involved in a particular task, it may actually stimulate activation in other regions that would not have normally been involved in a targeted task (E. Fehr, personal communication). Some researchers are

of right DLPFC. Further complicating matters, little treatment difference was actually observed (48% of unfair offers were accepted under rTMS; 42% under sham rTMS).

⁸The Knoch et al. (2006) results are consistent with behavioral work by Skitka et al. (2002), who showed participants a number of case studies of people who had contracted AIDS in different ways. Different cases made the victim appear more or less responsible (e.g., sexual contact versus a blood transfusion). Participants were asked for each case study to indicate whether the individual should be given subsidized access to drug treatment. Half of the participants made their decisions under cognitive load, while half made their decisions under no load. Participants were less likely to advocate subsidized treatment under cognitive load, suggesting that deliberation played a role in overcoming self-interest.

already combining rTMS with fMRI, and we will undoubtedly continue to learn about this promising procedure.

SUMMARY

In the domain of social preferences, the growing neuroscientific literature is highly supportive of a dual-system account of behavior. For example, Greene et al. (2001) and Koenigs et al. (2007) present evidence suggesting that personal moral dilemmas elicit prepotent emotional responses that must be cognitively overridden in order to make judgments incongruent with the prepotent response. The findings of Sanfey et al. (2003) and Knoch et al. (2006) both suggest that fairness preferences and self-interest operate via different systems, though they come to conflicting conclusions regarding which desire is the prepotent response in ultimatum games. While the Sanfey et al. (2003) results are correlational, Knoch et al. (2006) experimentally manipulated activation in right DLPFC and can thus draw causal conclusions about its role in ultimatum game behavior. However, given the uncertainty that still surrounds the rTMS procedure, future research should continue to examine how self-interest and fairness preferences interact at the neural level.

CONCLUSION

Neuroeconomics has bridged economics and psychology, largely because of movement within economics. Recent models in economics (Benhabib & Bisin 2005, Bernheim & Rangel 2004, Brocas & Carrillo 2006, Fudenberg & Levine 2006, Loewenstein & O'Donoghue 2004) have come to embrace a multiple systems perspective, which has long been popular among psychologists (Chaiken & Trope 1999, Posner & Snyder 1975, Schiffrin & Schneider 1977). Although neuroeconomics has not yet produced many findings that directly challenge assumptions held within psychology (only one of the neuroeconomics papers discussed above, Shiv et al.

2005, was published in a psychology journal), the field will undoubtedly eventually focus on issues of importance to both fields. For example, psychologists have often questioned how multiple systems interact to influence behavior. They may compete, or one system may provide a default response that can subsequently be overridden by another system, hypotheses that Evans (2008) respectively refers to as "parallel-competitive" and "default-interventionist." Economists who attempt to formally model the interaction of multiple systems are certainly interested in this question, and it is only a matter of time before neuroeconomists attempt to address it empirically.

Although neuroeconomics has encouraged positive changes within economics, reactions to neuroeconomics within economics too often seem to take one of two extreme forms. On the one hand, neuroeconomics has inspired some economists to adopt more psychologically realistic views of the world. This is undoubtedly beneficial to those economists and to the field. However, such views probably should have been adopted much earlier based on behavioral research. The overweighting of neural relative to behavioral evidence is illustrated in the bibliographies of the five new economic models mentioned above. For example, only one cites Chaiken & Trope's (1999) well-known review of dual-process research, whereas citations of neuroscientific studies abound. On the other hand, some economists, still reeling from the incorporation of psychology into economics and the rise of behavioral economics, are even more aghast at the infiltration of economics by neuroscience. They reject the "new phrenology" (Harrison 2005, p. 794) based on the argument that neural data cannot refute economic models, which make predictions about behavior rather than underlying processes (Gul & Pesendorfer 2005). According to this view, the failure to find neural correlates of "as-if" processes in economic models is not a failure of the models, but rather a failure to test them properly. Economists generally

evaluate assumptions about underlying processes based on the accuracy of their implications, and psychologically implausible assumptions are often tolerated if they lead to satisfactory behavioral predictions.

However, to the extent that correct assumptions about underlying processes make better (and fresh) predictions, researchers should strive to refine those assumptions. Neuroeconomic research aims to facilitate this refinement and suggest new models. Indeed, as discussed above, neuroeconomics has already inspired a spate of individual choice models within economics.

Beyond its potential for refining economic theories, a better understanding of the neural processes underlying behavior could have other far-reaching consequences. For example, economists have typically assumed an equivalence between preference and welfare—i.e., that satisfying people's preferences will make them better off. However, dual-process models of behavior challenge this assumption by postulating the existence of different systems with competing motivational propensities.

Neuroscience methods also hold out the promise of making it possible to measure happiness more directly, or at least mechanisms more proximal to the experience of happiness, which could have profound implications for public policy. Currently, it is widely believed that it is impossible to make interpersonal comparisons of desire or well-being. Deprived of such data, economists have been very reluctant to take a strong position on issues of resource distribution. Person A may have 10 times as much wealth as person B, which might lead one to assume that person B would benefit more than person A would be hurt by a transfer of wealth from A to B. However, lacking any ability to compare the two individuals' utilities, such an inference would be logically unsound; perhaps person A has a much greater appreciation of luxury than B, so that overall happiness would actually be enhanced by a further transfer of wealth from B to A. Neuroscientific measurement of hedonic

states might help to disarm such logical defenses of inequality.

Looking ahead, neuroeconomics will continue to capitalize on the latest technologies developed by neuroscientists. Ideally, the technology will become increasingly portable (e.g., wearable sensors). Critics of laboratory research often lament the alien-like, context-free nature of experiments. Studies in which participants must remain almost perfectly still inside multi-ton magnets are even more vulnerable to such critiques. Another important technological advance is known as hyperscanning, which refers to the simultaneous scanning of several interacting brains (Montague et al. 2002).⁹ Finally, the combination of multiple methods (e.g., rTMS and fMRI) will undoubtedly lead to new insights.

Armed with rapidly improving technology and new insights emerging from neuroscience and psychology, we believe that the future of neuroeconomics is bright. Its promise is great, in part, because 50 years of dominance by the rational choice model has left so many important questions unanswered. What, for example, is the enormous appeal of gambling? Why are disputes, whether between individuals or countries, so often jointly destructive? What causes the boom and bust cycles that are so clearly present in financial and other markets? How does advertising work? Why do credit cards promote spending? Why do people fail to save for retirement? A refined understanding of human behavior has the potential to shed light on these and many other important phenomena, and a better understanding of neural processing, in turn, cannot help but inform our understanding of human behavior.

⁹King-Casas et al. (2005) used hyperscanning to examine behavior in a repeated trust game. They found that activation in the trustee's head of caudate originally responded to the revelation of the investor's decisions, but this activation eventually came to precede such revelation, indicating that the trustee had developed a model to predict the investor's likely next move. Tomlin et al. (2006) similarly studied a repeated trust game and found that activation along the cingulate cortex distinguishes between the revelation of one's own decision and the revelation of the decision of one's opponent.

SUMMARY POINTS

1. Neuroeconomics has further bridged the once disparate fields of economics and psychology, largely due to movement within economics. Change has occurred within economics because the most important findings in neuroeconomics have posed a challenge to the standard economic perspective.
2. Neuroeconomics has primarily challenged the standard economic assumption that decision making is a unitary process—a simple matter of integrated and coherent utility maximization—suggesting instead that it is driven by the interaction between automatic and controlled processes.
3. Neuroeconomic research has focused most intensely on decision making under risk and uncertainty, but this line of research provides only mixed support for a dual-systems perspective.
4. The extent to which intertemporal choice is generated by multiple systems with conflicting priorities is perhaps the most hotly debated issue within neuroeconomics. However, a majority of the evidence favors a multiple systems perspective.
5. Neuroeconomic research on social preferences is highly supportive of a dual-systems account, although the most prominent studies come to conflicting conclusions regarding how self-interest and fairness concerns interact to influence behavior.
6. Neuroeconomics may ultimately influence psychology indirectly, via its influence on economics (e.g., by inspiring economic models increasingly grounded in psychological reality), and directly, by addressing debates of interest within psychology (e.g., whether multiple systems operate sequentially or in parallel to influence behavior).

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Argues that neural data cannot refute economic theories, which are silent regarding underlying processes. The most prominent critique of neuroeconomics.

Ambitiously combined fMRI and lesion patient data to test various explanations for ambiguity aversion. Results implicated immediate negative emotions.

Unlike most neuroeconomic studies that rely on correlational evidence, Knoch et al. use rTMS to experimentally manipulate activation in DLPFC.

Found that insula activation correlated negatively with spending, suggesting people do not control their spending strictly by considering opportunity costs.

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Concluded that limbic/paralimbic structures are preferentially recruited for intertemporal choices involving immediately available rewards, as opposed to fronto-parietal regions.

Results suggested unfair ultimatum game offers elicit a negative emotional response favoring rejection. Knoch et al. (2006) questioned this interpretation.

Attributed loss aversion to an asymmetric response to gains and losses within dopaminergic targets rather than to multiple systems.

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