Neuroeconomics

Andrew S Hart, *University of Washington, Seattle, Washington, USA*
Mark E Walton, *University of Oxford, Oxford, UK*
Paul EM Phillips, *University of Washington, Seattle, Washington, USA*

Introductory article

Article Contents

Online posting date: 15th March 2009

Neuroeconomics is an emergent multidisciplinary field that strives to understand how and why humans make decisions. It brings together behavioural methods and sophisticated computational theories from microeconomics, an understanding of emotional influences on behaviour from psychology, and human functional neural imaging and electrophysiological recordings in animal models from neuroscience. Moreover, the neuroscientific contribution to this field is now beginning to incorporate molecular, pharmacological and physical interference techniques which can test the causal relationship between neural function and behaviour. Research in neuroeconomics has uncovered potential representations of value and costs within the brain. Studies of decision-making in social environments have also revealed key emotional components of decision-making that may help to explain some deviations from optimal or rational decision-making in humans. Although it still has many challenges to overcome, neuroeconomics stands poised to benefit both microeconomic theory and neuroscience through shared techniques and ideas.

Introduction

Guided by the common drive to develop normative and descriptive theories of decision-making behaviour, experimental psychology and economics have existed for decades as parallel fields. In spite of their common motivations, the two communities rarely entered into a dialogue with each other or exchanged methods and ideas. This barrier was created by conceptual differences between the fields. Economists assumed that they had no access to internal states, so they formulated their theories based on behaviours, either observed or idealized. Psychologists, however, tended to put a great deal of emphasis on investigating the internal states that might govern the relationships between environmental factors and behaviours. The advent of cognitive neuroscience with its noninvasive techniques in human subjects, particularly functional magnetic resonance imaging (fMRI), which allows the recording of human brain activation with good spatial and temporal resolution, has finally placed researchers on both sides of the divide one step closer to the goal of observing internal states. These new techniques have inspired a dialogue among economists, psychologists and neuroscientists that is set to bring new developments in all three areas. This confluence of ideas from multiple disciplines has been dubbed Neuroeconomics. **See also**: Brain Imaging: Observing Ongoing Neural Activity; Cognitive Neuroscience

ELS subject area: Neuroscience

How to cite:
Hart, Andrew S; Walton, Mark E; and, Phillips, Paul EM (March 2009) Neuroeconomics. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0021399

Approaches to Decision-Making

Economists historically sought out to describe the actions of *Homo economicus*, an idyllic and completely rational human decision maker, whose goal in every action is to maximize value. Value-based decision-making requires a systematic evaluation of costs and benefits of actions available to us, followed by the selection of an appropriate action to complete the choice. Value can be considered an objective quantity in the environment, such as three oranges or £2, but economists quickly discovered that economic behaviours rarely follow the heuristics of value maximization, and humans are often irrational decision makers, relying heavily on social factors and effects. For example, someone might prefer 3 oranges to £1, but, paradoxically would prefer £10 to 30 oranges. Economists accounted for this deviation in behaviour by introducing the concept of utility, the subjective experience of value within the environment. The exact relationship between value and utility is unknown, but most agree that it is nonlinear, and as total value increases, the increase in utility for each additional unit of value diminishes. As a brief aside, it should be noted that the behaviours that interest economists are not necessarily financial decisions, and in many cases, they do not involve money or any other form of currency. A decision to spend 2 h at a pub rather than 2 h exercising is just as valid and interesting an economic problem as a decision to buy an expensive insurance policy for protection against an unlikely loss.

Using the concept of utility, Kahneman and Tversky formalized prospect theory to describe how humans respond to risk. Prospect theory states that when faced with several options, a human will pick the one that will yield the maximum positive change in utility (or minimum loss) after all costs and benefits have been considered. Kahneman and Tversky observed decision-making behaviour in human subjects to generate utility curves. They found that the shapes of the curves showed that their subjects were averse to losses as well as risky gains, often choosing smaller deterministic rewards over larger probabilistic rewards. The use of behavioural experiments as a method in economics was perhaps an early sign of the convergence of economics and psychology, as the behavioural economic practices of offering real incentives to participants and avoiding deception have now been adopted as the standard operating procedure in neuroeconomics.

Although using behavioural techniques has led to a great deal of progress in economics, economists often remained skeptical that they could use such behaviours to infer the thoughts and feelings that make up the process of choosing. By contrast, experimental psychology and neuroscience have a long history of developing theories of decision-making that include internal states. Psychological theories also tended to include motivational, social and affective components that could account for deviations from rationality. However, until recently, hypotheses that involved internal states in decision-making could not be tested directly by looking at brain activity but instead had to be assessed indirectly from measures such as reaction times and patterns of performance. **See also**: Brain Imaging: Localization of Brain Functions

However, recent work has changed the nature of the field. Using model-based approaches, neuroscientists have been able to test computational models of processes such as learning and decision-making by directly relating them to data from brain imaging and electrophysiological experiments. These types of experiments lend themselves to the use of more sophisticated decision-making tasks that approach the complexity of those used in economics. This line of work serves to benefit both neuroscience and economics by using neural data and complex choice tasks to develop better computational theories of decision-making. These theories often include internal processes such as the evaluation of options available in the environment, the representation of anticipated outcomes of actions, action selection and the evaluation of outcomes.

Neurobiology of Reward

In addition to economic decisions in humans within financial systems, it appears likely that all animal species engage in very similar decision-making processes as they forage for primary rewards such as food, shelter and sex. Thus, the first clues in neuroscience as to the representation of value in the brain have come from the studies of reward that combined Pavlovian conditioning with neural recordings in animals. Early work suggested that in rodents, neurons in the midbrain increase their rate of firing in response to classically conditioned cues that reliably predict food and water rewards. These responses were found to be independent of the physical properties of the stimuli (such as tone frequency) and modulated by the motivational state of the animal. That is, neurons in hungry rats responded more to tones that predicted food than to tones that predicted water, and vice versa for neurons in thirsty rats. **See also**: Pavlov, Ivan Petrovitch

In the early 1990's, Schultz and colleagues were able to show that dopaminergic neurons in the ventral tegmental area (VTA) and substantia nigra pars compacta (SNc) of the midbrain show similar cue-evoked changes in the activity in primates. Although initially these neurons show brief bursts of activity to unexpected fluid reward in thirsty animals, after prolonged training these responses occur at the presentation of the first cue predictive of a reward rather than the reward itself. The signals recorded in dopamine neurons are akin to error signals present in a popular computational model of learning, the temporal difference model. This is one of the first examples of how a normative model could be applied to neural data. Moreover, these changes in firing rate scale with both reward magnitude and reward probability, suggesting that the change in firing rate could represent the expected utility of anticipated rewards. **See also**: Basal Ganglia and the Regulation of Movement; Dopamine; Learning and Memory

Subsequently, similar findings have come from fMRI studies in humans, with the dopaminergic midbrain and several of its primary target regions, such as the ventral striatum and the frontal lobe being activated first by unexpected juice rewards and then by conditioned cues during a classical conditional task equivalent to that used with Schultz's monkeys. A similar network of regions also appears activated by nonprimary rewards such as money and, as for the juice, the activity scales with the amount of money that is expected and its likelihood of being received. More recently, it has been shown that the size of the signal in response to money is also influenced by personality factors such as introversion and the amount of monetary assets that a person possesses. Moreover, in humans, neural responses to pain and to financial loss also seem to involve overlapping circuits. These results demonstrate a convergence of findings in human and nonhuman models of reward and suggest that the neural representation of primary rewards might be common across species and these might largely overlap with the regions involved in evaluating monetary value in humans. **See also**: Cerebral Cortex

 ENCYCLOPEDIA OF LIFE SCIENCES © 2009, John Wiley & Sons, Ltd. www.els.net

Neurobiology of Decision-making

Research on the neural representation of value has been extended from simple learning paradigms into the realm of choices with multiple alternatives in both animals and humans. Bergman and colleagues recorded from midbrain dopamine neurons while monkeys were performing a 'two-armed bandit task' where the animals can choose between two options that differ in the likelihood of a reward being delivered. These choice trials were intermingled with 'reference' ones in which only one option was presented. The neural activity on these reference trials proved to be a better predictor of the monkeys' decision-making behaviour on choice trials than the actual rewards received in these trials, and indeed, the responses on choice trials scaled with the values of the monkeys' ultimate choices. These results suggest that dopamine neurons carry a representation of the value of future actions, a critical component in any model of decision-making.

Other studies on nonhuman primates have implicated important roles for neurons in a variety of cortical regions in aspects of decision-making. For example, Platt and Glimcher discovered neurons in the lateral intraparietal area (LIP) of cortex that fire at a higher frequency when the monkeys are about to make eye movements that would earn a larger proportion of the total available reward. Over a range of decisions, this change in activity is correlated to the ratio of the chosen reward magnitude to the total reward available in each trial. **See also**: Cerebral Cortex

Most of these experiments in animals have varied either the magnitude or likelihood of a single type of juice or food reward. However, many everyday decisions involve an assessment of disparate and abstract potential benefits. Several lines of evidence have indicated that prefrontal cortex might be important for assessing the relative value of such outcomes. For instance, neurons in the orbitofrontal cortex (OFC), a subregion of the frontal lobe, have been shown to encode the value of available rewards based on their subjective preference. This representation of value is independent of other sensory, motoric or mnemonic processes, suggesting that the brain contains a representation of the values of available options that is independent of the methods used to obtain them. Moreover, the valuation as coded by the neurons of OFC is independent of the other available options (i.e. whether a particular item is the best or worst available). This finding could have strong implications for economic theory, as economists have long struggled with the concept of transitive preferences. That is, if someone prefers an orange over three bananas, and they prefer three bananas over four apples, then they should prefer an orange over four apples. However, no behaviourally derived theory in economics can prove transitive preferences, as subjects often demonstrate paradoxical behaviour, such as choosing four apples over an orange in this example. The above findings provide economists with a putative neural representation of economic value that could be used to interpolate between goods in the environment.

If OFC neurons reliably represent the value of economic goods, then the degree of OFC activation in response to a novel good could be used to accurately predict preferences in hypothetical decisions. For example, if OFC activation is higher in response to a pineapple than to an orange, then we could say that one prefers a pineapple to an orange, even if he or she has never been presented with the choice. Preferences are often revealed through purchasing behaviour, so knowing whether one might prefer a pineapple over an orange could translate to knowing that he or she will pay more for a pineapple than for an orange.

When studied with fMRI, humans show similar contributions of networks of subcortical and cortical regions when making financial decisions between different goods. As with the work in animals, this has demonstrated that there is not a single unitary system for assessing value in the brain, but instead several, possibly competing, systems representing different aspects of value. For instance, Knutson and colleagues have studied a variety of purchasing scenarios and have shown that the activity in the ventral striatum during the presentation of products available for purchase is a predictor of future preference and, in a financial investment task, of making a risky investment. Other regions, such as the insula and medial prefrontal cortex, also reflect other aspects of investing, purchasing and selling, such as when prices seem particularly high or low or when subjects are likely to make safe investments. Intriguingly, the activation of these brain regions is often a better predictor of purchases than the subjects' own reported preferences. Together these results suggest that people's preferences and financial deliberations can be tracked in their brains, and that this information may provide important insights into how such purchase decisions are made.

Representing costs

The study by Knutson and colleagues highlights an important feature of decision-making that is not to be overlooked: the representation of costs. A cost is a mechanism to obtain an outcome that alters the net utility of the overall transaction, including delays in reward, the physical effort or persistence that is required to gain the reward, and of course, paying money. The studies of financial loss and purchasing mentioned above have implicated anterior cingulate cortex and insula as representing financial losses and excessive prices, respectively.

Studies in which subjects choose between options which differ in the delay to the reward suggest that the evaluation of immediate outcomes versus distant ones may engage partially dissociable neural systems. The limbic system, including dopamine neurons, and their cortical targets are activated more strongly when subjects choose immediately available rewards over delayed rewards and show diminishing activation when delayed rewards are chosen. The limbic system is considered a primitive part of the brain that is primarily engaged with satisfying basic needs and reproduction. In contrast, both immediate and delayed rewards activate lateral frontal cortical regions. These regions are generally engaged with higher level cognitive functions, and indeed they are more strongly activated when subjects are faced with more difficult choices between immediate and delayed rewards. Thus it appears that human decisions involving delayed gratification engage multiple neural systems. One system strongly discounts delayed rewards while the other does not discount delayed rewards. This finding invites the hypothesis that when making decisions, humans are often using multiple, competing systems, and that behaviours might depend on which system wins out over the other. Similar conclusions can be drawn from a subfield of neuroeconomics that deals with social decision-making. **See also**: Cognitive Neuroscience; Limbic System

Social decision-making

With increasingly complex behavioural tasks coming into use in neuroscience, much work has been done in the field of social decision-making. This branch of neuroeconomics uses head-to-head behavioural tasks in which the outcomes depend not only on the subjects' decisions but also on the decisions of another subject, a confederate, or a computer, and often incorporates game theory from economics for the interpretation of behaviour. The cases where behaviour deviates from the predictions of game theory offer a unique opportunity for neuroscience to educate the theories of economics.

A commonly used social decision-making task called the ultimatum game demonstrates the power of research in this area. In the ultimatum game, one player must choose how to divide up a sum of money between oneself and a responder. The responder can either accept or reject the proposer's decision. If the responder accepts, then the money is split up according to the proposer. If the responder rejects the offer, then neither player receives any money. Game theory, which assumes that both players will behave in order to maximize their own payoff, predicts that the proposer would offer very little money to the responder and the responder would accept any offer made by the proposer. However, players rarely behave in this way. Rather, the responders tend to reject low offers, even when the games are played in single trials, so they stand to gain nothing from future interactions by punishing selfish propositions. Although game theory cannot explain this behaviour, neuroscience can offer some insight into the internal processes that generate these decisions. During this game, players with higher activation in the insular cortex, a region implicated in emotional responding, tend to reject low offers more frequently. These findings invite the possibility of including emotional states in future theories of social decision-making, as offers that widely deviate from an inequitable of the money could be interpreted as unfair or in violation of social norms.

Emotional responding may not be the only explanation for subjects' behaviour in the ultimatum game. Findings from a study using a similar task, known as the modified trust game, suggest that the opportunity for punishment or vengeance may be a reward in itself. In the modified trust game, 2 subjects are each endowed with 10 arbitrary currency units. Subject A must choose to either invest his endowment in subject B or keep his endowment. If subject A chooses to keep his endowment, the game ends and both players keep 10 currency units. If subject A chooses to trust subject B, the 10 monetary units are immediately quadrupled to 40 units and given to subject B. Subject B may either defect and keep all 50 units or reciprocate and return 25 units to subject A. At the end of this round, both subjects are given an additional endowment of 20 units, and subject A has the option of punishing subject B in the event of a defection. Subject A can pay for money to be taken from subject B at an inflated rate of 2 to 1, so subject A can pay as many as 20 units for subject B to be punished by as many as 10 units. As with the ultimatum game study above, subjects face each other only once, so subject A stands no chance of benefiting from influencing the future behaviours of subject B. Even under these conditions, subjects in the A role chose to pay for the punishment of defectors. Using a brain scanning technique known as positron emission tomography (PET), researchers discovered that under conditions where punishment is both desirable and effective, the caudate nucleus shows greater activation than when punishment is either merely symbolic or not desirable.

Caudate activation correlated with the chance to punish suggests that in the modified trust game, the opportunity to punish is positively reinforcing, or possibly even satisfying as activation of this and other basal ganglia nuclei tend to accompany primary rewards and cues that predict rewards. The authors also describe a positive correlation between the amount subjects are willing to invest in punishment and the degree of caudate activation under conditions when inflicting punishment is desirable. Together these results suggest that vengeance, or the opportunity to punish violators of reciprocity, could be a valuable commodity.

Although the above studies demonstrate compelling correlations between measures of brain activity and social and economic factors, the goal of research in the field of social decision-making is to establish causal relationships between focal brain activation and behaviour. Further investigation using the ultimatum game has begun to approach this goal. In this game, a region of the lateral prefrontal cortex is activated as responders decide whether to accept or reject an offer, and activation is stronger when offers are inequitable. Lateral prefrontal cortex is thought to be involved in executive control and inhibition of urges. Using powerful magnetic stimulation at the scalp, researchers have been able to temporarily disrupt function in this region in human subjects, causing them to accept low, inequitable offers from other human players more frequently. This finding suggests that the lateral prefrontal cortex plays an important role in reducing selfish, vengeful or emotion-driven behaviour in social settings.

 ENCYCLOPEDIA OF LIFE SCIENCES © 2009, John Wiley & Sons, Ltd. www.els.net

Future Directions and Challenges

The above social decision study demonstrates how neuroeconomics could in the future be used to aid our understanding of psychiatric disorders such as obsessive compulsive disorder, addiction or borderline personality disorder. In these disorders, patients seem to misvalue their available alternatives and respond abnormally in social situations. Computational models are already being applied to the study of addictive drugs and their effects on valuation and decision-making, with the hope of tracking changes in decision-making through the different stages of addiction. Moreover, with further utilization of the broad range of interference tools available in neuroscience such as genetic knockout animals, behavioural pharmacology and focal brain lesions, a better grasp on causal relationships between brain function and decision-making can be obtained. **See also**: Knockout and Knock-in Animals

Although it is a promising young field, neuroeconomics still has some important challenges to overcome. Although the techniques and behavioural tasks have reached a great deal of sophistication, there is still some question as to how closely behaviour in the lab relates to decision-making in real world situations or financial markets. This is especially important in the case of social decision-making, in which nonverbal communication and personal space make up an important component of the social experience. Such characteristics of social settings are difficult to simulate inside an fMRI scanner. Also, neuroeconomics experiments tend to use money as a reward, but the relationship between money and primary rewards such as food, water or sex, is not clear. Money may be so deeply ingrained in human behaviour that it is interchangeable with primary reward, or it may represent consumable rewards that can be obtained in the future. For the total integration of the field, this relationship needs to be explored fully to temper comparisons between human studies that use monetary reward and human and animal studies that use primary rewards.

Neuroeconomics also faces an important conceptual challenge. The concept of competing neural systems that regulate rational versus emotion-based decisions has not been universally accepted, and many researchers in the field take the view that neural systems engaged in decision-making contain both rational and emotional components and contribute to decision-making in a more graded fashion. This debate is still awaiting the critical evidence to rule out either hypothesis. **See also**: Addiction

Further Reading

Glimcher PW (2003) *Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics*. Cambridge, MA: MIT Press.

Knutson B and Bossaerts P (2007) Neural antecedents of financial decisions. *Journal of Neuroscience* **27**: 8174–8177.

Lee D (2008) Game theory and neural basis of social decision making. *Nature Neuroscience* **11**: 404–408.

Loewenstein G, Rick S and Cohen JD (2008) Neuroeconomics. *Annual Reviews of Psychology* **59**: 647–672.

McClure SM, Laibson DI, Loewenstein G and Cohen JD (2004) Separate neural systems value immediate and delayed monetary rewards. *Science* **306**: 503–507.

Padoa-Schioppa C (2007) Orbitofrontal cortex and the computation of economic value. *Annals of the New York Academy of Sciences* **1121**: 232–253.

Phillips PEM, Walton ME and Jhou TC (2007) Calculating utility: preclinical evidence for cost-benefit analysis by mesolimbic dopamine. *Psychopharmacology (Berl)* **191**: 483–495.

Platt ML and Huettal SA (2008) Risky business: the neuroeconomics of decision making under uncertainty. *Nature Neuroscience* **11**: 398–403.

Rangel A, Camerer C and Montague PR (2008) A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience* **9**: 545–556.

Sugrue LP, Corrado GS and Newsome WT (2005) Choosing the greater of two goods: neural currencies for valuation and decision making. *Nature Reviews Neuroscience* **6**: 363–375.