Chapter 1
Neuroeconomics—An Introduction

Martin Reuter and Christian Montag

Abstract The present chapter provides an introduction into the young discipline of neuroeconomics and into the present *Neuroeconomics* book. Historical aspects, core concepts and future research avenues are presented.

1.1 Historical Aspects

Neuroeconomics is a very young scientific discipline that constitutes an interdisciplinary symbiosis of economics, psychology and the neurosciences. The general aim of neuroeconomics is to study human decision-making with a focus on the neural mechanisms thereof. The official establishment of the discipline was marked by the foundation of The Society for Neuroeconomics in 2005.

Research in this field is prolific and of high quality, however, scepticism remains, especially among those scientists who retain a purist vision of their respective disciplines. History has taught us that great achievements are made possible only by the combined expertise of scientists from different fields. For example, only through such successful interdisciplinary research could man have

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M. Reuter (✉)
Department of Psychology, University of Bonn, Bonn, Germany
e-mail: martin.reuter@uni-bonn-diff.de

M. Reuter
Center for Economics and Neuroscience (CENs), University of Bonn, Bonn, Germany

C. Montag
Department of Molecular Psychology, Institute of Psychology and Education,
Ulm University, Ulm, Germany
e-mail: christian.montag@uni-ulm.de

C. Montag
Key Laboratory for NeuroInformation, Center for Information in Medicine,
School of Life Science and Technology, University of Electronic Science
and Technology of China, Chengdu, People's Republic of China

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flown to the moon; astronomers working in isolation could never have achieved this dream, but with input from other disciplines (e.g. informatics, mathematics, physics, etc.) mankind's dream of walking on the moon became a reality.

Cognitive neuroscience, which emerged during the 1970s, is the youngest member of the neuroeconomic trio, while the disciplines of psychology and economics have been around for over one hundred years. For decades the two disciplines seemed to live in an uneasy parallel, arguably ignoring each other. This is surprising, given that the understanding of human behaviour is intrinsic to both disciplines. Of note, the scientific worldviews and the methodological approaches utilized by each discipline differ dramatically. Whereas economists try to establish a formal theory explaining human behaviour in an axiomatic way, psychologists build and refine theories through an empirical approach. Roughly speaking, economists have traditionally favoured a theoretical—and psychologists an empirical—approach. Since the launch of the journal of *Experimental Economics* in 1998 (and in view of the chairs for behavioural economics newly created at Universities throughout the world), it is clear that this strict differentiation between the theoretical economics and empirical psychology no longer holds. Nevertheless, such historical traditions are of importance; even today the two disciplines show marked differences that are far-reaching, which manifest in different theoretical foundations and methodological and statistical approaches, all of which serve to undermine successful interdisciplinary research efforts.

Whereas economics had not made direct acquaintance with the neurosciences prior to the establishment of the new discipline of neuroeconomics, the idea of investigating the role of the brain in human behaviour is an old one in psychology. For decades psychologists have used electroencephalography (EEG; see the method Chap. 19 by Debener et al. in this book) to investigate cognitive and emotional processes. Therefore, the invention and scientific application of magnetic resonance tomography (MRI; for an introduction see the method chapters on MRI by Markett (fMRI; Chap. 20), Gaser (MRI; Chap. 21) and Rüber (DTI; Chap. 22) in this book) in the 1990s proved a logical step for psychologists interested in subcortical processes that are not explicitly measurable through EEG. The subdiscipline of Biological Psychology makes use of all kinds of techniques that characterize the neurosciences, incorporating, in addition to EEG and MRI, genetics, psychophysiology, endocrinology, etc. In order to help bridge the gap between the "subdisciplines" of neuroeconomics, the present book deliberately features a broad methods section, which gives a scholarly introduction into neuroscience techniques relevant to this field (see PART VII of this book).

1.1.1 Economic Models and Their Parallels in Psychology

As mentioned above, economic models of human behaviour are axiomatic and try to establish algorithms valid for all participants across different situations. This idea is mirrored in classical experimental psychology, with the difference that experimental psychology uses experimental conditions to analyse behaviour. In Personality Psychology, however, the central tenet recognizes that large variability exists across participants, even in strictly controlled experimental settings or natural environments; a phenomenon referred to as individual differences.

A prominent economic model in neoclassical economics is *utility maximization*. According to utility maximization, people make their best choices according to their desires, knowledge and resources. The term *utility* does not refer to a good's quantity or monetary value per se in determining the decisions of an agent, but to the utility they obtain from the item. According to Marshall (1920, p. 78) "utility is correlative to desire and want", but desire and want can only be inferred indirectly by "the price which a person is willing to pay for the fulfilment or satisfaction of his desire". Although utility maximization makes correct predictions in a wide range of settings and situations including politics, markets and social life, its validity has been questioned, e.g. by *Prospect Theory* (Kahneman and Tversky 1979). Whereas the concept of *expected utility, which* originates from *Utility Maximization Theory,* postulates that alternative choices are valued by weighting the hedonic utility of possible outcomes against the chances of those outcomes actually occurring (e.g. in gambles), *Prospect Theory* claims that people do not always show a numerical evaluation of probabilities, but that outcomes are valued according to two aspects: a reference point (reference-dependent value) and an absolute utility. The reference-dependent value is thought to represent the valuation of past experiences and future aspirations and is therefore related to learning (past) and motivation (future). Most prominently, *Prospect Theory* explains why people grant more weight to losses than to gains, a phenomenon called *Loss Aversion*. There is empirical evidence across different cultures and ethnicities that, on average, losses are valued about twice as large as equal-sized gains. Of note, *Prospect Theory* has gained empirical support from the neurosciences. Using an fMRI study, Tom and colleagues have demonstrated that different brain activity patterns are correlated to the amount of gains and losses (Tom et al. 2007). Interestingly, they did not identify different brain circuits coding for gains and losses, but instead identified a unique system—the ventral striatum—that has become famous in the neurosciences as the brain's reward centre. Gains were expressed by an increase—and losses by a decrease—of the BOLD (blood oxygen level dependent) response in the ventral striatum.

Utility Maximization Theory focuses on economic decisions taken by a single agent in isolation. In contrast, *Game Theory* has extended the idea of utility maximization to social situations, e.g. it makes predictions of how the choices of other peoples influence the choice of an individual. Behavioural economics (partly influenced by psychology) has developed a battery of different games (e.g. Trust Game, Public Goods Game, Prisoner's Dilemma, etc.; *for an introduction to economic games* see Chap. 2 *by Civai and Hawes in this book*), which test the assumptions made by *Game Theory*. However, the empirical data do not always yield support for the theory. Naturally, people take into account the choices—or putative choices—of others when making their decisions, but their behaviour is often incongruent with the traditional economic view of man as a *homo* *economicus*. It is stated that the homo economicus makes decisions guided by self-interest (i.e. the maximization of personal benefit), that his decisions are completely rational and that all information necessary for making a choice is available. Results from the dictator game where player 1 (the dictator) has to split an endowment with an anonymous person (player 2) show that people do not behave in a manner congruent with that expected according to the view of man as a homo economicus (i.e. to take all the money and to award no money at all to player 2) (Camerer 2003). Instead, cross-cultural studies have shown that the "dictator" is far more cooperative, with mean allocations to the receiver (player 2) of about 28 % (Engel 2011). Based on the fact that this game, in its original version, is played as a 'one shot' game, i.e. the dictator has no reason to fear punishment from player 2 in a subsequent interaction; the dictator game is thought to be a measure of pure altruism.

In addition to the influence of others on people's choices (*Game Theory*), there are other crucial factors that influence economic behaviour. One of the most prominent factors studied in neuroeconomics is the relationship of the time lag between the decision and its consequences, referred to as *temporal discounting*. Interestingly, psychologists have investigated this topic for decades as *delay of gratification* (Mischel et al. 1989). In his seminal 'Marshmallow Study' at Stanford University in 1972, Mischel devised an experiment in which children were afforded the opportunity to 'earn' marshmallows. If the children could resist eating the first marshmallow they were offered, they were promised a second one, i.e. they would receive two marshmallows instead of one. The duration each child resisted the temptation to eat the initial marshmallow was analysed, and it was subsequently investigated whether or not delaying gratification correlated with future success. While the majority of the approximately 600 child participants attempted to resist the urge to eat the first marshmallow, only one-third delayed gratification long enough to get the second marshmallow. Analyses suggested that the age of the children was a crucial factor in influencing the child's success on this task. With increasing age, the ability to defer gratification increases. These findings have since been extended to adult samples, using various kinds of reinforcement. Intelligence (positive association) and gender (females were superior in resisting an immediate small reward in favour of a delayed bigger reward; evolutionary factors are discussed to account for this gender effect) turned out to be further prominent predictors of the ability to defer gratification. Under the label *temporal discounting* this phenomenon was investigated by means of functional magnetic resonance imaging (fMRI). McClure et al. (2004a) could identify distinct neural systems responding to immediate and delayed rewards. Whereas the limbic system is activated by immediate rewards ($t = 0$) the prefrontal cortex responds to both immediate and delayed rewards ($t > 0$), but more so when the delayed option is chosen. These findings hold true for monetary reinforcement as well as for primary rewards, e.g. sex (McClure et al. 2004b). The dissociation between cortical and subcortical brain regions with respect to immediate rewards supports the role of the limbic system (comprising the ventral striatum that is also named "the reward centre") for drives and instincts and the role of the prefrontal cortex for impulse control and cognitive processes. The latter are essential for evaluating offers and for deferring rewards until a future time point. There is plenty of evidence that the more a person discounts a delayed reward, the more likely that person is to exhibit a range of behavioural problems, including clinical disorders (e.g. drug addiction, impulse control disorders). The ventromedial prefrontal cortex (vmPFC) has shown to be involved in impulse control and in individual propensity to engage in risky behaviours (Bechara et al. 2000, 2002).

1.2 What We Have Learned from Animal Models

The crucial question when referring to findings from animal research is whether results can be extrapolated to humans. Preclinical trials—typically conducted in rodents—for the development of new drugs targeted at the treatment of human diseases, clearly answer this question with "yes". Excellent animal models for a range of psychological phenomena, e.g. anxiety, are available and do allow for predictions of the anxiolytic effects of a certain substance in humans. Even for those more complex behaviours relevant to the field of neuroeconomics, animal model exist. For example, Chen et al. (2006) were able to demonstrate that Capuchin monkeys are able to use tokens to purchase food from experimenters and that they prefer to trade with those experimenters who offer the best deals for their "money". In other words, even New World monkeys understand the principles of the market. Nonetheless, it is evident that the transfer from animal model to human is not always successful or feasible. Ethical concerns are a crucial consideration in this respect.

The invention of imaging techniques [e.g. MRI, positron emission tomography (PET)] has made it possible to study the human brain during task performance. Although PET imaging requires the administration of a radioactive ligand into the central blood system, it is a safe technique that can be used for research purposes with humans. More invasive techniques, such as microdialysis (a sampling technique for the continuous measurement of free, unbound concentrations of neurotransmitters or hormones in the extracellular fluid of brain tissue) or single-cell recordings (for assessment of the firing rate of neurons) in the living brain are, of course, not possible in healthy humans for ethical reasons. However, the neurosciences have provided many groundbreaking animal studies with broad relevance to neuroeconomics. As mentioned above, reinforcement and reward are crucial for decision-making, although other context variables also have a tremendous influence on our choices. The biological system most prominently related to reward is the dopamine (DA) system (Schultz et al. 1997). Its relevance was first identified in the context of studies on drug addiction. It was suggested that the dopaminergic system is the final common pathway of reward since almost all substances with the potential of causing addiction act via the DA system, either directly or indirectly (Spanagel and Weiss 1999). These findings could be extended to naturally occurring rewards (primary reinforcers like food or sex). The crucial question of how the

DA system could encode signals of reward is best studied in animal studies (for a review see Schultz 2013).

In a seminal study by Tobler et al. (2005), the activity of midbrain dopamine neurons in Macaque monkeys was recorded while cues signalled the probability of receiving a primary reinforcer (juice) of varying magnitude. This experiment tried to explain how the brain disentangles the probability and magnitude of reward. Keeping the probability of reward constant, the firing rate of the DA neurons increased monotonically with the expected liquid volume. The DA neurons were also able to encode the expected reward value, i.e. the combination of magnitude and probability. In a further step the authors conducted an experiment in which the reward outcomes were explicit rather than probabilistic. They used conditioned stimuli that explicitly predicted various amounts of liquid ($p = 1$). For example, a conditioned stimulus normally indicates the deliverance of 0.15 ml juice. They subsequently followed the conditioned stimulus with an unpredicted stimulus; either a smaller (0.05 ml) or larger (0.50 ml) volume of liquid; in response to which the firing rate of the dopaminergic neurons decreased or increased respectively. In a final experiment, Tobler et al. used one stimulus that predicted the delivery of either a small or a medium volume of juice with equal probability and a second stimulus that predicted a medium or a large volume with equal probability. Results indicated that for both conditioned stimuli, the deliverance of the, respectively, larger stimulus resulted in an increase—and that the deliverance of the, respectively, smaller stimulus resulted in a decrease—of the neuronal firing rate. Surprisingly, the identical medium volume delivery had opposite effects on neuronal activity, depending on the prediction. The prediction is in turn influenced by a *framing effect*. A medium amount of juice is attractive when compared to a small volume of juice, but unattractive in comparison to a large volume. The authors argue that, given the infinite number of reward values that are possible, this is an adaptive process. Thus, the firing rates of the dopaminergic neurons adapt to the coding of reward value in order to have a greater capacity for coding the likelihood of reward outcomes. Results showed that dopaminergic neurons encode a combination of magnitude and probability; the so-called expected reward values and that the response of the dopaminergic neurons depends on framing effects (for a concise review on the behavioural dynamics and neural basis of the framing effect please see Chap. 9 by X.T. Wang et al. in this book).

The effects of expected reward have a discrete neural signature in human decision-making, as demonstrated in a seminal study by Preuschoff et al. (2006). Using a simple gambling task in an fMRI setting, the authors varied expected reward and risk in an uncorrelated manner. Risk is a consideration because many decisions in daily life have to be made under conditions of uncertainty. Expected reward and risk were both represented in dopaminergic innervated brain regions, however, there was a temporal dissociation in their processing. The brain first processes information related to reward expectancy and later risk information. Besides the aforementioned study by Preuschoff et al., there are numerous examples in the literature of findings from animal studies being mirrored in neuroeconomic studies on humans. For example, Roiser et al. (2009) investigated the influence of framing effects on human decision-making and its neural activation patterns. They found that amygdala activation was stronger in those trials where participants made choices in congruence with—compared with those made counter to—the frame, but that this effect was only apparent in subjects carrying the short allele (s-allele) of the serotonin transporter polymorphism (5-HTTLPR; for more information on genetics see Chaps. 4 and 23 by Reuter and Montagin this book), a genetic variant related to neuroticism, depression and anxiety (Roiser et al. 2009).

1.2.1 Validation of Theoretical Models on Human Decision Making in Animals

As described above economists have developed theories (e.g. utility maximization; game theory, etc.) to predict human decision-making. Researchers from cognitive psychology and mathematics have established such theoretical models, albeit with a different focus. The best studied of these models try to explain choices via the simplest form of decision an individual can make—the choice between two alternatives. The focus here lies on the interdependency of choice probability and response time (RT). The most familiar expression of this relationship is the *speed–accuracy trade-off*, which characterizes the decision-maker's dilemma of being forced to negotiate between the competing demands of response speed and response accuracy (Bogacz et al. 2010). Many decisions are based on information that accumulates over time. Although the probability of making a correct or favourable decision increases with the amount of information we have gathered, sometimes we are forced to make quick and ill-informed decisions (e.g. to prevent harm). The development of *Sequential Sampling Models* has increased the theoretical understanding of such decision processes, however, it was the empirical validation in animal models (i.e. single-cell recordings in monkeys) that initially helped to test and refine these models. David Sewell and Philip Smith (see Chap. 14) provide a thrilling and comprehensive introduction to a research area in which theoretical mathematical frameworks and computational neuroscience meets empirical neurophysiological animal research. Through recent advances in imaging techniques, these models have now also been successfully tested in humans (Forstmann et al. 2010).

1.3 Ecological Validity

One of the most severe criticisms of neuroeconomic research is the frequent lack of ecological validity in studies. What can we learn from human decisions that are registered in fMRI scanners; a loud environment where movement is extremely restricted and where social interaction partners are presented—if at all—via video glasses (Mäki 2010). Imaging techniques like MRI, and PET are fantastic tools for allowing us to register brain activity, even in subcortical brain regions, while stimuli are processed. However, these techniques are not made for field studies, in which participants are observed in their natural environment. However, history has demonstrated that experimental approaches applied in the laboratory can indeed provide valuable insights into human behaviour and have thereby helped to legitimize the discipline of experimental economics. The same success is demonstrable for neuroeconomic studies using imaging techniques. Neuroeconomics permanently strives to establish ecological validity in any way possible. Implementing monetary reward in the behavioural games is one of these provisions. Decisions must be related to real consequences for the decision-maker, in order to be ecologically valid. It can be assumed that engagement in an economic game, which is played for monetary stakes, allows even the (fMRI) scanner environment to fade into the background.

Imaging studies are still common in neuroeconomics and have greatly boosted the success of the discipline. However, alternative neuroscientific techniques that are not limited to scanner facilities or laboratories are becoming increasingly prevalent. Molecular genetics is a key example in this instance. Behaviour can be studied in participants' natural environment and the participant subsequently provides a cell sample (e.g. by means of a noninvasive buccal swap) for genetic analyses. This approach ensures that participants are not influenced by the experimenter while exhibiting their natural behaviour. Most economists embarking upon neuroeconomic study are initially unaware that molecular genetics can provide information on the brain. Genes code for neurotransmitters, hormones, receptors and enzymes relevant for brain metabolism. Static genetic variants, called polymorphisms, exert a permanent influence on these gene products, by modulating the expression or the structure of gene products. In recent years a new field has grown from molecular genetics: epigenetics. Epigenetics dispels the ancient myth that genes are like an unstoppable computer programme, started at the moment when the semen and egg of our parents have fused. Prior to the introduction of epigenetics, genetic research often occasioned strong resentment among the general population, as it was considered synonymous with fatalism—a thing you cannot change. Epigenetic research has served to change this view of genes as destiny. Epigeneticists have demonstrated that the environment can and does influence our genes; not the static genetic polymorphisms, but rather the *expression* of our genes, by changing the methylation patterns of the genes. Thus, the relationship between genes and behaviour/environment is *bidirectional* (for a more detailed introduction, please see the genetics Chap. 23 in the methods section of this book and Chap. 4 "Genes and Human Decision Making").

Genetic approaches are not limited to field studies, but are also suitable for laboratory experiments. Neuroeconomics studies have used this method successfully and it will certainly become more and more important in the field. In a seminal study, Israel et al. (2009) have reported an association of a single nucleotide polymorphism (SNP; rs1042778) on the oxytocin receptor gene (OXTR) and prosocial fund allocations in the dictator game. This finding was replicated in an independent sample and serves to corroborate animal and human studies in demonstrating the pivotal role of the hormone oxytocin for prosocial behaviour (for a review see Ebstein et al. 2009).

1.4 Future Perspectives in Neuroeconomics

No matter how strongly neuroeconomists strive to improve prediction models on human decision-making through use of neuroscientific methods, criticism will always be present. It is impossible to convince every sceptic that biological variables can help us to better understand human behaviour and that neuroscientific approaches are helpful in verifying and refining theoretical economic models. On the whole, however, most criticism pertains to serious concerns, which must be taken seriously. The exciting possibilities offered by neuroscientific methods carry with it the risk of overselling the findings (Rubinstein 2008). The mass media contributes to this by exaggerating its reports of solid scientific work. We take this opportunity to discuss two such examples. We recently published a neuroeconomics study entitled “Investigating the genetic basis of altruism: The role of the COMT Val158Met polymorphism” (see a detailed description of this study in Chap. 4 in this book). The newspapers wrote articles on this study with headlines like this: “Altruism gene makes people generous”. It is obvious that altruism is not a monogenetic phenotype, but is subject to influence both from many genes, and from environmental effects. Therefore, there cannot be “an (a single)” altruism gene. The second example demonstrates that researchers sometimes tend to oversell their scientific findings. Kuhnen and Chiao (2009) published an article based on a sample of 65 participants entitled “Genetic determinants of financial risk-taking”. The Scientific American reported this study with the headline “My genes made me invest: DNA implicated in financial risk-taking”. One can debate the connotations of the word “determinants”, but it is obviously related to “determinism”, implying that there are no other sources of variance relevant for risk-taking, besides the 5-HTTLPR polymorphism investigated in this study. For the sake of Scientific American, it must be noted that the word “implicated” reflects the scientific value of this study very well, much better, in our opinion, than the phrase “genetic determinants”. Thus, a modest interpretation of scientific results in the field of neuroeconomics is essential to increase the respectability of the discipline.

It is obvious that the methodological spectrum of neuroscientific techniques has dramatically increased over the last years. Neuroeconomics is no longer limited to fMRI studies. We see EEG-, genetic-, endocrinological-, and TMS—studies, to name but a few methods, and the use of such methods will dramatically increase in future research. The paradigms and games used in neuroeconomic research will also become more and more elaborate in the endeavour to disentangle the subcomponents involved in economic decision making. Finally, the introduction of field studies will further enrich the spectrum by allowing researchers to test laboratory hypotheses in “real life”.

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