Neuroeconomics

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Abstract

In recent years, researchers in economics, psychology, and neuroscience have joined forces in the study of decision-making processes to form the new discipline of neuroeconomics. Neuroscientists turned to theories in economics and psychology to make sense of the increasing amounts of neurobiological data. At the same time, economists and psychologists turned to neuroscience for mechanistic constraints on their theories. Neuroeconomics studies tackle a host of topics, from financial choices through reinforcement learning to social decision making. Combining behavioral techniques with brain imaging in humans and electrophysiological recordings in animals, as well as complementary techniques, this interdisciplinary research has already generated new insights about the neural architecture of decision making. The neural mechanisms of some of the behavioral decision processes are increasingly understood, but many challenges remain. Extending neuroeconomics research to psychiatric disorders and incorporating new research tools are promising avenues for future studies.

THE HISTORY OF NEUROECONOMICS

INTRODUCTION

How does one choose between an apple and an orange? We can ask this question at several different levels. At the behavioral level, we may be interested in accurately predicting individual choices. At the algorithmic level, we can explore the neural mechanisms that underlie the observed choice behavior. Yet another level of inquiry is examining the mental states that give rise to the observed choice behavior. For centuries, researchers in economics, neuroscience, and psychology have studied decision making as largely separate disciplines. Researchers in each discipline have employed very different strategies to study one of these aspects of decision making.

Since the 1930s, neoclassical economists have essentially strove to predict human choice behavior based on rigorous mathematical models. These models were typically "as if" models, in the sense that they were not required to accurately describe the algorithm implementing the choice process, but

rather to correctly predict behavior. As Paul Samuelson and others have come to realize, making a small number of simple and reasonable assumptions, or "axioms" about choice behavior, such as "if a person prefers apples to oranges she will not also prefer oranges to apples," allows us to describe the decision maker's behavior "as if" they are trying to maximize some "utility" function. On the basis of these axioms, Von Neumann and Morgenstern (1944) developed the expected utility (EU) theory, a model for choice between uncertain outcomes, which was later extended by Savage (1954) to take into account the decision maker's subjective estimation of outcome probability (subjective EU).

At the same time that these economists were seeking to predict behavior, neuroscientists were aiming to reveal the mechanisms underlying the same behavior. For decades neurological research essentially depended on brain lesions in humans and animals. In this approach, behavioral deficits are correlated with the particular brain injury in an attempt to infer the function of the damaged neural system. Perhaps the most famous example is the 1848 case of Phineas Gage, a young railroad worker whose brain was penetrated by a steel rod (Neylan, 1999). Despite his remarkable physical recovery following the accident, Gage has exhibited substantial changes in personality and decision making, providing the first evidence in humans for the involvement of the prefrontal cortex, the part of the brain most affected by the accident, in decision-making processes. While brain lesions were very helpful in identifying general associations between brain structures and particular sensory, motor, or cognitive functions, they could provide little information about the neural algorithms that are implemented in each of these structures.

Advances in both economic theory and neurobiological techniques during the second half of the twentieth century led researchers in both of these disciplines to look to psychology, and eventually toward each other, in what turned out to be the birth of neuroeconomics.

On the economics side, economists began to note examples of choice behavior which was not compatible with neoclassical economic theory. In several cases, human choices violated one or more of the core axioms of the theory. Allais was the first to describe such violation in what is known as the "Allais paradox" (Allais, 1953), followed by Ellsberg, who described the "Ellsberg paradox" (Ellsberg, 1961). In a series of seminal studies published in the 1970s and 1980s Kahneman and Tversky have documented numerous substantial behavioral deviations from EU theory, demonstrating that these deviations were the rule rather than the exception (Tversky & Kahneman, 1974, 1981). The work of Kahneman and Tversky suggested to many economists and psychologists that economic models could benefit from psychological data and insights. These economists and psychologists formed the discipline of *behavioral economics*, a union of economics and psychology.

While these processes were taking place in the economics world, neuroscientists were also experiencing considerable transformations in their research. The introduction of novel data collection techniques markedly increased the ability of neuroscientists to investigate the neural circuits underlying higher cognitive functions. The first advance was made in the 1960s, when recording of neural activity in the brains of awake behaving animals became available. The next development occurred in the 1980s–1990s, when noninvasive imaging methods in humans, in particular positron emission tomography (PET) and functional magnetic resonance maging (fMRI) became widely used. These tools enabled neuroscientists to examine dynamic changes in neural activity while humans and other animals were engaged in complex behavior. The ability to record the activity of single neurons in awake behaving animals, and to image the activity of populations of neurons in humans, allowed much more than a simple correlation between neural activation and observed behavior. The analysis tools for making use of these new techniques and the large quantities of data that they generated, however, were not well developed. Similar to economists, neuroscientists have also begun to look to psychology, in order to use models of cognitive function in designing their experiments and analyzing their data. Instead of correlating a damaged brain area with impaired cognitive function, neuroscientists could now look for correlations between neural activity and hidden variables of the mental models. These studies gave rise to the new discipline of cognitive neuroscience, a union of neuroscience and psychology.

The formation of behavioral economics and cognitive neuroscience prepared the ground for what followed. Starting in the mid-1990s researchers in each of these disciplines, who were studying decision making, began to look to the other discipline. Several cognitive neuroscientists considered the use of economic theory as a normative theory against which they could examine their neurobiological data. At the same time, a few economists contemplated employing the mechanistic and algorithmic properties of the human nervous system as constraints on their models. Both of these processes set the stage for the emergence of the new discipline of neuroeconomics.

EMERGING FIELD

Shizgal and Conover were probably the first to explicitly apply economic theory to neurobiological data (Shizgal & Conover, 1996). In a review paper, these authors used economic theory to describe the neurobiology of choice in rats pressing a lever to directly stimulate reward-related neurons in their brains. Shortly afterwards, Platt and Glimcher (1999) published a highly influential study in which they showed that neurons in monkey parietal cortex encoded both the probability and the magnitude of expected juice

rewards, compatible with a role for these neurons in encoding the EU of the rewards. A similar approach was adopted in a human study by a group of experts in economics, neuroscience, and psychology. Breiter, Aharon, Kahneman, Dale, & Shizgal (2001) combined neuroimaging with economic theory to study the neural responses to expectation and experience of monetary gains and losses. The experimental design was based on Kahneman and Tversky's prospect theory (Kahneman was also one of the authors), testing two principles of the theory: that the evaluation of an uncertain option depends on whether it is presented as a gain or a loss, and that losses loom larger than gains of the same magnitude.

An explicit call for neuroscientists and economists to join forces in the study of decision making was made shortly afterwards by Glimcher in a 2003 book. Glimcher asserted that economics could provide a normative theory for the study of the neurobiology of higher cognitive function. In the next few years, a growing number of neurobiological papers in humans and other animals relied on economic theory in the design and analysis of their experiments. These papers examined the neural mechanism of a variety of behaviors, including reinforcement learning (Lee, Seo, & Jung, 2012), intertemporal choice (Kable & Glimcher, 2007), decision under risk and uncertainty (Platt & Huettel, 2008), valuation of goods of different types (Levy & Glimcher, 2012), social decision making (Lee, 2008) and a variety of decision biases. Some of these studies are described in the next section.

While neuroscientists widely appreciated the potential contribution of economics to neuroscience and quickly embraced the emerging field, the economic community was slower in its acceptance of neuroeconomics, and is still divided regarding the usefulness of neurobiological insights to economics theory. Perhaps the most famous opposition to neuroeconomics in the economics community was made by Gul and Pesendorfer (2008). These scholars argued that the goal of economic theories was to make predictions about behavior and that the actual machinery by which choice is accomplished must remain irrelevant to economists. In recent years, however, a growing number of economists have been advocating for considering neurobiological data in the development of economic theories. Camerer and colleagues first made the case for neuroeconomics from the economics side (Camerer, Loewenstein, & Prelec, 2005), arguing that the neural mechanisms of decision making should provide constraints on possible theories of decision making and may direct future studies in economics. In other words, these scholars proposed a shift from the "as if" models to models that use neural data in order to describe the actual decision mechanisms. As described later, substantial empirical support for this approach now exists.

In parallel to the first instances of interdisciplinary research combining economics, psychology, and neuroscience, several meetings and conferences

were held to bring together scientists from these different disciplines. These meetings eventually led to the formation of the Society for Neuroeconomics, which has been holding annual meetings since 2005, featuring the most recent studies in neuroeconomics. In 2008, the Society published a volume entitled "Neuroeconomics: Decision-Making and the Brain," which was edited by Glimcher, Camerer, Poldrack, and Fehr, and authored by many central scholars in the field. A new and largely modified second edition of this volume was published in 2014 (Glimcher & Fehr, 2014), summarizing nearly all of the most recent advances in neuroeconomics. This book serves as an excellent introduction to the discipline, as well as a handbook for researchers in the field and a textbook for students. Many of these researchers and students belong to specialized centers for neuroeconomics, which were open in many universities around the world. These centers provide both training to emerging neuroeconomists and support for established scientists, who, together with scholars in traditional departments for neuroscience, psychology, and economics, continue to investigate the behavior and neurobiology of decision making. Although neuroeconomics has only been around for a little over a decade, researchers in this discipline have made substantial progress in understanding various aspects of the neural architecture of decision making. Many questions, however, remain open, and it will be interesting to witness how the field evolves within the next few years. Some of these accomplishments and open questions are described here.

CUTTING-EDGE RESEARCH AND CENTRAL FINDINGS

Decision theories generally agree that the decision-making process consists of first assigning a "subjective value" to each available option and then choosing the most valuable option (Kable & Glimcher, 2009). These values need to be learned, stored, and modified when circumstances change. Typically, intentions and preferences of other agents also need to be taken into account. Numerous recent studies have employed a neuroeconomics approach to study each of these aspects of decision making. Owing to space limitations I briefly survey some of the most notable studies—the reader is encouraged to turn to the further readings for additional information.

The Neural Representation of Value

To be able to choose between an apple and an orange, the decision maker needs to estimate the value of each piece of fruit using some "common currency." One of the most solid findings that came out of neuroeconomics research is the identification of a valuation system in the brain, which

encodes values precisely in that manner. Accumulating evidence from a large number of studies strongly supports the existence of such a system. A common feature of most of these studies is that they used the choices that each participant made to infer her unique preferences, and then searched for "psychometric-neurometric matches" or correspondence between the behavioral measurement and the neural measurement. This approach, which was first employed in studies of perceptual decisions (Newsome, Britten, & Movshon, 1989), has proved to be very useful in studying economic or "value-based" decisions. Recording neural activity in the orbitofrontal cortex in monkeys, Padoa-Schioppa and Assad (2006) identified neurons whose activity was compatible with a common-currency representation of value. The monkeys made choices between pairs of different juices at varying quantities. On the basis of these choices, Padoa-Schioppa and Assad estimated the subjective value of each juice type at each quantity, and showed that a substantial number of their recorded neurons encoded that "offer value" on a common scale. fMRI studies soon yielded similar results. In one study, Kable and Glimcher examined how the value of immediate and delayed rewards is encoded in the brain by having subjects make choices between possible gains of different monetary amounts at different times of receipt (Kable & Glimcher, 2007). Critically, Kable and Glimcher used the participants' behavior to infer the subjective values that options of different delays and amounts held for each individual participant. They were then able to show that activity in three brain areas—the medial prefrontal cortex, the striatum (part of the basal ganglia) and the posterior cingulate cortex—is correlated with this measure of subjective value. This finding was of importance not just for neuroscientists but also for economists, because it was not compatible with a prominent economic theory of intertemporal choice. Thus, this study is a good example for the potential of neurobiological data to falsify existing economic theories and to generate constraints for new theories. Two of the same brain areas, the medial prefrontal cortex and the striatum, were also indicated as a common currency valuation system in another study published the same year. In that study, Tom, Fox, Trepel, & Poldrack (2007) compared the effect of anticipated rewards (monetary gains) and anticipated punishments (monetary losses) on neural activation in the whole brain. Activity in the medial prefrontal cortex and the striatum was modulated by the magnitude of both rewards and punishments. When participants anticipated a larger reward, activity in these two brain areas increased. When participants anticipated a larger loss, activity in the same brain areas decreased. Moreover, activation patterns reflected the individual's idiosyncratic aversion to losses, as estimated from their behavior. These two initial studies in humans were followed by a surge of studies examining various aspects of the neural representation of value.

Subsequent studies have shown that the same brain areas encode the value of a host of different rewards and punishments, including appetitive (Levy & Glimcher, 2011) and aversive (Plassmann, O'Doherty, & Rangel, 2010) food items, as well as other consumables (Chib, Rangel, Shimojo, & O'Doherty, 2009). A recent meta-analysis (Bartra, McGuire, & Kable, 2013) of over 200 of these studies confirmed this notion of a single, common-currency, valuation system.

The Learning of Subjective Values

Where do these values encoded in the medial prefrontal cortex and the striatum come from? One of the main sources of information about value is learning by experience, another area where research has made great strides. Substantial research has pointed to a role of the neurotransmitter dopamine in this type of learning (Dayan & Niv, 2008). In a seminal work, Schultz, Dayan, & Montague (1997) have shown that a theoretical algorithm from computer science (Sutton & Barto, 1998) provides a surprisingly good description of the activity of dopaminergic neurons in the monkey brain stem. The firing rate of these neurons seemed to signal the difference between the obtained and expected juice rewards, or the "reward prediction error," a signal that can drive learning. At the start of the experiment, juice was generally unexpected, and so whenever the monkey received a drop of juice, the dopaminergic neurons increased their firing rate. With time, however, the monkey learned that rewards were associated with visual or auditory cues that preceded them. He learned, for example, that after hearing a certain tone, he was likely to receive a reward. The intriguing observation of Schultz and his colleagues was that in the course of learning the dopaminergic neurons shifted their response from the reward to the reward-predictive cue. After several presentations of the cue followed by the reward, the appearance of the cue fully predicted the subsequent reward, which therefore did not generate a "reward prediction error" any longer. The cue itself was now the unpredicted rewarding event, and it was in response to these predictive cues that the dopaminergic neurons now increased their firing rate. Similar reinforcement learning signals have now been observed by many groups in several brain areas in both animals and humans. For example, fMRI studies have identified neural signals that reflect prediction errors in the striatum, a major target area of dopaminergic projections (O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003). This type of learning is known as "model-free"—discrepancies between expected and actual outcomes directly affect future expectations. More recent studies have also turned to examine "model-based" types of learning, in which the animal or the human constructs a cognitive model of the decision

situation, taking into account internal and external factors beyond the simple stimulus–outcome associations. These studies have identified neural correlates of both model-free and model-based learning (Daw, Gershman, Seymour, Dayan, & Dolan, 2011), and suggest a promising avenue for probing individual differences in value learning.

SOCIAL DECISION MAKING

Decisions are seldom made in isolation. An increasing number of neuroe-conomics studies incorporate social aspects in their experimental designs. Behavioral economics provides a convenient framework for many of these studies in the form of game theory. Von Neumann and Morgenstern, the fathers of the EU theory, also laid out the basis for game theory, in which decisions are affected by choices made by many players with competing interests. These decisions are complicated, because they require the decision maker to infer the beliefs and intentions of other behaving agents, and these beliefs and intentions in turn also depend on the decision maker's actions. Although humans and animals typically deviate in their behavior from the precise predictions of the theory, game theory, just like EU theory, provides a useful benchmark for quantifying these behavioral deviations and searching for their neural correlates. In monkeys, these studies usually employ simple paradigms, such as the well-known *rock-paper-scissors* game. In one example, using the slightly simpler game of *matching pennies*, Lee and colleagues (Lee, 2008) have examined how monkeys' choices are affected by changes in the strategies of their opponent. In matching pennies, each of two players chooses one of two available options. One player wins if both players make the same choice, the other wins if the choices are different. The monkey played the game against a computer opponent, whose game strategy was systematically manipulated by the experimenters. What they changed, essentially, was the degree to which the computer exploited the monkey's choice history in making its own choices. The researchers found that monkeys were, in fact, able to adapt their behavior, making their choice patterns more random, and thus more difficult to exploit, with each increase in the computer's level of sophistication. While the monkeys were playing that game, the experimenters recorded the activity of neurons in the dorsolateral prefrontal cortex and found that those neurons encoded the monkey's past choices and rewards (Barraclough, Conroy, & Lee, 2004), providing information that could be used to update the monkey's estimate of future rewards.

In humans, more complex game-theory-based paradigms are frequently used, examining levels of trust, cooperation, and preferences for the well-being of others. McCabe, Houser, Ryan, Smith, & Trouard (2001) were

the first to use game theory in an fMRI experiment, in which participants had to decide whether to trust another player. Results showed that those participants who tended to trust their opponents had higher neuronal activation in regions of the medial prefrontal cortex while playing against humans compared to playing against computers. A similar trust game was used a few years later by Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr (2005), but, critically, in their study the brain levels of oxytocin, a neuropeptide that is thought to play a role in social attachment, were increased before they made their decision. Kosfeld and colleagues found that those participants treated with oxytocin were subsequently more trusting, compared to a control group. This study is probably the earliest example demonstrating the potential role for neuroscientific data in shaping economic theory. Game-theory paradigms are also used to probe mentalizing processes, namely, the ability of humans to understand the mental states of others and to predict their behavior based on this understanding (Hampton, Bossaerts, & O'Doherty, 2008). Finally, a few studies have directly examined charitable giving, revealing neural activity in reward-related brain structures in response to charitable donations, even when those were mandatory (Harbaugh, Mayr, & Burghart, 2007). While one should be careful of making inferences from neural activation about behavior, this result is consistent with an account of "pure altruism," suggesting that people are capable of experiencing rewarding sensations in response to the good fortune of others.

OPEN QUESTIONS AND FUTURE DIRECTIONS

The field of neuroeconomics continues to expand. Many questions have been at least partially answered, but many more are still waiting to be solved. In the next few years, neuroeconomics will continue to look for the missing pieces for a comprehensive understanding of the neural architecture of decision making. At the same time, it is likely to broaden its scope to additional questions. In particular, a promising avenue for neuroeconomics research is to apply its rigorous analytical tools to the study of impaired decision processes, which are common in mental disorders.

A Complete Model of Choice

One of the major goals of neuroeconomics is to obtain a complete neural model of the choice process. While we know a great deal about how values are encoded in the brain, it is less clear how those values are used to produce choice. How are values compared to each other to select the option of the highest value? How does this selection in turn guide action? Recent findings

suggest that at least part of the choice process takes place in the medial prefrontal cortex, the same brain area whose activity also represents the values of available options. Single-unit recordings in monkeys (Strait, Blanchard, & Hayden, 2014) and magnetoencephalography (MEG) recordings in humans (Hunt *et al.*, 2012) identified signals in this brain area whose magnitude was correlated with the difference between the values of available options, an essential computation for choice. Choice-related signals were also identified, however, in the activity of neurons in the posterior parietal cortex (Louie & Glimcher, 2010). The posterior parietal cortex is ideally suitable to accommodate a choice process. First, it is spatially organized such that activity of specific neurons is linked to specific spatial locations, and can therefore conveniently encode the subjective values of items in these spatial locations. Second, a choice generated in this brain region can be directly communicated to the appropriate motor brain areas, to generate the required motor action that will implement the choice. More research is needed to paint a full picture incorporating the different components of the choice process. This picture will likely also involve additional brain areas that have been shown to have a role in valuation and choice, such as the posterior and anterior cingulate cortices, the amygdala and the insula.

THE NEUROECONOMICS OF PSYCHIATRY

The bulk of neuroeconomics research focuses on healthy individuals, in an attempt to illuminate the neural mechanisms underlying decision-making processes in the intact brain. Recently, however, a few researchers have begun to apply neuroeconomics techniques to the study of mental illness (Sharp, Monterosso, & Montague, 2012). This extension of the scope of neuroeconomics research from the normal to the abnormal seems obvious. Current psychiatric research is largely based on self-report questionnaires. While certainly useful, such questionnaires may be biased, as they require the individual to reflect upon behavior. Instead of asking participants what they *would* do, neuroeconomics techniques allow researchers to observe what participants *actually do*, and to study the neural mechanisms of this actual behavior. Neuroeconomics is likely to offer novel insights on mental disorders, which could direct more personally tailored interventions.

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