

# NeuroEconomics: An overview from an economic perspective

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## Abstract

Until now, economic theory has not systematically integrated the influence of emotions on decision-making. Since evidence from neuroscience suggests that decision-making as hypothesized in economic theory depends on prior emotional processing, interdisciplinary research under the label of “neuroeconomics” arose. The key idea of this approach is to employ recent neuroscientific methods in order to analyze economically relevant brain processes. This paper aims to provide an overview of the current state of neuroeconomic research by giving a brief description of the concept of neuroeconomics, outlining methods commonly used and describing current studies in this new research area. Finally, some future prospects and limitations are discussed.

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## 1. Introduction

Economics traditionally conceptualized a world populated by rational, self-interest guided, unemotional maximizers. Despite the undisputable success of economic models based on the homo oeconomicus concept, their limitations are nowadays hard to ignore. Experimental and behavioral economics have repeatedly revealed deviations from this classical theory. Subjects show non-opportunistic or reciprocal behavior and other “anomalies” and “paradoxes” that are not explicable with the traditional concept [17]. Consequently, psychological ideas were formalized and translated into testable predictions, thus leading to extended models of economic behavior. Rather than ignoring non-rational behavior, concepts like bounded rationality, bounded willpower or bounded self-interest arose and it was realized that economic behavior is frequently influenced by emotions and subconscious processes [5,39]. Since these “anomalies” were replicated in field experiments [44] focusing on the homo oeconomicus does not seem to be a promising option for advanced economic research [16,70,76].

Consequently, in the early 1970s extended economic models were developed using inputs from other scientific fields.

For instance, the integration of psychology led to the development of *behavioral economics* [15,59], out of which several new models on decision-making evolved. A well-known example is depicted in Fig. 1. It contains a dual-process model that distinguishes between the two systems “intuition” and “reasoning”.

This model was introduced to explain seemingly contradictory results of experimental studies of judgments under uncertainty. Despite their unquestionable explanatory value, “intuition” and “rationality” are theoretical constructs. The existence of these underlying cognitive systems was postulated from observation and analysis of behavior, which in turn is used to explain behavior. Criticism from traditional economics concerns this *circular reasoning* as well as the fact that – in contrast to market shares, unemployment rates and economic growth – theoretical constructs are neither observable nor objectively measurable. The only way to solve this dilemma was to use tools or methods that enable researchers to investigate behavior in a new, more objective way. Since neuroscience provides these tools, researchers in several disciplines started to use neuroscientific tools in order to observe brain activities that underlie behavior.

However, the approach to analyze behavior from a neurobiological perspective offers different possibilities. Our ability to explain behavior scientifically with any kind of

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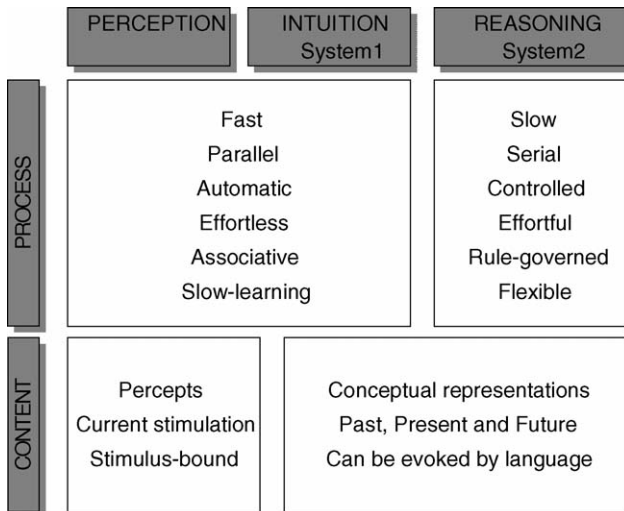


Fig. 1. Dual process model taken from [36].

analysis depends on the complexity of the respective system on one hand, and the available scientific tools on the other hand.

It is a futile attempt to try and explain the function of a human brain based on modeling individual activities of all estimated  $10^{11}$  neurons and their interactions. Models must reduce this complexity by defining larger structures as functional units. With presently available methods, neuroscience allows to investigate brain structures that can be looked upon as such functional units.

Attempting to link both disciplines – economics and neuroscience – it becomes evident that they have to learn a lot from each other [5,71]. The protagonists of this interpretation defined *neuroeconomics* as the application of neuroscientific methods to analyze and understand economically relevant behavior [16]. This definition represents the current mainstream understanding of neuroeconomics. Compared to the model of the *homo oeconomicus* it implies a totally different idea of man. From a neuroscientific perspective his counterpart is the *homo neurobiologicus*, whose behavior and social and economic nature are the result of neurobiology. It is the latter that largely determines his thinking and feeling, deciding and acting, as well as his buying and selling, i.e. his economic life [5]. In this understanding neuroeconomics can contribute to create models of economy that are based on a realistic description of human behavior and the comprehension of the driving forces of this behavior.

Appreciating possible contributions of neuroscience to economic modeling requires a basic understanding of the applied neuroscientific methods such as functional imaging of the brain. Section 2 therefore provides an introduction to these methods for economists. Results from current neuroeconomic research are outlined in Section 3. Possible implications for economic theory will be discussed and future research prospects will be envisioned in Section 4.

## 2. Overview of selected neuroimaging techniques currently used in neuroeconomics

In principle all kinds of neuroscientific tools can be used to investigate economic decision-making. Table 1 summarizes the prevalent methods currently employed in neuroeconomic research. They can be roughly grouped into two categories according to the underlying mechanisms: procedures for measuring electromagnetic activity of the brain and those sensitive to changes of cerebral blood flow or metabolism.

### 2.1. Electromagnetic recordings

#### 2.1.1. Electroencephalography (EEG)

EEG measures voltage fluctuations on the scalp. The underlying ion currents occur rather remote from the electrodes (across skin, skull and meninges) in surface-near cortex areas and result from changes in membrane conductivity elicited by synaptic activity and intrinsic membrane processes [46]. An electrode on the skin virtually “sees” the summed potentials generated by a large number of neurons.

While EEG with a temporal resolution of milliseconds and below can easily detect the time course of neural activity, spatial resolution is mainly limited by the so-called *inverse problem* [35]. As an infinite number of source configurations can generate identical potentials on the skin, estimated solutions of the inverse problem, i.e. source localization, therefore require appropriate a priori assumptions about sources and volume conduction to yield physiologically meaningful data [4,51].

#### 2.1.2. Magnetoencephalography (MEG)

MEG is sensitive to changes of magnetic fields that are induced by the electrical brain activity. The temporal resolution can be compared to that of the EEG, so that this modality can, e.g. resolve the temporal sequence of different cortical activities involved in decision-making [9]. However, in contrast to the EEG, MEG is also able to depict activity in deeper brain structures [2,8,9]. The *inverse problem* basically applies to MEG as well, so that source localization depends on valid assumptions, too. Integrating the different brain imaging techniques could further improve currently existing models of source localization [46].

Table 1  
Frequently used neuroimaging techniques

Changes in electric activity	Changes in cerebral blood flow/metabolism
Electroencephalography (EEG)	Positron emission tomography (PET)
Magnetoencephalography (MEG)	Functional magnetic resonance imaging (fMRI)

## 2.2. Methods measuring metabolic or hemodynamic responses to neural activity

### 2.2.1. Positron emission tomography (PET)

Positrons, the antiparticles of electrons, are emitted by certain radio-nuclides. These nuclides have the same chemical properties as their non-radioactive isotopes and can replace the latter in biologically relevant molecules. After injection or inhalation of tiny amounts of these modified molecules, e.g. modified glucose (FDG) or neurotransmitters, their spatial distribution can be detected by a PET-scanner. This device is sensitive to radiation resulting from the annihilation of emitted positrons when they collide with ubiquitously present electrons. From the detected distribution information concerning metabolism or brain perfusion can be derived and visualized in tomograms. Spatial resolution is quite high (about 3–6 mm), but temporal resolution is low (several minutes to fractions of an hour). As radioactive tracers are used, the application to healthy test persons is restricted.

### 2.2.2. Functional magnetic resonance tomography (fMRI)

fMRI is currently the most frequently used functional brain imaging technique. Magnetic resonance scanners produce sets of cross sections – tomograms – of the brain, exploiting weak but measurable resonance signals that are emitted by tissue water in a very strong magnetic field after excitation with a high frequency electromagnetic pulse. The acquired resonance signals can be attributed to their respective spatial origin, and cross sectional images can be calculated. The signal intensity, coded as gray value of a picture element, depends on water content and certain magnetic properties of the local tissue. In general, structural MR imaging is used to depict brain morphology with good contrast and high resolution.

The ability to visualize brain function by MRI depends on the fact that increased neural activity of a brain region is followed by a hemodynamic response. Albeit the mechanisms of this so-called *neurovascular coupling* are still not fully understood, the increased perfusion of activated brain tissue is the basis of the so-called Blood Oxygenation Level Dependent (BOLD)-effect: hemoglobin, the oxygen carrying molecule in blood, has different magnetic properties depending on its oxygenation state. While oxy-hemoglobin is diamagnetic, deoxy-hemoglobin is paramagnetic, i.e. it locally distorts the magnetic field, leading to a local signal loss. In activated brain tissue the increased oxygen consumption is overcompensated by the blood flow response. Thus, during activation deoxy-hemoglobin is partly replaced by oxy-hemoglobin, leading to less distortion of the local magnetic field, i.e. to increased signal intensity.

In contrast to PET-scans, no absolute levels of brain activity can be measured. The well-known color-coded statistical parametric activation maps (SPMs) are generated from elaborate statistical analyses of fMRI time series comparing signal intensity during different activation states.

Temporal and spatial resolution of fMRI depends on scanning technology on the one hand and on the underlying physiology of the detected signal intensity changes on the other hand.

With current scanner technology structural images are usually obtained with a resolution of about 1 mm × 1 mm × 1 mm voxels (the equivalent of a pixel (picture element) in a volume), while fMRI voxels typically have edge lengths of about 3–5 mm. As a rule temporal resolution of fMRI is between 1 and 3 s. For evaluation one must take into account that the cerebral blood flow (“CBF”) response to a brain activation is delayed by about 3–6 s.

The unquestionable attractiveness of the method results from a balance between temporal and spatial resolution on the one hand, allowing whole brain scans in less than 3 s, and on its non-invasiveness on the other hand, permitting repeated measurements in healthy volunteers *ad libitum*. In addition, the choice of scanning parameters allows increasing one parameter at the expense of the other. Recent fMRI approaches show that for some neural systems the temporal resolution can be improved down to milliseconds [56] and spatial resolution can be increased to the level of cortical columns as basic functional units of the cortex [37].

In summary, all currently available neuroimaging techniques have advantages and disadvantages. While the *where* of brain activity is more easily assessed by fMRI or PET, the question of *when* – e.g. the discrimination between parallel and sequential processing – can be more precisely answered by EEG or MEG. Thus, the method (or even a combination of several techniques) should be chosen carefully, depending on the economic question to be answered.

## 2.3. An outline of neuroeconomic studies

### 2.3.1. Study design

At the beginning of a neuroeconomic project a meaningful problem or hypothesis must be formulated. Already this first step is sometimes difficult to accomplish, because scientists of both involved fields – i.e. economists and neuroscientists – need to cross the borders between different approaches and terminologies to be able to communicate and understand each other’s methods and scientific problems.

After developing a hypothesis the applicability of neuroscience, i.e. its ability to answer the question specified should be ascertained. Subsequently, the most suitable method or combination of methods needs to be determined. Translating the scientific question into a sound stimulation paradigm or study design, as devoid of possible confounders as possible, constitutes another critical issue. Various mistakes can be made right at the beginning of a study that may later obstruct data analysis (see R. Savoy’s article in this issue).

### 2.3.2. Comparing brains

When neuroeconomic studies collect data from groups of individuals, there are certain steps to be taken to enable data analysis across several individuals. Trivial as this might

sound: like fingerprints there are no two brains identical to each other. In order to be able to compare activations across individual subjects, the brains are usually spatially *normalized* to a template brain, i.e. they are transformed so that they are similar in overall size and spatial orientation. Generally, the aim of this transformation is to bring homologous brain areas into the closest possible alignment.

In this context the Talairach stereotactic coordinate system is used. Talairach and Tournoux [74] introduced three important innovations: a coordinate system to identify a particular brain location relative to anatomical landmarks; a spatial transformation to match one brain to another; an atlas describing a standard brain, with anatomical and cytoarchitectonic labels. The coordinate system is based on the identification of the line connecting the anterior commissure (AC) and posterior commissure (PC)—two relatively invariant fiber bundles connecting the two hemispheres (see Fig. 2). This line, the AC–PC line, defines the y-axis of the brain coordinate system. The origin is set at the AC. The z-axis is orthogonal to the AC–PC-line in foot–head direction and passes through the interhemispheric fissure. The x-axis is orthogonal to both the other axes and points from AC to the right. Any point in the brain can be identified relative to these axes, which define the Talairach coordinate system.

A lot of analysis software like, e.g. SPM currently uses templates created by the Montreal Neurological Institute (MNI), based on the average of many normal MR scans. Although similar, the Talairach and the MNI templates are not identical, and care has to be taken to assign localizations given in MNI coordinates correctly to, e.g. cytoarchitectonically defined brain areas like the Brodmann areas (see below). Due to the great variability of brain anatomy and function this problem is anything but trivial. A detailed description of this issue can, e.g., be found in [12].

### 2.3.3. Data interpretation

The fact that certain brain functions, like speech or vision, are processed in dedicated brain areas has been common

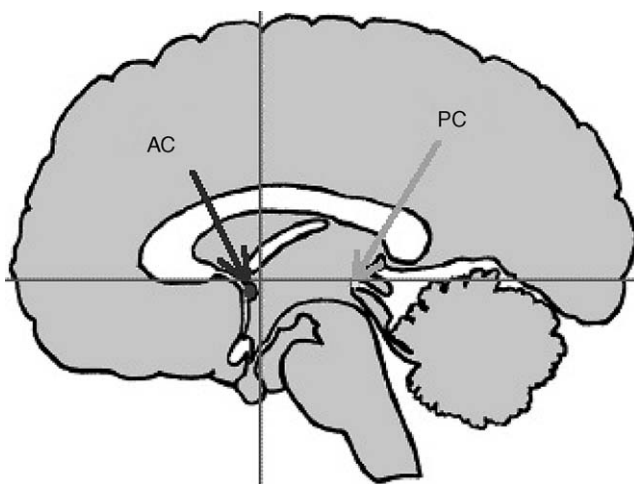


Fig. 2. The AC–PC-line.

knowledge for quite some time. Before the emergence of non-invasive neuroimaging techniques patients with brain lesions caused by trauma or disease were studied. Since then it is known that for instance the destruction of parts of the occipital lobe leads to cortical blindness, and aphasia can be a consequence of lesions in the temporal (Wernicke's area) or frontal lobe (Broca's area). More complex functional losses result from lesions of the ventromedial prefrontal cortex, as in the well-known case of Phineas Gage. When this part of his frontal lobe was destroyed in an accident 1848 his personality and social behavior were severely altered, whereas his intellectual capabilities largely remained intact [73].

Experiments with intra-operative direct brain stimulation can be given as an example of other historic sources of knowledge about localizing brain functions [58].

Another, older, approach to describe brain localizations is derived from microscopic anatomy. The foundations were laid by Brodmann almost 100 years ago [13]. According to variations of cytoarchitecture in stained brain sections he divided the human cortex into 52 distinct areas, the Brodmann areas (BAs, Fig. 3).

The convention of relating activation foci to these cytoarchitectonically defined areas was adopted early in functional imaging and results of activation localizations are often ascribed to BAs in neuroimaging studies (for example, see [24]). However, their microanatomical (rather than functional) derivation has to be kept in mind. Although for some areas (e.g. the motor cortex, BA 4) there seems to be a good correlation between areas delineated by cytoarchitecture and their function, this relation is less certain for other areas (for details, see [12]). A closer correlation may possibly be revealed by recent microanatomical approaches, utilizing, e.g. receptor autoradiography to analyze the regional and laminar distribution of various neurotransmitter receptors in order to delineate distinct brain areas [82].

Currently our knowledge about the localization of even more complex brain functions (e.g. decision-making or emotions) is expanding at an enormous pace, which is mainly due to the development of non-invasive brain imaging research techniques. The sources of knowledge mentioned above resemble only a fraction of the various available methods, which as a whole provide the necessary background for the interpretation of neuroeconomic studies. It should be noted, however, that even the most refined neuroscientific tools currently available are rather coarse compared to the complexity of our central nervous system and that we are far from an in-depth understanding of the brain. For a rather compact review of the history and future of *Human Brain Mapping* see, e.g., Ref. [65].

## 3. Current topics in neuroeconomic research

### 3.1. Preferences

*Preferences* play a substantial role in economic theory [70,72] since they have a significant influence on economic

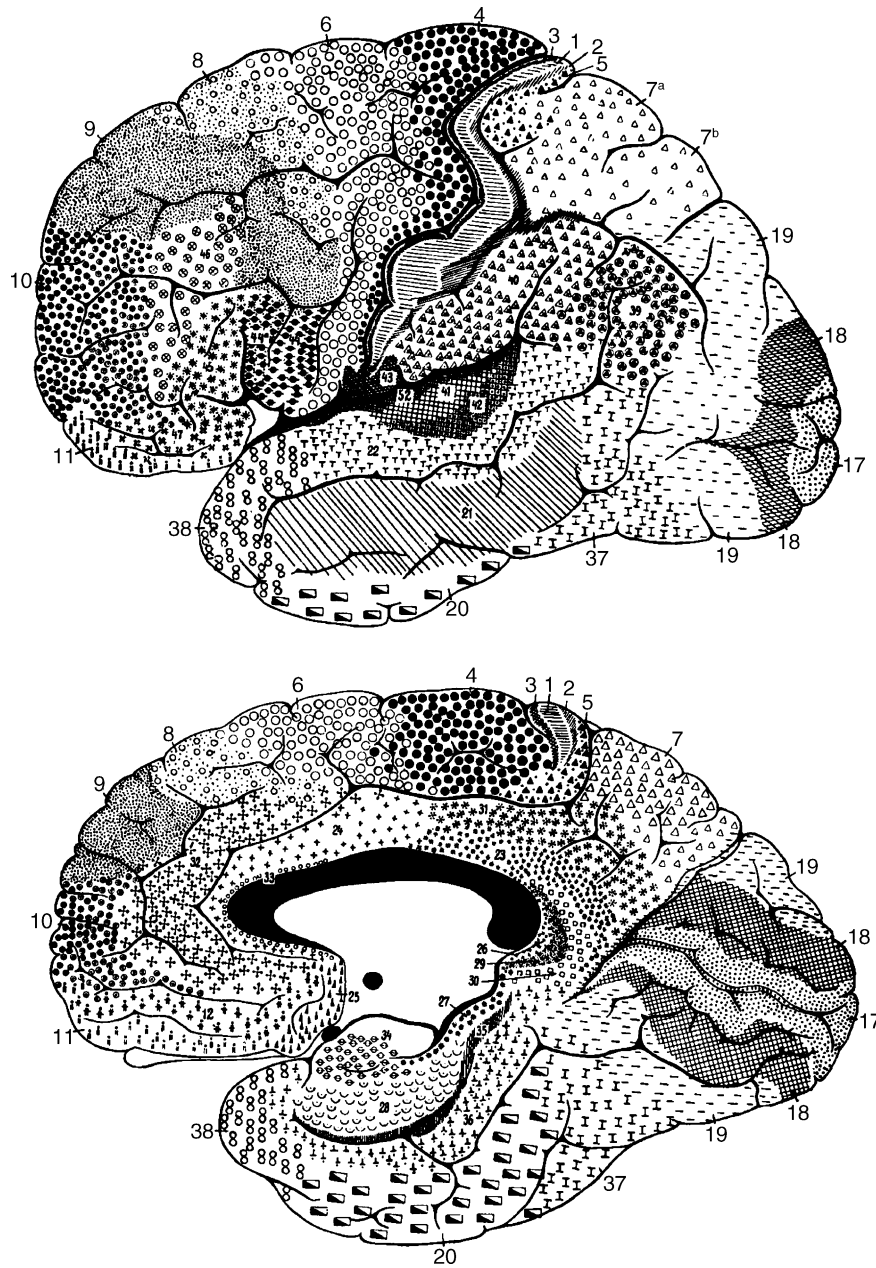


Fig. 3. Lateral and medial aspect of the human brain. The Brodmann areas (BAs) are represented by the various symbols.

decision-making (e.g. brand preferences). Moreover, preference judgments, i.e. selecting one of several brands in a department store, occur frequently in every-day life.

Until recently *preference* – as a theoretical term – could not be observed directly and had to be assessed for instance by questionnaires or observation of behavior. By now neural correlates of preference were detected in several neuroimaging studies. For instance, Deppe et al. [24] could show that in a simulated buying decision task between sensorily similar fast moving consumer goods only a subject's preferred brand elicited a distinct mode of decision-making. In their fMRI-study, 22 subjects were asked to make binary deci-

sions between different brands of sensorily nearly undistinguishable consumer goods. As one result Deppe et al. found reduced activation in the dorsolateral prefrontal, posterior parietal and occipital cortices and the left premotor area (Brodmann areas 9, 46, 7/19 and 6) only when the target brand was the subjects' favorite one. Simultaneously activity was increased in the inferior precuneus and posterior cingulate (BA 7), right superior frontal gyrus (BA 10), right supramarginal gyrus (BA 40) and most pronounced in the ventromedial prefrontal cortex ("VMPFC", BA 10).

There are some more studies that indicate that the VMPFC is a central neural substrate in preference judgment [49,57].

In future it might be possible to reveal differences in cortical processing of seemingly similar preferences or show that ostensibly different preferences have a similar neural correlate [79]. For instance there might be preferences that are predominantly influenced by emotions or other more deliberative ones. Based on the fact that highly emotional events are often remembered clearly, vividly and with great detail, one can hypothesize that preferences built on emotions are more robust than preferences built on deliberation. Sharot et al. support this hypothesis [68].

A better understanding of preferences might be useful for more concise predictions of market reactions (e.g. to advertising) or estimations of elasticity of demand [16].

### 3.2. Utility and the rewarding system

Measuring the utility derived from a good objectively presents a problem for researchers, because utility is always subjective and depends on the circumstances. The neural bases of the (expected and experienced) *utility* constitute a further facet of neuroeconomic research (for a delineation of the concept of utility and preference see [27]). However, neuroeconomic methods might contribute to solve these problems, because in several studies where people gain some useful good (i.e. money, juice or other incentives) by judgments, activation can be observed in the so-called “reward areas” of the brain ([29]; see also the article of Peterson et al. in this issue). Therefore, the “feeling” of utility may correlate with the activation in the rewarding systems of the brain.

It is possible that activity in this rewarding system also influences investor behavior, e.g. the general disposition to sell winners too early (see Ref. [69] and [55]). Investing money and gaining returns might correlate with activation in the rewarding systems of the brain, e.g. the ventral striatum [53] or more general the orbitofrontal prefrontal cortex–amygdala–Nucleus Accumbens (NAc)–circuit [50]. Knutson and Peterson [40] find that monetary payoffs induce some activation in the Nucleus Accumbens. The NAc is densely innervated by dopaminergic fibers originating from neurons in the midbrain [53]. As it is possible that the greater release of dopamine after an unexpected reward leads to accepting a risk more easily [5] it is also possible that dysfunction in the OFC–amygdala–NAc reward circuit might explain extreme risk-seeking behavior in some cases.

### 3.3. The social brain: fairness, altruism and trust

While preferences and utility are due to research on *individual* decision-making, neuroeconomics also covers the field of social behavior (e.g. cooperation). As outlined before, in classical theoretical approaches the assumption of self-interest is crucial to modeling economic decision-making. However, if this assumption is juxtaposed to the data acquired from studies in experimental economics, various problems arise (see e.g. [10,34,54]). In the ultimatum game, two players are offered a chance to win a certain amount of money.

One of the players (the proposer) suggests how to split the money. The responder may accept or reject the offer. If he accepts, both get the share agreed to, if he refuses the offer, none of them receives any money. Obviously, a selfish homo oeconomicus will offer his opponent the smallest share possible because game theory suggests that the responder will accept it. Yet in experiments conducted by game theorists the most frequent outcome is a fair (i.e. 50:50) share [17]. Moreover, several studies report that in about 50% of all games responders who are offered some 20% off the total amount choose to reject the offer although this means missing out altogether [15]. Why do people do this? With fMRI Sanfey et al. were able to prove that perceived *unfairness* correlates with activations in particular regions of the brain, i.e. the anterior insula and the dorsolateral, prefrontal cortex (“DLPFC”) [64]. What does this mean to economists?

1. *Anterior insula* activation is consistently seen in neuroimaging studies focusing on pain and distress [25], hunger and thirst [75] and autonomic arousal [19]. The insula has also been dealt with in surveys on emotion, in particular involvement in the evaluation and representation of specific negative emotional states [14]. Consequently, the activation in the anterior insula is a reflection of the responders’ negative emotional response to an unfair offer [64].
2. In contrast to the insula region, the *DLPFC* is usually linked to cognitive processes such as goal maintenance and executive control [52]. Thus, the DLPFC activation observed by Sanfey et al. may indicate that despite the unfair offer, people still try to accomplish the goal of accumulating as much money as possible. As indicated by the higher rejection rates, an unfair offer is more difficult to accept. Hence higher cognitive effort may be required to overcome the strong emotional tendency to reject the offer [64].

Conceivably, people in the ultimatum game experience conflicting emotions when confronted with unfair offers. Up to a certain level, the DLPFC controls the action. Therefore, one accepts the offer although it might not be fair. But if the offer decreases, the activation in the insula gets more intense up to the point where emotion dominates and the offer is rejected. Possibly, people behave this way in order to avoid negative feelings, i.e. the feeling of having accepted an unfair offer. Neuroscientists suggest that this kind of behavior may be rooted in evolution [5]. This notion corresponds to some statements in economic literature [7,54,78]. Moreover, recent studies about evolution theory support this supposition and demonstrate that in groups of people both fairness and defection inevitably occur [26]. An fMRI-study conducted by McCabe et al. supports this assumption. Based on the evidence that the ability for mental state attribution involves the prefrontal cortex, McCabe and colleagues hypothesized that this area is involved in integrating theory-of-mind-processing and cooperative actions. Studying lesions implies that the PFC is engaged in social cooperation [63]. Therefore, we

can conclude that there is a relation between the activity in the PFC and the ability to cooperate with other humans.

In a similar context the existence of *altruistic punishment* arises. “Altruistic punishment” means that individuals punish others, although the punishment is costly for them and yields no material gain [31]. In an experimental economic study Fehr and Gächter hypothesized that *free riding* causes strong negative emotions. These emotions trigger (altruistic) punishment [31]. In a complementary PET-study, de Quervain et al. were able to prove that people derive “satisfaction” from punishing norm violations and that the activation in the dorsal striatum reflects the anticipated satisfaction from punishing defectors [22]. In the light of these results one might say that altruistic people who punish others for transgressing a rule tend to reward themselves for their behavior. For this kind of behavior brain areas such as the striatum and the medial prefrontal cortex have been shown to play an important role [39]. As evidenced by several MRI-studies on the prisoner’s dilemma, cooperation is associated with activations in brain areas that have also been linked to reward processing [61]. Integrating these results into studies on organizational behavior to help explain the interplay of intrinsic and extrinsic reward, e.g. in the context of the *motivation crowding effect* [32], might be interesting.

The construct of *trust* might be based on concepts similar to altruism [20]. Trust is generally considered a precondition to achieve economic growth, individual income, democratic stability, government performance and, in general, cooperation [3]. Since cooperation is a basic element of modern societies, investigating trust is high on the agenda of economic research. In classical theoretical approaches trust is defined as a rational calculation. For instance, a specific model explains the existence of trust by means of three variables: (1)  $p$ , the likelihood of making a profit (a gain). This equals the probability that the recipient of trust actually behaves in a trustworthy manner; (2)  $L$  (for losses), the potential loss that occurs if trust is betrayed and (3)  $G$  (gain), the potential gain if the recipient of trust in fact proves to be trustworthy [18]. The normative hypothesis of this model is that an actor will always be trusted if the following assumption applies:

$$p \times G > (1 - p) \times L$$

This simple model seems convincing but it leads to some kind of “trust mathematicum”, computed trust [77]. In practice, a number of questions remain unanswered: how would the ‘giver of trust’ determine the exact value of  $p$  in an unfamiliar situation, for example, at the beginning of a new business relationship? If all actors by definition behave opportunistically, where does trust evolve? And why does trust exist between anonymous traders on the Internet [6]? It seems far more realistic that trust built on the basis of simple and emotional heuristics and will be reciprocated within certain limits. By now, there are first studies that investigate the influence of hormones like oxytocin [81] or cortisol (see the article of Takahashi in this issue) on trust. In order to measure neural

correlates of trust using event-related hyperscan-fMRI (“h-fMRI” which means that two volunteers are measured parallel in two scanners), King-Casas et al. made a simple modification to a single-exchange trust game to make the model more realistic by changing the originally single-round format to a multi-round format in which the same two individuals (one designated the “investor”, and the other the “trustee”) played 10 consecutive rounds. Their findings suggest that especially the caudate nucleus is involved in trust-building and reciprocity in economic exchange [38]). The caudate nucleus is commonly active when learning about relations between stimuli and responses [66].

### 3.4. Insights on dynamic concepts: learning, memory and knowledge

In western economies innovations are considered important for economic growth. Therefore, economic policy is aiming to establish an innovative, knowledge-creating society [41]. One major concept in the context of knowledge management is *learning*. So far, economic researchers know little about the neural foundations of learning [76]. Therefore, a theory of learning may be closely connected to the field of neuroeconomics [80]. A good starting point for this theory might be the *prediction error hypothesis* [50,60]. The core concept of this hypothesis is the prediction error  $\delta(T_i)$ . It is defined as followed:

$$\delta(T_i) = r(T_i) + \gamma V(T_{i+1}) - V(T_i)$$

where  $r$  is the occurrence of rewards at a current instance  $T_i$  in a sequence of time steps  $T_i$  [ $i = 1, 2, \dots$ ],  $V(T_i)$  an estimated value as a function of  $T_i$  and  $\gamma$  is a scale factor for future rewards. When  $\delta$  is positive, then the estimation  $V(T_i)$  was too pessimistic and vice versa. It is suggested that dopaminergic neurons generate a prediction error signal correlates with  $\delta(T_i)$  [5,60]. Several studies have been performed to test this hypothesis with fMRI [50]. By now, fMRI experiments have identified a set of reward related brain structures including the OFC, the amygdala, the ventral striatum and the medial prefrontal cortex.

If one defines *knowledge* as individual problem-solving capability, it is evident that memory and learning are the fundamental bases of knowledge. For instance, if in an experiment consumers have to judge whether the price for a certain product is acceptable or not, they have to be aware of the common price. In practice it is well-known that people are not able to name prices for a wide range of products in all kinds of business sectors [30]. Therefore, it seems possible that price has only little influence on buying behavior. As anybody can imagine, in most cases the opposite is true. How can this be explained? Price knowledge for some products could be assumed to become an automatic process which is typically hard to articulate as price-decision may be unconscious [62]. Or, as Bechara and Damasio pointed out [5]: “Thus knowledge without emotional signaling leads to the dissociation between what one knows or says and how one

Table 2  
Overview of first neuroeconomic studies (in chronological order)

Author	Theoretical background	Problem	Method	Results
Breiter et al. [11]	Behavioral decision theory, prospect theory	Neural responses to expectancy and experience of monetary gains and losses	fMRI	Activation changes in the sublenticular extended amygdala (SLEA) and orbital gyrus were triggered by expected values of the prospects. Responses to experience of rewards increased monotonically with monetary value in the nucleus accumbens, SLEA, and thalamus. Responses to prospects and outcomes were generally, but not always, seen in the same regions. Overlaps with activation changes seen previously in response to tactile stimuli, gustatory stimuli, and euphoria-inducing drugs were found.
McCabe et al. [47]	Behavioral decision theory, game theory, particularly trust and willingness to cooperate	Neural correlates of cooperative behavior	fMRI	Within the group of cooperative subjects the PFC showed activation changes when subjects are playing a human than when they are playing a computer. Within the group of non-cooperators, no significant activation changes in the PFC between computer and human conditions were found.
Erk et al. [29]	Behavioral decision theory, social interactions	Neural correlates of social rewards	fMRI	Products symbolizing wealth and status lead to increased activity in reward-related brain areas.
Smith et al. [71]	Behavioral decision theory, game theory, in particular ambiguity, risk, gains and losses	Neural correlates of attitudes about monetary gains or losses and risk or ambiguity	PET	Participants turned out to be risk averse in gains and risk-seeking in losses; and ambiguity-seeking in neither gains nor losses. Interactions between attitudes and beliefs triggered neural activation changes in dorsomedial and ventromedial brain areas.
Sanfey et al. [64]	Behavioral decision theory, game theory, in particular ultimatum game	Neural correlates of decision-making processes during the Ultimatum Game	fMRI	Unfair offers lead to activity changes in brain areas related to both emotion and cognition. Increased activity in anterior insula for rejected unfair offers suggests an important role for emotions in decision-making.
Ambler et al. [2]	Behavioral decision theory	Neural correlates of product choices	MEG	Brain activations in product choice differed from those for height discrimination and a positive relationship between brand familiarity and choice time was found. Neural activation during choice task involved brain areas responsible for silent vocalization. Decision processes took approximately 1 s and can be seen as two halves. The first period seems to involve gender-specific problem recognition processes. The second half concerned the choice itself (no gender differences).
Knutson and Peterson [40]	Behavioral decision theory, expected utility	Neural correlates of monetary rewards, review of several studies	fMRI	Increasing monetary gains activates a subcortical region of the ventral striatum in a magnitude-proportional manner. This ventral striatal activation is not evident during anticipation of losses. Actual gain outcomes instead activate a region of



Table 2 (Continued)

Author	Theoretical background	Problem	Method	Results
de Quervain et al. [22]	Behavioral decision theory, altruism, cooperation	Neural bases of “altruistic punishment”	PET	the medial prefrontal cortex. During anticipation of gain, ventral striatal activation is accompanied by feelings characterized by increasing arousal and positive valence.
McClure et al. [49]	Behavioral decision theory, preferences	Neural correlates of preference for culturally familiar drinks	fMRI	Sanctions against defectors activate reward processing brain regions. For the anonymous task, a consistent neural response in the ventromedial prefrontal cortex is reported that correlates with subjects’ behavioral preferences for these beverages. In the brand-cued experiment, brand knowledge for one of the drinks had a dramatic influence on expressed behavioral preferences and on the measured brain responses.
McClure et al. [48]	Behavioral decision theory, temporal preferences	Neural correlates of immediate and delayed monetary rewards	fMRI	Two separate systems were found to be involved. Parts of the limbic system are activated by decisions involving immediate rewards. Activity changes in the lateral prefrontal cortex and posterior parietal cortex were triggered by inter-temporal choices. The relative engagement of the two systems is directly associated with subjects’ choices, with greater relative fronto-parietal activity when subjects choose longer term options.
Deppe et al. [24]	Behavioral decision theory, preference decisions of consumers	Influence of implicit brand information on individual economic decisions	fMRI	Only the presence of a subject’s favorite brand leads to a distinctive mode of decision-making, activating regions responsible for integrating emotions.
King-Casas et al. [38]	Behavioral decision theory, game theory, trust game	Neural correlates of trust reciprocity and reputation in a multi-round trust game	Hyperscan-fMRI	The authors suggest that the head of the caudate nucleus processes information about the fairness of a social partner’s decision and the intention to repay with trust.
Abler et al. [1]	Behavioral decision theory	Neural correlates of omission relative to receipt of reward (frustration)	fMRI	The authors found a neural correlates of frustration in form of decreased activation in the ventral striatum and increased activation in the anterior insula and the right medial prefrontal cortex.
Deppe et al. [23]	Behavioral decision theory, credibility judgments of news headlines in the context of different magazine frames	Neural correlates of framing effects and prejudgements	fMRI	The credibility of ambiguous news headlines is biased by the magazine brand, in which the news headline is published. These framing effects correlate with activation changes in the medial prefrontal cortex.

decides to act”, e.g. at the point of sale. Therefore, explicit price knowledge might follow some kind of inverted U-shape as function of purchase-frequency. It is low for both, products whose prices we really do not know and products the prices of which we only know by intuition or, gut feeling. In between it is high. Neuroeconomic research may provide some insights on this hypothesis by investigating the neural correlates of price knowledge.

### 3.5. Towards a neural theory of economic decision-making

Although the debate about the role of emotion, cognition, memory and information processing in decision-making has grown over the years, scientists have yet to reach a consensus on these terms (see e.g. [5]). This holds particularly true for the role of emotions in decision-making [5,43]. To the

best of our knowledge there are just a few articles published in major economic journals, which address the concept of emotions explicitly [5,28,43,45]. Perhaps economists have ignored the role of emotions in decision-making because of its “checkered history” [5]. However, when defining emotions as a collection of changes in body and brain conditions [5,21], neuroeconomic studies seem to be a promising approach to gain insights in the role of emotions in economic decisions. According to the literature in neuroscience, emotions play an important role in the survival of man [5,23]. Consequently, it seems to be quite logical, that many of our decision are influenced (not just biased in a negative sense) by emotions [33,80]. By localizing brain activity during specific decision and relating these functions neuro-anatomically, methods of functional brain imaging are able to visualize different dissociated neural networks which are assumed to be responsible for emotions in decision-making. It will be a challenging task for neuroeconomics to identify emotions significant for economic decision-making and the context in which they occur.

Introducing the *somatic marker hypothesis* Bechara and Damasio suggest that (economic) decision-making is influenced by somatic states that can be stimulated by so-called “primary” and “secondary inducers” [5]. “Primary inducers” are defined as learned states that cause pleasurable or aversive states. “Secondary inducers” are entities generated by the recall of a personal or hypothetical emotional event. According to this hypothesis several brain structures are involved in triggering somatic states in decision-making. The *amygdala*, which is seen “as a critical substrate in the neural system necessary for triggering somatic states from primary inducers”, plays a prominent role. In contrast, the *VMPFC* is crucial to triggering somatic states from secondary inducers. Unlike the amygdala response, which is sudden and habituates quickly, responses of the *VMPFC* are deliberately slow and longer lasting.

Although it has not been tested in economic decision-making yet, some researchers found evidence in favor of the somatic marker hypothesis. In the aforementioned study, Deppe et al. report some significantly increased activity in the *VMPFC* when subjects had to decide on their “first-choice-brand” [24]. Another important finding is reported in this issue by Deppe et al. In an event-related fMRI study, the authors show that individual activity changes in the *VMPFC* correlate with the degree of susceptibility of an individual to a judgment bias. Furthermore, the article of Volz et al. published in this issue provides evidence that a part of PFC, the posterior frontomedian cortex (BA 8), correlates with uncertainty in decision-making. These findings are consistent with the role of the *VMPFC* as suggested by the somatic marker hypothesis and provide new insights into how people address the problem of (economic) decision-making.

Until now there are only a few groups worldwide that explicitly conduct “neuroeconomic” research on economic decision-making. Table 2 shows a selection of the empirical

studies carried out in this field so far (other synopsis can be found in [16] and [80]).

#### 4. Conclusion and remarks

Although still a young discipline, neuroeconomics has made some interesting contributions to economic theory. While first studies can be characterized as explorative research, researchers now focus on concepts crucial to modern economic theory such as fairness, trust, altruism, memory, learning and knowledge. At present, investigations of decision-making processes, which have already been performed for decades, in both disciplines separately, are of particular importance. In order to gain a deeper understanding of the ‘economic man’, neuroeconomics broadens the concepts of behavioral economics by means of neuroscientific tools. These tools enable economic research on brain processes, which in economic research have so far been looked upon as black box.

Neuroeconomics deals with measurements of the actual behavior of man and related brain functions. It does not propose ideal or optimized models of behavior or systems. Especially, as in the field of neuroeconomics several disciplines cooperate, care must be taken to prevent misinterpretation of experimental results.

All measurement techniques employed to investigate brain functions in principle give physical information about specific physical measures. For most techniques it is generally accepted that these measures allow statements about brain functions, however, the measures remain indirect, and statements that are valid in a certain setting may not be valid at all in a different one. Brain function is still a field with many open questions, and while there are functional relations that are understood in general, the more detailed processes are still unclear.

The fact should always be remembered that in a strict sense most experiments are only able to give evidence for a correlation between fulfilling a specific task and brain activity of specific areas. This must not be misunderstood as a proof for an actual causal relation.

Similar to psychology, models can be built that allow to relate (normal or pathologic) behavior of man to individual brain activities. However, it is always mandatory to state the limits, outside which the model is not valid, and one has to be aware of the fact that also new findings may render a previously accepted model invalid. All statements about brain functions that control economic relevant behavior rely on:

- That the measured quantities give true values, not only noise or results of systematic errors.
- That the spatial and temporal assignment of measured quantities to brain structures is correct.
- That the model relating the measured quantities to brain activity is still valid in the actual measurement.

- That models and statements about typical functions of specific brain structures are correct and valid also in the actual case.
- That the tested person actually reacts to the stimulus that shall be investigated and is not distracted by other activities (there is always a lot of confounding factors).

In the light of the relative imprecise knowledge about emotion related brain functions one has to resist the temptation to generalize a result found in a specific setting. Even if it would fit perfectly to a proposed model, generalization might be premature. Other settings and other tasks may employ totally different reaction systems.

A critical review of own results and previous results is always necessary. Especially if own interpretations rely on previously published work, one has also to critically assess whether the interpretation of the older results is still valid in the light of later research.

Keeping all this in mind neuroeconomic researchers may reach their goal: To provide a descriptive decision-making theory, which is not restricted to economic theory and more realistic than that of the homo oeconomicus.

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