Chapter 1 Neurobiology of Decision Making: Methodology in Decision-Making Research. Neuroanatomical and Neurobiochemical Fundamentals

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Abstract The research into decision making relies on psychology, neurobiology, pathology as well as economics and it encompasses factors that play a leading role in the process of making decisions on the neural level, regardless of the fact if they are made consciously or subconsciously. From the psychological point of view decision making is a process where cognitive, emotional and motivational aspects play a vital role. Studies on the brain magnetic nuclear resonance imaging reveal that decision-making processes begin before an individual is able to realize it. Neurochemistry has identified several neurotransmitters that are differently associated with decision-making processes, the most important ones being dopamine, serotonin, cortisol, oxytocin and prolactin. Due to a complicated nature of neurotransmitters, the mechanisms that implicate their production are to fully understood yet and it is still not quite known how they work. From the neurochemical perspective, the control of decision-making processes is determined by good communication among different parts of the brain that is regulated by the levels of serotonin. Decision making is a complex process which is possible due to processes taking place in many parts of our brain. However, neuroanatomically speaking, it is the prefrontal cortex that plays a pivotal role in coordinating these processes. To some extent decision making is based on an assumption that people are able to predict other people's behavior and step into their shoes. This capability results from individual preferences and beliefs. Social neuroscience allows us to see neural mechanisms underlying the human ability to represent our intentions. Neurobiology, in turn, strives to explain how relevant moral decisions appear in our brains and how they can modify our emotions. Studies on neurobiological background of our decision-making processes give us better insight into the presumably bounded human rationality as well as into the role of emotions, morality and empathy. Also,

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these studies contribute to our knowledge about the course of decision-making processes and their adaptive value.

Keywords Experimental economics • Definition • Good experiment • Features

1.1 Introduction

Making decisions is a vital, but, at the same time, a trivial part of human lives. Decisions about even the simplest of choices can sometimes get difficult, thus forcing us to analyze gains and losses.

The study into decision-making processes is a field of science which, on the one hand, integrates the knowledge of psychology, medicine, neurobiology, physiology or pathology, while on the other hand—of economics, ethics, philosophy or law. Continuously progressing neurobiological research into decision making is a significant part of the neuroeconomic theories which deal with such problems as how much human behavior, including the economic one, is influenced by emotions, and how much it is ruled by rationality. These theories address factors that play a leading role in decision making on the neural level, regardless of the fact if decisions are made consciously or subconsciously. From the adaptive point of view, good decision making requires integration of many relevant data, motivations with the knowledge concerning potential consequences of the resulting action (Bayer 2008). In order to gain an insight to these processes neurosciences have turned to methods of neuroimaging, especially the functional one.

From the psychological point of view, decision making is a complicated and multi-stage process determined by cognitive, emotional and motivational aspects. In the pre-decisional phase a problem is defined and information about available options is collected; in the consecutive phase the preferred options are identified and the right decision is made, while in the post decisional phase the decisionmaking process is assessed and evaluated (Svenson 2003).

Neurobiology perceives the human brain as an organ which, as a result of evolution, stores and processes information. It is an organized system where the extensive number of operations, prepared and conducted by the brain itself, is taking place. Decisions associated with the undertaken actions arise out of the neuronal processes of self-organization as well as of a massive number of sensory data coming from the external and internal environment as well as from the knowledge stored in the functional brain architecture.

Complicated physical and chemical neural processes have brought the neurobiologists to the conclusion that decisions are determined by the pre-conditions influencing specific neural networks. The concept of the neural origin of decisions is in strong opposition to the view accepting the presence of free will and puts in question the importance of the decision making 'I' that could act as the free will which singlehandedly is able to induce the brain to initiate a series of processes. According to neurobiologists, a human being is able to make their decisions consciously and rationally as a result of neural processes taking part in their brain that is subject to physical and chemical processes, similarly to any other function of the brain. However, the information processing in the brain which leads to conscious decision making involves neural systems that are completely different from the ones involved in unconscious events, thus bringing entirely different results (Merkel and Roth 2008). We still have insufficient knowledge as to how these processes differ (Singer et al. [2004\)](#page-15-0).

1.2 Methods of Research into Decision Making

In order to understand and assess the role of individual brain structures and occurring there functional, bioelectrical and neurochemical processes which underlie and accompany decision making, specific studies need to be conducted. Noninvasive and constantly improved imaging methods make it possible to observe the activity changes in particular brain structures during initiating the decision, preference assessment, risk-taking or the execution of other tasks. What is more, the analysis of measurements obtained at rest and in experimental conditions enabled the researchers to recognize the parts of the brain that are activated in the course of performing different tasks.

The available monitoring methods can be divided into the ones that provide images of the brain structures (computed tomography—CT, nuclear magnetic resonance—NMR, anatomopathological tests) and the ones that monitor its functions (functional NMR—fNMR, electroencephalography—EEG, positron emission tomography—PET). Additionally, the researchers have at their disposal other, more technically challenging methods that create new opportunities for monitoring the neurochemical or neurophysiologic brain activity.

Today, the elementary method of brain imaging used in experimental studies and in pathology diagnostics is the nuclear magnetic resonance (NMR). Technological advancement has brought even more precise high-field imaging devices (7 T). The functional nuclear magnetic resonance (fNMR) is a brain imaging method monitoring changes in the magnetic field. It assesses the amount of oxygen transported to various parts of the brain, thus visualizing which parts of the brain become active when making specific decisions. The effect of structural changes (such as the focal lesions or the lesions in cerebral cortex) on decision making, e.g. in brain-aging processes, can be monitored by means of conventional neuro-imaging methods, such as computed tomography or magnetic resonance imaging.

The resonance technology facilitates the assessment of morphological lesions in the brain tissue. Metabolic irregularities are detected by means of proton magnetic resonance spectroscopy (1H-MRS) which allows for a quantitative viability measure of brain metabolites and for an insight into its chemical composition (Demaerel [1997](#page-13-0)). Another, relatively new technique of imaging is the diffusion NMR that resolves the diffusion water movement in the inter- and intra-cellular fluids within the brain (Thijs et al. [2001\)](#page-15-1). The diffusion of water molecules within the brain is anisotropic, therefore in a way of mathematic transformations we can obtain the so called Apparent Diffusion Coefficient (ADC) maps in the brain. Due to this neuroimaging technique the changes in the brain can be detected within minutes, in contrast to conventional tests such as KT and NMR that take hours. There are the following diffusion techniques: Diffusion Tensor Imaging (DTI) that can be used in diagnosing lesions in white matter tracts and Diffusion-Weighted Imaging (DWI) which is highly effective in resolving various forms of the brain pathology. The above methods have been recently applied in the neuroeconomic research.

Before the introduction of DTI specific tracts within the brain could be traced only by means of neuropathological tests. Apart from the analysis of lesions in some parts of the brain, DTI allows neuroscientists to focus their interests on the networks that link these lesions. Thus emerged the opportunities to study various networks within the brain, as well as their parts (Chiang et al. [2009\)](#page-13-1). The diffusion tensor and a new technique called tractography, which also visualizes white matter tracts, have become the methods that can be used not only in the clinical practice, but also in behavioral psychology or in neuroeconomic research (Johansen-Berg and Behrens [2006\)](#page-14-0).

PET is a very accurate scanning technique where a radioactive tracer is transported to the parts of the increased neuronal brain activity, thus allowing detection of the structures that are most activated during the performance of an individual task. The practical disadvantage of this method is the procedure of the tracer preparation, its stability and cost.

Other brain imaging methods use a laser beam with near-infrared wavelength, which allows to track the blood flow that absorbs light of different wavelength depending on its oxygenation. What is registered is the light reflected by the brain. Such methods include: NIRS (near-infrared spectroscopy), DOT (diffuse optical tomography) that enable researchers to build brain activation maps, and EROS (event-related optical signal) that shows changes taking place in activated neurons. Unfortunately, this method can only be used to examine cerebral cortex and its disadvantage is its poor spatial resolution.

EEG, that monitors solely the bioelectric brain activity, is a relatively cheap method whose accuracy was not initially appreciated but, along with the technological advancement and the introduction of multichannel devices, has become more and more popular.

There are also brain stimulation methods such as transcranial magnetic stimulation (TMS) where after transcranial stimulation the maps of brain activity typical of a given task are made.

Extremely interesting opportunities are created by methods of neurobiological observation due to which we can monitor processes in single neurons or in their groups. After placing an ultra-thin microelectrode in the cell body, the changes in neural stimulation can be monitored. These method are used in experiments on animal brains. In one of the first neuroeconomic studies the researchers analyzed how single neurons in a monkey's brain respond to the changes in value and to a reward (Glimcher [2003\)](#page-13-2). It is also possible to map single neurons by means of

single neuron imaging (SNI) where electrodes are implanted in specific neurons, which can be done due to genetic engineering and imaging techniques (Kawasaki et al. [2007\)](#page-14-1). Unfortunately, it is an invasive method that cannot be applied in studies on humans. Nevertheless, it creates the opportunity to measure directly the activity of neurons.

Other, interesting solutions are offered by optogenetics chosen "the Method of the Year" by the journal Nature in 2012. In a technologically complicated way genes of light-sensitive proteins are injected into specific animal brain neurons and then the secretion of neurotransmitters is monitored by means of light (Deisseroth [2011\)](#page-13-3).

Psycho-physiological methods correlate various psycho-physical functions with physiologic responses, thus testing, e.g., what effect positive and negative emotions have on heart rate, ventilation rate, blood pressure or skin conductivity. One of the most common methods in this group is galvanic skin response (GSR). The method is used, for instance, to assess the reactions of anxiety associated with risky decisions (Bechara et al. [2000](#page-13-4)). Another interesting method is eye-tracking (ET). These methods have long been known, the observations are easy to record and interpret, which explains their popularity.

Vital information can be obtained by correlating the findings of examinations of anatomo-pathological brain structures associated with the decision-making related activity. This method is applied in diagnosing neurological patients with impaired decision-making skills and poor evaluation of the consequences of the decisions they have made. The example is a study where healthy individual's ethical opinions were compared with the opinions of patients with damaged ventral-medial part of prefrontal cortex (Koenigs et al. [2007\)](#page-14-2). It was observed that the patients' choices were much more rational and ethical than those made by healthy individuals in the control group.

When analyzing methodology of neuroeconomic research it is clear that the majority of researchers use one or two methods. It seems to result from the cost of individual tests or from other kind of difficulties.

1.3 Brain Activity and Decision Making

The first answers to the question how human brain works in terms of volitional processes were suggested by the outcomes of B. Libet's experiments in the 1980s (Libet [1985\)](#page-14-3). He observed the electrical activity of the brain during a simple task of voluntary flexing the wrist and discovered the so called readiness potential that occurred about a second before the motor act, while the very awareness of the will to flick the hand preceded the movement by about one fourth of a second. That meant that the brain had made the decision before the individual became aware of it.

The fact that the decision-making processes begin before the individual becomes aware of them has been confirmed by studies using the functional nuclear magnetic resonance (fNMR). Subjects examined by the NMR scanner were asked to decide whether they wished to add or subtract two figures. It was observed that the neural activity allowing to predict if the subject intended to add or subtract emerged app. Four seconds before they actually became aware of that decision (Haynes et al. [2007\)](#page-14-4).

The results of that study caused some controversy, primarily leading to a conclusion that there was no free will. Williams wrote in New Scientist: "Unconscious processes result in making a decision long before conscious thinking begins" and "the brain probably makes decisions before its owner does" (Williams [2013\)](#page-15-2). Coyne, the evolutionary biologist, said in his column "So it is with all of our other choices: not one of them results from a free and conscious decision on our part." (Coyne [2012](#page-13-5)). The above concepts that our decisions associated with conscious acts and their planning are made solely in our subconsciousness should be approached with caution as it is still highlighted that free will plays an important role in decision making.

Studies on humans and apes found that principally two neural systems were involved in financial decision making (McClure et al. [2004](#page-14-5)). The first system, consisting of the structures of the limbic and paralimbic systems embracing the ventral part of striatum, prefrontal and orbitofrontal cortex and a part of hippocampus, became active when the option of immediate benefit or loss was available. But when the decision concerned the delayed option, the second system, composed of posterior parietal and lateral prefrontal cortex, took over. However, that hypothesis was not confirmed in subsequent studies. Instead, it has been revealed that the limbic system is not particularly involved in decisions concerning immediate options (Bayer et al. [2007\)](#page-13-6). In subjects making decisions associated with obtaining most immediate benefits the highest activity was observed in the ventral striatum and the posterior and anterior cingulate cortex (Kable and Glimcher [2007](#page-14-6)). Those structures were also engaged in the delayed benefit decision making but their activity was much weaker than in the case of the decisions concerning immediate benefits.

1.4 Neurobiochemistry of Decision Making

Neurobiochemistry has defined several compounds—neurotransmitters—that are related with decision-making processes. The most important are dopamine, serotonin (Rogers 2010), cortisol, oxytocin and prolactin which are chemical substances controlling the transmission of electric impulses between neurons. Their role is to mobilize the brain to undertaking specific tasks (Bayer et al. [2007](#page-13-6)).

In order to assess the relationship of dopamine with various economic factors, such as risk or benefit delay, the studies were conducted on single neurons in monkeys. It has been found out that the dopamine midbrain neurons influence the decisions concerning consumption of fluids and foods (Schultz [2006](#page-15-3)) as well as

error prediction (Schultz et al. [1997](#page-15-4)). The studies suggest that the delayed benefit decisions are also connected with the dopamine neurons (Kobayashi 2008).

The studies on relations of serotonin with economic behavior were based on pharmacological interventions in humans. The researchers applied rapid tryptophan depletion (RTD), the technique of temporary reducing brain serotonin by ingestion of an excess of neutral amino acids in the reduced presence of serotonin precursor, i.e. tryptophan. The studies compared the economic behavior of the treatment and the control group. It was found that RTD considerably altered decision-making processes in gambling tasks and made the treatment group choose the more likely of the two possible outcomes more often than the control group (Talbot et al. [2006\)](#page-15-5). On the other hand the subjects who followed RTD had poorer ability to distinguish the volume of the expected rewards attributed to specific choices (Rogers et al. [2003\)](#page-14-7).

The findings of the research into the relationship between brain serotonin and the approach to risk are inconclusive. Some studies do not confirm the correlation between risk taking and the levels of serotonin (Rogers et al. [2003](#page-14-7); Talbot et al. [2006\)](#page-15-5), while the others provide evidence that there is a dependency between serotonin levels and neuroticism, loss avoidance or aversion which are individual attributes closely related with risk avoidance (Gonda 2008, Murphy et al. [2008\)](#page-14-8). Another scientific project investigated the impact of two neurotransmitters, serotonin and dopamine, on risk taking and confirmed their mutual vital role (Kuhnen and Chiao [2009\)](#page-14-9). It is generally assumed that serotonin interacts with dopamine in triggering the signals of prediction processes (Denk et al. [2005,](#page-13-7) Tanaka 2007). It has been observed that the importance of delayed rewards is ignored when serotonin levels are low (Schweighofer et al. [2008](#page-15-6)). The brain activity of both the dopaminergic and and serotonergic decrease with aging, which aggravates cognitive disorders. This explains specific changes in economic behavior occurring that are age-related or accompany neurodegenerative conditions such as Alzheimer's disease or other dementia syndromes (Mohr et al. [2010\)](#page-14-10).

Also, the location of numerous subcortical nuclei in brainstem and hypothalamus that control the production and transport of neurotransmitters to various parts of brain as well as to specific parts of body apart from the brain. Due to complicated character of these chemical compounds it has not been fully explained yet what mechanisms implicate their production and what their effect is. In neurochemical terms, what conditions the control of decision-making processes is good communication among different parts of brain which is regulated by serotonin concentration. Its level rises at the moment of getting satisfaction from making an important decision, while its deficit can cause lowered self-control capacity. There are different levels of neurotransmitters in each cerebral hemisphere. In the rightbrain the concentration of noradrenalin and serotonin, playing fundamental roles in activating and suppressing emotions, is higher. The left hemisphere is richer in dopamine that is responsible for concentration and attention, which are vital in decision making. It also controls the right-brain inhibiting the actions that are regarded improper from the social point of view. The more the right hemisphere controls one's personality, the individual will be vulnerable to their own impulses and emotions in decision making (Denk et al. [2005;](#page-13-7) Rogers [2011\)](#page-15-7). The influence on decision-making processes of other chemical substances present in the central nervous system, such as norepinephrine is increasingly being recognized (Eckhoff et al. [2009](#page-13-8)).

What is essential for the proper neurochemical functioning of the brain is the right concentration of glucose, the deficit of which can lead to anxiety, agitation and aggressive behavior.

It needs to be remembered that in decision making the functional state of the brain is important, but also the condition of the whole body. Fatigue, exhaustion, dehydration, misbalance of homeostasis contribute to making wrong choices.

1.5 Neuroanatomy of Decision Making

Decision making is a complex process that is possible only due to the processes taking place in many parts of the brain (Lee et al. [2007\)](#page-14-11). From the neuroanatomical point of view, however, it is prefrontal cortex that plays a crucial role in their coordination (Krawczyk [2002\)](#page-14-12). Neuropsychological studies, particularly the neuroimaging ones, have defined the areas of prefrontal cortex that are pivotal for decision making. Also, the research into the relationships of anatomopathological lesions with changes in the patient's functioning allowed for evaluating the importance in decision making of specific cortex areas such as orbitofrontal cortex (Volz and von Cramon [2009](#page-15-8)), dorsolateral prefrontal cortex (Lee and Seo [2007](#page-14-13)) and anterior cingulate cortex (Rushworth and Behrens [2008\)](#page-15-9).

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Orbitofrontal cortex has extensive connections with sensory analysis structures olfactory, gustatory, visual and somatosensory cortices, as well as with corpus striatum being a part of the reward system. Such neuroanatomic conditionality allows orbitofrontal cortex to participate in perception and generation of responses to stimuli of the primary reward value. It results in decisions associated with need satisfaction (Rolls [2004](#page-15-10)). Additionally, this part of the cortex is responsible for the analysis of the individual stimuli value. The example is a patient with damaged orbitofrontal cortex who, despite preserved high level of declarative knowledge and problem-solving skills, was experiencing difficulty in making decisions in simple, everyday situations as well as in adapting to the environment (Eslinger and Damasio [1985\)](#page-13-9). It was observed that patients with lesions of orbitofrontal cortex performed tasks disregarding their high costs, expected immediate and big profits

and were not able to accept a long-term perspective (Bechara et al. [2000\)](#page-13-4). That allowed to make the somatic marker hypothesis, according to which the emotional response related to the options to choose is possible due to the connections between orbitofrontal cortex with amygdaloid nuclei and with hippocampus (Bechara et al. [1994\)](#page-13-10).

It has been proven that orbitofrontal cortex also participates in generating responses to abstract cues, such as the financial ones, and that it is where value is attributed to individual objects (Plassmann et al. [2007\)](#page-14-14). The fNMR tests have clearly shown in which parts of orbitofrontal cortex are activated in response to financial benefits and losses (O'Doherty et al. [2001](#page-14-15)). Particularly strong activation of this brain area occurs when decisions are made in the circumstances of uncertainty (Hsu et al. [2005](#page-14-16)).

Particularly strong activation of orbitofrontal cortex with connections to the reward system facilitates active recognition and sustenance of profit-generating behavior and suppresses behavior resulting in financial loss. It occurs when the decisions are associated with substantial financial rewards or penalties (Elliott et al. [2000\)](#page-13-11).

The sensitivity of the neurons in orbitofrontal cortex to a reward stimulus triggers subjective stimulus value on the continuous scale and dissociates the options to be chosen (Grabenhorst and Rolls [2009\)](#page-13-12). What also takes place in this cortex is the adaptation to environmental changes, long-term monitoring of their effects and extinguishing the response to stimuli whose reward value is decreasing (Krawczyk [2002\)](#page-14-12).

The activation of orbitofrontal cortex subside when the stimulus is delayed. Therefore it has been observed that in human decision making the value of delayed stimuli tends to decline (Green and Myerson [2004\)](#page-13-13).

$1.5.2$ 1.5.2 Dorsolateral Prefrontal Cortex

It is the dorsolateral prefrontal cortex where the decision-making process is recognized and where thus obtained information is used to control the decisions (Krawczyk [2002](#page-14-12)). What is essential for decision making, this cortex stores information about the decision maker's environment in the short-term memory and then processes this information (Lee and Seo [2007](#page-14-13)). The dynamics of human decisionmaking processes depends on intellectual evaluation and adaptation to the environ-ment where the decisions are made (Gigerenzer [2007](#page-13-14)).

In the dorsolateral prefrontal cortex other relevant operational memory-related tasks are performed, such as storing information, including the affective ones, out of which the decision goals and options are chosen (Krawczyk [2002](#page-14-12); Goldman-Rakic [1996](#page-13-15)). Other vital functions of the dorsolateral prefrontal cortex include:

• shaping the rules of proper decision making and referring them to new situations on the basis of previous experience (Wallis and Miller [2003](#page-15-11)),

- simultaneous processing of information about environmental conditions and about the reward value of environmental stimuli (Kobayashi et al. [2007\)](#page-14-17),
- integrating information about physical and abstract attributes of individual decision options and their motivational importance (Sakagami and Watanabe [2007\)](#page-15-12),
- distinguishing and categorizing newly perceived stimuli and, on that account, making choices out of options with similar attributes and similar subjective usability (Krawczyk [2002](#page-14-12)),
- categorizing new stimuli and attributing them with reward values (Pan et al. [2008\)](#page-14-18),
- planning, controlling and adapting behavior to temporarily and prospectively important rules and consequences (Sakagami and Niki [1994](#page-15-13)),
- selecting responses adequate to the present stimulus, predicting its reward value and planning the response accordingly (Wallis et al. [2001\)](#page-15-14),
- modifying behavior on the basis of previous decisions (Hare et al. [2009](#page-14-19)).

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Anterior cingulate cortex plays a specific role in making decisions in the conditions of uncertainty as it is responsible for choosing between responses to two or more competing stimuli. The level of activity of this cortex is directly proportional to the intensity of the conflict. Basing on the observation of increased activity in cingulate cortex after having made wrong decisions it has been found that due to this mechanism a human being is able to continuously monitor the correctness of their behavior (Carter et al. [1998\)](#page-13-16).

Other vital functions of the anterior cingulate cortex include:

- altering the chosen activity after the wrong decision has been recognized; predicting the potential value of the selected choices and evaluating their costs and pay-off (Walton et al. [2007\)](#page-15-15),
- choosing between an available small reward and the substantial but effort-based one (Walton et al. [2002](#page-15-16)),
- decreasing the decision-making uncertainty (Yoshida and Ishii [2006](#page-15-17)),
- initiating the choice of the decision which is the most accurate in given circumstance (Rushworth et al. [2007](#page-15-18)),
- observing and collecting information about other people's behavior that leads to making interpersonal or broad-range social decisions (Rilling et al. [2002\)](#page-14-20),
- predicting negative consequences of decisions that have been made and analyzing the uncertainty of the consequence assessment (Rilling et al. [2002\)](#page-14-20),
- integrating cognitive aspects of the decision uncertainty with the autonomic arousal that accompany negative consequences of decision making; creating conditions for decision verification and correction (Critchley et al. [2005](#page-13-17)).

1.6 Brain Processes: People's Behavior Prediction and Empathy vs. Decision Making

Decision making is to some extent based on the assumption that people are able to predict the behavior of others and empathize with them. This ability results from individual preferences and beliefs. Social neuroscience provides insight into neural mechanisms underlying our capacity to represent intentions, beliefs and desires of other people and to share other people's feelings, e.g. to empathize. Empathy makes people less selfish, allows them to share emotions and feelings with others, thus motivating them to make decisions oriented at other people. Studies on empathy indicate that the same affective brain neural circuits are automatically activated when we are feeling pain as well as when we see others in pain. Therefore, while making decisions, empathy often directs our emotions at other people.

Developmental and social psychology as well as cognitive neuroscience focus on human ability to assess and predict various states, such as desires, opinions, intentions, of other people. A study was conducted on the brain activity during the choice- and belief-related tasks (Bhatt and Camerer [2005\)](#page-13-18). It revealed the involvement of the medial part of prefrontal cortex, i.e. the anterior cingulate cortex. This part of the brain takes part not only in reading other people's thoughts, intentions and beliefs, but also helps refer to one's own states of mind. It assists in creating decoupled representations of our beliefs about the state of the world (Frith and Frith [2003\)](#page-13-19).

Similar research concentrated on searching for neural mechanisms being a basis for human ability to represent other people's goals and intentions solely by observing their motor acts. Such an approach stemmed from the observation that neurons in premotor cortex in macaques' brains activate both when the monkey makes a hand movement and when it observes another monkey or a human making the same hand movement. It was a remarkable discovery of the fact that the so called mirror neurons reflect the neural origins of imitation which is vital in the decision-making context (Rizzolatti et al. [1996\)](#page-14-21). The system of mirror neurons may be the basis for our ability to empathize with mental states of other people, ensuring that we automatically simulate their acts, goals and intentions and adapt our decisions to this.

Apart from the ability to understand other people's state of mind, people are also able to empathize, i.e. to share other people's feelings in the absence of any emotional arousal. What is more, humans can feel empathy toward others in many different emotional situations, both elementary such as anger, fear, sadness, joy, pain or desire, and more complex, such as the sense of guilt, embarrassment or love. Relying on the perception models explaining behavior and imitation, the researchers proposed a neuroscientific model of empathy, implying that the mere observation or image of a person in a given emotional state automatically activates the representation of this state in the observer together with the related responses of their autonomic and somatic systems, thus strongly influencing their decisionmaking (Preston and de Waal [2002](#page-14-22)).

The research by Singer has proved that both strong stimuli (pain) and the awareness that someone important to us feels pain activate the same pain neural circuits. That finding implies that if a person dear to us suffers from pain, suffering will also appear in our brain (Singer et al. [2004](#page-15-0)). It seems that the ability to emphasize could have developed from the same system which creates the representations of human inner states and it helps predict and understand other people's feelings associated with some event, e.g. with a decision that has been made.

The results of Singer's study suggest as well that empathic response is automatic and does not require active assessment of other people feelings. Volunteers subjected to neuroimaging did not know that the experiment examined empathy. The analysis confirmed that the ability to emphasize is individually diversified.

What is important for understanding decision-making processes is the fact that emphatic responses appear also when individuals who undergo brain imaging tests do not know the person who receives the pain stimulus. The findings of studies on empathy can contribute to better understanding of social preferences, especially of behavior considered honest and dishonest. These findings show that many people have a positive opinion about those who behaved honestly in their decision making and are regard negatively those who behaved dishonestly. Such a pattern of preferences suggests that people prefer to collaborate with honest partners, advo-cating penalties for dishonest competitors (Fehr and Gächter [2000\)](#page-13-20).

1.7 Neurobiology of Moral Dilemmas vs. Decision Making

From Aristotle to I. Kant to J.S. Mill, moral philosophy theories say that the primary role in making moral decisions is played by brain. In the light of modern developmental psychology, rationality is perceived as the foundation of moral choices. On the other hand, sentimentalists contended that emotions play the primary role in moral decision making. A. Smith wrote in 1759 that morality comes from understanding other people and the feeling of sympathy toward them. His view finds its appreciation in the concepts of modern sentimentalists, such as (Haidt [2006\)](#page-14-23).

Neurobiology attempts to find out how moral decisions appear in the brain and how these decisions van by modified by emotions. It is the doctors who face particularly controversial moral dilemmas in their everyday practice, having to choose between two bad solutions, e.g. which accident victim they are to help first, being aware that their decision reduces the other victim's survival odds. The economists also have to decide which poorly performing company or bank should be given access to funding.

The studies of lesser-evil decisions are based on M.D. Hauser's Moral Sense Test (MST). It is a series of hypothetical situations where subjects choose one of several difficult solutions (Hauser [2007\)](#page-14-24). What is interesting, fNMR tests show that time of response is longer when the decisions are associated with the choice of a utilitarian solution than when they require violating personal moral standards (Hauser [2007](#page-14-24)).

In the famous Thomson's Trolley Dilemma where the decision has to be made whether to redirect the runaway trolley from the its current course and save five people standing on the track and kill one person standing on the alternative track. The question is: is it morally acceptable to hit the switch to turn the trolley to save five people at the expense of the one? (Thomson [1978\)](#page-15-19). The majority of tested subjects decide to hit the switch, regarding such a choice as the utilitarian solution, thus following J.S. Mill's view that moral acts are the ones that make people happier.

The decision of another type has to be made in the Footbridge Dilemma where a trolley heading for a group of several people can be stopped by pushing a stranger off the bridge and onto the tracks. Unlike to the previous moral dilemma, most subjects do not decide to push off the stranger, which may result from the fear of violating the moral standard: Do not kill.

There is an interesting explanation of the above decisions based on the double effect doctrine credited to Thomas Aquinas which says "An act which causes a certain ethically negative effect and which would be morally unacceptable if performed intentionally can be morally justified when performed with the intent to cause another, morally justified effect and only becomes its unintentional, although predictable, effect" (Galewicz [2001\)](#page-13-21).

Hence, the act which is an effect of specific decisions will be acceptable when: its effect is good, brings at least as much good as its abandonment, will not be performed in bad faith and will be an effect of the action rather than the bad outcome. According to such approach, saving people in the Footbridge Dilemma does not satisfy the last criterion (people have been saved as a result of killing one person), this is why most subjects do not make this decision. In the Trolley Dilemma the death of one person was caused by hitting the switch (the death was 'just' induced).

Modern moral psychologists J. D. Greene and J. Haidt maintain that although decisions concerning the above moral dilemmas are connected with violating moral standards, they still have ethical character. In the Trolley Dilemma the decisions are of non-personal nature, while in the Footbridge Dilemma, they are definitely personal decisions. When facing decisions that may lead to hard consequences, most people accept non-personal violation of moral standards, while rejecting personal violation of these rules.

1.8 Conclusions

Decision making is closely connected with neurobiological, neurostructural, neurochemical and psychological mechanisms. They take place in specific parts of the brain, particularly in the prefrontal cortex, an area integrating connections with individual decision options. This process prepares relevant preferences with reference to current needs of a decision maker. Studies on neurobiological background of decision making give better insight into the human implied bounded rationality

and into the role of emotions, morality and empathy. Moreover, these studies contribute to the knowledge about the course of decision-making processes and their adaptive value.

References

- Bayer HM, Lau B, Glimcher PW (2007) Statistics of midbrain dopamine neuron spike trains in the awake primate. J Neurophysiol 98:1428–1439
- Bechara A, Damasio AR, Damasio H, Anderson SW (1994) Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 50:7–15
- Bechara A, Tranel D, Damasio H (2000) Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. Brain 123:2189–2202
- Bhatt M, Camerer CF (2005) Self-referential thinking and equilibrium as states of mind in games: fMRI evidence. Games Econ Behav 52:424–459
- Carter CS, Braver TS, Barch DM et al (1998) Anterior and the online monitoring of performance. Science 280:747–749
- Chiang MC, Barysheva M, Shattuck DW et al (2009) Genetics of brain fiber architecture and intellectual performance. J Neurosci 29(7):2212–2224
- Coyne JA (2012) Column: why you don't really have free will, US Today. [http://usatoday30.](http://usatoday30.usatoday.com/news/opinion/forum/story/2012-01-01/free-will-science-religion/52317624/1) [usatoday.com/news/opinion/forum/story/2012-01-01/free-will-science-religion/52317624/1.](http://usatoday30.usatoday.com/news/opinion/forum/story/2012-01-01/free-will-science-religion/52317624/1) Accessed 1 Jan 2012
- Critchley HD, Tang J, Glaser D et al (2005) Anterior cingulate activity during error and autonomic response. NeuroImage 26:885–895
- Deisseroth K (2011) Optogenetics. Nat Methods 8:26–29
- Demaerel P (1997) In vivo localized single-voxel proton magnetic resonance spectroscopy of intracranial tumors. Int J Neuroradiol 3:94–100
- Denk F, Walton ME, Jennings KA, Sharp T et al (2005) Differential involvement of serotonin and dopamine systems in cost-benefit decisions about delay or effort. Psychopharmacology 179:587–596
- Eckhoff P, Wong-Lin K-F, Holmes P (2009) Optimality and robustness of a biophysical decisionmaking model under norepinephrine modulation. J Neurosci 29(13):4301–4311
- Elliott R, Friston K, Dolan R (2000) Dissociable neural responses in human reward systems. J Neurosci 20:6159–6165
- Eslinger PJ, Damasio AR (1985) Severe disturbance of higher cognition after bilateral frontal lobe ablation: patient EVR. Neurology 35:1731–1741
- Fehr E, Gächter S (2000) Cooperation and punishment in public good experiments. Am Econ Rev 90(4):980–994
- Frith U, Frith CD (2003) Development and neurophysiology of mentalizing. Philos Trans R Soc Biol Sci 358:459–473
- Galewicz W (2001) Tomasz z Akwinu o zabijaniu. Znak 7(554):81–97
- Gigerenzer G (2007) Gut feelings. The intelligence of the unconscious. Allen Lane, London
- Glimcher P (2003) The neurobiology of visual-saccadic decision making. Annu Rev Neurosci 26:133–179
- Goldman-Rakic PS (1996) Regional and cellular fractionation of working memory. Proc Natl Acad Sci U S A 93:13473–13480
- Grabenhorst F, Rolls ET (2009) Different representations of relative and absolute subjective value in the human brain. NeuroImage 48:258–268
- Green L, Myerson J (2004) A discounting framework for choice with delayed and probabilistic rewards. Psychol Bull 130:769–792
- Haidt J (2006) The happiness hypothesis: finding modern truth in ancient wisdom. Basic Books, New York
- Hare TA, Camerer CF, Rangel A (2009) Self-control in decision-making involves modulation of the vmPFC valuation system. Science 324:646–648
- Hauser MD (2007) Moral minds: how nature designed our universal sense of right and wrong. HarperCollins, New York
- Haynes JD, Sakai K, Rees G et al (2007) Reading hidden intentions in the human brain. Curr Biol 17:323–328
- Hsu M, Bhatt M, Adolphs R et al (2005) Neural systems responding to degrees of uncertainty in human decision-making. Science 310:1680–1683
- Johansen-Berg H, Behrens TE (2006) Just pretty pictures? What diffusion tractography can add in clinical neuroscience. Curr Opin Neurol 19(4):379–385
- Kable JW, Glimcher PW (2007) The neural correlates of subjective value during intertemporal choice. Nat Neurosci 10(12):1625–1633
- Kawasaki H, Adolphs R, Kaufman R et al (2007) Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. Nat Neurosci 4:15–16
- Kobayashi S, Kawagoe R, Takikawa Y et al (2007) Functional differences between macaque prefrontal cortex and caudate nucleus during eye movements with and without reward. Exp Brain Res 176:341–355
- Koenigs M, Young L, Adolphs R et al (2007) Damage to the prefrontal cortex increases utilitarian moral judgements. Nature 446(7138):908–911
- Krawczyk D (2002) Contributions of the prefrontal cortex to the neural basis of human decision making. Neurosci Biobehav Rev 26:631–664
- Kuhnen CM, Chiao JY (2009) Genetic determinants of financial risk taking. PLoS One 4:e4362
- Lee D, Rushworth MF, Walton ME et al (2007) Functional specialization of the primate frontal cortex during decision making. J Neurosci 27:8170–8173
- Lee D, Seo H (2007) Mechanisms of reinforcement learning and decision making in the primate dorsolateral prefrontal cortex. Ann N Y Acad Sci 1104:108–122
- Libet B (1985) Unconscious cerebral initiative and the role of conscious will in voluntary action. Behav Brain Sci 8:529–566
- McClure SM, Laibson DI, Loewenstein G, Cohen JD (2004) Separate neural systems value immediate and delayed monetary rewards. Science 306:503–507
- Mohr P, Li S-C, Heekeren HR (2010) Neuroeconomics and aging: neuromodulation of economic decision making in old age. Neurosci Biobehav Rev 34:678–688
- Murphy SE, Longhitano C, Ayres RE et al (2008) The role of serotonin in nonnormative risky choice: the effects of tryptophan supplements on loss-aversion in healthy adult volunteers. J Cogn Neurosci 21:1709–1719
- O'Doherty J, Kringelbach ML, Rolls ET et al (2001) Abstract reward and punishment representations in the human orbitofrontal cortex. Nat Neurosci 4:95–102
- Pan X, Sawa K, Tsuda I et al (2008) Reward prediction based on stimulus categorization in primate lateral prefrontal cortex. Nat Neurosci 11:703–712
- Plassmann H, O'Doherty J, Rangel A (2007) Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. J Neurosci 27:9984–9988
- Preston SD, de Waal FB (2002) Empathy: its ultimate and proximate bases. Behav Brain Sci 25 $(1):1-20$
- Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C (2002) A neural basis for social cooperation. Neuron 35:395–405
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. Cogn Brain Res 3:131–141
- Rogers RD, Tunbridge EM, Bhagwagar Z et al (2003) Tryptophan depletion alters the decisionmaking of healthy volunteers through altered processing of reward cues. Neuropsychopharmacology 28:153–162
- Rogers RD (2011) The roles of dopamine and serotonin in decision making: evidence from pharmacological experiments in humans. Neuropsychopharmacology 36(1):114–132
- Rolls ET (2004) The functions of the orbitofrontal cortex. Brain Cogn 55:11–29
- Rushworth MF, Behrens TE (2008) Choice, uncertainty and value in prefrontal and cingulate cortex. Nat Neurosci 11:389–397
- Rushworth MF, Behrens TE, Rudebeck PH, Walton ME (2007) Contrasting roles for cingulate and orbitofrontal cortex in decisions and social behavior. Trends Cogn Sci 11:168–176
- Sakagami M, Niki H (1994) Spatial selectivity of go/no-go neurons in monkey prefrontal cortex. Exp Brain Res 100:165–169
- Sakagami M, Watanabe M (2007) Integration of cognitive and motivational information in the primate lateral prefrontal cortex. Ann N Y Acad Sci 1104:89–107
- Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. Science 275:1593–1599
- Schultz W (2006) Behavioral theories and the neurophysiology of reward. Annu Rev Psychol 57:87–115
- Schweighofer N, Bertin M, Shishida K et al (2008) Low-serotonin levels increase delayed reward discounting in humans. J Neurosci 28:4528–4532
- Singer T, Seymour B, O'Doherty J et al (2004) Empathy for pain involves the affective but not sensory components of pain. Science 303(5661):1157-1162
- Talbot PS, Watson DR, Barrett SL, Cooper SJ (2006) Rapid tryptophan depletion improves decision-making cognition in healthy humans without affecting reversal learning or set shifting. Neuropsychopharmacology 31:1519–1525
- Thomson JJ (1978) Killing, letting die, and the trolley problem. Monist 59:204–217
- Thijs VN, Adami A, Neumann-Haefelin T et al (2001) Relationship between severity of MR perfusion deficit and DWI lesion evolution. Neurology 57:1205–1211
- Volz KG, von Cramon DY (2009) How the orbitofrontal cortex contributes to decision making—a view from neuroscience. Prog Brain Res 174:61–71
- Wallis JD, Anderson KC, Miller EK (2001) Single neurons in prefrontal cortex encode abstract rules. Nature 411:953–956
- Wallis JD, Miller EK (2003) Neuronal activity in primate dorsolateral and orbital prefrontal cortex during performance of a reward preference task. Eur J Neurosci 18:2069–2081
- Walton ME, Bannerman DM, Rushworth MF (2002) The role of rat medial frontal cortex in effortbased decision making. J Neurosci 22:10996–11003
- Walton ME, Rudebeck PH, Bannerman DM, Rushworth MF (2007) Calculating the cost of acting in frontal cortex. Ann N Y Acad Sci 1104:340–356
- Williams C (2013) Brain imaging spots our abstract choices before we do. New Sci 218(2913):16
- Yoshida W, Ishii S (2006) Resolution of uncertainty in prefrontal cortex. Neuron 50:781–789