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Table of contents

1. Introduction

Standard economic theory is based on the concepts of self-interest, rationality and utility maximization (Wilkinson, 2008, p. 5). From this point of view cooperation only occurs if the benefit outweighs the cost. However, cooperative behavior and cooperation are fundamental concepts vital for society. People have to work together and rely on each other in any society, culture and age. Especially modern societies strongly depend on cooperation between strangers.

People pay taxes although tax evasion is possible and buy bus tickets although controls are rare. People contribute to society, although their contribution does not count. Society would not collapse if one person does not pay taxes. The self-interested, rational and utility maximizing “homo oeconomicus” would not fit in this society. He would not pay taxes or buy bus tickets, because he benefits more from the money than society does.

This raises the question if the standard economic models are wrong. Maybe people are not rational, self-interested and utility maximizing. The concept of the “homo oeconomicus” has therefore been challenged by a number of new approaches from other scientific fields.

This thesis will discuss three interdisciplinary approaches: Psychological knowledge of behavior is incorporated in the theory of behavioral economics. Neuroeconomics combines neuroscience with economics and tries to find answers on the neural level. The third approach of genoeconomics reminds us that genes have to be taken into account and wants to find out, how much of our behavior is carved into our genes and how much we can shape by living.

The aim of this thesis is to show that economics can benefit from interdisciplinary approaches in the form of new theories, methods and ways of thinking.

2. Cooperative behavior in the light of behavioral economics

2.1. Aim of behavioral economics

Behavioral economics tries to answer economic questions by incorporating psychological knowledge into economic theories. Self-interest and utility maximization is one of the main-characteristics of the so-called homo oeconomicus. People are thought to maximize their own benefit without caring about others. In the last decades, however, a large number of experiments showed that this is not necessarily the case. Behavioral economics tries to find out why such discrepancies between standard economic theory and actual human behavior exist and why people cooperate when standard economics would assume otherwise. In this chapter different behavioral economic methods and current findings will be discussed to show how behavioral economics can contribute to economic research of cooperation.

2.2. From standard economic theory to behavioral economics

Before the strict division of economics and psychology, economists often contributed theories to psychology. Adam Smith for example wrote besides his famous "*The Wealth of Nations"* the book *"The Theory of Moral Sentiments"*, in which he discussed human behavior from a psychological point of view (Camerer, Loewenstein and Rabin, 2004, p. 5).

This "drifting apart" of psychology and economics started at the beginning of the 20^{th} century. At this time economists wanted to transform economics into a natural science, whereas in psychology Freud's theory was very popular (Camerer, Loewenstein and Rabin, 2004, p. 5). His theory was not like a natural science at all, because introspection and interpretation of dreams cannot be part of a natural science. Natural science focuses on observable phenomena which can be measured and reproduced by an independent person. Different opinions on science led to the drifting apart of economics and psychology.

The gap between the two sciences became smaller again as behaviorism became more popular in psychology. Psychologists like Watson, Thorndike and Skinner were also only interested in human behavior because all behavior can be changed by learning and therefore intentions are neglectable (Sternberg, 2009, p. 8).

The differences between the two disciplines increased again as soon as cognitive psychology became the leading paradigm in psychology, because then intentions and motivations became important for psychology. Behavior was no more just a reaction to the environment but the human mind creates and actively changes the impression of the environment and therefore cannot be neglected any longer. Not only behavior itself is therefore important and this is a main difference to economics, where observable actions and shown preferences count.

Behavioral economics tries to close this gap by using psychological knowledge to solve economic problems and to improve economic theories. Simon (1956) was the first to try to break the basic assumption of rationality in neoclassical economics. He made the term “bounded rationality” popular, which means that humans are not able to be rational due to cognitive limitations. Kahneman and Tversky showed that we are all prone to cognitive biases and use heuristics due to for example complexity or time pressure which may lead us in the wrong direction.

Behavioral economics assumes that humans don not only want to maximize their own utility, but also their utility in relation to others. People have so-called other-regarding preferences like reciprocity, fairness and altruism. This approach does not assume that standard economics is wrong but it wants to extend the standard theory of rational choice (Ho, Lim & Camerer, 2006). Common methods to prove other-regarding preferences and prosocial behavior are experiments and games.

2.3. Experiments in behavioral economics

This chapter describes which methods behavioral economists use to measure cooperativeness and what their advantages and disadvantages are. Behavioral economists heavily rely on laboratory experiments. That is remarkable, because experiments were not used very often by economists in the past, because they tended to rely on mathematical theories and empirical data from the field.

In an experiment one or more parameters of a specific condition are systematically changed and the effects of these changes are measured. The factors which are varied are called independent variables and the effect of a change is called dependent variable (Hogg & Vaughn, 2008, p. 9). To make sure that only the independent variables are modified in one condition, control of as many confounding variables as possible is necessary (Hogg & Vaughn, 2008, p. 10). Confounding variables are any effects on the dependent variables from any source other than independent variables. The control of confounding variables guarantees that only independent variables are responsible for the change of the dependent variable which can be improved by random allocation of participants to the different conditions.

An experiment can be used, for example, to investigate which effect money has on cooperation. The independent variable is the amount of money, which can be changed in different conditions. The dependent variable is the level of cooperation and confounding variables might be the culture of the country or the relationship of the participating people. To avoid any effect of culture in this example, people from different cultures should be put randomly into every condition of the experiment. After eliminating the effect of all confounding variables it is obvious that any change in cooperation in the different conditions is due to changes in the amount of money.

2.4. Advantages and disadvantages of experiments

A big advantage of experiments is that it is possible to draw causal conclusions. A laboratory experiment reduces the possible explanations of a certain behavior in the ideal case to one reason. Empirical data collected on the field on the other hand allows different explanations for a specific behavior, because it is almost impossible to manipulate the environment in a way that only one reason remains, because the environment is so complex.

A second big advantage of an experimental approach is that it is possible to change the conditions very easily (Falk & Heckman, 2009). Due to the fact that experimental designs are held simple, it is possible to extract the effect of one change of the design directly. In the “real” world it is almost impossible to change only one condition, because the world’s complexity and nobody knows how different aspects interact with each other and which effect a change of one variable might cause.

A third advantage is the easy replicability of experiments (Falk & Heckman, 2009). By using this very controlled environment, which reduces the decision of the person to its very core and avoids “noise” of other variables as much as possible, experiments can be replicated. This would be impossible in the field, because so many things in the real world influence the results, for example the weather, the day of the week or any other factor which the scientists do not or cannot take into account. The best way to prove any results of any research is by replicating them.

Another advantage is the cost factor. Using a laboratory saves time and money, because there is no necessity to search participants in the needed environment. You can create any environment in the lab and fill it with random people or with the group necessary for the experiment. All you need are computers and software which are the core of every lab. Nowadays computers are cheap and to perform simple experiments you do not need expensive software. A second cost factor is the payment for the participants, which is common in economics but not in psychology, to make sure that the participants have a proper incentive to act according to their true preferences.

A big disadvantage of a laboratory experiment, on the other hand, is that it might be difficult to convert the results of the lab to the real environment, because an experiment is always an artificially created situation, which will never happen this way in the real world. In the real world people do not know exactly how their behavior might affect other people and what their effort levels and output are, because these variables are not completely observable. It is impossible to avoid this problem, so it is important to keep that in mind and to test theories and hypothesis by using experiments and empirical data.

A second disadvantage could be a selection effect, which means that most samples consist of students, especially economics students, and therefore many critics argue that these samples are biased and not reflecting the “real” population (Falk & Heckman, 2009). Students are easy to find for teaching experimenters and they are often more motivated to participate, because they get money or a grade in exchange for participation. This critique is justified and it has been tested if non-students would act differently in the experiments. There have been several experiments with other groups like CEOs and the results were almost the same as in the student design of the experiment (Fehr & List, 2004). Another interesting result is that behavior of participants with different socio-economic background does not differ significantly in a one shot public goods game (Gächter, Herrmann & Thöni, 2004). The reason why the results do not differ among different groups might be that the decisions made in these experiments are so simple that socio-economic background has no influence.

Another common point of criticism is that the stakes are too low and therefore participants act differently than they would in the real world. When stakes increase, behavior becomes more selfish and more like assumed in the standard economic theory. Ultimatum games in Indonesia with a stake of the income of three months, however, showed that the results did not change significantly even if the stakes were very high (Cameron, 1999). The same insignificant difference in results was found in Russia, where students were offered up to three times of their monthly income in a gift exchange market game (Fehr, Fischbacher & Tougareva, 2002).

A fourth problem is that participants might have other reasons for their behavior than intended by the experimenters. It is quite common that participants understand the purpose of the experiment and therefore might act in a way to help the experimenter to get the “right” results. This is possible, because designs are often simple and straight forward, especially if participants study economics and have learned about similar experiments before. This phenomenon is called “demand characteristics”, because participants show characteristics which are demanded by the experimenter (Hogg & Vaughan, 2008, p. 11).

2.5. Games

The most common way to test cooperative behavior in the laboratory is to use games. A game is a setup in which two or more persons are asked to act while their behavior is observed.

2.5.1. Prisoner´s dilemma

One of the most famous examples of a game and the fact that people can cooperate even if it is better to deceive according to self-interest maximization is the prisoner´s dilemma (PD).

The setting of the classical PD is that two players are imprisoned and they are accused of a crime. Both players have to decide whether to confess or to stay silent, but they cannot communicate with each other. If both stay silent, they get a low punishment (1, 1). If both confess, they get a high punishment (5, 5). With only these two options it is clear that both prisoners would stay silent. The third possible outcome, however, makes the dilemma visible. If one confesses and the other one stays silent, the confessor becomes a key witness and is not punished, while the silent player gets a very high punishment (0, 10). If they act in pure self-interest, they will not cooperate and therefore confess because they would expect the other player to confess. The other player expects this behavior and reacts by confessing to avoid the worst outcome, where the other prisoner confesses while he stays silent (10.0). In the end both are worse off, because they did not cooperate. The outcomes are visualised in figure 1.

		Suspect B	
		Confess	Not confess
Suspect A	Confess	5,5	0,10
	Not confess	10,0	1,1

Table 1: Outcomes of a prisoners´ dilemma (Wilkinson, 2008, p. 337)

In empirical studies approximately fifty percent of the games in one shot situations end in cooperation, which is contrary to self-interest theory (Wilkinson, 2008, p. 337). This game measures conditional reciprocity, which will be explained in chapter 2.7.1. In a sequel PD the players only cooperate if no one defects in earlier rounds of the game. As soon as one player stops cooperating, the other will do so as well and cooperation ends with the result that reciprocity is conditional (Falk & Fischbacher, 2006).

2.5.2. Ultimatum game

This game, introduced by Güth, Schmittberger and Schwarze (1982), consists of two players; one is the proposer and the other one the responder. The proposer gets a fixed amount of money from the experimenter and has to decide how much he keeps and how much he gives the responder. The responder has two options: He can either keep the money the proposer offers and both get their share of the money or he rejects the offer and both players get nothing.

If the assumptions of the standard economic theory that all humans are rational and utility maximizing holds, the result should be that the proposer can offer any amount above zero, because the responder would be better off and therefore not reject even the tiniest amount of money. Empirical data, however, shows that responders reject offers below 20% of the available amount (Levitt & List, 2007). Knowing that most people would reject a very unfair offer, most proposers offer 25-50% of the money they got (Levitt & List, 2007).

The Ultimatum game measures the responder's negative reciprocity, which means punishing unkind behavior, because the responder has the power to reject the offer of the proposer and therefore to punish him for unacceptable offers (Levitt & List, 2007). For the proposer this game is a measure of fairness, because he can decide how to distribute the money (Levitt & List, 2007).

A big advantage of this game is that it is really simple and therefore easy to explain, to implement and to monitor.

2.5.3. Dictator game

The dictator game is similar to the ultimatum game, but the difference is that the responder cannot reject the offer of the proposer. He has to accept it and cannot punish the proposer for an unfair offer. Therefore, this game is a measure of altruism, fairness and inequity aversion, because the proposer has no incentive at all to give the “responder” any share of the money, because the responder has no possibility to punish him and the players do not know each other (Levitt & List, 2007). Nevertheless around 60% of the people give money to the responder, but the proposers are less generous with an average share of around 20% (Levitt & List, 2007). Standard economic theory would assume that nobody would give any share of the money at all, so 20% is an impressive proof that social preferences exist.

2.5.4. Trust game

In the trust game player A receives an endowment from the experimenter. Player A has the opportunity to send some of his money to player B, knowing that B can either keep the money or send some or all the money back to player A. The money sent to B is multiplied by the experimenter with a factor bigger than 1, which makes both players better off, if A sends money to B and B sends some of it back (Berg, Dickhaut & McCabe, 1995).

Assuming that the players act according to the standard economic theory and therefore act rationally and utility maximizing, B has no incentive to send A money back, because A has no way to punish him for his unkind behavior. A anticipates this behavior, because it would be rational and therefore A would not send any money to B with the result that A keeps all the money and no transaction happens. Empirical data on the other hand shows that A sends on average approximately 50% of his endowment to B and B returns around 50% of the money to A (Berg, Dickhaut & McCabe, 1995). Again we see that people are showing social preferences and are not acting fully rational.

This game leads to good results, if you want to measure trust of A and trustworthiness of B. A has to trust B if he sends him money and B acts trustworthy if he returns money to A (Levitt & List, 2007). Additionally, this game is a good indicator for positive reciprocity of B, because he has the opportunity to reward A for his behavior (Levitt and List, 2007). Therein lies a problem of the trust game. It possible to know, if A acts out of trust or reciprocity. Furthermore A can send money to B because of other-regarding preferences unconditional of other people like altruism or inequity aversion or out of spitefulness towards the experimenter to let him pay as much as possible (Harrison, 2008).

One way to get rid of these confounds, is to modify game designs according to Cox (2004). In his article Cox (2004) uses a so called triadic design to avoid confounds and to identify trust and reciprocity behavior. Instead of playing only one trust game, he lets the players play three different games in an across subject design. This means that players change every round to avoid learning or strategy effects. The first game, an investment game, is similar to the trust game described above except that both players receive an endorsement. The second game is a dictator game, where the first player of the first game chooses the amount the second player gets and the third game is a dictator game, where the second player has the choice of how much he gives the first player of the first game (Cox, 2004). According to Cox (2004) the advantage of this design is that it is possible to find out if the players act out of altruism or out of reciprocity and trust, because the trust game shows, if the players act out of reciprocity or trust and in the dictator games they show if they act out of altruism. Nevertheless this design cannot clarify if the players act out of inequity aversion or spitefulness and it is not clear either if the players act out of reciprocity or trust. This might be found out, if an ultimatum game is added. A disadvantage of this design is that it takes much longer and is therefore more expensive and exhausting for the participants.

2.5.5. Gift exchange game

The gift exchange game is an experiment which is constructed like a typical employer employee relation with an incomplete contract (Fehr, Kirchsteiger & Riedl, 1993). In this experiment player A offers player B a salary and player B chooses an effort level in response (Falk & Fischbacher, 2006).

Principal agent theory predicts in this case that player B will choose the lowest possible effort level, no matter how much salary he gets, because he has no incentive to do otherwise, since A cannot control his behavior. A anticipates this behavior and therefore offers the lowest possible wage with the result that B indeed chooses the lowest possible effort and both act rationally as the model predicts.

Empirical data and everyday experience, however, show that employers, in our case A, pay more than necessary, because they want bigger efforts. Employees, in our case B, show more effort than predicted, which leads to a positive wage effort relation (Falk & Fischbacher, 2006). It can be derived from the data that employers do not want employees that accept the lowest possible wage, because in that case they expect that these workers will not work hard enough (Fehr & Falk, 1999). Market experiment wages are significantly above the minimum wage level and stayed there even when minimum wages were abolished again (Falk, Fehr & Zehnder, 2006).

Similar to the trust game this game is a good measure of trust and trustworthiness (Levitt & List, 2007). A, the employer, trusts B, the employee to show more effort if he increases his salary. On the other hand, B is considered trustworthy if he indeed shows more effort when A offers a higher wage than the minimum.

2.5.6. Public goods game

In a standard public goods game four players are endorsed with the same number of tokens. First every player has to decide how many of them he wants to keep and how many he wants to put into the pool. After everybody has made their decision, the tokens in the pool are multiplied by a specific factor and then equally divided among the players. (Chaudhuri, 2011)

If all the players were acting only out of self-interest, the best strategy would be to keep all the money, if everybody else in the game puts his money in the pool. The person, who keeps his money, has most in the end, because he gets his share of the pool and his whole endorsement. However, if everybody thinks like that, nobody will put any money in the pool and everybody is worse off.

Experimental results show that participants contribute on average 40% to 60% of their endorsement and that contribution declines over time as more players tend to free ride (Chaudhuri, 2011). Ways to increase contributions are to allow communication, to implement a threshold or to increase the factor the money is multiplied by in the pool (Ledyard, 1995, cited in Chaudhuri, 2011).

2.5.7. Possible variations in games

- One-shot vs. iterated interaction games

One-shot interaction means that a game only lasts one round. In iterated interactions the game takes more than one round. The Differences are that it is not possible to build reputation to learn the behavior patterns of the other players and that there are no learning effects in a one-shot interaction game.

- Across subject vs. within subject interaction

In an across subject design the playing parties change every round of a game. This design is also called stranger condition. In a within subject design the players stay the same for the whole game, which is also called partner condition. The difference is that there are no learning effects or strategic thinking in an across subject design. Every round of an iterated game in an across subject design is a one shot game with all its advantages and disadvantages.

- Face to face vs. computer interaction

Another important decision is if games should take place in front of computers or face to face. People act less selfish, when they interact face to face, because they can talk and actually see their counterparts and their reaction and therefore social norms are activated.

Another way to use computers is to create standardized settings. Rilling et al. (2002) for example let the participants play prisoner´s dilemmas on a computer. Under one condition they told the players that they would play against a computer and in the second condition they told them that they would play against humans, whereas in fact they always played against a computer. That way you can standardize the answers of the opponent of the participant, which reduces complexity and possible problems due to uncommon or irrational choices. Results showed that players acted significantly less cooperative, when they were told that they play against a computer (Rilling et al., 2002; Suzuki et al., 2011).

- Earned vs. endorsed money

It is standard in economic experiments to give the participants money for their effort. Normally they get a fixed amount of money to play with in the experiment and according to their performance in the game they get paid out. So it is possible that players do not value the money they get before the experiment, because they got it without effort.

To test whether there is a difference if the players have to earn the money to play with in the experiments or if they get it for free from the experimenter, Oxoby and Spraggon (2008) modified a dictator game by adding the so called receiver earnings treatment, in which the proposer gets his capital to allocate in the game depending on the performance of the responder in an exam. The more questions the responder answers correctly the more money the proposer starts the game with. He afterwards has to decide, how much of the money he keeps and how much he gives the responder, who actually earned the money. This treatment should create a moral conflict, because the proposer has the power to keep all the money, but the responder earned it and so it would be unfair to do so.

Wealth (CAN$)	Mean (percent)	Median (percent)	Offers between (percent)			
			0 percent	1–49 percent	50 percent	51–100 percent
Baseline dictator treatment						
10	23.5 (4.717) [20]	20	35.00	35.00	30.00	0
20	20.22 (3.604) [23]	25	26.09	60.87	13.04	0
40	20 (3.776) [18]	18.75	11.11	77.78	11.11	0
Receiver earnings treatment						
10	27.5 (7.665) [16]	20	37.50	25.00	25.00	12.50
20	46 (4.220) [35]	50	2.86	40.00	25.71	31.42
40	63.83 (3.663) [32]	75	0.00	15.63	15.63	62.86

Table 2: Percentage offers by treatment and wealth level (Oxoby & Spraggon, 2008, p. 706)

The results in table 2 show that the offers were higher in the receiver earnings treatment than in the standard dictator treatment and increased the better the responders were at the exam (Oxoby & Spraggon, 2008). This indicates that it makes a difference if the money was earned or simply endorsed.

- <u>Height of stakes</u>

Normally the person gets a show up fee and/or he can earn money according to the decisions he makes during the experiment. To keep the costs low the stakes are normally relatively low, usually up to 15 €. A point of criticism therefore might be that the stakes are too low to make people care. It would be very expensive to increase the stakes and therefore Cameron (1999) tested, if the height of the stakes changes the results of ultimatum games. To keep the costs low, they conducted the experiment in Indonesia, where they let people play for stakes up to three months of their income (Cameron, 1999). The results in figure 1 show that even very high stakes could not crowd out cooperation, especially the behavior of the proposer did not change with the height of stakes (Cameron, 1999).

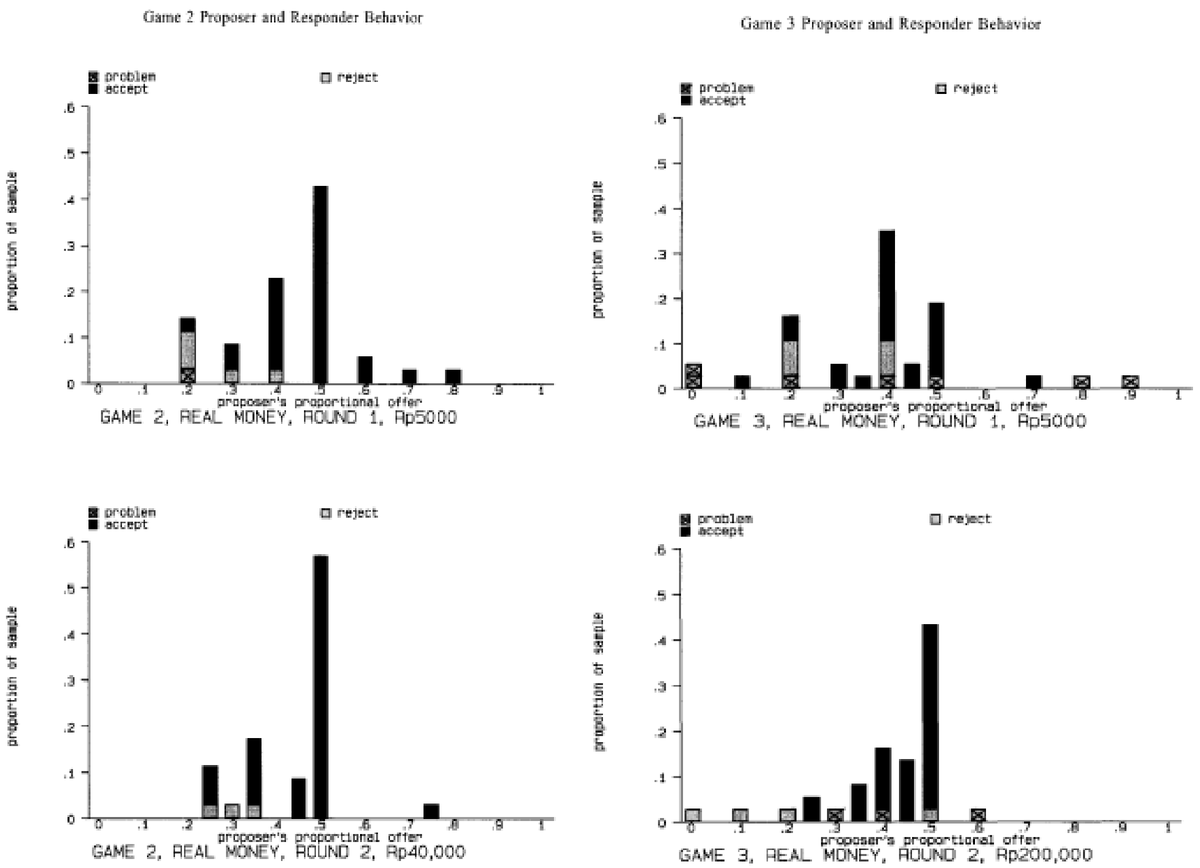

Figure 1: Left: Proposer and responder behavior at stakes of 5000 and 40000 rupees (Cameron, 1999, p. 52); Right: Proposer and responder behavior at stakes of 5000 and 200000 rupees (Cameron, 1999, p. 53)

Therefore the relative height of the stake compared to the income of the participants showed no impact on the behavior in ultimatum games. Cooperation is not decreasing in dependency on the height of the stake.

Another experiment investigated the influence of the absolute height of the stake on the cooperation rate. Absolute here means the height of the number. Furlong and Opfer (2009) tested in prisoner´s dilemma games if cooperation rates change if the numeric values of the stakes are higher, even if the money value stays the same. The higher the reward for cooperation the higher is the rate of cooperation in this kind of game, because it becomes more preferable than defection. They compared games, where they varied for example the stakes for cooperation between 3$ and 300¢ and all other outcomes in the same way between dollars and pennies, so that the money value was the same, but the numeric values were different (Furlong & Opfer, 2009). Results showed a significant difference in cooperation rates. Players cooperated more, when the stakes were posted in pennies, which is remarkable, because the money values of the stakes were the same in the dollar and penny conditions (Furlong & Opfer, 2009). This proves that the height of the number has an influence on the cooperation rate, because the higher the number the more it looks like, even if this is not the case.

2.6. “Typical” results in an experiment of cooperative behavior

A good experiment to measure cooperation is the public goods game. To maximize the outcome of all players, all players should invest their complete stake. If they cooperate, they earn the highest possible amount of money. In these experiments people cooperate in the first rounds and put some of their money in the pool, but the contribution rate decreases over time.

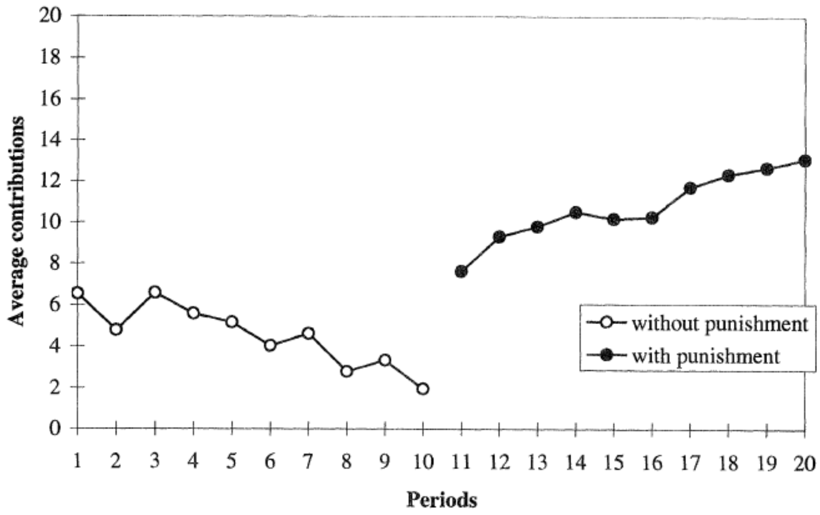

Figure 2: Average contributions over time in the stranger treatment (Fehr & Gächter, 2000, p. 986)

The white dots of figure 2 show a result typical of basic cooperation experiments: The cooperation level starts higher than expected by standard economic theory and declines over time. This figure also shows that the public goods game is a very variable game. There are many factors that can be implemented like a "punishment" and "stranger" condition in this case which can be seen for the graph with black dots. This flexibility makes it possible to test many hypotheses concerning cooperation just by modifying the conditions of the game, which would be very difficult and time and cost intensive in the field.

2.7. Reasons for cooperation

2.7.1. Reciprocity

Reciprocity means that people respond to other peoples´ behavior with the same behavior (Fehr & Gächter, 2000), even if no material gains are expected (Fehr & Fischbacher, 2002). This behavior seems clear, when we interact with friends and relatives, but it even occurs, when complete strangers meet each other (Nowak & Sigmund, 1998).

Reciprocity can be categorized in different ways. Positive reciprocity means that people react kindly to kind actions towards them and negative reciprocity means that people react negatively to negative actions (Fehr & Gächter, 2000). Positive reciprocity is the rewarding aspect of reciprocity and negative reciprocity is the punishing aspect.

Applied to cooperative behavior, positive reciprocity means that people are willing to cooperate if others act cooperatively. This might be an explanation why humans cooperate in gift exchange games, although it would be rational not to cooperate.

One kind of reciprocity driven cooperation is called conditional cooperation, which means that one person cooperates if the other person also does so (Fischbacher, Gächter & Fehr, 2001). This is known as the ”tit for tat“ strategy (Axelrod & Hamilton, 1981). In the first round players usually cooperate to show the other player that they are willing to do so.

This attitude towards cooperation might be a signal that a person is very reciprocal. Even in situations, where incentives not to cooperate are high, these people remain reciprocal and contribute the same amount of money (Fischbacher, Gächter & Fehr, 2001). This form of reciprocity is also called direct reciprocity.

Fischbacher, Gächter and Fehr (2001) found out that in a one-shot public goods game 50% of the people were conditional co-operators, who were willing to contribute more the more others contribute. The figure below also shows that 30% are free-riders and contribute nothing no matter how much the other players contribute. The third group of players show “hump-shaped” behavior. They cooperate on the low contribution levels and free-ride as soon as contribution levels rise above a specific level.

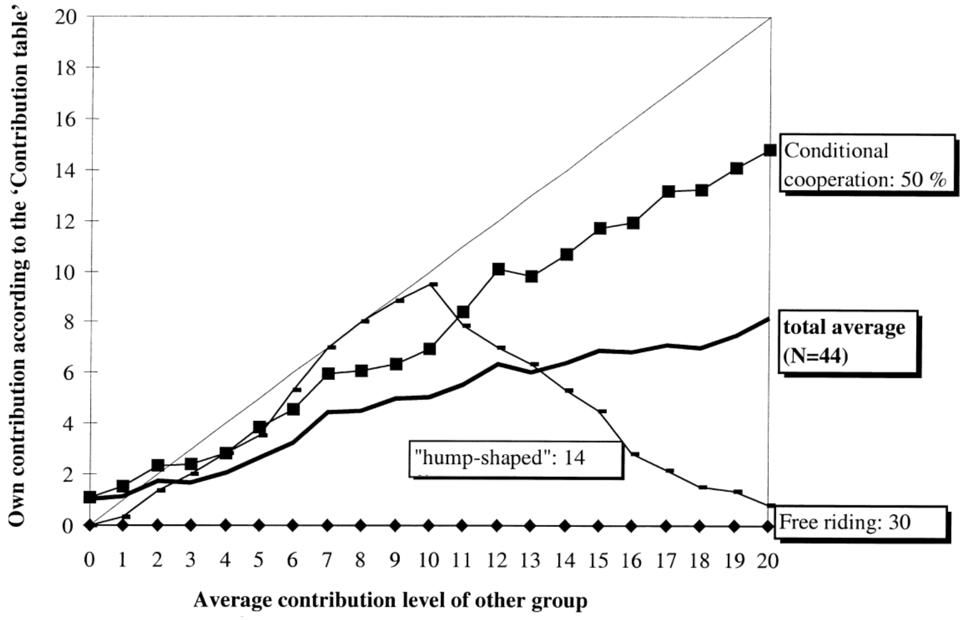

Figure 3: Average of the own contribution compared with average contribution of other members (diagonal=perfect conditional) (Fischbacher, Gächter & Fehr, 2001, p. 400)

This coexistence of co-operators and free-riders has the effect that small changes in the setting of the game can change the result and that not all members of the group have to be cooperative in nature to provide the overall result of cooperation (Gintis et al., 2003).

Indirect reciprocity might also be an important reason for cooperation. Indirect reciprocity means that a third person knows how a player behaved in a specific game or situation and reacts according to it (Engelmann & Fischbacher, 2009). This concept is related to reputation building. If somebody knows the history of a person, he also knows how he is likely to react in the future and this reputation might change decision behavior. To make a cooperative system based on indirect reciprocity work, two conditions must be met. First, it is necessary that good reputation will be rewarded and second, people have to be willing to invest into their reputation (Engelmann & Fischbacher, 2009).

So there are different forms of reciprocity like direct or indirect and positive or negative reciprocity, which are all important for cooperative behavior. Direct reciprocity is one explanation why two people cooperate in a repeated interaction. If there is no repeated interaction cooperation can still happen due to indirect reciprocity, which is similar to reputation. But even in one-shot public goods experiments approximately 50% of the participants are cooperative, on the condition that the other participants are cooperative. They are so-called conditional co-operators. Kind behavior in answer to kind behavior of others is called positive reciprocity. Negative reciprocity, on the other hand, describes the punishing aspect of reciprocity. Interestingly enough, people tend to punish even if it is costly for them (Fehr & Gächter, 2000).

2.7.2. Incentives

Punishments and rewards are a way to increase cooperation. Punishing selfish behavior and rewarding cooperative behavior looks like a straight forward and transparent way to promote cooperation. Fehr and Gächter (2000) added a punishment condition to a public goods game. The first stage of that game consisted of a standard public goods game with standard results (cooperation above standard economic prediction but decreasing over time). In the second stage it was possible to punish other players by reducing their income. This was done by buying punishment points and assigning them to the other player. After this modification cooperation rates increased and stayed high (Figure 2), although those punishment points were costly and therefore reduced the income of the punisher as well. This result is contrary to standard economic theory, which predicts that no punishment would happen, because it would also reduce the income of the punisher.

A disadvantage of punishment is that it reduces the efficiency of the outcome, because income gets lost by punishing. A way to avoid this is to replace punishment with redistribution. This means that punishment does not only reduce the income of the free-rider but it also increases the income of the co-operator, rewarding him. Sausgruber and Tyran (2007) showed experimentally that this is a possible mechanism to induce cooperation with a “costless” sanction (Figure 4).

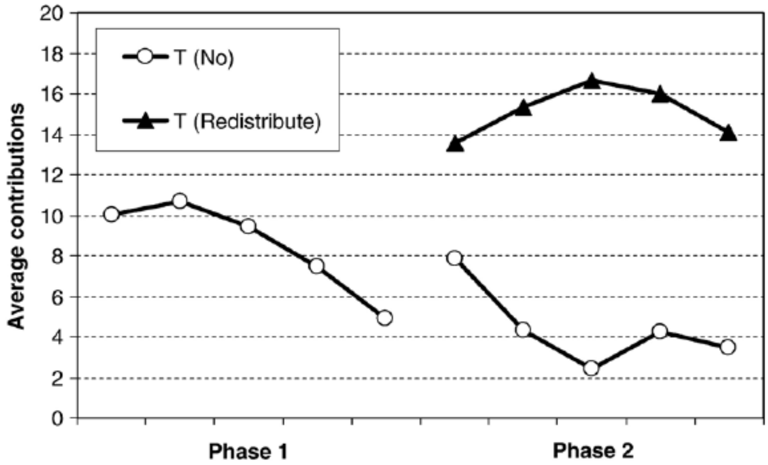

Figure 4: Average contributions over time in basic (white dots) and redistribution condition (black triangles) (Sausgruber & Tyran, 2007, p. 336)

2.7.3. Inequity aversion

An individual is inequity averse if he dislikes outcomes that are perceived as inequitable (Fehr & Schmidt, 1999, p. 820). This means that every person has a different threshold of perceived inequity aversion. It depends on the reference outcome which he uses for the specific situation so the relative outcome matters (Fehr & Schmidt, 1999; Bolton & Ockenfels, 2000).

This attitude can explain why some people give money in the dictator game (Fehr & Schmidt, 2006). They want to reduce inequality and raise the other player to their own level. It also can explain why people punish selfish behavior in the ultimatum game by rejecting too low offers and it helps to understand why this level of rejection is different for each person. Everyone has a different point of reference outcome which he defines as unequal.

2.8. Differences in culture

Cooperative behavior seems to differ across cultures. Herrmann, Thöni and Gächter (2008) conducted public goods games in 16 different regions of the world and the results, visualized in figure 5, show that there are differences between different cultures. The results of the left figure are not as surprising as those of the right one. In the left part of figure 5 public goods game were played without the possibility to punish antisocial behavior. Tendencies are the same across all cultures. Contribution decreases over time. The right part reflects the results of public goods games, conducted with the possibility to punish antisocial behavior. The results show that there is cross-societal variation. In some pools high contribution was as much punished as low contribution, whereas in others only low contributors were sanctioned and in some the extent of antisocial punishment even removed the effect of punishment to enhance cooperation (Herrmann, Gächter & Thöni, 2008). One possible explanation is that some punish those who deviate from the norm, regardless in which direction, to bring them back in line (Herrmann, Gächter & Thöni, 2008). The reason is that they are suspicious of others who are too generous and therefore do not act according to the norm (Herrmann, Gächter & Thöni, 2008).

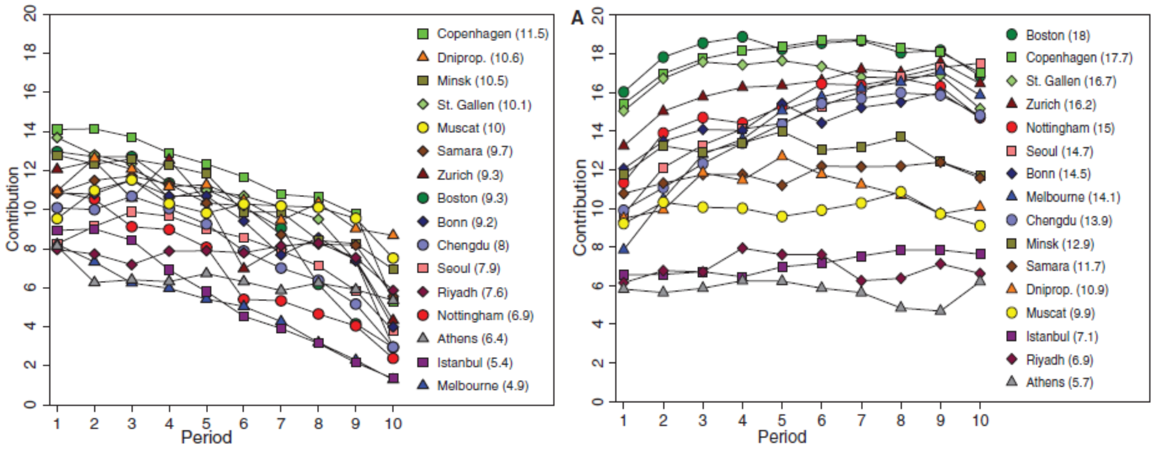

Figure 5: Left: Differences in cooperation across cultures <u>without</u> punishment (Herrmann, Thöni & Gächter, 2008, p. 1365); Right: Differences in cooperation across cultures <u>with</u> punishment (Herrmann, Thöni & Gächter, 2008, p. 1364)

2.9. Ways to increase cooperation in games

After explaining some reasons for cooperation, it is possible to use this knowledge to show how to increase cooperation.

Using reciprocity to increase cooperation might be accomplished by using partner conditions in experiments and showing the decision history of the participants to build up reputation.

It can be assumed that 50% of the people are conditional co-operators and cooperative equilibria are fragile because of free riders and “humped-shaped” behaving people. Therefore it is important to choose the right members for the games, like in real organisations, where some “rotten apples” might spoil the whole group.

Another possible approach to increase cooperation in games is to allow communication between the players. Isaak and Walker (1988) showed in a modified trust game that communication increases the contribution rate. The possibility to communicate with the other players might increase the willingness to cooperate, because that way they might express their feelings and their possible disapproval with words instead of punishment. Houser and Xiao (2005) modified an Ultimatum game by giving the responder the possibility to tell the proposer his feelings after accepting or rejecting the offer. The results in figure 6 show that the possibility to express emotions reduced the rejection rate significantly when only 20% of the money was offered (Houser & Xiao, 2005). So many offers are rejected to show disapproval and if other ways are offered to express oneself, people prefer cost-efficient ways.

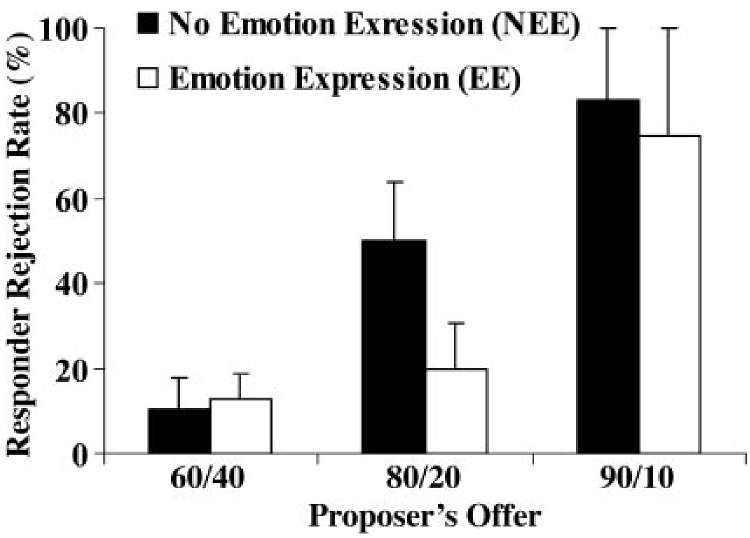

Figure 6: Rejection rates of several offers dependent on emotion expression(Houser & Xiao, 2005, p. 7400)

A proven way to increase cooperation is to add a possibility to sanction selfish behavior (Fehr & Gächter, 2002). Sanctions do not have to be monetary. Sausgruber and Tyran (2007) improved the rate of cooperation by making redistribution possible. The big advantage of this approach is that redistribution is more efficient than a costly punishment mechanism. The costs of punishment are lost for all players and reduce the pot, whereas distribution only shifts money from one player to the other. . The cultural background has to be taken into account, when introducing a punishment opportunity, because not in all cultures punishment leads to higher cooperation (Herrmann, Thöni & Gächter, 2008).

Zelmer (2003) identified in a Meta-study of 27 lab experiments that three variables were highly significantly responsible for an increase in cooperation in public goods games: “Marginal per capita return”, “Communication allowed” and “Constant groups for session”. This means that the highest increase in cooperation occurs in a setting, in which the pool is multiplied by a high factor, communication is allowed and the players stay the same for the whole experiment.

3. Cooperative behavior in the light of neuroeconomics

3.1 Definition of Neuroeconomics

It is very difficult to find a single definition for neuroeconomics that fits for all research in this field. It is obvious that neuroeconomics combines neuroscience and economics, but in which way and to which purpose, is still not finally determined yet. Neuroscience might help to answer fundamental questions of economics, because its aim is to understand how the brain works on a mechanical level, namely on the level of neurons and synapses. By knowing how the brain functions neuroscience wants to find out how thoughts and choices work. So neuroscience chooses an inductive approach to generate knowledge. Although both sciences share the goal to understand human behavior, research strategies have been very different. As already mentioned above, economics uses mainly mathematics and nowadays experiments whereas neuroscience uses experimentally obtained data from the brain, like brain images or animal experiments. Neuroeconomics tries to combine these two approaches.

Fumagalli (2010) shows this diversity of definitions by giving different definitions from different groups of researchers that show different foci and goals. Some experts do not see neuroeconomics as a new field but rather as an extension or application of economics or a new method for economic research, whereas others consider it a new interdisciplinary discipline (Fumagalli, 2010).

Neuroeconomists believe that this combination of economics and neuroscience is one step towards a unification of economics and psychology (Fehr & Camerer, 2007). Both disciplines focus on human behavior, but separated at the beginning of the 20th century. Neuroscience might be able to bring them together again, because it offers a common ground of methodology, data, definitions and theories on the neural level. It would be possible for both disciplines to communicate in a language both fields understand.

3.2 Fields of Neuroeconomics

Ross (2008) distinguishes two fields of neuroeconomics: “Behavioral economics in a scanner” (BES) and “Neurocellular economics” (NE).

“Behavioral economics in a scanner” is behavioral economics using methods of neuroscience. A main characteristic of BES is that it is assumed that specific behavior leads to an increased activation in particular parts of the brain (Vromen, 2011). Furthermore, BES is used to generate more data to confirm questions from behavioral economics. BES, for example, registers brain activity of people in an ultimatum game inside an MRI scanner. This is one reason, why neuroeconomics have often been criticised. It is argued that in the end it is just behavioral economics with fancy machinery, a marketing gag of behavioral economics but nothing new.

“Neurocellular economics” or “economics of neural activity” uses modelling techniques and theories of economics to make models of brain cell activity or brain organisation. It is possible to use economic theory for explanations how the brain works, because brains and markets have in common that they are both parallel processors (Ross, 2008). According to Ross (2008) they both learn and optimize the same way. Thinking in an economic way helps for example to understand the model of the midbrain/striatal dopamine circuit. This circuit is responsible for rewarding and integrates attentional cueing, value estimation and motor response preparation (Ross, 2008). This integration is similar to those of economic models of utility, but instead of money, dopamine signals are the currency of the brain and therefore maximized (Harrison & Ross, 2010).

Although both fields are called neuroeconomics there are differences between them. BES uses neuroscientific knowledge to reject standard economic theory, whereas NE uses standard economic theory to study neural behavior and does not want to reject it but rather enrich it (Harrison & Ross, 2010). Across these differences there is common ground that it is necessary to develop new economic models and theories, because the predictive power of standard economic theory is poor (Vromen, 2011). Additionally, both fields believe that neuroscience can help and enrich economics especially as far as choice theory is concerned (Vromen, 2011).

Most of the criticism on neuroeconomics is not headed towards NE but towards BES, but this differentiation has been widely ignored by critics so far. This thesis will focus on BES, because most of the research about cooperative behavior was done in that field.

3.3 Basic neuroanatomy

This chapter offers a very brief introduction to neuroanatomy. The main areas of the brain will be presented and allocated to specific areas of the brain. Furthermore it will be explained, what neural activity is and how it works. Finally some important brain regions will be explained more closely, because they are of interest in neuroeconomics of cooperative behavior, like the reward circuit and the limbic system.

3.3.1 Orientation in the brain

Knowing directions is crucial for orientation. Figure 7 introduces the specific terms that are used in anatomy when talking about directions in the brain. If you take the centre of the brain as a reference point, the front side is called anterior. Posterior is the term that refers to the lower side of the brain. The upside area of the brain is called dorsal. Ventral is the opposite direction of dorsal. The midline divides the brain in two parts. Medial is used to describe any area closer to the midline whereas lateral refers to any area further away from it. (Pinel, 2007, p. 63)

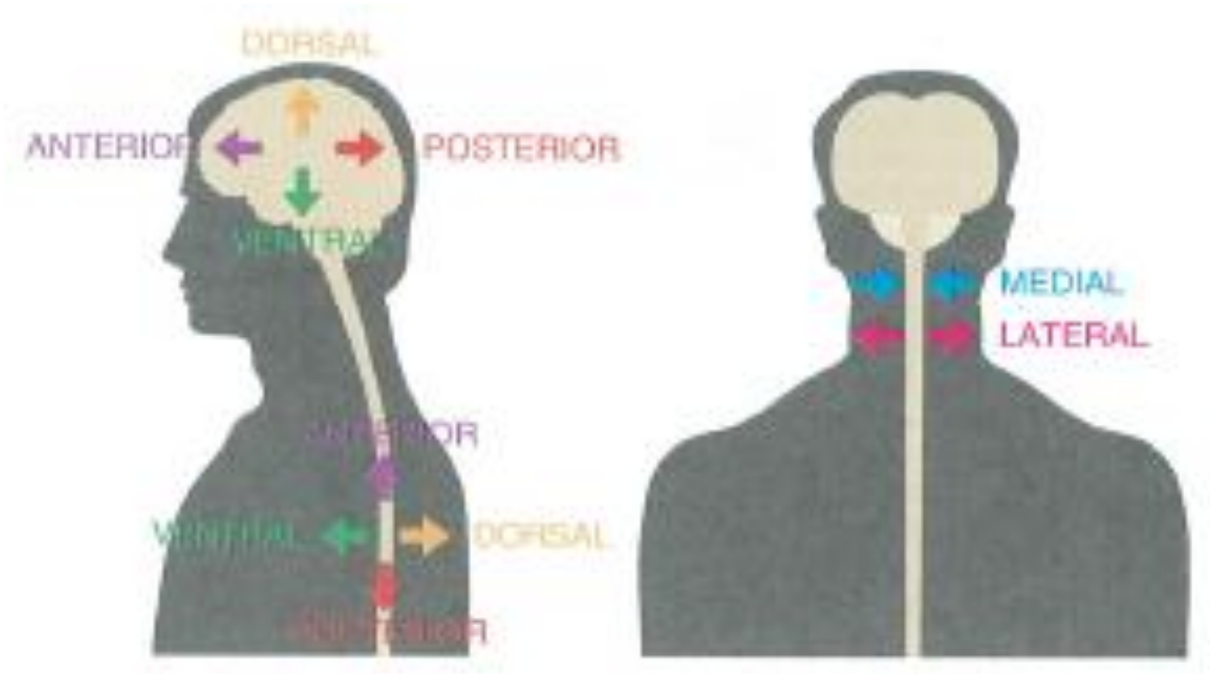

Figure 7: Anatomical directions in a human (Pinel, 2009, p. 63)

3.3.2 A map of the brain

The human brain has three major parts: The brain stem, which is the connection between the brain and the spinal cord and the oldest part of the brain, the Cerebellum, a rippled part under the cerebrum and the cerebrum, the largest and youngest part of the brain (Bear et al., 2007, p. 209). The cerebrum is subdivided into four parts. The frontal lobe lies at the front of the brain, the parietal lobe at the vertex, the temporal lobe closest to the stem and the occipital lobe at the back of the brain. The left and the right half of the cerebrum are anatomically the same but have different functions.

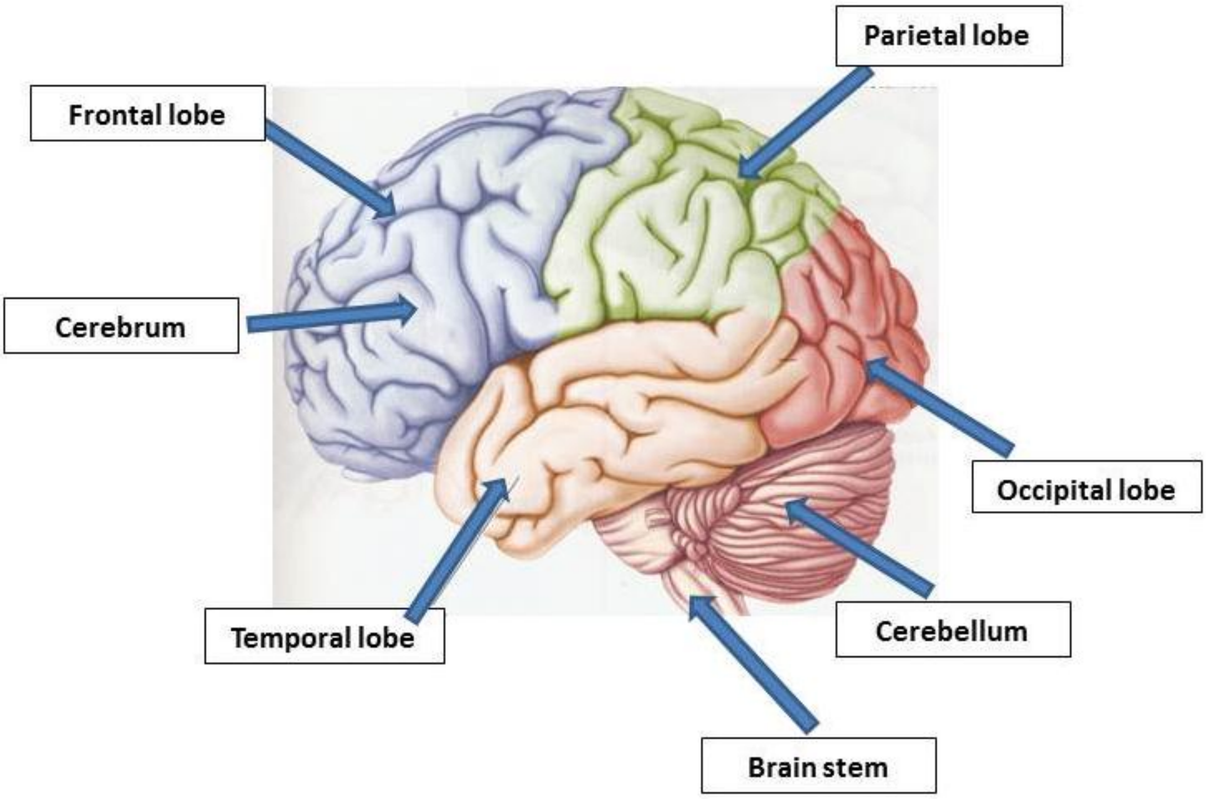

Figure 8: Areas of the human brain (Bear et al., 2007, p. 209)

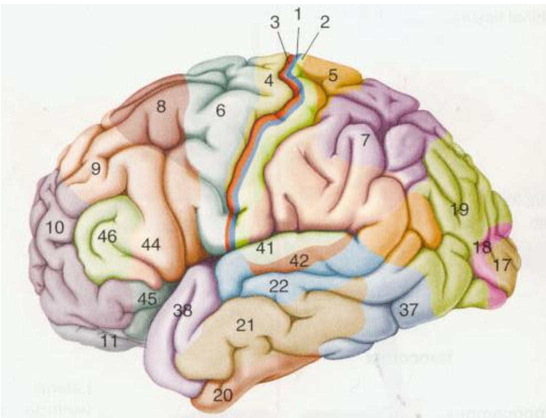

Figure 9: Brodmann areas in the human brain (Bear et al., 2007, p. 198)

Another way to divide the cerebrum is by splitting it up into zones. The cytoarchitectural map by Korbinian Brodmann numerates 46 zones according to their cytoarchitecture (Bear et al., 2007, p. 198).

3.3.3 Neural activity

The body uses current to transmit information within the body. Without any action the current inside the neuron is about -65 mV. As soon as a signal above a certain threshold reaches the neuron, the neuron depolarizes. This means that by changing its voltage, it sends a signal to the next neuron to which it is connected via synapses. Chemical synapses release neurotransmitters which bind to receptors of the next neuron and lead to an action potential in the next neuron, which releases neurotransmitters and so on. Electrical synapses, on the other hand, allow direct transfer of current from one neuron to the other.

After depolarization the neuron has a refractory period. In this phase the neuron cannot be stimulated and returns to its negatively charged state to make new depolarisation possible again.

3.3.4 The pleasure/reward centre

The pleasure centre of the brain rewards certain behavior to reinforce it. This is one reason why drugs work. Pleasure is created by the release of the neurotransmitter dopamine along the nigrostriatal pathway (green in figure 10) and the mesocorticolimbic pathway (red in figure 10). So the most important areas for pleasure and reward in the brain are the prefrontal cortex, the limbic system, the amygdala, the striatum, the anterior cingular cortex and the nucleus accumbens (Pinel, 2009, p. 392).

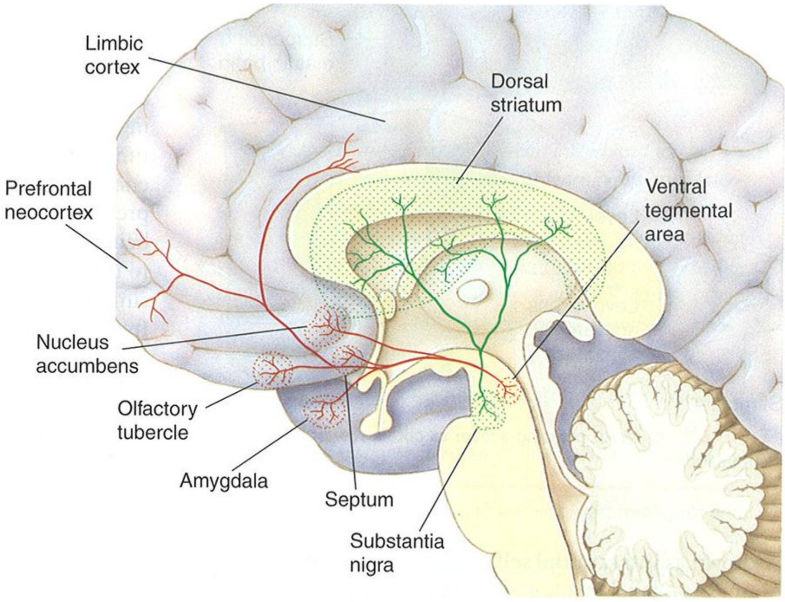

Figure 10: The mesotelencephalic dopamine system in the human brain (Pinel, 2009, p. 392)

3.3.5 The limbic system

The limbic system is responsible for the experience and expression of emotion (Pinel, 2009, p. 71). The main structures of the limbic system are the amygdala, the hippocampus, the cingular cortex, the fornix, the septum and the mammillary body (figure 11).

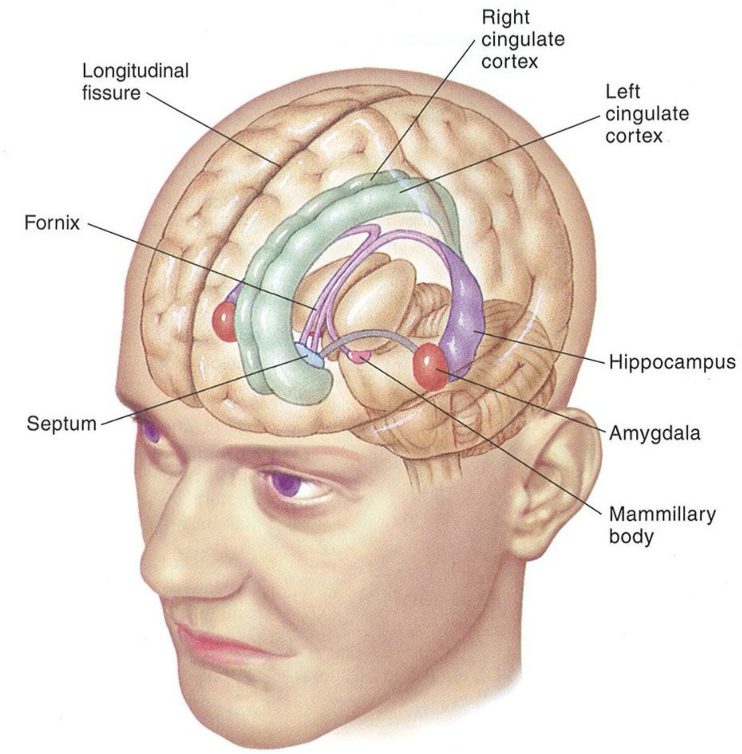

Figure 11: The major structures of the limbic system (Pinel, 2009, p. 71)

3.4 Methods of neuroeconomics

3.4.1 Neuroeconomic research in practice

Most neuroeconomic studies consist of two parts, the economic and the neuroscientific part. The underlying economics of neuroeconomic experiments are the same as mentioned in chapter 2 and games (ultimatum, trust, dictator,…) are widely used. Games are ideal for this kind of research, because test persons must not move at all in an MRI scanner. During an ultimatum game, for example, it is possible to lie completely still and nevertheless make decisions. The neuroscientific part of the experiments is to measure what the brain does during the experimental task.

The most common ways to make the brain´s answers visible are neuroimaging techniques and lesions. Each of these methods has its advantages which will be shown in the following chapter. Also the application of hormones like oxytocin as a neuroeconomic method will be discussed, as it is an uncommon but interesting path for the topic of cooperation.

3.4.2 Neuroimaging techniques

There are several imaging techniques which are used in neuroeconomic research. The most common are fMRI, PET and EEG.

- fMRI – functional magnetic resonance imaging

Like the MRI technology fMRI uses electromagnetic waves to measure activity in specific brain regions. The difference is that fMRI uses the so-called BOLD signal (Wager et al., 2009, p. 154). "BOLD" stands for "Blood Oxygen Level Dependent" and means that the differences in blood oxygen levels in different brain regions are visualized. fMRI can measure these differences, because oxygen saturated blood has different magnetic attributes than blood with an increased CO_2 level. These differences are an indicator for altered brain activity, because the brain needs oxygen to run and therefore high oxygen levels mean high activity. So fMRI is an indirect measure for brain activity.

fMRI has several advantages (Wager et al., 2009, p. 155):

- fMRI has been used since the 1970s for medical purposes, so there are facilities available, which can be used for neuroeconomic research.
- fMRI has a high spatial resolution, which means that this method can visualize very accurately where brain activity happens. (Other methods are better in visualizing when brain activity happens and how it changes over time like the EEG, which are therefore called methods with high temporal resolution.) To

overcome this disadvantage it is possible to combine EEG with fMRI to increase temporal resolution.

- fMRI technique does not need any injection of radioactive markers, because only the blood oxygen level is determined. Therefore multiple scans are considered safe for the test person.

- <u>PET – positron emission tomography</u>

PET is a powerful tool to measure the overall activity of the brain (Wager et al., 2009, p. 157). In principle PET exploits the fact that the brain needs glucose to operate. As soon as neural activity increases, the activated neurons of the brain demand glucose to get the energy needed. Therefore neuroscientists inject radioactive-labelled glucose, usually ^{18}F-fluorodeoxyglucose, as a tracer into the carotid. The body transports it into the brain, because it cannot differentiate between the “normal” and the modified glucose (Pinel, 2007, p. 134). Inside the brain the glucose derivative cannot be metabolised and remains at places of high neuronal activity, where it decays and emits positrons (Wager et al., 2009, p. 156). These positrons collide with neighbouring electrons, which annihilates both particles, and emit two photons in opposite directions which are detected by photoreceptive sensors around the test person´s head. This information is sent to a computer, where it is interpreted and presented as a three dimensional image of the brain. Therefore it is possible to locate the exact position of the annihilation of the positron and the electron (but not the distribution of the tracer), which means that PET is an indirect measure of brain activity (Wager et al., 2009, p. 156).

Several advantages of PET (Wager et al., 2009, p. 154):

- PET shows the activity of the brain better than fMRI.
- Due to the fact that PET uses a radioactive tracer, it does not suffer from magnetic artefacts like fMRI.
- The tracer makes it easier to measure the blood flow and the areas of activity in the brain.

- <u>EEG</u>

EEG measures the electric activity of the brain, which is the sum of action potentials, postsynaptic potentials and electric signals of skin, muscles, blood and the eyes (Pinel, 2007, p. 137). If all these activities are measured, however, it is not possible to pinpoint down a single source, which makes causal explanations very difficult.

Thus, EEG is mainly used to identify different levels of consciousness (for example sleep), which correlate with certain EEG – wave frequencies (Pinel, 2007, p. 137).

Advantages of EEG:

- No injection of radioactive tracer necessary
- Cheap compared to fMRI or PET
- High temporal resolution (but low spatial resolution, but solvable via combination with fMRI)

• Interpreting the results of neuroimaging techniques

It is very important to know that the results of neuroimaging techniques are presented in statistical probabilities or correlations. This means that the colourful regions of the brain in the pictures are nothing more than statistical probabilities of occurrence. fMRI pictures, for example, show t values of occurrences of activities. In the marked regions activity is significantly higher than in other regions. Given the fact that thousands of fMRI studies have been done yet, it is very likely that some effects are just artefacts or coincident.

3.4.3 Lesions

First neuroscientific research "happened", when people changed their behavior due to injuries of the brain caused by accidents, attacks or aging. People with Parkinson disease for example tend to be more honest than the normal population due to changes in the brain (Nobuhito et al., 2009). These changes are caused by specific lesions of the brain due to the disease.

Lesions can be differentiated into permanent or temporal lesions. In experiments, permanent lesions are inflicted by knife cuts, radio-frequency current or removing of brain mass (Pinel, 2007, p. 143).

- Cryogenic blockade

Temporal lesions are made by cryogenic blockade, TMS (transcranial magnetic stimulation) or DCS (direct current stimulation). Cryogenic blockade means that the area of interest of the brain is cooled down so that neural activity stops but no damages occur (Pinel, 2007, p. 143).

- TMS (transcranial magnetic stimulation)

TMS uses a magnetic field to change neural activity in a certain brain area. It is still unclear how TMS exactly works, but applied frequencies below 1 Hz decreases and above 1 Hz increases neural activity (Weber, 2011, p. 52; Sandrini, Umilta & Rusconi, 2011). A disadvantage of this method is that its application is limited to areas not deeper than 2-3 cm, because the magnetic field is losing strength rapidly on its way through the brain (Sandrini, Umilta & Rusconi, 2011).

- DCS (direct current stimulation)

DCS uses a constant stream of current instead of a magnetic field to reduce brain activity (Weber, 2011, p. 53). This stream of current changes the probability that incoming neural signals lead to postsynaptic firing (Wagner et al., 2007). An advantage of DCS in contrast to TMS is that test subjects do not feel the current and therefore it is easier to distract them (Weber, 2011, p. 53).

A big advantage of the use of lesions is that, if behavior changes after a lesion, you know exactly which region of the brain is responsible for the change. This means that it is possible to deduce a causal relation between a change in behavior and the destruction/inhibition of a certain brain area (Umilta, 2011). Of course, it is illegal to set permanent lesions in humans for scientific purposes only. Therefore stroke or tumor patients qualify as subjects for scientific research on lesions. Temporal lesions might be a solution, but these methods still bear a risk, because the effects of DCS, TMS or cryogenic blockade are not clearly understood yet (Pinel, 2007, p. 136).

3.5. Chances of Neuroeconomics

Neuroeconomics is a young discipline with a lot of potential. Although the contribution to the field of economics is small yet (McCabe, 2008), there are several ways in which neuroeconomics can be useful for economics.

Brain imaging or studies of people with brain damages in specific brain regions are additional sources of data, which can be used to confirm economic hypotheses and theories (Spiegler, 2008). Increased demand will improve the methods and reduce costs of these still expensive machines. So not only economics benefits from neuroeconomics but also medicine and other disciplines that use these methods do. Maybe it will be standard one day to measure brain data to get published in economics.

Knowing the "construction plan" of the brain can be useful to answer economic questions and to understand why people act the way they do. Neuroeconomic results can be added to economic theories and that way improve predictions of economic models. Today this map of the brain is still incomplete and so we do not understand exactly how the brain works.

Padoa-Schioppa (2008) argues that neuroeconomics can contribute to economics also via psychology.

"Neural data can and do lead to better psychological theories, and psychological insights can and do lead to better economic theories." (Padoa-Schioppa, 2008, p. 449)

Although the three disciplines of neuroscience, psychology and economics work on different levels of cognition, all of them are interested in human behavior. Economics tries to address human behavior globally with one set of formulas (Glimcher & Rustichini, 2004). Psychology works one level below on the individual level and neuroscience works on the cellular level. They might benefit from each other, if they are unable to answer questions by themselves.

Unfortunately there are still economists who think that economics does not need neuroscience or psychology like Gul and Pesendorfer (2005). One chance of neuroeconomics might be a step towards the unification of economics, psychology and neuroscience into one discipline that studies human behavior (Glimcher & Rustichini, 2004). Mathematical (economics), mechanistic (neuroscience) and behavioral (psychology) measures and constructs could be brought together in the future for the benefit of all (Fehr & Camerer, 2007). Economics and psychology could offer the theoretic framework and the object of analysis whereas neuroscience could contribute the methods and the language.

Contributions of neuroeconomics are still small, but it is an area with a lot of potential for the future. However, there is plenty of skepticism about the value of neuroeconomics. Whereas this chapter dealt with possible ways in which neuroeconomics can contribute to economic theory, the next chapter will take a closer look at these concerns.

3.6. Critical thoughts on neuroeconomics

3.6.1. Justification issues

There is intense discussion about whether economics can benefit from neuroeconomic research at all. Critics argue that neuroeconomics does not answer any relevant economic questions the way it is used today. It is just an additional source of data for questions of behavioral economics (Ortmann, 2008; Rustichini, 2005). Putting people into a scanner is not enough to justify a new field of economics. Additionally, neuroeconomic research is flawed in many ways as will be explained in this chapter.

According to Gul and Pesendorfer (2005) neuroeconomics makes two claims: The first says that psychological and physiological evidence are relevant for economics Gul and Pesendorfer (2005) respond that this is not the case. They argue that neuroeconomics cannot falsify any standard economic model, because economics "*address different questions, utilize different abstractions, and address different types of empirical data*" (Gul & Pesendorfer, 2005, p.1). Neuroeconomics or neuroscience in general wants to know more about the functioning of the brain whereas economics cares about individual choices. These different fields of interest lead to different data. Neuroeconomic data has therefore no value for economics, because the two disciplines have a different focus of interest. Different scientific traditions of neuroscience and economics lead to different meanings and abstractions of constructs like risk aversion according to Gul and Pesendorfer (2005), which therefore cannot be compared. They point out, however, that this does not mean that one definition is better than the other, they are simply different.

The second claim of neuroeconomics says that economic welfare analysis should focus on true utility instead of choice utility (Gul and Pesendorfer, 2005). The concept of true utility assumes that a choice is not the expression of what people really want, but rather of what they think they want. This assumption makes it clear, why neuroeconomics is so often criticized. Neuroeconomics rejects one of the basic assumptions of economics, namely that choice is the expression of people´s true will. If this is not the case, economic theory has a legitimation problem. In neuroeconomics choices are strongly influenced by the environment (for example framing) or unconscious factors like priming[1]. Considering these two different concepts of choice, Gul and Pesendorfer (2005) conclude once again that neuroeconomics cannot be used in the context of economics.

Any factor that might influence a person’s choice is seen as an information problem by Gul and Pesendorfer (2005): According to them, wrong choices are only due to a lack of information. As soon as people find out that they are influenced, they will counteract and thus choose what they really want.

Gul and Pesendorfer´s approach is a very fundamentalistic one according to Camerer (2008), because it isolates economics by denying any importance of non-choice data. Gul and Pesendorfer (2005) reduce all inconsistencies of behavior to a lack of information, which can be solved by telling people that they are wrong and by making them learn. Even Camerer (2008) agrees that it might be possible to see these anomalies as information problems, but using constructs or theories of other fields might be more elegant and simple than constructing for every psychological phenomenon an information problem. The central assumption of the information problem argument is that all behavior is conscious choice, which can be changed, if

[1] A prime is the presentation of a stimulus that affects the recognition of the following stimulus (Neely, 2003, cited in Sternberg, 2009).

you tell the choosing person that he might be in danger of acting irrational and let him learn. This is a noble attitude towards human learning behavior but Friedman (1998) showed in the "Monty-Hall Problem"[2] that people make irrational decisions even if they were told so and therefore had the opportunity to learn.

Another central assumption of neuroeconomics is that it is possible to track down the exact region of the brain that is responsible for a decision. According to Umilta (2011) this might be seen as a modern form of phrenology[3], where every region of the brain is responsible for one function, because this is not the case.

According to Umilta (2011) it is a common misconception that the brain can be separated into independent structures that are responsible for specific neural activities and that every thought or action can be traced back to a specific mental process. Assuming this modularity of the brain and the mind should make it possible to track down specific areas of the brain that are responsible for specific actions of the mind in an almost one-to-one fashion. (Umilta, 2011) This approach is neither new nor the only approach towards the organisation of the brain. Besides the former approach of phrenology exists a holistic approach towards the organisation of the brain. This means according to Umilta (2011) that there are no specific brain areas that are solely responsible for thoughts or feelings.

Another problem related to the topic is called "reverse inference fallacy" (Umilta, 2011; Poldrack, 2006; Harrison & Ross, 2010). Reverse inference in neuroeconomics means concluding from the activation of region A to a cognitive process B (Poldrack, 2006). Most brain regions, however, have more than one function and therefore may light up during scans due to many reasons (Cabesza & Nyberg, 2000). This means that neural activity does not necessarily have to be connected to the function tested

[2] There are three doors to choose from. There is a prize behind one door. The subject has to choose one door. Afterwards the experimenter opens one of the two doors not chosen. He opens one, which does not contain a prize. Two doors are left closed. The subject can switch to the other closed door or remain at his previously chosen door. Afterwards his chosen door is opened and he gets a prize if he has chosen the right one. The optimal strategy is to switch after the first round.

[3] Phrenology is a „science" of the 19th century, which tried to correlate the structure of the head with different behavioral traits like destructiveness, imitation or hope, because it was believed that the form of the skull reflects the form of the brain and the form of the brain is related to personality traits. (Bear et al., 2007, p. 10)

in the experiment. Therefore we cannot extract the effect of the experiment from the effect measured (Poldrack, 2006) and as a consequence it is very difficult to draw causal conclusions from brain images (Harrison & Ross, 2010).

Another problem of imaging techniques is the so called “ground noise” (Ortmann, 2008). It is not possible to live without basic brain activities and these signals “pollute” brain images. Even controlling for these activities does not help, since most regions have more than one function. Another source of noise is the fact that lying in a scanner or having electrodes fixed on one´s head is an uncommon experience and might therefore influence the results as well.

3.6.2 Methodological issues

Methodological issues are a big problem of neuroeconomic research. To generalize results it is necessary to use a representative sample. Nowadays, most studies prefer healthy and young people, because experiments can be exhausting or even painful, if you get contrast substances injected.

Sample size is a second problem. Scanner time is very expensive and therefore the samples are often reduced to a critical size which can reduce the power of the study and therefore make interpretations more difficult (Harrison, 2008).

False positive results are another problem in neuroeconomic studies, if the significance levels are not corrected when dealing with multiple comparisons (Bennett et al., 2009). Corrections are necessary, because the brain is divided into about 130.000 voxels (three dimensional units for MRI imaging) and during one MRI many thousands of images are made of each of them. This raises the probability of false positive results. Although it is common to decrease the level of significance to $p<0{,}001$ per voxel and only interpret results if the cluster size is at least 8 voxels, Bennett et al. (2009) showed that this might not be enough. They argue that statistical corrections are necessary but not always done properly in published articles. In 26% of the articles in the journal NeuroImage, a journal with an impact factor between 5 and 6 and specialized in brain imaging studies, the corrections were not properly done and therefore results might include false positive voxels (Bennett et al., 2009). Worth mentioning is the second part of the article of Bennett et al. (2009), where they show how results get distorted, if corrections are not done properly. They put a dead salmon in an fMRI and examined the brain activity of the dead fish. Without statistical corrections the salmon did show brain activity. After correcting for multiple comparisons the salmon returned to his true dead state.

Vul et al. (2009) focused on another statistical problem of fMRI studies of emotion, personality and social cognition. They showed that correlations in fMRI studies between brain activity and personality measures might be higher than expected when looking at the reliabilities of the compared measures. Reliability is an upper bound of correlation and Vul et al. (2009) were puzzled by the fact that some studies reported higher correlations than possible due to their expected correlation between personality measures and fMRI data and tried to figure out why. The reason for these too high correlations was that they had been computed incorrectly. Some authors only counted voxels whose correlations between individual voxels and a certain other measure passed a certain threshold. This “method” leads to a higher correlation, because it neglects all other voxels whose correlations are low and thus speak against the correlation as demonstrated in figure12.

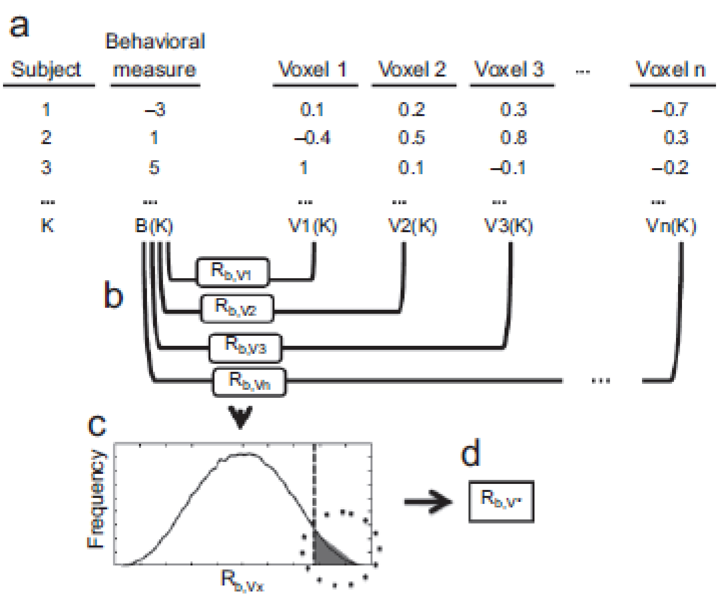

Figure 12: Demonstration of how puzzling high correlations might happen. Every measure is correlated with an individual voxel. Only those voxels whose correlations are beyond a specific threshold are used for the final correlation analysis between the activated voxels and the behavioral measure. (Vul et al, 2009)

Using this method to demonstrate the relation between, for example, intelligence and height would mean that you only use participants for the correlation analysis who have an IQ beyond a specific threshold and then conclude results for the whole sample. This is nonsense, a way in which data was processed in some fMRI studies analysed by Vul et al. (2009).

Another major problem concerning brain images is the problem of causality. These images of the brain – though very sophisticated ones– are just images. You cannot be sure whether the activation depicted in them is due to an independent variable or to any other variable which cannot be controlled. The complexity of the brain makes it very difficult to establish causality, because to guarantee causality, it is necessary to be sure that only one variable is responsible for the change in brain activity.

The BOLD signal is an indirect measure of brain activity and the mental activity associated with the area and thus causes controversy as well. The central assumption is that the more oxygenated blood there is in a specific area the higher is the brain activity and the higher the activity in a specific area the more is this area involved in the task presented during the fMRI (Umilta, 2011).

This assumption is a big one. That the brain needs oxygen to work is common knowledge, but nobody knows how much oxygen it takes for a specific area to work properly. Maybe the amount of oxygen needed to generate a specific amount of activity varies between different brain areas and/or is not linear. A more efficient area would not be represented properly in the fMRI. Assuming that brain activity means mental activity in the first places is already a big assumption already discussed above.

Even if we knew the relation of blood needed there is still the problem of pre-emptive blood flow, found by Sirotin and Das (2009) and summarized well by Leopold (2009) (Harrison & Ross, 2010). Sirotin and Das (2009) taught two monkeys that they get juice if they fixate a certain visual stimulus. They measured the BOLD signal and the underlying neural activity separately and both measures showed a good, but not perfect, match. In the second condition they did the same experiment without the visual stimulus. The results showed that there was blood flow even if there was no stimulus, which led to a significant mismatch of the BOLD signal and neural activity (Sirotin & Das, 2009). The explanation was that the brain pre-emptively sent blood to brain regions by an unknown anticipatory mechanism in expectation of a stimulus. For neuroeconomic research this means that expectations have to be taken into account, because if participants know or have a clue what is about to come this might change the results significantly. Knowing that most of the participants are students of economics or psychology, it is possible that they know what the experiments are about and unconsciously change the results due to expectations.

Another problem of brain images is the way results are created. Every experiment needs an experimental and a control condition. The effect of the experimental condition is computed by subtracting the results of the experimental condition from those of the control condition and by dividing the result by the standard deviation of the sample. In neuroeconomic experiments this means that in an fMRI the BOLD signal is measured, when the subject is lying in the scanner either doing nothing or doing the experiment. Both results are subtracted from each other and divided by the standard deviation of the sample and this is the experimental effect. Umilta (2011), however, points out that cognitive subtraction only works if mental functions and brain activities and their change over time are known in great detail. Thus, even the simplest of tasks are very difficult to analyse due to the complexity of the human brain (Umilta, 2011).

3.6.3 Ethical issues

Neuroeconomic experimenters find themselves confronted with ethical problems as well, like for example the injection of contrast substance into healthy human beings. This contrast substance is radioactive although exposure is very low. How much suffering is acceptable for science, because those injections can be painful? Electromagnetic fields of fMRI bear health risks as well (Zichy, 2011, p. 318).

Jones (2007) points out that transcranial magnetic stimulation (TMS), which leads to a temporal lesion of the brain, is not of minimal risk either. Possible side effects might range from headaches to seizures of psychosis. Knoch, Pascual-Leone and Fehr (2007) therefore only used 1-Hz repetitive TMS, whose risks are minimal for populations without predisposing conditions. Additionally, they followed the guidelines, chose only volunteers and gave them all information they needed about TMS, including possible side effects and discomforts.

Another point of discussion is deception. In some experiments participants are told that they play against a human, whereas they play against a computer. This may sound harmless besides the fact that deception might change reasons for specific behavior and therefore falsify results. But where is the limit of deception, where do we draw the line?

Besides the studies themselves the use of the results poses an ethical issue (Zichy, 2011, p. 319). In 1-8% of the studies the brain imaging techniques show irregularities like tumors (Zichy, 2011, p. 319). Heinemann et al. (2008) recommend for brain imaging studies that the scientist should inform the test subject that incidental findings might occur and that those will be reported to the subject if they want to know them. According to Zichy (2011, p. 321), there are three more problems that might occur in the future, if results are not used in an ethical way.

The first problem occurs if scientists really encode the brain and know which region is responsible for which function. This will lead to us becoming transparent individuals.

The second problem is about controlling behavior or actions of individuals. Knoch et al. (2009) showed that disruption of the prefrontal cortex influences the ability to build reputation (cf. 3.7.1.). In the future scientists may be able to disrupt, for example, the brain area which is responsible for aggression. This will confront humanity with big ethical questions.

The third problem according to Zichy (2011, p. 322) is that we might be able to use the resources of the brain directly without the owner of the brain as a “super-computer”. This sounds like Science Fiction, but nevertheless might be possible in the distant future.

3.6.4 Summary

There are three fields of criticism on neuroeconomics: justification, methodology and ethics. Methodological problems are the easiest to solve in theory. It is possible to increase sample sizes and make them representative for the population. Alpha corrections to avoid false positives are easily feasible as well. Ethical issues can be met by installing or strengthening ethic committees which already exist in most universities and have to allow research beforehand. Justification problems are best solved by trying to get results which are new and useful for economic theory. The next chapter shows a number of results of neuroeconomic research and makes chances and issues visible.

3.7. Neural basis of cooperative behaviour

This chapter gives insight into the current neuroeconomic research of cooperation. The most important structures involved are the prefrontal cortex and the reward system. Of special interest in the prefrontal cortex are the right dorsolateral prefrontal cortex (rDLPFC), the ventromedial prefrontal cortex (VMPFC) and the anterior cingulate cortex (ACC). In the reward system the focus will be put on the striatum. After a short presentation of studies that will confirm that the PFC and the reward system are important for cooperation, the studies will be analysed in the light of the critical areas of legitimation, methodology and ethics, to show that these problems are also relevant for articles that were published in big journals like Nature or Science.

3.7.1. Prefrontal Cortex (PFC)

The PFC lies at the very anterior end of the frontal lobe approximately in the Brodmann areas 9-14, 45 and 46. It is assumed that the prefrontal cortex plays an important role in cognitive control, the ability to form thoughts

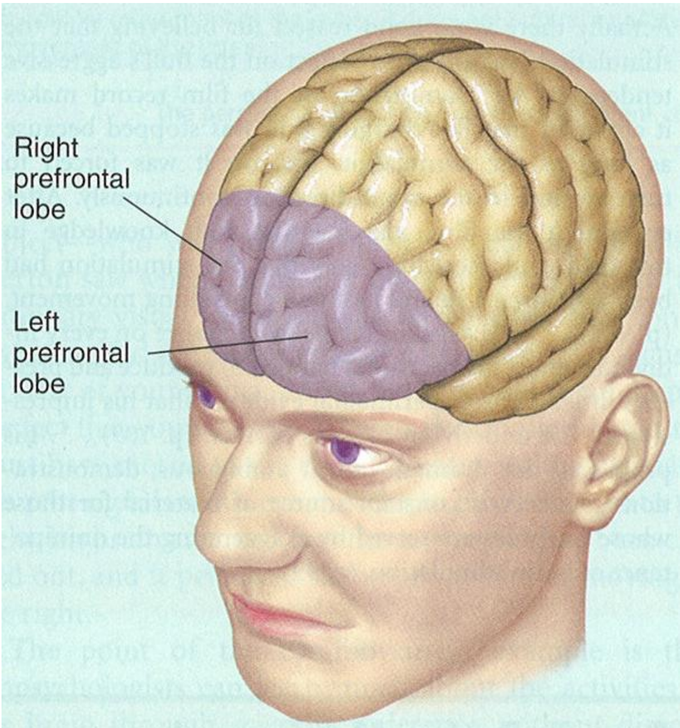

Figure 13: The left and the right prefrontal lobes (Pinel, 2009, p. 16)

and action according to the internal goals (Miller & Cohen, 2001). This means that the PFC is important for top-down processes that are conscious and related to internal representations of goals. Applied to cooperation this means that the PFC compares the options and results of social and self-interest preferences and has to mediate the conflict.

- Right Dorsolateral Prefrontal Cortex (DLPFC)

Results of neuroeconomic studies show that the right DLPFC plays an important role in cooperative behavior (Knoch et al., 2006; 2008; 2009; 2010; Rilling et al., 2007; Sanfey et al., 2003; Suzuki et al., 2011).

Suzuki et al. (2011) conducted an fMRI study, where 17 participants were scanned while playing random matching repeated prisoner´s dilemmas and the partners were changed every round. To make indirect reciprocity or reputation building possible they showed the participants histories of the previous actions of their partners. Experimental results of this study show that people tend to cooperate more with people with good or unknown records than with those with bad, non-cooperative records (Suzuki et al., 2011). Results of the fMRI showed that there was increased neural activity in the right DLPFC, when players were interacting with partners with bad records and therefore not cooperating (Suzuki et al., 2011). That higher activation of the right DLPFC leads to higher rates of defection was also shown in the study of Rilling et al. (2007). The right DLPFC therefore seems to be responsible for long term thinking (Knoch et al., 2009) and for inhibiting predominant responses in a top-down manner (Miller & Cohen, 2001). This means that the predominant response in this study might have been to cooperate (Suzuki et al., 2011) and the higher activation of the right DLPFC in the bad record condition made the participants overcome this desire.

Now we know that the right DLPFC shows higher activation in a game that measures cooperation due to indirect reciprocity, but we cannot draw the causal conclusion that the right DLPFC lights up because of indirect reciprocity. Brain imaging methods alone cannot prove that the right DLPFC is solely responsible for the results.

To confirm this causal relationship Knoch et al. (2009) disrupted the right and the left DLPFC of 87 subjects with repetitive transcranial magnetic stimulation (rTMS) and let them play trust games, where under one condition the players knew the decision records of their partners in the game. Results showed that disruption of the right DLPFC negates the effect of the decision records and therefore cooperative behavior did not increase in the condition with known records (Knoch et al., 2009). Participants were unable to include long term information into the decision due to the lesion set.

Additionally, higher activation of the right DLPFC led to changes in behavior for the sake of long term maximisation of utility in Suzuki et al. (2011), whereas participants with reduced right DLPFC activation in Knoch et al (2009) did not change their behavior despite knowledge of past records. So it is possible to conclude that there is a causal relationship between activation of the right DLPFC and the ability to build reputation or to be able to reciprocate indirectly.

Another function of the DLPFC is cognitive control, which means that actions are in line with the internal goals (Miller & Cohen, 2001). When facing an unfair offer, this internal conflict between maximisation of income and rejecting the unfair offer leads to an increased activation of the right DLPFC (Sanfey et al., 2003). A lower activation of the right DLPFC leads therefore to an increased acceptance rate of unfair offers because of the missing conflict. To test this hypothesis, Knoch et al (2006) used rTMS to disrupt the right DLPFC of players and let them play ultimatum games. The results, illustrated in figure 14 confirmed that inhibition of the right DLPFC leads to higher acceptance rates of unfair offers when playing against human partners. (Knoch et al, 2006).

This study allows the causal conclusion that the higher right DLPFC activity in a conflict between fairness motives and self-interest is the more probable it is that fairness motives are executed (Knoch et al., 2006). An important aspect of fairness is punishing unfair behavior. Assuming that the lower the activity of the right DLPFC is the less important fairness motives are, low activity of the right DLPFC would lead to a decrease in altruistic punishment. Knoch et al. (2008) tested this hypothesis by inhibiting the right DLPFC of 128 participants playing one-shot ultimatum games. Punishing unfair behavior in the ultimatum game happens by rejecting offers, so that nobody gets any money. Results confirmed indeed that punishment of unfair behavior decreased if the right DLPFC was inhibited (Figure 14) (Knoch et al., 2008).

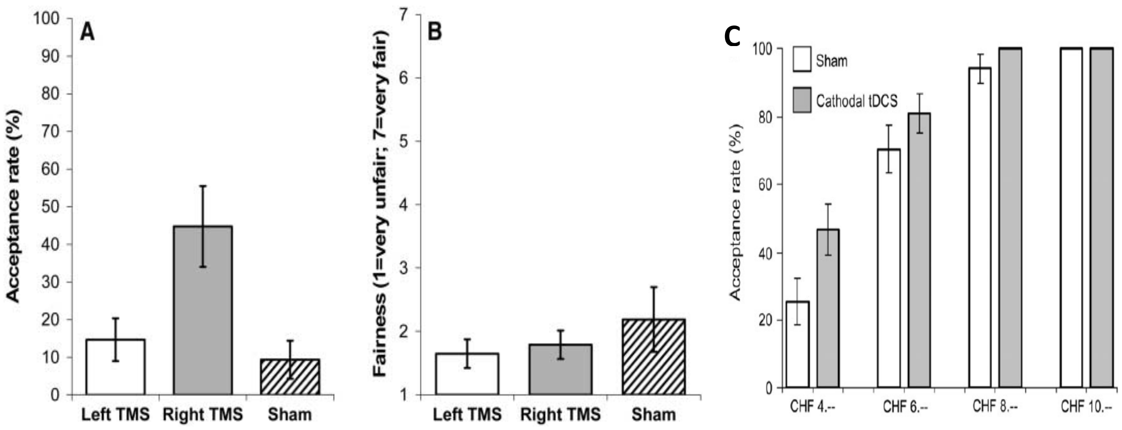

Figure 14: Left: Acceptance rates of the different treatment groups (Knoch, 2006, p. 829); Middle: Perceived unfairness of offers across treatment groups (Knoch, 2006, p. 829); Right: Acceptance rates of different offers across treatments (Knoch, 2008, p. 1989)

An EEG study of Knoch et al. (2010) confirms the relationship between neural activity in the DLPFC and acceptance rates of unfair offers. They let the participants play ultimatum games while simultaneously using EEG to measure cortical activity and found significant positive correlations between resting current density in the right lateral PFC and acceptance rates of unfair offers (Knoch et al., 2010). The level of activity in this area is also a good predictor of individuals' punishment behavior, because prediction worked for fair and unfair offers and can therefore be used independently from that measure (Knoch et al., 2010)

Another interesting result of Knoch et al. was that although acceptance rates were higher, the perception of the offer did not change despite the inhibition of the right DLPFC (Figure 14, right) (Knoch et al., 2006; 2008). This means that subjects accepted unfair offers, even if they were aware of the offers being unfair. They were unable to execute the social norm of fairness which might pose a threat to society if this method was abused and carried out on a large scale. Thus, the importance of the right DLPFC for social appropriate behavior was confirmed (Knoch et al, 2006).

- Ventromedial Prefrontal Cortex (VMPFC)

The results of different studies indicate that the VMPFC plays an important role for cooperative behavior (de Quervain et al., 2004; Rilling et al., 2002; 2004; Koenigs & Tranel, 2007; Tricomi et al., 2010). This area is associated with the integration of cognitive operations for a higher goal and with involvement in difficult choices (de Quervain et al., 2004). This means that the VMPFC is involved in taking others into account. Tricomi et al. (2010) showed that VMPFC activation is associated with the social preference of inequality aversion. Patients with VMPFC damage on the other hand are short tempered, angry and irritable (Koenigs & Tranel, 2007). Brain imaging studies and a lesion study will be presented to confirm the importance of this brain region for cooperative behavior.

The VMPFC showed higher activation in iterated prisoner´s dilemmas and in ultimatum games, when comparing the activation levels of costly *vs.* costless punishment of the opponent (de Quervain et al., 2004). Costly punishment led to higher activation of the VMPFC than costless punishment, which reflects the inner conflict that arises under the first condition. Contrary to costless punishment the player has to sacrifice his own money for punishing unfair behavior. Additionally, people with lesions in this area tend to reject unfair offers in ultimatum games more often than healthy people (Koenigs & Tranel, 2007). A possible explanation for this phenomenon is that they are unable to see the benefit of the offer and only perceive the unfairness of the behavior and punish it.

In the prisoner´s dilemma the activation of the VMPFC was higher, when both players were cooperating, which is again an indicator that this area is responsible for the integration of different cognitive operations like taking others into account (Rilling et al., 2002; 2004). These activations only occurred when the games were played between humans (Rilling et al., 2004). There was no significant activation in conditions where a computer was the opponent.

- Anterior Cingulate Cortex (ACC)

The ACC is associated with cognitive control and the detection of cognitive conflicts (Botvinick et al., 2001). The anterior cingulate cortex showed higher activation for unfair offers in ultimatum games (Sanfey et al., 2003). In this case the cognitive conflict is caused by the wish of getting at least a little money set against the temptation of punishing the opponent for his unfair offer. The feeling of envy also leads to an activation of the ACC. In this case the cognitive conflict lies within the person, because one`s self-concept is threatened by others (Takahashi et al., 2009).

3.7.2. Reward System/Striatum

Many neuroeconomic studies showed activation of the striatum in situations related to cooperative behavior (Rilling et al., 2002; 2004; de Quervain et al., 2004; King-Casas et al, 2005; Tom et al., 2007; Seymour et al., 2007; Fliessman et al., 2007 and Tabibnia et al., 2008). The striatum consists of the putamen and the caudate and is part of the reward system.

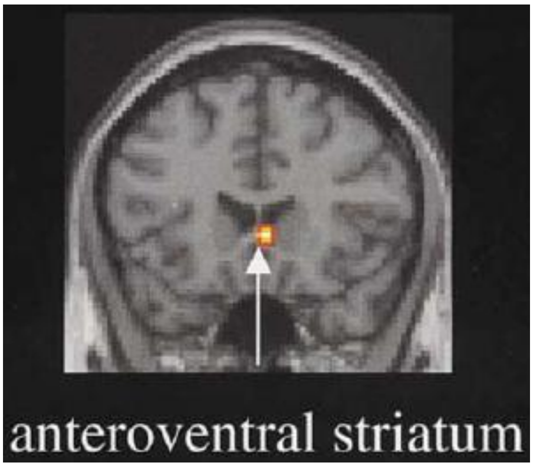

Figure 15: Anteroventral striatum in an fMRI (Rilling et al., 2002)

It is assumed to be activated because mutual cooperation is rewarding and this reward makes us overcome the temptation to act selfishly and therefore leads to further cooperation and to the next "kick" (Rilling et al., 2004). Rilling et al. (2002) made an fMRI study, where the participants played iterated prisoner´s dilemmas and stated in post scan interviews that mutual cooperation was the most satisfying outcome for them. To find out if the rewarding effect of cooperation depends on the social interaction or on the maximisation of the benefit of the game, they let the participants play the same game against computers. Under this new condition no stratial activation occurred. Therefore, it was confirmed that this effect is only related to social interactions with humans (Rilling et al., 2002). The opposite results were found regarding the effects of defection. There it had no influence whether the participants played against computers or humans. Both conditions showed decreased striatal activation and the loss of expected material rewards was always perceived as negative (Rilling et al., 2004).

It could be shown that not only a bad result itself - in our case defection - leads to a reduced reaction of the striatum. Even the prospect or the expectation of getting betrayed is enough to decrease activation levels of the striatum (Rilling et al., 2004). Most humans are loss averse, which means that they do not like losing and therefore try to avoid it. The neural correlate of loss aversion is thus the striatum, which shows less activation, whenever a loss is expected. The striatum, on the other hand, is activated in the case of positive expectations. It shows increased activity in actions that are related to rewards (Rilling et al., 2004; Seymour et al., 2007). The prediction or expectation of a positive reward or punishment, particularly altruistic punishment, activates the anterior part of the striatum and the prediction or expectation of negative events leads to an activation in the posterior area of the striatum (Seymour et al., 2007). This result of Seymour et al. (2007) is contrary to the result of Rilling et al. (2004), who measured less activation in the striatum, whenever losses were expected. It speaks against Rilling et al. (2004) that their results had a p-value of only 0.03, which is too low for fMRI studies due to the risk of false positive results, as explained in section 3.6.2. The two studies used completely different methods, which might influence comparability. Whereas Rilling et al. (2004) let the participants play one-shot prisoner´s dilemmas, Seymour et al. (2007) let them play a simple lottery without a social context. Seymour et al. (2007) offer a second explanation besides the mentioned methodological differences: According to them, it might be possible that the experimental setting, where you get a certain sum of money for participating creates a positive frame that leads to positive expectations for the task and therefore influences the activity of the striatum (Seymour et al., 2007).

The experiments cited above show that the striatum is related to the good feeling of cooperation by making cooperation and even punishment of defection rewarding. Fliessbach et al. (2007) wanted to find out if social comparison influences the reward processing function or if only the absolute height of the reward matters. Their hypothesis was that the activity of the reward system is higher, the higher the relative reward is (Fliessbach et al., 2007). To test their hypothesis they let participants do an estimation task in pairs, while they were both in an fMRI scanner. The task was constructed in a way that both participants had a high chance (80%) of getting all the items right (Fliessbach et al., 2007). Then they were told how much person A would get and how much person B. If both of them had all the items right they were told three different relative heights of income: both got the same amount of money, or player A or player B two times more income. To check if the absolute height was important, they constructed each condition in a way that the players got the same relative amount but different absolute amounts of money (for example: high= 60€; low= 30€).

The results in figure 16 show that the activation of the ventral striatum strongly depended on the relative height of the payment. The BOLD signals of the different conditions did not change significantly under conditions with absolute high and low incomes, but there was a significant increase as far as the relative height of the income was concerned. The BOLD signal was stronger in the condition where the tested person got more than the other participant. If both got the same amount, there was only little hemodynamic response, although they got money. Lower responses were measured, if the participant got less than the other person, although they still got money. (Fliessbach, 2007)

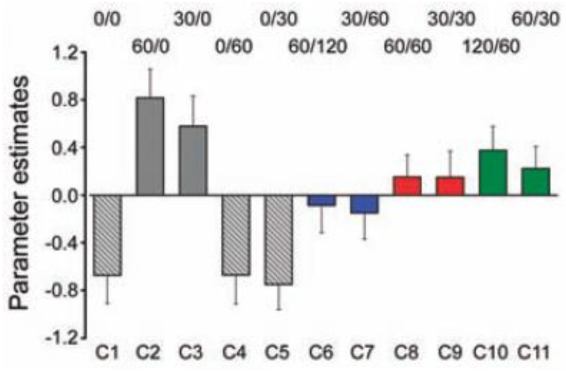

Figure 16: Parameter estimates of activation across scenarios with different relative income (Fliessbach, 2007, p. 1307)

This shows that not only the absolute amount of a reward is important for striatal activity, but also the relative income has to be taken into account. The study of Tabibnia et al. (2008) confirms that the fairness of an offer moderates the effect of a reward on the striatum or the reward system in general.

De Quervain et al. (2004) showed that punishing the loss of expected material rewards or unfair behavior in general can also be rewarding and activates the dorsal striatum. It is not enough to punish symbolically, only punishment that reduces the defector´s outcome activates the dorsal striatum. The more activated the dorsal striatum gets, the higher is the willingness to punish defectors, even if it is costly for oneself (de Quervain et al., 2004).

The activity level of the striatum is not only an indicator of current expected loss or reward, but also a predictor of how a person will act and react in the future (King-Casas et al. 2005). In iterated prisoner´s dilemmas King-Casas et al. (2005) found out that response magnitude and response timing were good predictors for future cooperation (King-Casas et al. 2005). Response magnitude reflects the expected future reward of the next rounds. If trust is high that the partner will reciprocate in the next rounds, the expected reward increases and this leads to a higher activation of the caudate which is part of the striatum. Response timing also changes over time, as participants get to know each other and learn how the other person reacts. This is taken this into account when calculating the expected future reward.

Another function of the striatum is that it makes us mistrust betrayers. Negative feelings due to low striatal activation are related to the betrayal so that we learn that betrayers should not be trusted again in the future (Rilling et al., 2004).

3.7.3. Oxytocin

For the topic of cooperative behavior hormones associated with social behavior are interesting and oxytocin is the most famous representative. Oxytocin is a neuropeptide that is released from the pituitary gland into the blood stream. The release is triggered by action potentials. It plays a key-role in the process of bonding (for example during childbirth) and is responsible for female milk secretion (Kosfeld et al., 2005). Oxytocin is also released in response to socially relevant stressors and to social interaction (Heinrichs & Domes, 2008). It affects the amygdala by lowering emotional and social stimuli that are associated with autonomic arousal and promote social interpretations of signals (Heinrichs & Domes, 2008).

Therefore Kosfeld et al. (2005) hypothesized that oxytocin might also promote prosocial behavior like trust. To test their hypothesis they gave the subjects intranasal oxytocin and let them play one-shot trust games with strangers. Results showed that investors (subjects who first give money to the trustees) transferred significantly more money when oxytocin was applied than the control group that received a placebo (Figure 17, left). On the other hand the amount transferred back to the investor by the trustee was not different between the two groups (Figure 17, right) (Kosfeld et al., 2005).

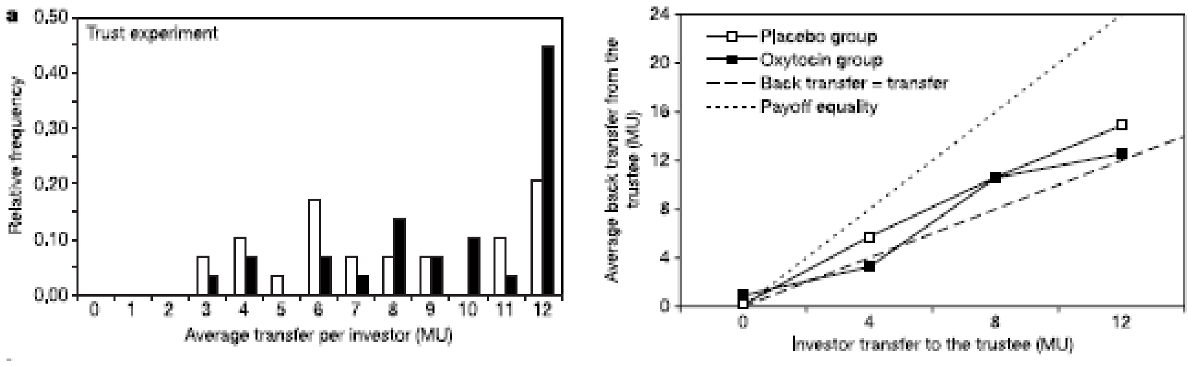

Figure 17: Left: transfer trustee to investor in trust games, Right: transfer investor to trustee in trust games (Kosfeld et al., 2005, p. 674-675)

This means that oxytocin promotes trust but not trustworthiness. Kosfeld et al. (2005) explained this result saying that investors and trustees face different situations. Trust is more important for the investors than for the trustees, for whom reciprocity is more important than trust (Kosfeld et al., 2005). This is why oxytocin affects investors more than trustees. Thus, it increases the willingness to bear social risks due to interpersonal interaction. Kosfeld et al. (2005) also showed that oxytocin does not work in an interaction where the social aspect is missing by letting a random mechanism determine the transfer of money back to the investor in the so called risk game. Under this condition both groups showed no difference in trusting behavior.

Kosfeld et al. (2005) showed that the application of oxytocin increases trusting behavior. To determine if and how oxytocin is at work in trusting behavior without artificial application, Zak et al. (2005) let the participants play one shot trust games and then measured oxytocin levels of trustees and investors. It is interesting that Zak et al. (2005) could not measure higher oxytocin levels in the investors but in the trustees they did. This contradicts the results of Kosfeld et al. (2005) mentioned above. No explanation for this contradiction is offered, however, although Zak was involved in both papers.

Baumgartner et al. (2008) expanded the design of Kosfeld et al. (2005) by an fMRI study to gain a deeper understanding of the neural mechanisms of trust. They found out that in the trust game the amygdala and the midbrain were less activated in the oxytocin condition, where the participants received intranasal oxytocin (Baumgartner et al., 2008). It is assumed that one function of the amygdala and the midbrain is the modulation of emotions, for example fear, and low activation of them indicates low levels of fear, which is good for cooperation (Baumgartner et al., 2008). This study again confirms that social interaction is necessary to make oxytocin work, because there was no significant difference between the oxytocin and the placebo group in transfers in the risk game condition where the results were solely determined by a computer.

3.7.4. A critical view on the results

All studies discussed in the last chapters offered interesting new insights into well-known economic problems. There were countless papers on experimental games before, but neuroeconomic research gave the topic a new direction. The combination of neuroscience and economics makes it possible to use neuroscientific knowledge for economic questions.

The most important contribution of neuroeconomics is in the form of additional data, which is used to decode the construction plan of the brain. This data is not only of interest for economists but also for other disciplines like psychology or neuroscience, because they are written in a language all fields understand. So neuroeconomics offers a common ground today and might lead to the unification of these three disciplines in the future.

Confronted with the immense complexity of the brain, neuroeconomic research can be said to be still at the beginning. As research mainly works on a descriptive level, neuroscientific findings are often rather speculations and assumptions than proofs. Brain imaging studies, for example, do not allow causal conclusions and whether specific forms of behavior can be matched to single brain areas in a one to one fashion is still a field of intensive research. Also methodological problems can distort the results, as shown above in chapter 3.6.2.. Therefore, neuroscientific results should be looked at critically and not be taken as absolute.

Looking at neuroscientific research papers, the method section tend to be strikingly short. Most only contain the number of participants, the game played and the used neuroscientific method. The numbers of participants make it clear why neuroeconomic research is criticised so much. They range from 14 (de Quervain et al., 2004, published in “Science”) to 87 (Knoch et al., 2010, published in “Psychological Science”) and are not representative as far age or education were concerned (most participants were students). According to Bortz and Döring (2006, p. 629) at least 22 subjects are necessary to calculate correlations with appropriate test power at a significance level of 0.05 under the condition that a big correlation is expected. The standard significance level for neuroeconomic research is 0.001, which increases the necessary sample tremendously, not considering the power or the expected effect sizes.

According to Bennett et al (2009) significance levels might be too high and therefore provoke false positive results. When corrections for multiple testing were done, this was hardly ever mentioned in the methods sections.

To evaluate the potential of those methods, besides significance effect sizes are important to know. The reason is that significance only tells if there is an effect, but does not tell the impact, therefore effect sizes are needed. Unfortunately effect sizes are often not documented in papers.

Knoch et al. (2009), however, do offer effect sizes in the supporting information of their paper on the disruption of the DLPFC with rTMS. They used multiple regressions to calculate the effect of TMS on the trustee in a trust game. The explained variance R^2 of the rTMS is a good measure for the effect. Unfortunately, only the R^2 for the whole multiple regression analysis with all predictors was given. Therefore it was not possible to extract the effect of the rTMS. According to Bortz and Döring (2006, p. 606) an R^2 of 0.01 reflects a small, 0.1 a medium and 0.25 a big effect. The whole model of Knoch et al. (2009) explains 13% of variance, which stands for a medium effect. Furthermore, they only calculated regressions for the condition, where the temptation to defect was highest. This means that TMS had a significant effect on the trustee in the trust game, but it was only medium for the whole model and limited to conditions with high temptation.

In the study of Knoch et al. (2008) tDCS was used to measure the effect of disruption of the right DLPFC of responders in an ultimatum game. The calculation of the effect size for Knoch et al. (2008) showed a medium effect. The effect size was calculated by transforming the Z-value of the difference of the most unfair offer between groups with and without tDCS into a correlation coefficient (Field, 2009, p. 550). This works by dividing the Z-Value (2.244) by the square root of the total number of participants (√64). The resulted correlation coefficient of 0.28 reflects a medium effect (Bortz & Döring, 2006, p. 606[4]).

Knoch et al. (2006) use rTMS to disrupt the right DLPFC and measure the effect on the responder. To calculate the size of the effect, the z-value was transformed in a correlation coefficient by dividing it (2.388) by the square root of total number of participants (√35). The result of 0.4 can be interpreted according to Bortz and Döring (2006, p. 606) as a medium to big effect.

Kosfeld et al. (2005) applied oxytocin on half of the investors of a trust game. The results demonstrated that oxytocin had a significant effect on trusting behavior. To find out how dangerous oxytocin is, the magnitude of the effect was calculated by dividing the z-value of the U-Test (1.897) between the oxytocin and placebo group by the square root of the total number of investors (√58). The result of 0.25 indicates a medium effect of oxytocin.

The medium effect sizes in all studies cited above show that manipulation of brain activity really works and has some effect. Therefore it is necessary to think about the implications of these results.

Furthermore, scientists have to be careful when using methods like TMS or DCS. The experience of manipulation can be disturbing for the participants especially when they are unable to defend themselves against it. Therefore strict controls of these methods are necessary, because they might bear risks that do not justify the research that is done now.

[4] small effect: 0,1; medium effect: 0,3; big effect: 0,5

4. Cooperative behavior in the light of genoeconomics

4.1. Definition and introduction into genetics

Genoeconomics is an interdisciplinary field that uses genetics, especially behavioral genetics, to study questions of economics. Its aim is to investigate which aspects of human behavior are related to genes and how much is related to other factors like education, personality, situation or society. Therefore genoeconomics targets a very fundamental question. How much of human behavior is determined by genes and how much is determined by the environment?

This question is called the nature *vs.* nurture conflict, which has been going on for thousands of years. To illustrate how important this question is let us assume scientists find out that human behavior is solely determined by the genetic code. This would mean that changes in the environment would not change the way humans act. Therefore, any intervention and investment into a person would be futile, because you know that he or she does not have the genetic equipment to make the investment work. On the other hand, if scientists find out that genes had no influence on human behavior, it would not make a difference who the natural parents of a child are, because the only thing that would count is who raises the child. It is extremely unlikely, however, that these extreme positions are true. Both nature and nurture are believed to form the human being.

4.2. A Brief introduction into genetics

4.2.1. DNA

DNA stands for deoxyribonucleic acid and is the blueprint of life. It consists of sugars connected with nucleobases, bound together by phosphates (Bazzett, 2008, p. 26). There are four different kinds of DNA bases: adenine, cytosine, guanine and thymine. DNA adopts the form of the famous double helix. The phosphates and sugars form the backbone and the nucleobases interact with their counterparts by hydrogen bonds.. Adenine always binds to thymine and guanine always to cytosine. These different base sequences are the construction plan of amino acids, which form proteins that are required for life (Bazzett, 2008, p. 33). DNA is stored in the cell core and the storage compartment is called chromosome.

4.2.2. Genes

Genes are the smallest essential piece of information for the construction of one amino acid. This information consists of three nucleobases which are called a codon. The genome is the sum of all genes and therefore contains all information of the organism. Amino acids are assembled in the cytoplasm outside of the cell core. To get the genetic information out of the core, messenger RNA is needed. Outside the core mRNA attaches to ribosomes, where the synthesis of the amino acids takes place. (Bazzett, 2008, p.43f)

4.3. Methods of genoeconomics

4.3.1. Heritability studies

The genotype is the genetic information humans receive from their parents while the phenotype describes how genetic information is “interpreted” in the offspring (Bazzett, 2008, p. 124). The variance of the phenotype is the sum of the variances of the genotype and the environment. Therefore heritability is the share of the variance of the phenotype that is explained by the genotypic variance (Visscher et al., 2008). Simply spoken, heritability is the variation in humans related to genetic variation or the share of the phenotype of human behavior that is heritable to the next generation. So 30% heritability means that if all humans were raised in the same environment, there would remain 30% of the variability that is visible now and if all humans were clones, there still would be a variability of 70% (Navarro, 2009).

Twin studies are the most famous approach to study heritability. These studies want to reveal the genetic part of human behavior by comparing monozygotic and fraternal twins. Monozygotic twins share the same genes and the same environment, whereas fraternal twins only share the same environment. The difference in behavior or traits of monozygotic and fraternal twins must therefore be related to genetic factors, because environments are the same. If the difference between monozygotic and fraternal twins is small, genetic contribution is low and therefore heritability is low. If the difference is high, genetics is strongly related to the variance in behavior or any other trait and heritability is high.

There are two big problems with twin studies. First, twins are not representative of the whole population (Navarro, 2008) and second, twins do not share an identic environment but only a very similar one. A second way to study heritability is by comparing adoptees with biological children raised in the same family (Beauchamp et al., 2011).

Heritability studies can tell us if a trait or a specific behavior is related to the genotype. But they cannot tell which genes and to which extent. Heritability serves as an upper limit of explained variance by the sum of single genes. Association studies can identify genes that are associated with specific traits or behavior.

4.3.2. Candidate gene association studies

Association studies compare allelic[5] frequencies for groups with specific attributes with a control group on a quantitative trait (Plomin et al., 2008, p. 108). In candidate gene association studies specific genes are assumed to be related to specific behavior and therefore the differences in these genes between high and low scoring subjects are calculated to measure the relationship. A problem is that these hypotheses are not supported well by theories because it might be possible that hundreds or thousands of genes are equally responsible for a single behavioral aspect. A second problem is that replication of results seems to be difficult (Plomin et

[5] Allele is an alternative form of a gene. Different blood types are different alleles of the same gene. (Bazzett, 2008, p. 44)

al., 2008, p. 110; Benjamin, 2010; Beauchamp et al., 2011). This is an indicator that these studies are underpowered, which would lead to high rates of false positive results. One possible solution would be to increase sample size.

4.3.3. Genome wide association studies

Genome-wide association studies examine variation of behavior due to genetic variation without *a priori* hypotheses (Navarro, 2009; Plomin et al., 2008, p. 111). This means that hundred thousands of markers are tested for a relationship to a specific behavior. This approach became possible due to the availability of microarrays, which can genotype possible genetic markers on a little chip (Plomin et al., 2008, p. 111f). This reduced the costs of genotyping to around 500$ per individual and they are still falling by half every second year (Benjamin, 2010). These studies result in many genes with small effect sizes that are associated with the researched behavior (Plomin et al., 2008, p. 113). This data mining approach leads to an increase in false positive results due to multiple testing of genetic association for hundreds or thousands of genes in the same sample and therefore alpha level corrections are necessary (Navarro, 2009). Without corrections chances would be high that positive results are just artefacts or coincidence due to the fact that you "asked the same person hundred thousands of questions". Therefore replication studies are crucial to detect these false positive results.

4.4. Possible contributions of genetics to economics

There are three ways in which genetics might contribute to economics in the future. First, genetic markers can be used as diagnostic tool. A profound knowledge of the function of specific genes might be used in screening tests to predict a certain behavior or to invest in prevention programmes, if genetic markers are known to be associated with specific diseases (Beauchamp et al., 2011).

Secondly, genetic information might be used as control variables in settings where omitted and reverse causality are an issue (Beauchamp et al., 2011). If we know that 40 % of the variation in behavior in the ultimatum game is associated with genetic factors, it might be possible to control the outcome of the game for the genetic part and therefore to lower bias (Beauchamp et al., 2011).

A third possible contribution of genetics to economics is that genetic data might be helpful in understanding different responses to the same intervention between different individuals (Beauchamp et al., 2011).

4.5. Issues in genoeconomics

4.5.1. Low test power

Test power is the probability that a test of significance rejects a hypothesis and the rejection is right (Bortz & Döring, 2006, p. 602). Three components influence test power: Level of significance, effect size and sample size (Bortz & Döring, 2006, p.603). The lower the significance level, the lower is the test power. The higher the effect size, the higher the test power and the bigger the sample, the higher is the test power (Bortz & Döring, 2006, p. 603).

Those three components illustrate why huge sample sizes are needed in modern association studies to identify genes which are associated with specific behavior. As explained above, significance levels must be corrected due to multiple testing to reduce false positive results leading to reduced test power. Furthermore, the genetic effect per gene is very small, because a combination of many genes is assumed to be responsible for complex social behavior like cooperation. The only component which can be influenced easily is the sample size and therefore huge sample sizes have to compensate small effect sizes and very small levels of significance. Beauchamp et al. (2011) give a good example what this means. At a significance level of 5% you need 4000 subjects to have the power of 50% to detect a marker that explains 0.1 % of the variance (Beauchamp et al., 2011 , p. 73). Now imagine the necessary sample size to get 80% of power at a significance level of 5×10^{-8} for a marker that explains only 0.01% of variance. You need ten thousands of subjects. This is one reason why replications of association studies fail that often. Most studies do not test enough subjects to reach sufficient test power and false positive results are the consequence.

4.5.2. False positives

Multiple testing and therefore correction of the significance level and underpowered studies lead to false positive results, which get published but do not hold in replication studies. This damages the reputation of genetic studies. Therefore scientists try to bundle their resources to conduct studies with sufficient sample sizes to get results that are replicable (Benjamin, 2010). The funds necessary are huge, but costs of genome encoding have fallen drastically in recent years (Plomin et al., 2008, p. 111; Benjamin, 2010). Additionally, guidelines were created to ensure high quality of reported results in genetic association studies. The STREGA initiative (strengthening the reporting of genetic association studies) for example has the aim to increase transparency in genetic research (Little et al., 2009). Areas covered in their guideline are for example population stratification, genotyping errors, replication, selection of participants, rationale for choice of genes, statistical methods and reporting of descriptive and outcome data (Little et al., 2009).

4.5.3. Ethical issues

The possibility of predicting the future by using genetic information leads to ethical problems. It is already possible to test individuals for a number of single-gene disorders like Huntington´s disease (Plomin et al., 2008, p. 107). Insurances and employers would pay a lot of money for this kind of information if testing was carried out on a larger scale.

In the distant future it might even be possible to predict a person´s behavior by reading their DNA. Predicting behavior is extremely difficult, because it is determined by a large number of genes. Therefore we would have to know every single involved gene and its interactions. Science fiction movies like GATTACA demonstrate how a possible future might look like, where it is possible to manipulate the genetic code to eliminate risk factors and to design babies with maximal potential. The society discriminates between those people designed and those conceived the common way. This movie is still science fiction, but the increasing availability of genetic data and the growing knowledge about the functions of specific genes, bear the risk that genetic information might be used for other purposes than science. Knowing that a person is prone to a certain illness like for example dementia is a very valuable piece of information. So we have to make sure that nobody misuses this new kind of data.

4.6. Genoeconomic results on cooperative behavior

This chapter focuses on the results of genoeconomic research related to cooperative behavior, particularly in connection with experimental games (cf. 2.5.). Its aim is to present results of current research and to show how genoeconomic research works. The results will be discussed according to their chances and issues related to genoeconomics.

It should be clear by now that people do not act like “homines oeconomici” in experimental games. An interesting question is how much of this variation in behavior is related to genetic variation? To calculate the heritability of cooperative behavior in games, Wallace et al. (2007) let monozygotic (MZ) and dizygotic (DZ) twins play ultimatum games and Cesarini et al. (2008) let them play trust games. Both studies used the same source of data, namely the “Swedish Twin Registry at Karolinska Institute” and had the same sample size of 658 individuals in 71 DZ and 258 MZ twins (Wallace et al., 2007; Cesarini et al., 2008).

The results showed that the acceptance thresholds did not differ between MZ and DZ twins in ultimatum games, but the acceptance thresholds of both MZ twins were correlated in contrary to those of the DZ twins which did not correlate at all as demonstrated in figure 18 (Wallace et al., 2007). Therefore heritability can be assumed.

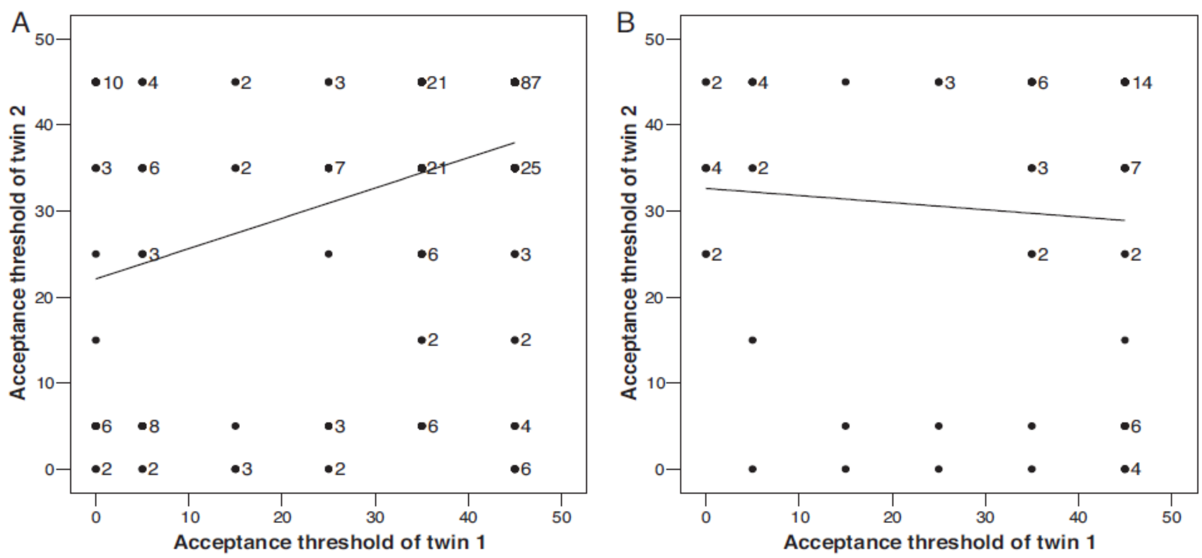

Figure 18: Scatterplot of ultimatum game acceptance thresholds for twin pairs: (*A*) Scatterplot for MZ twins, (B) Scatterplot for DZ twins (Wallace et al., 2007, p. 15632)

Cesarini et al. (2008) demonstrated that behavior in trust games is heritable. MZ twins behaved more similar than DZ twins and a heritability index of 20% was calculated for the Swedish sample (Cesarini et al., 2008).

These twin studies resulted in a heritability index of more than 40% for ultimatum games and around 20% for trust games (Wallace et al., 2007; Cesarini et al., 2008). This means that 40% of the variation in the ultimatum game seems to be related to genetic effects. Assuming that ultimatum games measure fairness, reciprocity and inequity aversion means that 40% of the variation in these variables might be related to genetic factors. In the trust game a heritability index of 20% means that 20% of the variation in trust and trustworthiness is related to genetics. The height of the index of trust and trustworthiness does not differ significantly (Cesarini et al., 2008). Variation in behavior in games might therefore be attributable to genes beside any other factors assumed by neuroeconomists or behavioral economists.

Environment therefore accounts for 60 respectively 80% of the variation. This means that genetics does not have the expected importance for cooperative behavior in trust or ultimatum games. One plausible factor for this observation might be due to culture. Cesarini et al. (2008) compared the trust games results of a Swedish sample with a US-American sample and behavior of MZ and DZ twins differed significantly between the two countries, which indicates huge differences between the two cultures as far as behavior in games is concerned. These observations confirm the results of Herrmann, Gächter and Thöni (2008) that cooperative behavior in games can vary strongly between different societies (cf. 2.8.).

Over all it can be said that genes contribute to cooperative behavior in games. It has to be determined, however, which genes are responsible for cooperative behavior. To answer this question other methods like candidate genes studies or genome wide association studies are available.

Hammock and Young (2005) showed that variation of the vasopressin 1a receptor predicts differences in social behavior of prairie voles. Based on these investigations Knafo et al. (2008) published a candidate gene association study, which showed that the length of the arginine vasopressin 1a receptor RS3 promoter region is also related to prosocial behavior in humans. Test subjects with short versions of this gene gave significantly less money in a dictator game than test subjects with long versions (Knafo et al., 2008).

The results of the presented studies confirm that cooperative behavior has a genetic component. Due to the fact that huge samples are necessary to find out which genes are responsible for cooperative behavior, it will take some time to identify specific genes and their impact. The presented candidate gene association study showed that vasopressin is associated with cooperative behavior but replication is needed, because the sample was rather small (203). With decreasing costs more studies will be conducted and new genes will be found and confirmed by replication studies, but as long as samples stay small, results should be treated cautiously.

5. Conclusion

The aim of this thesis was to introduce interdisciplinary approaches which might be helpful for economics. It was demonstrated with care how different fields handle the topic of cooperation.

Behavioral economics uses psychological knowledge to enrich or reject economic theories. The concept of the homo oeconomicus was extended by other-regarding preferences. People do not only care about their own benefit, but also take others into account. Experimental games like the ultimatum game or the prisoner´s dilemma were used in many of the presented studies to demonstrate these other-regarding preferences. Although incentives, especially punishment, showed an effect in behavioral economic studies, they were mainly seen as a way to "communicate", to tell other people that they are not acting according to the norm. Therefore redistribution worked as well as punishment and the possibility to communicate or to express ones feelings led to higher cooperation.

Reciprocity and inequity aversion are examples of other-regarding preferences which were demonstrated in various studies with many different games.

Neuroeconomics tries to combine neuroscience and economics. Economists use methods of neuroscience like brain imaging and temporal lesions to proof economic theories. This approach has been criticized a lot due to methodological, justification and ethical problems. The biggest chance of neuroeconomics is that it might be able one day to unify psychology, economics and neuroscience since all these disciplines research human behavior on different levels.

The most interesting neuroeconomic studies were the lesion studies of Knoch et al., because they were very controversial. They used current or magnetic fields to influence the activity of the brain and brought astonishing results concerning the function of the prefrontal cortex. To evaluate how much effect those methods had, effect sizes were calculated and resulted in medium sized effects, which means that this technology has to be taken seriously and handled with caution.

Another way to influence people is to use hormones. The example of oxytocin showed that the application of the bonding hormone changed cooperative behavior and has to be handled with care.

Brain imaging studies showed that the prefrontal cortex and the reward system are related with cooperation. Due to the fact that imaging studies are just correlative, no causal conclusions can be drawn from them. Lesion studies could be used to confirm the results of the brain imaging studies.

The third interdisciplinary approach discussed was genoeconomics. The main methods of genoeconomics are heritability studies and association studies. The results showed that cooperative behavior is indeed heritable. To find out which genes are related to cooperative behavior, association studies are necessary. One problem is that huge samples are needed, because the effect of each gene is very small. Otherwise studies would be underpowered which can lead to false positive results.

All three of the approaches under discussion showed interesting new ways towards the research of cooperative behavior and gathered promising information of how cooperation works. Especially the field of genoeconomics is still in its beginnings, but one can be sure that many more interesting results and striking findings towards the understanding of cooperation will follow in the future.

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List of Figures

List of Tables

Abstract (English)

Standard economic theory and especially the concept of the "homo oeconomicus" have been challenged by a number of new approaches from other scientific fields.

This thesis will discuss three interdisciplinary approaches: Psychological knowledge of behavior is incorporated in the theory of behavioral economics. Neuroeconomics combines neuroscience with economics and tries to find answers on the neural level. The third approach of genoeconomics focuses on the role of genes related to economic behavior. To demonstrate how these approaches work, findings on cooperation were presented and chances and problems of the interdisciplinary approaches discussed.

Behavioral economics uses experimental approaches and could show that people are not solely self-interested. They are also showing other-regarding preferences like reciprocity or inequity aversion. Neuroeconomic research found out that the prefrontal cortex, a mediator between social- and self-interest, and the reward system are activated when decisions concerning cooperation had to be made. Genoeconomics could prove that cooperative behavior has a genetic component.

This thesis showed that other fields of science can contribute to economic questions. Although there are still problems to solve, interdisciplinary approaches can enrich economics.

Abstract (German)

Die Standard Ökonomie und im Besonderen das Konzept des „Homo Ökonomicus“ wird durch neue Ansätze aus anderen Forschungsgebieten herausgefordert.

Diese Diplomarbeit stellt drei interdisziplinäre Ansätze vor. Die Verhaltensökonomie nutzt Wissen aus der Psychologie. Die Neuroökonomie kombiniert die Neurowissenschaften mit der Ökonomie und versucht so, Antworten auf neuronaler Ebene zu finden. Der dritte Ansatz, genannt Verhaltensgenetik der Ökonomie (genoeconomics), konzentriert sich auf die Rolle, die Gene bei für die Ökonomie interessanten Verhaltensweisen spielt. Um zu demonstrieren, wie diese Ansätze forschen, werden die jeweiligen Ergebnisse zum Thema Kooperation vorgestellt und die Chancen und Probleme der interdisziplinären Ansätze diskutiert.

Die Verhaltensökonomie nutzte experimentelle Ansätze und konnte zeigen, dass Menschen nicht nur egoistisch sind. Sie zeigen soziale Präferenzen wie Reziprozität oder Aversion gegen Ungleichheit. Die Neuroökonomie konnte zeigen, dass der präfrontale Cortex, ein Vermittler zwischen Egoismus und Gemeinschaftsinteresse, und das Belohnungzentrum aktiv sind, wenn Kooperationsentscheidungen getroffen werden müssen. Die Verhaltensgenetik der Ökonomie konnte zeigen, dass kooperatives Verhalten eine genetische Komponente besitzt.

Diese Diplomarbeit konnte zeigen, dass auch andere Wissenschaften Beiträge zur Ökonomie leisten können. Auch wenn es noch Probleme gibt, können diese interdisziplinären Ansätze die Ökonomie bereichern.

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