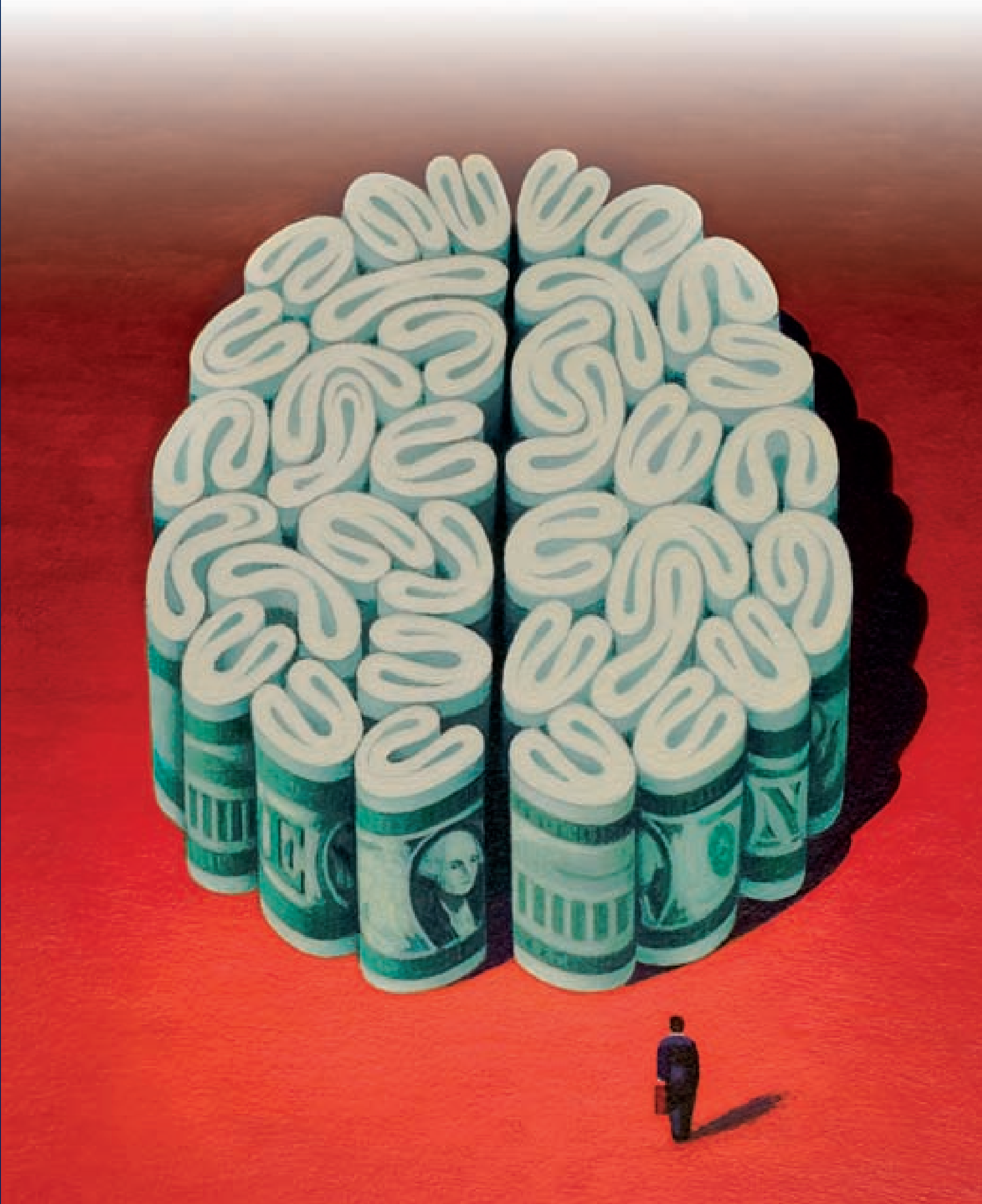
KAISA HYTÖNEN

Context Effects in Valuation, Judgment and Choice

A Neuroscientific Approach



Context Effects in Valuation, Judgment and Choice
A Neuroscientific Approach

Context Effects in Valuation, Judgment and Choice
A Neuroscientific Approach

Effecten van de context op keuzes, oordelen en waarderingen
Een neurowetenschappelijke benadering

Thesis

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Chapter 1

Introduction

Neuroeconomics emerged during the last decade as a new interdisciplinary field that aims to facilitate a profound understanding of decision-making processes through the integration of knowledge and insight from the disciplines of economics, psychology and neuroscience. To date, various aspects of decision making have been studied as part of the neuroeconomics discipline, ranging from risk and valuation to intertemporal choice and social decision making. In addition to the emergence of neuroeconomics, the prospect of using neuroscientific tools to understand human decision behavior has also garnered attention in the field of marketing. This research area, known as consumer neuroscience or neuromarketing (Smidts, 2002), is closely related to the broad range of research interests in neuroeconomics. The resulting work is often published and presented in similar forums to neuroeconomic experiments. Both neuroeconomic and neuromarketing research are also generally referred to as decision neuroscience (Sanfey, 2007; Shiv et al., 2005).

Both neuroeconomics and neuromarketing have investigated the neuronal networks related to valuation and choice behavior[1]. Research themes in neuromarketing have for instance included the evaluation of TV commercials (Ambler, Ioannides, & Rose, 2000; Astolfi et al., 2008; Rossiter, Silberstein, Harris, & Nield, 2001), processes related to brand perception (Schaefer, 2009; Yoon, Gutchess, Feinberg, & Polk, 2006), trade-off difficulty (Hedgcock & Rao, 2009), salesperson's interpersonal mentalizing skills (Dietvorst et al., 2009), and the effectiveness of celebrities in advertising and persuasion (Klucharev, Smidts, & Fernandez, 2008; Stallen et al., 2010). Broadly speaking, two different research perspectives can be taken in addressing neuromarketing topics (Ariely & Berns, 2010; Smidts, 2002):

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[1] For a detailed review, please see Chapter 2.

1. Theory generating and theory testing using tools from neuroimaging. The goal is to increase process-level understanding of consumer behavior.

2. Gathering information on the quality of the marketing stimulus and predicting consumer choices by means of neuroimaging. This 'stimulus-centered approach' aims at providing reliable information above and beyond regular methods of marketing research, improving for instance the design of packages, effectiveness of commercials and quality of products.

Until recently the largest part of the literature has concentrated on understanding the processes underlying consumer behavior. For instance, neuromarketing has studied why context variables influence the hedonic experience of goods. One experiment indicates that brand information can influence the consumption experience by higher level processes related to retrieval of brand information from memory (McClure et al., 2004). In contrast, another study found that the price of wines directly modulates the activity in a brain area related to hedonic experience, integrating the low-level sensory taste perception with flavor expectancy based on price information (Plassmann, O'Doherty, Shiv, & Rangel, 2008). Interestingly, these valuation areas have also been found to correlate with later purchase behavior and willingness to pay for goods (Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007; Plassmann, O'Doherty, & Rangel, 2007), which indicates the potential for the second, marketing stimulus-based approach.

Recently, the marketing stimulus-centered approach has gained more attention in the literature. As already mentioned above, neuronal activations to product displays correlate with the future purchase behavior (Knutson, et al., 2007). A recent study indicates further that neuronal responses to products predict future willingness-to-purchase to a similar degree, irrespective of whether consumers pay attention on the product displays or not (Tusche, Bode, & Haynes, 2010). In another example, the brain signals evoked by anti-smoking ads have been reported to improve the prediction of future reductions in smoking above and beyond traditional self-report measures (Falk, Berkman, Whalen, & Lieberman, 2011). Another study indicates that the self-related processing occurring in the brain during personally tailored anti-smoking messages predicts smoking cessation four months later (Chua et al., 2011).

Neuroeconomics and neuromarketing have attracted attention both among academics and the general public. The academic interest is indicated by the emergence and expansion of the Society of Neuroeconomics and the Association of NeuroPsychoEconomics and the active participation of researchers in annual conferences arranged by these two societies. Furthermore, the academic community is actively publishing articles in neuroeconomics and neuromarketing. By the end of 2010 there were 44 hits in the Web of Science® search engine[2] for review articles in neuroeconomics[3]. The number of publications in neuromarketing[4] at that time was lower, with one review article and 26 other types of reports. However, the field of neuromarketing does not have such a well-established standing and terminology as neuroeconomics does and thus the terms used in the search are less likely to be included in the reports that could be considered a part of neuromarketing. Both neuroeconomic and neuromarketing research have also been widely discussed in the popular press and on internet forums. Most notably, neuroeconomics and neuromarketing have inspired the authors of such books as "Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics" and "Foundations of Neuroeconomic Analysis" by Paul W. Glimcher (Glimcher, 2003, 2011), a pioneering researcher in neuroeconomics, and the best-seller "Buyology" (Lindstrom, 2008), which introduced neuromarketing to the general audience.

The emergence of neuromarketing has also attracted commercial interest which led to the introduction of neuromarketing consulting firms already at the early stage of academic research (Harrison, 2008). Intriguingly, using neuroimaging methods as a marketing tool was patented in the United States as early as in 2000 (Zaltman & Kosslyn, 2000), which was four years before the publication of the first widely acknowledged neuromarketing study which compared preference formations in relation to two common beverages, Coca-Cola and Pepsi (McClure, et al., 2004). The Nielsen Company recently acquired

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[2] The search engine is available at www.isiknowledge.com. The following data bases were used: Science Citation Index Expanded from 1945 onwards and Social Sciences Citation Index from 1956 onwards.

[3] Searching for 'neuroeconomics' or 'neuroeconomic' in the title, abstract or keywords.

[4] Searching for 'neuromarketing' or 'consumer neuroscience' in the title, abstract or keywords.

NeuroFocus Inc., the market leader in neuromarketing-driven consumer research, indicating the great commercial interest in the use of neuroscientific tools in marketing research (Nielsen Holdings, 2011). Also in the Netherlands the first neuroeconomic research and consulting company, Neurensics, recently started providing its services (Neurensics, 2011).

Neuroeconomics and neuromarketing have also faced opposition and criticism. For instance, neuroeconomics has been criticized for hiding the lack of new (economic) insights by story-telling, for attempts to falsify economic theories by using inappropriate measures[5] and for insufficient data analysis methods (Gul & Pesendorfer, 2008; Harrison, 2008). Some of these highlighted problems arise from an initial brain-centered approach of neuroeconomic studies, which was adopted to increase the understanding of the neural architecture related to decision making. To a large extent, neuroscientific methods do still hold promise for economics and that may be realized with continuing method development and more careful consideration of research questions (Clithero, Tankersley, & Huettel, 2008; Harrison, 2008). In addition, the emergence of neuromarketing has come paired with debate on the ethical aspects, including consumer privacy rights and free will and also the use and storage of personal medical data (Ariely & Berns, 2010; Fisher, Chin, & Klitzman, 2010; Murphy, Illes, & Reiner, 2008; Wilson, Gaines, & Hill, 2008). Some of this debate reflects science-fiction-like future scenarios where ‘mind reading’ is possible inconspicuously in everyday market situations as well as in the controlled laboratory environments used in current neuromarketing research. In addition to the academic debate on the usability of neuroimaging tools, there are also concerns that companies specialized in commercial applications of neuromarketing might be offering excessively high hopes to their clients at this early stage of academic research (Ariely & Berns, 2010; Fisher, et al., 2010). In 2010 these concerns led to the launch of a “NeuroStandards” project by the Advertising Research Foundation (ARF). Preliminary findings indicate that the quality of research varies between vendors and that further scientific development is necessary. The ARF concludes that the current neuromarketing methods can provide additional insights but do not replace the traditional research tools (Advertising Research Foundation, 2011).

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[5] The argument against neuroeconomics is that economic models do not make predictions about neural processes and thus brain imaging data cannot support nor refute the models.

This doctoral dissertation uses neuroscientific methods to investigate processes related to consumer decision making and judgment. The aim of this dissertation is to apply neuroscientific research methods to gain a better understanding of how prior experiences and social environment influence current choices and judgments. The dissertation contributes to the literature by highlighting the biological mechanisms that link prior experiences to current actions and social environment to judgment, which potentially informs future behavioral experiments and models of sequential choice and judgment. In the context of the present topic, the dissertation also discusses the previously stated concerns regarding neuroeconomics and neuromarketing. The next section introduces the research questions asked in the dissertation and after that this chapter concludes with an outline for the rest of the dissertation.

1.1. Research Questions

Imagine a woman who joins a group of friends for a night out at a local casino, but who has no intention of spending any money gambling. Rather than being drawn by the game play, she is motivated by the prospect of spending a relaxing evening with friends. Upon entering the casino, she experiences the uncomfortable feeling of being different from those around her: everyone else seems to be gambling. She finally relents, decides to join in and starts playing cautiously with small monetary bets. She enjoys a run of luck at first, which encourages her to take more risk by increasing her bets. After all, she has just won and, consequently, has ‘extra money’ to spend that she didn’t have at first. Over the course of the evening, she realizes that she has lost more money than she has won. In an attempt to get back to break-even, she chooses a game that offers the prospect of recouping all her losses. In doing so, she fails to recognize that this game involves more risk than she was willing to take earlier.

Consumers make their judgments and choices often as a part of a sequence of events. In the example scenario, the actions of the consumer are motivated and reasoned on the basis of the surrounding environment and past events. First, she changes her mind about spending money on gambling after observing the behavior of others, then increases her bets ‘because she previously won some extra money’ and finally attempts to recoup her losses by increasing the level of risk she takes on. Most research efforts have, however, been directed to consumer decision-making processes in isolated situations, both behaviorally and in neuroscience studies. Thus, this dissertation addresses the general question:

> *How do social or financial experiences influence future judgments and choices?*

This general question is addressed in two different contexts. First, path dependence in choice is investigated in the context of risky decision making. As described in the example scenario above, in certain situations consumers' risk appetite may fluctuate as a function of prior outcomes. The dissertation tests whether these changes in risk appetite are driven by modulations in the affective and deliberative processes that are evoked by prior gain and loss experiences.

> *Are path-dependent behavioral adjustments in risky choice underlined by affect or cognitive deliberation?*

In addition to the above dual-process hypothesis on path dependence, the dissertation also considers another possible explanation for the path dependence in risky choice. In detail, the dissertation questions whether past lotteries function as a frame of reference for the evaluation of subsequent lotteries. If the valuation of the latter lotteries depends on the preceding ones, this naturally also modifies the perception of the general choice problem. Thus, the dissertation addresses the question whether prospects are valued in respect to the previous states instead of in absolute terms.

> *Is valuation of risky prospects done relatively to past states or in an absolute manner?*

Second, the dissertation investigates how experiences in the social environment influence subsequent judgments. In other words, we study the mechanisms of social conformity that is illustrated in the example by the consumer's willingness to change her opinion towards gambling after she had observed the gambling behavior of others. Specifically we ask whether conformity to the previously observed group opinion is driven by similar brain mechanisms to those operating in basic trial-and-error learning.

> *Is social conformity driven by basic learning mechanisms?*

This dissertation does not only study the dependencies between past financial and social events and the subsequent behavioral patterns but its main goal is to study the mechanisms that lead to the observed behaviors. This interest is motivated by the idea that mechanism-level information can inform future development of effective and efficient interventions for such contextual effects. The dissertation explores the cognitive processes that contribute to path dependence in choice and environmental influence on judgments. In detail, the dissertation investigates whether the changes in choice behavior are driven by affect and cognitive deliberation and how judgments are influenced by basic learning mechanisms. The questions are investigated using an exploratory, neuroscientific approach. The idea is to test process-level hypotheses by recording brain activation while consumers are performing decision or judgment tasks.

1.2. Outline

This dissertation is divided into three parts. The first part introduces relevant background theory and methods in neuroeconomics. Chapter 2 gives a general overview of the field and its methods. The main body of the chapter concentrates on brain mechanisms that are related to valuation and decision making. Chapter 3 elaborates on the details of functional magnetic resonance imaging (fMRI). fMRI is currently the most common method in neuroeconomic research and it is also used in the experiments of this dissertation. This chapter has two goals. First, it aims to give a short introduction to the basics of the method for those readers who are not familiar with fMRI. Second, it discusses the limitations and advantages of using fMRI as a research tool in neuroeconomics and elaborates on the additional value that fMRI can provide above other methods in neuroscience and behavioral economics.

The second part presents an fMRI data set that explores path dependence and valuation in risky choice. Chapter 4 investigates the brain mechanisms that underlie increasing risk appetite after both previously experienced gains and losses. In detail, we use neuroimaging tools to test the hypothesis that gains and losses increase affective processing and decrease deliberative brain networks, and that the modulations in these two mechanisms drive the changes in risk appetite. Chapter 5 looks at the data from valuation perspective: we test whether identical risky lotteries are valued differently depending on past history.

The third part of the dissertation investigates how subjective judgments are influenced by the social environment. We study modulations in judgment in social context since it has been previously well documented that judgments are strongly influenced by the social environment (Cialdini & Goldstein, 2004). Chapter 6 reports fMRI findings on social modulation of facial attractiveness ratings where decision-makers adjust their ratings to conform to the average rating of other people. We test whether such changes in judgment are driven by reinforcement learning mechanisms, i.e. whether people experience that deviation from a general group opinion is an error in behavior that needs to be corrected.

Chapter 7 concludes with a general discussion. First, the chapter summarizes the main findings of the fMRI experiments, and then analyzes the contributions and limitations of the research. The dissertation concludes with a consideration of interesting avenues for future research, both with regard to the present research topic as well as to the field of neuromarketing in general.

Part I

Theory and Methods

Chapter 2

A Neuroeconomic Perspective on Valuation and Choice

Abstract

Neuroeconomics is a developing field that utilizes methodologies from neuroscience, psychology and economics to study the brain networks that are activate during decision making. In this chapter, we outline the primary methods used by neuroeconomics and examine how this field can help build better models of decision making. First, we review research related to valuation processes that occur in the brain, and discuss the properties of the human reward circuitry which reacts to both the anticipation and receipt of financial and hedonic rewards. These reward areas also appear to encode the overall attractiveness of risky prospects, integrating value and probability information. Next, we discuss the balance between emotional and cognitive control areas in the brain, which have a central role to play in behavioral framing effects. We conclude with a discussion of how a better understanding of the brain processes can increase our knowledge of why decision making in the real world often strays quite far from the predictions made by standard utility maximization accounts.[6]

2.1. Introduction

In recent years neuroeconomics has emerged as an exciting interdisciplinary field, with the stated aim of combining knowledge from economics, psychology, and neuroscience in order to increase the understanding of decision-making behavior. The combination of these different disciplines has provided an opportunity to begin specifying the brain basis of decision making, as well as informing

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[6] An adapted version of this chapter, including all the illustrations, was published in the *Wiley Encyclopedia of Operations Research and Management Science* (Hytönen & Sanfey, 2011).

theoretical models of decision making. In addition, there is now the growing awareness that many of the findings from the field can potentially have implications for more practical decision analysis situations.

According to the classical economic perspective (Bernoulli, 1738), decision-makers approach choice situations by analyzing the attainable outcomes and their associated probabilities. The well-known expected utility model of decision making under risk is a good formulation of this behavior, with this model based on an axiomatic foundation that reflects a rationality assumption on the part of the decision-maker (von Neumann & Morgenstern, 1947). Despite the model's theoretical elegance and normative appeal, it has been often demonstrated that it does not provide an adequate description of typical decision making, and neuroeconomic studies are beginning to demonstrate how a better understanding of the neural processes involved can help explain these discrepancies.

In this chapter we will first provide some brief details about typical methods used in neuroeconomic studies, before examining how knowledge about the valuation system in the human brain can yield insight into how decisions are made, and how this knowledge can in turn help build better models of decision and choice. We will then discuss a particularly well-known behavioral anomaly, the framing effect, and how understanding of the brain's emotional mechanisms can lead to better models of this behavior, before concluding with some general observations about the relevance of this new discipline for decision analysis.

2.2. Methods

One important approach to neuroeconomics has been to utilize the varied set of methods developed by neuroscientists to examine higher-level cognitive processes. These methods vary widely both in their use and in terms of what questions they can answer, but together they provide a highly flexible set of tools for examining the neural substrate of decision making. Broadly speaking, they can be divided into two types, those that observe the normal functioning brain and those that examine perturbations in these normal functions.

The most frequently used methods measure the degree of 'activation' of various brain regions while people are making choices and decisions. For instance, the commonly-used method of fMRI[7] leverages the physiological fact that changes

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[7] See Chapter 3 for further information on the method.

in neural blood flow leads to corresponding changes in local magnetic properties of the brain, which in turn can be detected by an MRI machine. These blood flow changes are thought to be directly related to regional neural activity, thus providing a measure which correlates with neural firing. The majority of the results we discuss in this chapter are based on fMRI studies, however other non-invasive measuring techniques are used by neuroeconomists, such as those that measure electrical (electroencephalography, EEG) and magnetic field (magnetoencephalography, MEG) changes evoked by brain activity. A promising new method for future research is fast optical imaging (event-related optical signal, EROS), which measures changes in optical scattering that are caused by neuronal activations (Gratton & Fabiani, 2010).

A different approach has been to examine the functioning of the disrupted brain to make inferences about normal behavior. Indeed, the study of decision-making processes in the human brain was largely motivated by behavioral deficits that were apparent in patients with brain damage. For example, brain lesions in the frontal lobes of the brain appear to be associated with uncontrolled behavior: patients take excessive risks regardless of their intellectual capabilities or other demographic or psychological factors. The lack of an appropriate skin conductance response to emotional stimuli in this patient group set forth the idea that brain damage to the frontal lobe interfered with behavior through inappropriate integration of emotional knowledge in the decision-making process (Bechara, Damasio, Tranel, & Damasio, 1997; Damasio, 1994), thus providing an important initial clue as to how the brain's organization related to decision processes. In addition to examining the behavioral deficits of patient with lesions, there are also methods to temporarily disrupt neural processing using electrical and magnetic signals in healthy participants, such as Transcranial Magnetic Stimulation (TMS). As an example, people's risk attitude changes when the functioning of their dorsolateral prefrontal cortex is disturbed with TMS (Knoch et al., 2006).

2.3. Preferences and Valuation

2.3.1. Reward Processing in the Brain

The functioning of the human brain and the nervous system is based on millions of brain cells called neurons, and in practical terms the brain is a vast network of

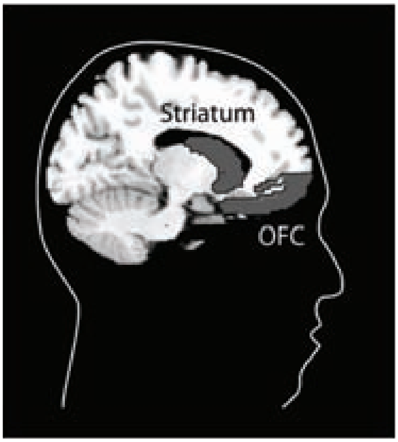


Figure 2-1. The striatum is located in basal ganglia at the center of the brain. The orbitofrontal cortex (OFC) is a subsection of the frontal cortex that is specialized in valuation. The figure indicates the approximate anatomical locations of the regions of interest.

neurons that communicate with each other. The human brain can be structurally divided into separate regions, some of which appear to have some specificity to certain functions.

Reward processing in the human brain is closely related to the neurotransmitter dopamine. Dopamine is mainly produced in the brainstem and then projected to multiple areas in the brain. Areas of the brain such as the striatum and the orbitofrontal cortex (OFC) receive input from these domapinergic neurons and are thought to process the rewarding value of stimuli (see Figure 2-1). Additionally, the ventromedial prefrontal cortex (VMPFC) is often mentioned in this context as well. Since the anatomical definitions of the medial OFC and the VMPFC are somewhat overlapping, and indeed often used in parallel to refer to the same location, we adopt here for simplicity the notation of using OFC when we refer to a prefrontal region that reacts to rewards (medial OFC and VMPFC) and punishments (lateral OFC) (Kringelbach, 2005).

The target regions of dopamine neurons have been shown to react to both primary and secondary rewards. Striatum activity increases with the receipt of primary rewards such as water and juice (Berns, McClure, Pagnoni, & Montague, 2001), and OFC activity reflects the rewarding value of stimulus in multiple different modalities like taste and olfaction (O'Doherty, 2004). In addition to primary rewards, both the striatum and the OFC react to the receipt of secondary rewards such as financial incentives (Delgado, Locke, Stenger, & Fiez, 2003; Knutson, Westdorp, Kaiser, & Hommer, 2000; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Thut et al., 1997). The OFC is also sensitive to more subjective features of the stimuli, and is involved in the calculation of the hedonic value of rewards (de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003; Kringelbach, 2005). The OFC even tracks modulations in the hedonic value that are driven by contextual information. One study indicates how the OFC correlates with the transfer of positive value from a celebrity presenter to a product (Stallen, et al., 2010). In another study where participants evaluated wine, the perceived pleasantness of the wine and the OFC activity varied as a function of retail price, though the actual wine consumed remained the same: high price increased the pleasantness estimation both in the brain and in the behavioral measures (Plassmann, et al., 2008). Of course, in terms of rational models, the consumption experience of identical wines should not depend on the surrounding context (price), but this research demonstrates that the brain's computations are not fully in accordance with a classical utility calculation process.

2.3.2. Anticipation and Evaluation of Future Rewards

In order to choose the option that provides the highest level of satisfaction, decision-makers need to anticipate the rewarding value of each outcome in the relevant choice set. As this is clearly an important issue to economic decision making, anticipatory reward mechanisms were among the first topics that were widely researched in neuroeconomics. The research to date indicates that the reward circuitry in the brain demonstrates increased activation not only when rewards are obtained but also during the anticipation of rewarding outcomes (Knutson, Adams, Fong, & Hommer, 2001; Knutson & Greer, 2008; O'Doherty, 2004). Importantly, these anticipatory patterns of activation are not just correlates of the subjective value of the reward, but also have an influence on future economic choices themselves. Negative anticipatory affect during decision making is related to an increase in risk aversion, and positive anticipatory affect in contrast is associated with an increasing risk seeking attitude (Kuhnen & Knutson, 2005).

In addition to anticipatory reward processing, decision-makers in risky choice scenarios must also take into account the probability of each outcome option in order to reach an overall estimate of the attractiveness of the prospects. In a typical experiment, participants encounter a series of uncertain prospects in turn, after which the prospects are resolved, revealing the gain or loss to the participant. As an example, in one task participants view eight cards face-down in random order, one of which is the target card. The task of the participants is to place a bet on the cards. If participant place the bet on the target card they win the bet, otherwise they lose an equal amount of money from their total earnings. The magnitude of the outcome is manipulated by providing the participants with either 1 or 5 Euros to bet with. The probability of receiving the reward is manipulated by allowing the participants to place the bet on either just one card (low probability) or on the corners of four adjacent cards (high probability). By using this paradigm, Yacubian and colleagues showed that both the striatum and the OFC encode anticipation of probabilistic rewards (Yacubian et al., 2006). The findings of this experiment indicate that both the reward magnitude and also the associated probabilities are directly encoded in the valuation network itself: the striatum and the OFC had higher activation levels in the high bet and high probability conditions than in the low bet and low probability conditions, respectively. Further, the results of this experiment show that the reward circuit also provides a measure for the overall desirability of a risky prospect as it encodes the expected value of a prospect, integrating the value and probability information for rewarding stimuli. Other fMRI experiments that have studied the valuation of risky prospects have reported similar findings in reward circuitry for manipulations of outcome magnitudes and probabilities as well as for the overall expected value of the prospect (Abler, Walter, Erk, Kammerer, & Spitzer, 2006; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Preuschoff, Bossaerts, & Quartz, 2006; Tobler, O'Doherty, Dolan, & Schultz, 2007; Yacubian et al., 2007). These findings indicate that both the magnitude of the outcomes and probability of receiving them can be processed via the basic reward mechanisms of the brain, suggesting that the evaluation of risky prospects does not necessarily require high level ‘rational’ calculations.

As prior research indicates, people do not react linearly to anticipated outcomes and their probabilities. The very early work of Bernoulli showed that outcomes are processed in a subjective manner rather than relying on the objective numerical value (Bernoulli, 1738). Typically the utility associated with one additional unit decreases as the outcome level becomes higher. Intriguingly, the activation in the striatum to anticipated monetary gains appears to have the same property: the incremental additions to the strength of the striatum activity become smaller as the magnitude of reward increases linearly (Pine et al., 2009). This property of the striatal response is in line with the decreasing marginal utility effect which is well-characterized at the behavioral level. This finding implies that the striatum might be involved in the calculation of subjective utility of the reward rather than simply reflecting the absolute reward value. Similarly to reward magnitude, the striatum does not react linearly to probabilities but instead it overweights small probabilities and underweights large probabilities (Hsu, Krajbich, Zhao, & Camerer, 2009). Similar nonlinear weighting pattern of probabilities is also apparent in the behavior of decision-makers (Kahneman & Tversky, 1979). These results imply that the behavioral deviations from linearity may have their roots in the properties of the reward system, both in terms of the sensitivities of the valuation and probabilistic nature of rewards and punishments.

Thus far we have discussed the anticipatory reactions related to the expectation of financial incentives. However, it is also the case that this mechanism may underlie decisions of a non-financial nature, suggesting that the basic reward system may be a mechanism for most, if not all, of the typical day-to-day decisions we take. For instance, the striatum has been shown to reflect the preference for a variety of consumer products (Knutson, et al., 2007; Knutson et al., 2008), as well as encoding the anticipatory value of hedonic outcomes (Sharot, De Martino, & Dolan, 2009). The striatum activity also reflects modulations in the expected hedonic value in a similar fashion to the way the OFC encodes the influence of price on the experienced pleasantness of wines. In an fMRI study participants evaluated the expected hedonic value of several potential vacations, after which participants were forced to make a choice between two options of similar desirability to them (Sharot, De Martino, et al., 2009). Behaviorally, a commitment to one of these previously equally valued options increased the self-reported hedonic value of the chosen option, and decreased the valuation of the unselected one. The change in the expected pleasure of the two vacation destinations was also reflected in the striatum, with higher activity here for the chosen option than for the rejected one. Another study indicated that the subjective hedonic expectations are indeed influenced by the basic reward processing mechanisms, with a pharmacological manipulation which increases dopamine levels also increasing hedonic expectations for future life events (Sharot, Shiner, Brown, Fan, & Dolan, 2009).

2.3.3. Reference Dependence of Valuation

Normative decision-making models, such as the expected utility model, assume that valuation is done in respect to the total amount of wealth. One of the main insights of prospect theory (Kahneman & Tversky, 1979), a descriptive theory of decision making under risk, is that decision makers tend to value outcomes in a reference dependent manner. In accordance with this theoretical model, the brain seems to process positive and negative outcomes differentially. The most dramatic example of reference dependence is that the gains and losses activate different brain networks. For instance, the calculation of the expected value of a prospect has been suggested to be performed by the striatum when calculating the expectation of gains (Tobler, O'Doherty, et al., 2007; Yacubian, et al., 2006) and by more affective brain structures (amygdala) when calculating the expectation of losses (Yacubian, et al., 2006). In addition, the anticipation of a negative outcome has been linked to a brain structure (insula) that is often associated with processing of negative experiences such as pain, whereas anticipation of rewards is reflected in the reward circuitry (Knutson, et al., 2001; Kuhnen & Knutson, 2005).

The reference dependence of striatum activity has been implied by multiple studies. In one early neuroeconomics study, participants played lotteries while undergoing fMRI. One type of lottery consisted of positive and zero outcome options whereas another type of lottery consisted of negative and zero outcome options. When people received the zero outcome from the negative lottery (a relative gain), striatum activity was higher than when the zero outcome was received from the positive lottery (a relative loss) (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001). In general the striatum seems to process the outcomes in respect to subjective expectation (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Yacubian, et al., 2006) though some parts of the striatum have recently been shown to reflect reference independent calculation, together with some sub-regions of the OFC (De Martino, Kumaran, Holt, & Dolan, 2009).

In addition to performing calculations with respect to other possible rewards, Tom and colleagues have shown that the striatum induces non-linear reactions to gains and losses in a task where participants made choices accepting or rejecting mixed gambles (Tom, Fox, Trepel, & Poldrack, 2007). The researchers found a common network, including the striatum and the OFC, that was activated for gains and deactivated for losses. These areas also showed a pattern of loss aversion, namely that the slope of the deactivation for losses was greater than the slope of activation for gains in a majority of participants. Therefore, the striatum again demonstrates some of the properties of descriptive models of risky choice, showing loss aversion rather than the patterns predicted by classical expected utility maximization. Also of interest was that during decision making, no brain areas where found that were specifically activated by evaluation of increasing losses, in contrast to other studies that have reported increased activity in emotional regions, such as amygdala and insula, for losses (Kuhnen & Knutson, 2005; Yacubian, et al., 2006). One possible explanation for this difference is that the Tom et al. study restricted analysis purely to the decision-making phase (decision utility), and excluded anticipatory effects (anticipated utility) by only resolving the lotteries after the fMRI scanning.

Besides the set of possible outcomes, also other contexts influence the valuation process, such as social aspects (Fliessbach et al., 2007; Klucharev, et al., 2008) and numerical representations of financial gains (Weber, Rangel, Wibral, & Falk, 2009). Fliessbach, et al. (2007) scanned two participants simultaneously with fMRI while they performed a simple visual counting task. Participants received monetary rewards of varying magnitudes for correct performance, whereas incorrect answers had no financial consequences, and participants were informed of the performance and rewards of both players. Of interest were trials where both were correct but one of the participants received a higher reward than the other. Across reward levels, participant's striatum activity was higher when they received more than their partner relative to when they received less than the other player, demonstrating that participants evaluated their outcome relative to that of their partner, as opposed to purely evaluating the payoff.

2.3.4. Summary and Implications

Studies in neuroeconomics have indicated multiple properties in the valuation network of the brain that either support or contradict the assumption of rational evaluation of risky prospects. One important property of the reward circuitry is that it appears to anticipate the utility of future outcomes, providing the decision-maker with necessary information for comparing the possible outcome options and selecting the most attractive course of action. Further, this circuit also informs the decision-maker of the desirability of risky prospects by integrating the subjective value and probability of expected outcomes, thus reflecting the overall attractiveness of risky alternatives. These results suggest that the valuation of risky prospects is done in the basic reward circuitry of the brain in accordance with the principles of expected utility maximization. However, another part of the literature indicates that the reward circuitry does not always behave as predicted by expected utility maximization model when the outcome values and probabilities are manipulated. For instance, the probabilities are represented in a non-linear fashion in the valuation process, reward circuitry processes outcomes as gains and losses relative to a reference point, and even arbitrary contexts such as the rewards of others and the numerical presentation of the financial rewards, influence the valuation of outcomes. None of these properties meet the requirements of expected utility maximization but they are reflected in the behavior of decision-makers and accounted for in descriptive models of decision making under risk (see e.g. Kahneman & Tversky, 1979).

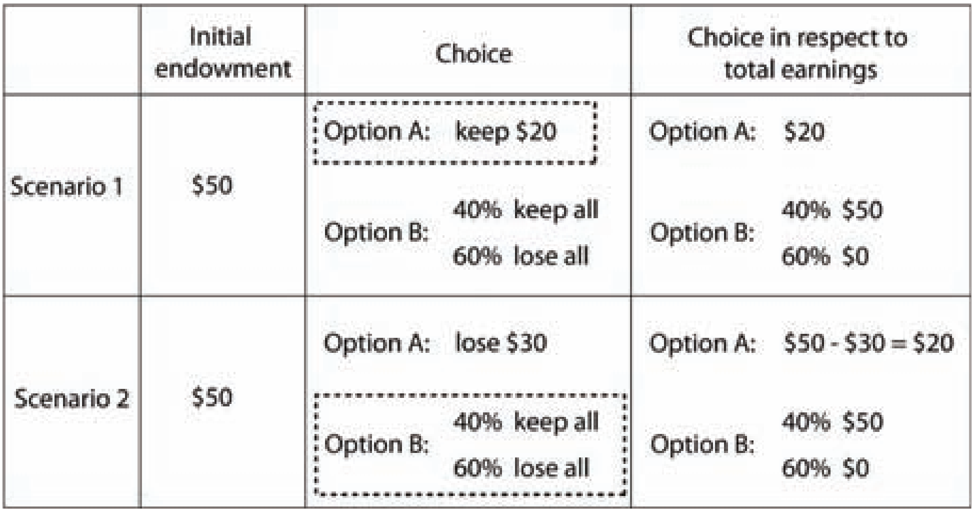
In sum, the brain evidence indicates that both the evaluation of the attractiveness of risky prospects and the behavioral biases observed in these estimations, are reflected in the reward circuitry of the brain. One implication of these findings is that the evaluation of risky prospects is not controlled by higher level deliberation, but that instead prospects are valued via more fundamental mechanisms, which also potentially explains the well-observed behavioral deviations from utility maximization.

When interpreting neuroscience findings it is important to take into account the so-called ‘reverse inference’ fallacy, which refers to the difficulty of inferring mental states of the decision-maker based on the activated brain regions, as one specific brain region can be involved in multiple processes (Poldrack, 2006). While there is a growing amount of evidence implicating the striatum and the OFC in the processing of rewards, it should not be concluded that these areas are reward-meters, where activity can be read off and taken as a metric of positive or negative valence. Despite this caveat however, the investigation of how the brain computes and processes reward and punishments offers a very useful window into basic decision making.

2.4. Framing Effect and the Brain

We have discussed above how behavioral findings such as loss aversion and reference dependent valuation can be observed at the neural level, and here we extend that by discussing another well-characterized behavioral anomaly, the framing effect (Tversky & Kahneman, 1981). The framing effect is a phenomenon where decision-makers display different preferences in choice situations which are identical other than for largely irrelevant contextual effects. For example, consider two packages of ground beef, one of which claims "75% lean" and the other "25% fat". Even though there is no difference in the actual product between these two packages, a majority of consumers prefers the "75% lean" beef over the one having 25% of fat (Levin, Johnson, Russo, & Deldin, 1985). The framing of information also influences how people react on a preventive health behavior advocacy, such as on campaigns against coronary heart disease or skin cancer, with negative frame being particularly effective when people process the given information intensively (Block & Keller, 1995; Maheswaran & Meyerslevy, 1990).

One explanation for the framing effect is that the decision-makers tend to be risk averse in the gain domain and risk seeking in the loss domain. For example, imagine the following two scenarios (see Figure 2-2). In the first scenario you are given $50 and then asked to make a choice between two options: keep $20 of the initial endowment or play a lottery where you have 40% chance of keeping the whole endowment and 60% chance of losing everything. In the second scenario, after you first received the initial endowment of $50, you are asked to choose: either lose $30 or participate in a lottery identical to that of the first scenario. Importantly, both of these scenarios are equivalent—they provide a choice between gaining $20 for sure and having a 40% chance of receiving $50. However, when people answer these questions separately, they tend to prefer the sure option in the gain domain (scenario 1: risk averse) and the lottery in the loss domain (scenario 2: risk seeking). Thus, the framing of the choice options influences the risk attitude of the decision-maker and causes preference reversals. This violates the invariance principle of normative decision-making models which holds that the preference structure is independent of the phrasing of the choice options. The framing effect can be observed in multiple types of decision, and even in participants groups who are dealing with risk on a daily basis, such as financial planners (Roszkowski & Snelbecker, 1990). As a practical example, when



	Initial endowment	Choice	Choice in respect to total earnings
Scenario 1	$50	Option A: keep $20	Option A: $20
		Option B: 40% keep all 60% lose all	Option B: 40% $50 60% $0
Scenario 2	$50	Option A: lose $30	Option A: $50 - $30 = $20
		Option B: 40% keep all 60% lose all	Option B: 40% $50 60% $0

Figure 2-2. Example scenarios for the framing effect. The dashed lines indicate typical choices that people make in line with the framing effect.

people consider selling their stock investments during an economic slump, it makes a difference whether they think about the money they can save or the money they will lose in case of selling. When people think about the money they could save by selling the stocks, they often prefer the safe option of selling the stocks and keeping the money (risk averse in gain domain), but when they think about the realized losses related to the sale, they prefer more risky courses of action (risk seeking in loss domain).

One possible explanation for this phenomenon is that the presence of risk in the choice situations elicits emotional reactions which intrude in the decision-making process (Loewenstein, Weber, Hsee, & Welch, 2001). Behavioral research suggests that increasing the emotional salience of the choice situation strengthens nonlinearities in the valuation process (Hsee & Rottenstreich, 2004) which leads to further deviations from risk neutrality (Mukherjee, 2010), thereby strengthening the framing effects. This hypothesis of emotional involvement in framing effects was tested by De Martino et al. in an fMRI study where participants made choices similar to those described above (De Martino, et al., 2006). Choices where participants adhered to the standard bias (safe choice in the gain domain and

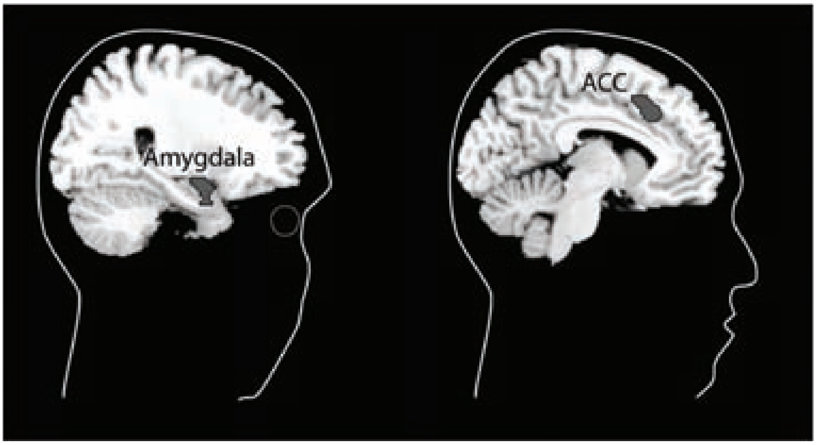


Figure 2-3. Framing effect is related to activity in amygdala and resisting the frame involves anterior cingulate cortex (ACC) activity. The image does not display the whole ACC (selection based on De Martino, Kumaran, Seymour, & Dolan, 2006). The picture on the right is a slice of the brain that is cut along the midline of the head. The picture on the left is a parallel slice taken from the brain at the level of eyes. This picture indicates the anatomical locations of the regions of interest, but does not represent data from the actual measurement.

lottery choice in the loss domain) were compared to those situations where participants chose in the opposite direction (lottery choice in the gain domain, and safe choice in the loss domain). This comparison showed activity in an area related to valuation and processing of emotional stimuli (amygdala), supporting the hypothesis that emotional processes contribute to the framing effects (Figure 2-3). The researchers also examined which brain mechanisms were related to resisting the framing effect, and found activity in a region that is commonly involved in conflict detection and cognitive control (anterior cingulate cortex; Figure 2-3). This implies that resistance to the framing bias requires detection of conflict between the rational course of action and an emotional tendency, and regulatory control of the emotional mechanisms to override the bias.

Framing effects are not equally strong in all individuals. In a follow up study the researchers were interested in these differences between individuals (Roiser et al., 2009). They hypothesized that genetic variation might be able to explain these differences, and examined variation in a gene 5-HTTLPR, which has previously been shown to modulate amygdala and anterior cingulate function. The results showed that people with the short allele form of the gene demonstrated strong behavioral framing effects, which were also reflected in the activation in amygdala. In contrast, the people with the long allele variant showed a weaker behavioral effect, which was not reflected in the pattern of amygdala activity. By performing a connectivity analysis between brain regions, the researchers were able to show that the coupling between anterior cingulate and the amygdala increased when participants with long alleles were countering the framing effect. This increase in the connectivity did not occur in the subjects with short alleles. Based on the results, the researchers claim that the participant group with the long alleles has more efficient dynamic regulatory control over the emotional amygdala reactions than the group with short alleles, which further leads to reduced behavioral framing effects. Thus, the results indicate both the role of emotional reactions and the regulation of those reactions in enhancing and controlling of behavioral framing effects, respectively, and how individual variability in the control mechanisms influences the sensitivity to the framing effects.

2.4.1. Summary and Implications

The fMRI experiments outlined here indicate the role of affective neural processes in driving the behavioral framing effects, and the importance of cognitive control in decreasing them. These findings imply that even when the decision situation does not have any clear emotional context, the presence of risky prospects can activate emotional brain regions. The effect of this emotional activation differs in positive and negative domains: in a positive frame involvement of emotional brain regions increases risk aversion, and in a negative frame the emotional activation leads to more risk seeking attitude. Additionally, the susceptibility of individuals to framing effects differs, and these differences can at least partly be explained by genetic variation. Overall, the findings support the idea that framing effects can be reduced either by decreasing the emotional reactions induced by risky prospects or by increasing the cognitive control during the decision process.

2.5. Conclusions

In this chapter we have outlined the importance of both reward circuitry and the balance of emotional and cognitive control in the evaluation of risky prospects, and we have described how these mechanisms can be related to decision biases that have previously been observed in the behavior of decision-makers. As this existing research suggests, neuroscience studies can provide insights in the decision-making processes, and give potentially valuable information for further development of economical models. Further, a better understanding of the neural architecture underlying behavioral biases may provide opportunities to minimize the errors associated with these processes.

This work also suggests that different biases may have different fundamental causes and so might differ in how easy they are to overcome. For example, biases associated with reward mechanisms might be more persistent than the biases that arise from the imbalance of emotional and control signals. Another important role for the striatum is as part of the learning mechanism in the brain (Schultz & Dickinson, 2000), which may imply that the biases that are reflected in the striatum activity are more difficult to overcome. One conception of the role of the striatum is that it is not engaged in the processing of rewards and punishments *per se*, but rather that it tracks so-called reward prediction error, that is, the difference between what we expect and what we receive (Hare, et al., 2008), thus computing gains and losses in respect to the reference point of expected outcome. If there is a bias in the calculation of the prediction error signals, these biases are continuously reinforced in the behavior, complicating efforts to overcome the resulting behavioral biases. For example, in a loss-aversion account, if outcomes that are worse than expected are followed by an exaggerated reward prediction error signal, this will lead to the learning of loss-averse behavioral patterns for choice situations involving losses.

Despite this however, research indicates that either neural or intentional control mechanisms have the ability to reduce the behavioral biases in certain conditions (Paulus & Frank, 2006; Sokol-Hessner et al., 2009). This may be because cognitive mechanisms can overcome more affective reactions that also enhance the biases. For instance, in the case of loss aversion there is evidence that points towards the role of emotions in enhancing the bias (De Martino, Camerer, & Adolphs, 2010; Knutson, et al., 2008), and that the decision-maker can reduce the influence of this emotional reaction in their decision-making process by intentionally choosing to use an emotion regulation strategy, such as a reappraisal strategy focusing on reinterpretation of the situation (Gross, 2002; Sokol-Hessner, et al., 2009). As discussed earlier in this chapter, framing effects are also driven by emotional mechanisms. The tendency of decision-makers to be risk averse in gain domains and risk seeking in loss domains appears to be related to increased emotional brain reactions, whereas resisting the biases involves use of cognitive control mechanisms. Those individuals who have better control over their affective responses show smaller framing effects than other people. Thus, these results also indicate the importance of regulation of emotional signals in reducing biases in the decision-making process, and suggest that it is possible that the framing effects in risky decision making could also be reduced by exerting intentional control over the emotional reactions with existing emotion regulation strategies. Overall, the role of emotional reactions in inducing decision biases, and the possibilities to reduce these influences with simple instructions to the decision-maker, are important aspects to take into account when designing decision support tools.

An important future step for neuroeconomics is to increase the understanding of individual variability in the sensitivity to decision biases. For developing the most efficient methods to reduce and control for the decision biases on an individual level, it is important to learn more about individual differences in choice situations, which will lead to better understanding of the brain mechanisms central to decision-making biases. In order to achieve a more complete picture of the neural calculations on an individual level, more attention should be paid to the functioning of larger brain networks involved in decision making. Some initial steps towards this goal have already been taken, for instance by categorizing people in different groups based on their genotype. Though neuroeconomics is a young field, it offers enormous potential for the better specification of decision-making behavior, and as such promises to open up interesting new avenues for decision analysis in the near future.

The literature outlined in this chapter represents a large body of neuroeconomic knowledge on valuation and reward-driven decision making. The later chapters of this dissertation build on this knowledge when discussing path dependence of risky decision making and social conformity. The first central theme in this literature review, valuation, is discussed in the second part of the dissertation in the context of a task on sequential risky choices. In particular, Chapter 5 investigates whether the valuation of risky gambles is done in the striatum and the OFC in respect to prior events or in absolute terms. Valuation account is also present in the third part of the dissertation concentrating on social conformity. In Chapter 6 we test whether disagreement with a group opinion functions as a social punishment ('negative reward') which drives future behavior towards the general opinion. The second central theme of this chapter was framing effects and the related emotional and control mechanisms. Chapter 4 continues this line of research and studies how emotion and cognitive control underlie path dependence in risky choice, i.e. how the frame of prior negative and positive events influences risky choice. Finally, Chapter 6 considers conflict areas in the brain when studying the conflict between participant's opinion and the opinion of others.

Chapter 3

Measuring Brain Activation with Functional Magnetic Resonance Imaging

Abstract

This chapter provides an introduction to fMRI as a tool in neuroeconomics studies and discusses the pros and cons of fMRI in comparison to other available methods for analyzing choice behavior. First, the chapter describes the origins of the fMRI signal, how the method restricts the experimental design, and the analysis procedures. The second half of this chapter discusses the limitations and advantages of fMRI in neuroeconomic studies in general and in the context of this dissertation.

3.1. Introduction

Magnetic resonance imaging (MRI) is a medical imaging technique that provides high spatial resolution images of arbitrary cross-sections of the human body. Since they were introduced commercially in the early 1980s, MRI techniques have become valuable imaging modalities for medical applications. Initially MRI techniques were used to obtain detailed anatomical information on the body structures but soon further technical developments enabled them to be used for functional measurements of brain activation. The basic structural MRI scans take multiple minutes to create precise photograph-like images of the brain structures, but nowadays the functional MRI measurements (fMRI) collect less detailed data from the whole brain within a couple of seconds, enabling the measurement of brain function. Since 1990s fMRI has revolutionized research in cognitive neuroscience by providing a non-invasive, radiation-free way of collecting functional brain data with high spatial resolution. The availability of fMRI methods has also boosted the recent expansion in neuroeconomics studies. The growing interest in using fMRI in research is reflected in the increasing number of

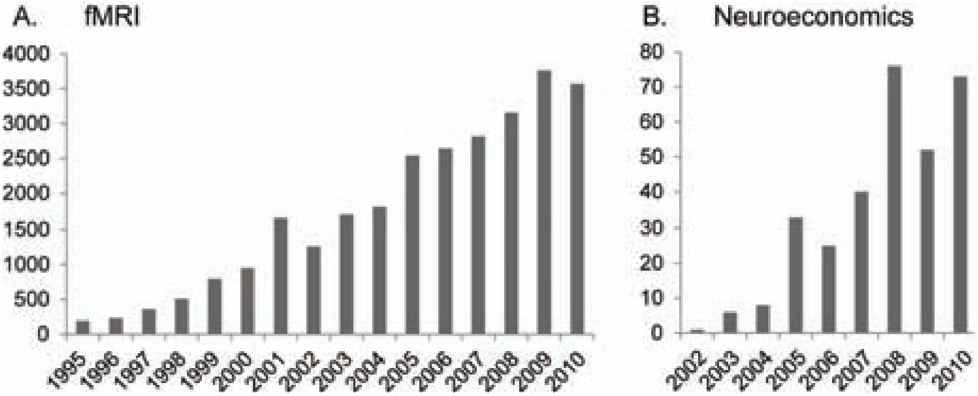


Figure 3-1. A. Number of publications which mention "fMRI", "functional MRI", "functional MR" or "functional magnetic resonance imaging" in the title, abstract or keywords. B. Number of publications that mention words "neuroeconomics" or "neuroeconomic" in corresponding fields. The searches were conducted with Web of Science® search engine (www.isiknowledge.com) using Science Citation Index Expanded and Social Sciences Citation Index databases.

publications which mention fMRI. Simultaneously the number of reports on neuroeconomics has been increasing substantially (Figure 3-1).

The remaining parts of this dissertation report on neuroeconomic studies that use fMRI techniques. This chapter provides a general introduction to fMRI for those readers unfamiliar with the method. This chapter does not, however, aim for a comprehensive description of fMRI measurements and design. For more detailed information on these issues, please see for instance (Huettel, Song, & McCarthy, 2009). The rest of this chapter is organized as follows. First, Section 3.2 introduces in brief the basic properties of fMRI signals and how fMRI measurements are done in practice. Thereafter, Section 3.3 describes the limitations and advantages of using fMRI as a tool in neuroeconomics. It also discusses the decision to use fMRI in this dissertation. The chapter ends with a short summary.

3.2. Technical Details

3.2.1. Origins of fMRI Signal

The MRI signal is based on a physical phenomenon called nuclear magnetic resonance that occurs when atomic nuclei interact with external magnetic fields. Each nuclear particle—a proton or a neutron—has a fundamental physical property called a *spin*, and a nucleus that has an uneven number of these nuclear particles, such as a hydrogen nucleus, possesses a *net spin*. The human body contains a lot of hydrogen nuclei and hence this is the most commonly used nucleus in medical imaging. Because a hydrogen nucleus has a net spin it gets a net magnetization when it is placed in an external magnetic field. In general, when a magnetic object is placed in a magnetic field, the object orients itself along the direction of the external magnetic field. However, MRI scanners are only able to detect the magnetized hydrogen nuclei when their magnetization direction is *not* along the direction of the external field. The MRI scanner thus first displaces the magnetization of hydrogen nuclei away from the direction of the external field ('excitation') and then starts registering the signal. With time the magnetized hydrogen nuclei return to alignment with the external field. The speed of this transition ('relaxation') depends on the properties of the surrounding tissue[8]. All in all, the formation of the structural images of the brain depends on the content of hydrogen atoms and other properties of the tissue. For instance, bones which have low hydrogen content are not clearly visible in MRI, and relaxation is in general faster in the vicinity of simple molecules, such as water, than close to more complex structures. MRI scanners have a strong constant magnetic field to achieve sufficient signal quality[9] and they use radiofrequency pulses (excitation) and

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[8] Two different processes influence the speed of relaxation. First, a nucleus is in a higher energy state when it is not aligned with the external magnetic field. Relaxation depends on the speed of energy transfer from the nucleus to the surrounding tissue. Second, when the magnetization of the hydrogen nuclei is displaced from the direction of the external magnetic field, the nuclei start precessing in the same phase about the external magnetic field. Surrounding tissue causes small variations in the magnetic field, which reduce the phase coherence of the hydrogen nuclei. This loss of coherence reduces the observable magnetization signal.

[9] Typically 1.5 T, 3 T, or even 7 T in research. For comparison, the earth's magnetic field is approximately 0.00003 – 0.00006 T.

weaker time-varying magnetic fields (localization gradients[10]) to create an informative signal.

The fMRI measurements of brain activation during task performance do not directly record neuronal activation but rely instead on an indirect measure of brain activity which is based on vascular changes in the vicinity of activated brain cells. Neuronal activation boosts energy consumption and local blood flow which increases the concentration of oxygenated hemoglobin at the activated brain sites. Different magnetic properties of oxygenated and de-oxygenated hemoglobin enable the measurement of blood oxygenation level-dependent (BOLD) contrast with fMRI. fMRI measures the activity within the whole brain at a high spatial resolution (e.g. 3 x 3 x 3 mm) with a fairly good temporal resolution in the order of seconds (~2s). Even though the temporal resolution of fMRI is low when compared to the high speed of electric activation in the brain cells or to the millisecond timescale of EEG and MEG, it is sufficient to capture the slow changes in the amount of oxygenated hemoglobin around the activated brain site.

3.2.2. Event-Related Experimental Design and Measurement Conditions

The use of fMRI imposes a number of requirements on an experimental design. In neuroeconomics the most commonly used design type is so-called event-related fMRI design[11]. Due to the slow nature of the dynamic changes in the blood flow in the brain (or hemodynamic responses), the fMRI signal changes that are caused by a neuronal activity are delayed (starts ~2 seconds after the stimulus and peaks ~6 seconds after the stimulus) and blurred (one single short event can cause a response of ~10 seconds). Another typical feature of fMRI data is the noisiness of the signal. Therefore, it is often necessary to repeat the interesting events many

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[10] The localization gradients (time-varying magnetic fields) enable the localization of the signal source in the three-dimensional space. First gradient ascertains that only one 'slice' of the brain is excited at a given moment in time (z-dimension). The second gradient modifies the phase of rotation of the magnetized hydrogen nuclei (y-dimension) and the third gradient adjusts the rotation frequency during the data collection (x-dimension). Each 'brain slice' can be separately reconstructed based on the phase-frequency space data.

[11] Another option would be to use a block design, where stimuli are presented in blocks of similar type of stimulus. The analysis is also based on comparing the activations of blocks to each other. Since neuroeconomics is generally interested in more transient events (such as observing a particular stimulus or making a choice), block designs are not very common. It is also possible to design an intermediate form of these two basic design options ('mixed design').

times to reduce the influence of noise[12]. To enable the statistical separation of the neuronal activities in different time points, the events need to be separated in time by delay periods and/or the stimuli need to be presented in randomized order. Furthermore, fMRI does not provide an absolute measure of activity level, introducing a need for a reference level or condition. While fMRI researchers collect a lot of data from one participant, fMRI experiments often include relatively small number of participants (12-30)[13], depending on the expected strength and variability of the effect sizes. For instance, for basic research in visual perception even 12 participants might be a sufficient number whereas when studying higher level mechanisms researchers generally aim for approximately 20-25 participants per experiment.

fMRI measurements are conducted with an MRI machine. During fMRI measurements participants are situated on a movable examination table inside a magnet bore at a high external magnetic field. The participant's head is placed tightly in position, e.g. with foam padding, to minimize artificial signal intensity changes due to head motion. While lying inside the MRI scanner participants can view visual stimulation from a screen at the end of the magnet bore with the help of a mirror system. Most research facilities also provide a range of MRI-compatible response devices, such as button boxes and joysticks. Generally the fMRI measurements do not cause any noticeable sensations in the participants[14], except for high acoustic noise.

3.2.3. fMRI Data Analysis and Reporting

After fMRI images have been reconstructed from the raw data collected by the MRI machine, the fMRI images are first pre-processed to correct for some known inaccuracies. For instance, the data from different points in the brain is collected at a different time point because the data is collected one 'brain slice' at a time. Thus, the data is corrected using the knowledge of the timing differences between the different brain slices. Another important correction is to reduce the distortions in

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[12] The number of repetitions depends on the size of the effect. Large effects may be detected even in one trial or block of stimuli whereas smaller effects require 15 or more repetitions.

[13] Also practical limitations influence this choice: fMRI scanning costs hundreds of Euros per hour and measurements take time because researchers can generally invite only one participant at a time.

[14] Some people might report e.g. 'tingling' or 'tapping' sensations due to harmless peripheral nerve stimulation.

the data that are caused by head movements of the participants[15]. The pre-processing steps also prepare the data for group-level analysis by fitting the data of individual participants into a common brain coordinate system[16]. Often the last pre-processing step is spatial smoothing that is essential for making the statistical inferences using random field theory.

The actual data processing generally begins with an analysis of each individual participant. The data from each point in space is modeled with a general linear model (GLM), using the expected data patterns as explanatory variables ('regressors'). With this 'first-level' GLM analysis the researcher gains knowledge on the explanatory power of each regressor in each location of the brain. With the help of statistical tests[17], the researcher finds out in which brain locations (or 'voxels', which correspond to three-dimensional pixels) the brain data co-varies with the expected brain activation pattern. A 'second level' of the fMRI data analysis uses summary statistics (contrast images) from the first-level analysis and tests which regressors are statistically significant in a certain brain location across the whole participant group. In practice, the second-level statistics test whether an effect observed in individual participants in a certain location is significant across the group of participants. The principle is similar to the standard statistical tests—the only differences are that the input to the statistical tests originates from the first-level statistics and not directly from the measurement data, and that many similar statistical tests need to be performed (one per voxel). Sometimes the research questions concern also individual differences in the brain activation between participants. If a researcher expects a correlation between the level of brain activation and one or more covariates, such as age, level of education or attitude to risk, the researcher can perform a multiple regression analysis on the second level or include the covariates in other appropriate models.

The statistical inferences in the fMRI analysis are susceptible to the multiple comparisons problem. The multiple comparisons problem arises due to the large number of statistical tests involved—one test per voxel adds up to millions of tests when all voxels within the brain volume are analyzed ('whole

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[15] The data is collected in the coordinate system of the scanner and not relative to the brain. Thus when the head moves the spatial locations in the data and in the brain do not correspond similarly to each other any more.

[16] There are multiple coordinate systems. Most common are Montreal Neurological Institute (MNI) space and Talairach space.

[17] Most often t-test.

brain analysis'). If each of these tests has a false positive rate of 5%, then understandably false positives are extremely likely in a whole fMRI data set. There are multiple ways of correcting for the multiple comparisons problem. A conservative way is to conduct a Bonferroni correction, by dividing the significance level α by the number of tests performed and using this corrected significance level for each individual test. This method is often too conservative for fMRI data sets because the fMRI data sets inherently have some level of spatial correlation, i.e. neighboring voxels are not independent of each other. The appropriate statistical threshold for a data set with spatial correlation can be found by dividing the significance level α by the number of *independent* observations instead of the *number* of tests. That is, the correction should be based on the number of independent data patterns rather than on the number of statistical tests. The lack of knowledge on the number of independent observations in an fMRI data set creates a challenge for this approach. A solution to this problem is to use mathematical random field theory which provides appropriate thresholds for smooth statistical maps[18]. In addition to the voxel-level inferences, the random field theory can also be utilized to cluster-level inferences[19]. For the cluster-level correction the researcher first needs specify an initial threshold to search for activated clusters of voxels (for instance, $Z > 3.1$ which corresponds to an uncorrected p-value of $p < 0.001$ on an individual voxel level). Based on the random field theory, it is possible to calculate the corrected cluster-level p-values taking into account the initial threshold and the size of the cluster. The cluster-level statistics are more sensitive in detecting activations than the voxel-level tests but this increase in sensitivity reduces the localizing power: individual voxels or small clusters may not reach the cluster-level criteria.

The statistical tests are often performed over the whole brain volume, i.e. for each voxel within the brain (whole brain analysis). In these cases the correction of the p-value also concerns the whole brain volume. Sometimes this is not reasonable, because the hypothesis does not concern the whole brain but only a certain brain area. In these situations it is possible to restrict the analysis to the

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[18] Random field theory utilizes a mathematical construct known as the Euler characteristic. Using information on the size, shape and smoothness of the statistical space, one can calculate the expected Euler characteristic for each threshold level. The expected Euler characteristic approximates the corrected p-value, i.e. family-wise error (FWE) rate.

[19] On the level of spatially connected voxels that show similar data pattern.

anatomical location of interest, or a region of interest (ROI). To ensure the validity of the statistical tests, the ROIs need to be defined by literature-based *a priori* hypotheses. It is worth noting that reducing the area of interest also diminishes the multiple comparisons problem and thus improves the statistical power of the test.

Similarly to other research reports, fMRI research should be documented in such a manner that the reader is able to replicate the research based on the given information. A great challenge in fMRI research is to find an appropriate level of reporting to meet the needs of readers. In addition to neuroscientists the papers are of interest to medical doctors, biologists, psychologists, physicists, statisticians, marketeers, and economists. Probably due to the multidisciplinary nature of fMRI research, there has been a great variability in the level of reporting. Recently a discussion on more fixed guidelines for fMRI research has been initiated (Poldrack et al., 2008). The basic guidelines include giving detailed information on the participants, design, data analysis, and statistical results. The statistical results are often reported in data tables that give basic information on the brain activations (name of the anatomical region, coordinates of the location and cluster size) and information on the statistical inference. In general, it is advisable to report p-values that are corrected for the multiple comparisons problem. The corrected p-values can be reported either on the cluster level or on the voxel level. On the voxel level, the value of a suitable distribution variable is also reported, such as T or F scores[20]. Instead of T and F scores, it is also common to report their transforms to Z scores[21]. In addition to the corrected statistical inferences, for completeness researchers often publish also uncorrected results. For instance, researchers may use the uncorrected threshold of $p < 0.001$ for each individual voxel. In these cases there is no quantified control of the multiple comparisons problem and most often the threshold is more liberal than the corrected thresholds.

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[20] Often the highest score (peak value) within the cluster.

[21] The random field theory applies to the Z-score maps so the Z scores are quite informative.

3.3. Limitations and Advantages of fMRI

3.3.1. Limitations

Regardless of its success in cognitive neuroscience, fMRI faces multiple challenges that make it vulnerable to criticism. One drawback of the method is that the current technical restrictions for the experimental set-up (Section 3.2.2) steer the experimental conditions away from naturalistic situations. This is particularly challenging for experiments studying social decision making that requires direct interaction and communication with other people. Previously this problem has been solved by having one person outside the MRI scanner communicating with the fMRI participants through a computer interface (Rilling et al., 2002), by collecting opponent's responses prior to the fMRI scanning (Halko, Hlushchuk, Hari, & Schurmann, 2009), or by providing artificial responses to the fMRI participant as opponent responses (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). With two MRI machines it is also possible to record the brain activations of two interacting participants (King-Casas et al., 2005). One might argue that the environmental limitations in the MRI scanner are always particularly impactful when studying higher-level cognitive functions, such as decision-making processes. Inevitably studies with the current fMRI set-up cannot reach similar degree of generalizability than field experiments, but their external validity might be reasonably similar to traditional laboratory experiments. The MRI surroundings do include more distracting factors than normal laboratory conditions, such as high acoustic background noise during measurements and restricted body movement, but on the positive side all of these distractions occur similarly during each experimental condition, decreasing the likelihood that the experimental effects are driven by these external factors. In fact, it could even be argued that in an unnatural way the constant distractions in the fMRI setting simulate the continuous stream of task-irrelevant stimulation which surrounds decision-makers outside the behavioral laboratories.

In addition to the limited generalizability, fMRI research is also challenged in its internal validity. In its typical form, fMRI research is correlative, and it indicates the brain regions that show design specific fluctuations but it does not imply a direct causal link between activity in the brain region and behavior. The interpretation of neuroimaging results also requires caution when inferring mental states or cognitive processes based on observed brain-activation patterns.

The inverse inference problem in fMRI research arises from poor functional specificity of brain regions to cognitive functions (Poldrack, 2006). Even though one particular brain area might be consistently activated in a certain cognitive task, the same brain areas might also be involved in other cognitive processes and tasks. For instance, even though the amygdala and insula are often found to process experienced and anticipated negative emotions, it might be misleading to imply that amygdala or insula activity is specific to negative emotions per se as parts of these structures can also be activated by positive events and emotions (Baxter & Murray, 2002; Craig, 2009). This limited functional specificity in contemporary fMRI research restricts the possibilities of inferring the mental state of decision-makers based on their brain activities[22]. This inverse inference problem should be kept in mind especially in neuroeconomics, where the temptation to draw conclusions on the mental states of decision-makers is high.

The interpretation of fMRI results is also complicated by the lack of an absolute measure for the brain activity. Standard fMRI methods only register relative changes in the activation levels (or blood flow). This leads to the need for relative comparisons and to interpretation issues, such as whether a difference between conditions is caused by increased activity in one condition or decreased activity in another. For instance, if a study design includes trials where participants win money and trials where they lose money, significant brain activation in win > loss contrast can be due to increasing brain activation during the win trials or due to decreasing activation during the loss trials. Also a direct comparison of activity levels between different brain regions is challenged by the lack of an absolute measure of brain activity in fMRI. Answering questions such as “which one of these regions is more activated by the stimuli?” are confounded by the lack of a common reference signal in the brain regions and by the fact that the vascular properties of the brain regions can differ, causing varying fMRI signal strengths with equivalent increases in the activation levels.

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[22] Inverse inference problem can potentially be decreased with time when the understanding of the function of each brain region increases with more fine-grained spatial resolution. Methods that provide better spatial resolution, such as single cell recordings in animal studies, are currently very useful tools for studying the functional specificity of brain regions.

3.3.2. Advantages of Neuroimaging over Behavioral Methods

The questions asked in this dissertation concern mainly the cognitive processes that underlie context and history effects in choice sequences. Considering the previously discussed difficulties in interpreting brain imaging findings, in particular the inverse inference problem, it is quite obvious that the high-level implications based on neuroscientific data are currently speculative and debatable. Even though neuroscience cannot currently provide conclusive evidence on the causes of behavioral biases in human decision making, the implications of the studies can later be tested and verified, or rejected, by behavioral studies[23]. One of the strengths of using neuroscience in studying decision behavior is that it enables a more exploratory approach to the processes that underlie the behavioral anomalies than more traditional behavioral methods. This process-level information can give valuable suggestions for interesting directions for future research, which potentially reduces the amount of trial and error in behavioral research. That is, the interpretations of the brain data can function as a guide to interesting new research questions. Furthermore, when developing theoretical accounts to forecast individual choice behavior, understanding the biological processes that create the behavior might improve the predictive power of the models both in previously tested and in novel contexts (Clithero, et al., 2008).

3.3.3. Advantages of fMRI over Other Neuroscientific Methods

From the vast range of neuroscientific research methods, fMRI is currently the most common choice in neuroeconomics when studying human participants. In comparison to other available methods[24], fMRI provides a combination of good spatial coverage and specificity as well as sufficient temporal precision[25]. Methods that register the electromagnetic fields caused by electrical signaling in the brain (EEG and MEG) provide much better time resolution in comparison to fMRI but those methods are poor in spatial localization, and they mainly provide information from the cortical (surface) layers of the brain. Nevertheless, most

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[23] Delgado, Schotter, Ozbay, & Phelps (2008) provide an example how understanding of the neural system can help in developing behavioral hypothesis and economical theory.

[24] See also Section 2.2.

[25] fMRI is also radiation-free, unlike some earlier methods that provide suitable spatial and temporal resolution. For instance, positron emission tomography exposes participants to ionizing radiation.

neuromarketing companies use currently EEG, due to its suitability for commercial analysis (high time resolution), and more flexible and natural experimental conditions. One promising new technology, fast optical imaging, combines some of the positive aspects of fMRI and electromagnetic measurements—fast optical imaging reaches similar spatial resolution to fMRI and similar temporal resolution to EEG and MEG. However, optical measurements are spatially restricted to the surface layers of the brain[26], and thus they cannot be used when studying deep brain structures. This is problematic for neuroeconomics, since many interesting brain structures, such as large parts of the reward circuitry, are located more centrally in the brain. Valuable information on neuroeconomics has been achieved by observing the behavior of patients with brain lesions (for instance Bechara, et al., 1997; Clark et al., 2008; De Martino, et al., 2010; Shiv, Loewenstein, Bechara, Damasio, & Damasio, 2005; Weller, Levin, Shiv, & Bechara, 2007), and by disrupting selected brain regions with magnetic or electric pulses (e.g. Fecteau et al., 2007; Klucharev, Munneke, Smidts, & Fernández, 2011; Knoch, et al., 2006). The advantage of these research methods is that they provide strong evidence on the causality between selected brain regions and behavior, but on the other hand these methods provide information only on a very limited number of brain sites, especially in comparison to fMRI that can provide whole brain coverage.

This dissertation reports studies that utilize fMRI methodology. fMRI is selected as the most suitable neuroscientific research tool based on the requirements set by the research questions. The questions that are asked in this dissertation are exploratory, aiming to test which type of processes underlie temporal and context dependencies in decision making. The questions do not make strong statements about the causal relations between a certain brain region and behavior (where lesion studies and/or electromagnetic stimulators would be most suitable) but instead suggest that multiple brain regions might be involved in a particular behavioral phenomenon. Furthermore, some of these regions of interest are located more centrally in the brain, which limits the possibility of using EEG, MEG and fast optical imaging that might otherwise be suitable, due to their superb temporal resolution. In sum, fMRI is best suited for the research

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[26] Optical imaging does not reach deeper than 3 cm below the head surface (Gratton & Fabiani, 2010).

questions in this dissertation that require exploration of brain activation patterns simultaneously in large portions of the brain.

3.4. Summary

This chapter discussed fMRI as a tool in neuroeconomics and described the central limitations and advantages of using fMRI. When comparing fMRI to other neuroscientific methods, fMRI provides a good compromise between brain coverage, spatial and temporal accuracy. The weaknesses of fMRI include the indirect way of measuring the brain activations (relies on blood flow changes) and correlative nature of the data. Also the measurement conditions in the contemporary fMRI scanners are much more restricted than in standard behavioral laboratories, and, due to noisy data, multiple within-subject repetitions of each condition are most often needed. In general, the interpretation of neuroscience findings has been criticized for the inverse inference problem: due to the lack of one-to-one mapping between brain regions and cognitive functions, it is not possible to infer mental states from neuroimaging data with certainty. Regardless, due to the possibilities of measuring signal changes from the whole brain, fMRI is a useful tool for exploring the biological mechanisms that underlie choice behavior. Even though the interpretation of these biological changes might be debatable, the neuroimaging data does objectively inform us of the reactions related to the experimental setting and of the brain processes that occur during decision making. These explorative findings, in turn, can motivate and guide future research.

Part II

Sequential Risky Choice

Chapter 4

Path Dependence in Risky Choice: Affective and Deliberative Processes in Brain and Behavior

Abstract

Decision-makers show increased risk appetite both when they gamble with previously won money, the house money effect, and when they have a chance to win back a prior loss, the break even effect. To study the origin of these well-documented effects, we use functional magnetic resonance imaging to record the brain activities of decision-makers, while they make sequential risky choices. Our behavioral data indicates that the two behavioral effects are persistent in a within-subject design in spite of many repetitions and the short timeframe required for neuroimaging experiments. Our brain data shows that the path dependence of risk attitudes is closely related to increases in affective mechanisms and decreases in deliberative brain networks. Moreover, in between-subject analyses, the strength of activation in these two brain networks explains the strength of both the house money and the break even effect. Interestingly, we also find that from gain/loss experience to subsequent choice, affective and deliberative processes appear to follow different time dynamics. This research illustrates how modern neuroimaging techniques can currently be utilized in behavioral economics and what kind of insights the neuroscientific research can provide for further exploration of path dependency.

4.1. Introduction

Over the past 25 years or so, behavioral experiments have convincingly demonstrated that the risk attitudes of decision-makers are often influenced by the outcomes of previous choices, indicating path dependence in choice behavior. Most notably, Thaler and Johnson (1990) show that decision-makers tend to take more risk if they have a chance to win back a prior loss, i.e., the decision-maker is willing to accept higher risks than she would otherwise do, in order to restore her previous level of wealth, also known as the 'break even effect' (BEE). Similarly, the decision-maker also has a greater risk appetite after experiencing a gain that is large enough to cover the potential losses in the current risky prospect ('house money effect', HME). As an example, reconsider the earlier scenario where a consumer was playing at a casino. After winning some money, she continued taking high risks with the money she had just won, because she felt that the money was not hers to begin with. It was casino's money, 'house money'.

Prior research indicates that path dependence of risk attitude is pervasive also outside the behavioral laboratory, and with large monetary stakes. For example, horse race gamblers display an increasing propensity to bet on long shots at the end of the racing day, presumably in an attempt to recover earlier losses (McGlothlin, 1956). Similarly, Chicago Board of Trade proprietary traders display a greater risk appetite in afternoon trading sessions after morning losses (Coval & Shumway, 2005)[27]. Moreover, Barberis, Huang, & Santos (2001) show that path-dependency can have a large effect on asset returns. The increase in risk appetite after a history of gain and loss experiences is also observed in the behavior of contestants in the popular TV game show "Deal or No Deal", where contestants make a series of choices over time between cashing out with a certain lump sum, or by taking a risk to continue playing the game, with uncertain consequences (Post, van den Assem, Baltussen, & Thaler, 2008). Another recent paper studying the behavior of online poker players indicates that the path dependence in risky choice extends to gaming situations where decision-makers are experts in the domain. Specifically, the study shows that experienced poker players have an increased level of risk appetite after big losses (Smith, Levere, & Kurtzman, 2009).

The present research uses an exploratory approach to study the mechanisms that underlie these behavioral anomalies. By employing modern neuroimaging techniques, we aim to provide a starting point for constructing a biologically plausible model of the processes that are driving the HME and BEE. By increasing our understanding of the mechanisms behind behavioral patterns, it

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[27] Locke & Mann (2009) find the same behavioral effect in the Chicago Mercantile Exchange but they challenge the interpretation and hypothesize that the effect is due to improvements in work-effort in order to reach a daily income target.

will be possible in the long run to provide more accurate forecasts of behavior in both existing and novel contexts. Furthermore, process-level understanding of these choice phenomena can explain behavioral differences between decision-makers, thus allowing more detailed predictions of individual behavior (Clithero, et al., 2008).

We design a within-subject experiment that aims to capture both the HME and the BEE, while controlling for all potential confounds in the choice problems and employing large real incentives. On the process level, we expect that gain and loss experiences induce an increase in affective mechanisms and a decrease in deliberative processes, and that these brain responses drive both the HME and the BEE. To test this hypothesis we use functional magnetic resonance imaging (fMRI) to record the brain activities of decision-makers while they make sequential choices. We also aim to disentangle the time dynamics of these two processes at different stages of sequential choices. Specifically, we examine the role of affective and deliberative processes when decision-makers are informed of an outcome, and further, how active these processes are when the decision-makers make the subsequent decision. Additionally, we test whether the brain activity can forecast future behavioral choices.

The remainder of this chapter is organized as follows. In Section 4.2 we introduce the theoretical background of path dependence in risky choice and formulate our hypotheses on affective and deliberative brain mechanisms. Section 4.3 describes our neuroimaging experiment. Section 4.4 reports both the behavioral and the neuroimaging results, providing insights into the dynamics of affect and deliberation and how these processes are related to choice behavior. In Section 4.5 we discuss the implications of our findings. Finally, in Section 4.6 we conclude with the final remarks on the contribution of our neuroimaging findings to behavioral economics.

4.2. Path Dependence, Affect and Deliberation

4.2.1. Theoretical Framework

Path dependence in risky choice was first proposed by Kahneman and Tversky (1979) when they introduced prospect theory. One distinguishing feature of the descriptive prospect theory relative to more normative expected utility theory (von Neumann & Morgenstern, 1947) is the reference-dependent valuation of

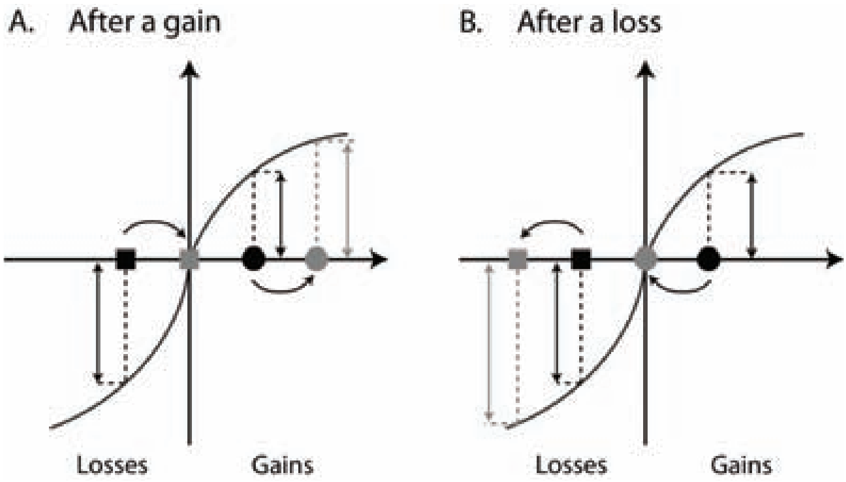

Figure 4-1. Picture presents a coin toss game where participant can win or lose one euro. Black square and circle present the actual prospect; Grey square and circle present the prospect after the integration of a prior outcome. A, Perception of the game following a gain of one euro. If the previous gain is integrated in the prospect, the prospective loss (indicated with the black up-down arrow above 'Losses') 'disappears' while the prospective gain increases (grey up-down arrow vs. black up-down arrow above 'Gains'). B, Similarly after a loss, the prospective loss increases and the gain 'disappears'. Note also that after a loss the participant has a possibility to gain back the loss which provides a larger improvement in value than a gain of one euro.

outcomes. In general, people tend to show moderate risk-averse behavior in the gain domain and risk-seeking behavior in the loss domain (framing effect; Tversky & Kahneman, 1981), as well as relatively strong risk aversion for mixed gambles due to a greater sensitivity to losses than to gains (loss aversion). These behavioral properties are captured in prospect theory by the shape of the value function, with diminishing sensitivity to increments in gains and losses, and also by having a steeper slope for losses than for gains of a similar size.

The increase in risk appetite after both gains and losses can be explained by insufficient adaptation of a reference point after prior outcomes (Kahneman & Tversky, 1979; Thaler & Johnson, 1990). After a positive outcome, when the next prospect contains losses that are smaller than the previous gain, decision-makers may integrate the initial gains with the outcomes of the future prospect, thus decreasing the influence of loss aversion in the future choice (Figure 4-1). After a negative outcome, when only the risky gamble provides a possibility to win back the previous loss ('break even'), decision-makers will integrate their prior losses with the current gamble, thereby promoting the risk-seeking tendency which predominates in the loss domain (Thaler & Johnson, 1990). Therefore, both the HME and the BEE can be interpreted as consequences of the nonlinearities in the value function, which account for loss aversion and domain-dependent risk attitude differences.

In the initial formulation of prospect theory the shape of the value function is assumed to reflect general psychophysical features of chance (Kahneman & Tversky, 1979) but recently the shape of the value function has been hypothesized to be more dynamic. The value function is now proposed to reflect a combined result of affective and deliberate processing systems, with the affective system driving the nonlinearities in valuation and the deliberative system valuing outcomes linearly (Hsee & Rottenstreich, 2004; Mukherjee, 2010). This new model proposes that the shape of the value function can vary depending on how strongly the two systems are involved in the processing of the decision problem. In general, converging evidence suggests that decisions are indeed influenced by an affective system, which is assumed to be fast, effortless, automatic, and associative, as well as by the deliberative system, characterized by slower and more effortful processing (Kahneman, 2003; Sloman, 1996).

The recent dual process expansion of prospect theory is supported by both behavioral and brain imaging findings. Behaviorally, affect-rich stimuli increase the curvature of the value function, which can be accounted for by assuming increasing use of a nonlinear affective processing system (Hsee & Rottenstreich, 2004). Neuroimaging research suggests that framing effects, which also relate to the nonlinear curvature of the value function, are also driven by affective neural processes whereas cognitive control mechanisms are more active when decision-makers act against the common framing biases (De Martino, et al., 2006). Interestingly, the functioning of these brain networks relates to between-subject differences in the strength of behavioral framing effects: A recent study by Roiser et al. (2009) finds that a participant group that exhibits only weak behavioral framing effects has increased connectivity between control and affective brain regions, suggesting the presence of an efficient dynamic regulatory control over the emotional reactions, whereas a participant group exhibiting large behavioral effects has weaker connectivity between the brain networks. These fMRI findings imply that a risky choice situation, without an obvious emotional valence, can evoke emotional processing, which may drive nonlinearities in valuation.

Similarly, loss aversion has been related to affective mechanisms in the brain. An fMRI experiment by Tom et al. (2007) indicates that the valuation mechanisms of the brain have a higher sensitivity to loss than to gain outcomes. Another study by Knutson et al. (2008) suggests that affective reactions in the brain (specifically in the insula) might increase the endowment effect and thus increase aversion for losses in selling situations. Further, patients who have a brain damage in another affect-related brain region (the amygdala) show a dramatically lower level of risk aversion than healthy people (De Martino, et al., 2010).

Given that path dependence in risky choice can be accounted for by nonlinearities in valuation, if we assume insufficient updating of a reference point, and given the recent research suggesting that nonlinearities in valuation might be particularly driven by affective mechanisms, we argue that the path dependence of risky choices is promoted by affective mechanisms, while deliberative mechanisms suppress path-dependent behavior. In detail, we propose that a high involvement of affective processes and a low involvement of deliberative processes in gain and loss experiences underlie path dependence in sequential risky choice[28].

Behavioral research on risk perception and planning provides initial support for this proposition, while also opposing findings have been reported. Monga & Rao (2006) report that positive affect following gain outcomes mediates positive expectations towards future risks and negative affect related to loss

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[28] It is to some degree still an open question as to whether 'affective process' is a unitary system in response to both gains and losses, or whether there is a complex network of affect-related mechanisms that are different for gain and loss situations. Similarly, we consider it an open question whether the 'deliberative process' is truly a single mechanism, or rather an aggregate description for a network of different processes involved in controlling behavior. Additionally, we have no a priori prediction on the timing of the affective and deliberative processes, but instead explore this as an empirical question and also test separately the processes that occur when gains and losses are revealed, and when the subsequent choices are made.

experiences creates more negative expectations, which might lead to risk aversion after losses. Indeed, Sullivan & Kida (1995) find that decision-makers do not show increased risk-seeking attitude after prior losses that could be regained but instead they persist on risk-averse attitude. In contrast, Andrade & Iyer, (2009) provide evidence for increasing risk appetite after negative outcomes. In their experiment, the negative emotion following a loss outcome correlates with increased risk-taking behavior in respect to prior plans of the decision-maker. In detail, the results indicate that the increase in risk appetite after actual losses depends on the strength of the negative emotion experienced during the decision-making process. However, this study does not find any differences in the risk taking behavior in respect to previous plans after gain experiences.

4.2.2. Hypotheses on the Brain Activity Patterns

While the human brain consists of structurally separable brain areas, the functional specificity of a single brain region is not clear-cut. Further, since the different brain regions are heavily connected with each other, a single cognitive process is often performed by a network of interacting brain areas. Here we limit our review to two central neuronal networks that relate to affective processing (the affective salience network) and deliberation (the executive-control system).

Increases in Affective Salience Network with Gains and Losses

The neuroscience literature indicates some specificity to the processing of positive and negative events. The processing of positive events and rewards is closely related to the functioning of the neurotransmitter dopamine. The dopaminergic neurons in the midbrain project to multiple brain areas, such as the striatum and the medial orbitofrontal cortex (mOFC), which are often reported to reflect valuation. For instance, these brain regions are known to activate for the receipt of both primary and secondary rewards, such as drinks (Berns, et al., 2001; Plassmann, et al., 2008) and financial rewards (Delgado, et al., 2003; Knutson, et al., 2000; O'Doherty, et al., 2001; Thut, et al., 1997), and they also reflect the hedonic value of rewards (de Araujo, et al., 2003; Kringelbach, 2005; Plassmann, et al., 2008). In line with the behavioral reference dependence of valuation, the reward circuitry also processes outcomes largely in a reference dependent manner, and a variety of contextual aspects have been shown to influence the evaluation of received outcomes, such as other possible outcomes (Breiter, et al., 2001) and the outcomes of others (Fliessbach, et al., 2007)[29].

Dopamine has an important role in guiding behavior (Schultz & Dickinson, 2000). In general, increased dopamine activity at the time of the receipt of rewards, as reflected in the midbrain and the striatum, reinforces the behaviors that lead to the rewarding outcomes. Indeed, recent neuroscience literature already provides some initial evidence that the reinforcement signals in the dopamine system (or the striatum) are linked to future risky choices (Cohen, 2008; Kuhnen & Knutson, 2005). Thus, based on the role of dopamine both in receipt of rewards and in guiding future behavior, the dopamine system and related brain regions are a good candidate for driving the increases in risk appetite after prior gains.

The negative affective brain mechanisms are less consistent across different studies in neuroscience. Multiple experiments show that the lateral parts of the OFC have increased activity when punishments are received (see Kringelbach, 2005 for a review). In contrast, other studies report that negative monetary outcomes decrease activity in the reward structures, such as the striatum (Tom, et al., 2007), or may even evoke activity in other affective brain structures such as the amygdala or the anterior insula (Kuhnen & Knutson, 2005; Yacubian, et al., 2006). The negatively valenced insula reaction also predicts an increase in risk aversion (Kuhnen & Knutson, 2005), which is suggested to indicate the role of negative affect in guiding future choice behavior.

Though the insula is often related to negative experiences, converging evidence indicates that the anterior insula reflects also positive affective arousal. This reaction in the anterior insula when experiencing subjective emotions co-occurs frequently with emotional parts of the anterior cingulate cortex (ACC). As summarized by Craig (2009), this network is consistently activated in studies that include affective arousal with a vast range of different types of emotions, ranging from love and happiness to anger, disgust, and social exclusion. Similar to other affective brain regions, also the anterior insula and the ACC have been linked to risky decision making in multiple studies, though there is little convergence in the conclusions—while some researchers report a positive correlation between anterior insula activity and safe choices (Campbell-Meiklejohn, Woolrich,

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[29] See Section 2.3 for more detailed information.

Passingham, & Rogers, 2008; Knutson & Bossaerts, 2007; Liu et al., 2007), others find a negative correlation (Clark, Lawrence, Astley-Jones, & Gray, 2009; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Platt & Huettel, 2008; Xue, Lu, Levin, & Bechara, 2010). For the ACC the results seem to be more consistent, pointing towards positive correlation between activity level and risky choices (Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009; Cohen, Heller, & Ranganath, 2005).

Earlier we proposed that high involvement of affective processes increases path dependence in risky choice, and that the affective reaction related to gains and losses increases risk appetite. Based on the review of the neuroscience literature on affective brain mechanisms, we form the following hypotheses:

> Hypothesis 1a: The affect-related, interconnected affective salience network, consisting of the midbrain, striatum, insula, parts of ACC, thalamus, and amygdala (Seeley et al., 2007), has stronger activity when experiencing gains and losses than when the outcome is relatively neutral.
>
> Hypothesis 1b: The activity in the affective salience network correlates positively with risky choices.

Decreases in Executive-Control Mechanisms with Gains and Losses

The brain has an interconnected network of brain regions that exert control over behavior. This network, including brain areas such as the dorsolateral prefrontal cortex (DLPFC), the ventrolateral prefrontal cortex (VLPFC), and lateral parietal cortices (Seeley, et al., 2007), is related to multiple controlling actions, ranging from inhibiting the execution of planed motor responses (Liddle, Kiehl, & Smith, 2001) to exerting self-control over dietary choices (Hare, Camerer, & Rangel, 2009). Previous research in neuroeconomics indicates the relevance of this network for controlling risky choices. For instance, Campbell-Meiklejohn et al. (2008) report increased activity in the parietal cortices when people decide to stop the risky behavior of chasing previous losses, thus indicating the role of the control network for increasing risk aversion in behavior. Moreover, two recent experiments show the causal relation between the right DLPFC and decreasing risk appetite. Knoch et al. (2006) temporarily block brain activity in the right DLPFC by using magnetic field pulses (transcranial magnetic stimulation, TMS). This disruption in the activity of the right DLPFC leads to a decreasing number of safe choices in comparison to a control group with intact activity in the right DLPFC. Fecteau et al. (2007) enhance the activity in the right DLPFC by using direct current stimulation technique, which lead to an increasing amount of safe choices.

In line with the second part of our proposition, we ask whether gain and loss experiences are related to decreased level of deliberative processes relative to more neutral outcomes and whether this decrease in deliberate processes is related to stronger path dependence in risky choices. In other words, we expect to see more activity in the executive-control network after neutral outcomes than when gains and losses are experienced. Hence, we form the following hypotheses:

> Hypothesis 2a: The deliberation-related, interconnected executive-control network, consisting of DLPFC, VLPFC, and lateral parietal cortices (including intraparietal lobule), has stronger activity related to neutral outcomes than when experiencing gains and losses.
>
> Hypothesis 2b: The activity in the executive-control mechanisms correlates positively with safe choices.

4.3. Experimental Setup

In order to conduct an investigation of the processes that underlie path dependence in choice behavior, we utilize fMRI methodology to record brain activity of decision-makers while they engage in risky choice situations (see Chapter 3 for details on the method).

4.3.1. Experimental Design

We developed an fMRI compatible sequential choice paradigm based on previous behavioral research by Post et al. (2008). In our paradigm the decision-makers do not experience actual gains and losses, but rather they experience relative changes in the expected value of a previously chosen prospect by means of an elimination of one prize option from the prospect. As growing literature suggests that reference points for gains and losses are expectation-based (Koszegi & Rabin, 2006; Koszegi & Rabin, 2007), we assume that once participants are initially endowed with a prospect, any changes (i.e. prize eliminations) in this prospect will be evaluated relative to the initial prospect. Based on previous research by Post et al., we expect that this type of relative changes and clear path dependence in risky prospects promote increases in risk appetite after relative gain and loss experiences, i.e. the HME and the BEE, respectively.

In detail, the participant's task was to choose between risky lotteries (risky choice: L) and 'sure-thing' amounts of money (offer choice: O) in the fMRI scanner. Each sequential choice problem (*trial*) consisted of either one or two choice stages depending on participants' behavior (Figure 4-2A). In the first stage of a trial, participants chose between a three-prize lottery and a riskless offer. An offer choice aborted the trial, with the participant proceeding to a new trial, while a risky lottery choice was followed by a random removal of one prize from the three-prize lottery. To increase participants' awareness that one of the prizes is removed from the lottery, they were asked to indicate one of three numbered pictures of identical briefcases, knowing that a randomly assigned and hidden prize inside will be removed from the lottery (33% chance of removing each prize). In the following outcome phase, participants were informed which prize was removed and which two prizes were still remaining in the lottery. After the outcome screen, participants entered a second choice stage where they chose between the reduced two-prize lottery and a new 'sure-thing' offer. Participants were not informed about the outcome of the two-prize lottery to avoid carry-over effects between the choice problems. At the end of the experiment, one of the planned 108 trials (participants may have repeated some trials twice, see below) was randomly selected and participants were paid the monetary outcome of that trial (on average 46 Euros). If the selected game had ended with a lottery choice on the second stage, the final outcome was resolved with a dice.

The choice problems were designed so that participants faced a set of 24 different lottery-offer pairs in the second choice stage three times, with each pair occurring in three different conditions (*trials of interest*; Figure 4-2B): once after a previously experienced gain (smallest prize removed), once after a neutral outcome (middle prize removed), and once after a loss (largest prize removed). Thus, this design enabled the comparison of choices between a two-prize lottery and an offer that were identical in numerical value, but which had different historical paths. The prizes in the three-prize lotteries varied from 1 Euro to 116 Euros, with the smallest and largest prize differing by 12 to 56 Euros. The middle prize was always equal to the expected value of the prospect. In addition to the

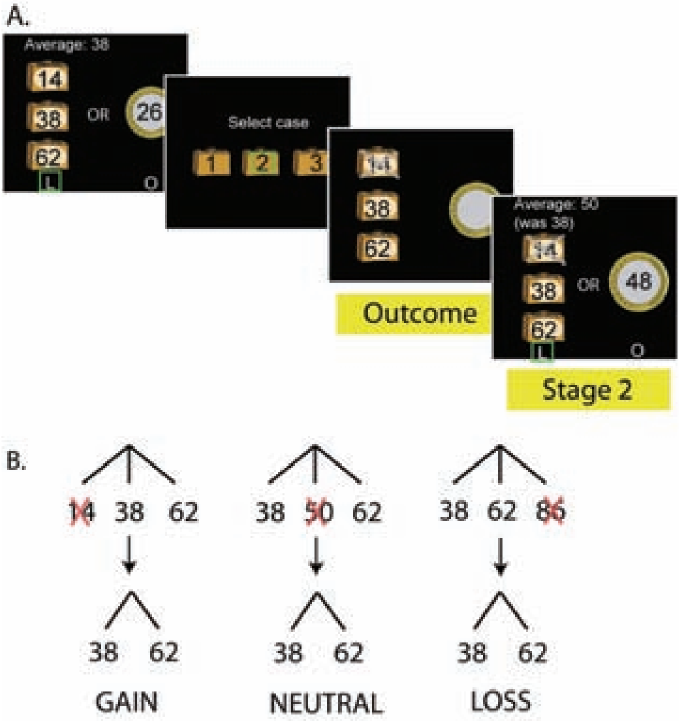

Figure 4-2. Sequential choice paradigm. A. After choosing the three-prize lottery (L) participants proceed to the random removal of one prize from the lottery. In the outcome phase participants learn which prize is removed from the lottery and thereafter they proceed to the second choice stage. In the data analysis we concentrate on brain activities that occur during the outcome screen and the second choice stage, and on the behavioral choices that are made on the second choice stage. B. The design enables the comparison of identical choices in the second choice stage. The conditions differ only in outcome history: gain, neutral or loss outcome. Each of the 24 different two-prize lottery–offer pairs is employed once after each type of outcome.

choice problems that were matched on the second stage lottery-offer pairs, the experiment also included 36 filler choices in order to keep the probabilities at the prize-elimination stage unbiased.

The offer amounts were set in the first choice stage to be considerably below the expected value of the lottery so that participants were encouraged to select the lottery and therefore would frequently proceed to the prize removal and second choice stage. To ascertain that the first stage choices were not trivial to an individual participant, the offers were dynamically adjusted to be as high as possible so that the participant still more frequently selected the lottery. If a participant aborted a trial of interest in the first choice stage by selecting the fixed offer, that trial was repeated once at the end of the experiment with a lower riskless alternative. The offers for the second stage choices were set at a level where an average participant would be indifferent between the lottery and the offer. The certainty equivalents of the lotteries were based on results from independent pretests with 20 participants. However, for some fMRI participants, these estimates did not work well. To avoid ceiling and floor effects in the second stage choice data, we excluded participants that gave less than 10% of lottery or offer answers on the trials of interest across all conditions (five participants did not pass this criterion). In 12 trials the offer amounts in the choice stages were manipulated to be either extremely low or extremely high in order to ensure that the participants kept paying attention to the trials. If participants were not successful in detecting at least half of these catch trials, they were excluded from further analysis (four people did not pass this criterion, one of whom also chose the same option too frequently in the second stage choice).

Prior to the scanning, participants read written instructions on the task, had a training session of ~7.5 minutes outside the scanner, and an additional short training session inside the scanner. The experimental trials were divided into two ~25-minute fMRI scanning sessions[30] that were separated by a ~5 minute break outside the fMRI scanner. The stimuli were presented with Presentation software (Neurobehavioral Systems). The choice problems were separated from each other by a jittered 4-5 second delay period. In the choice stages participants had 5.5 seconds to respond (after a forced delay of 1.5 seconds), using one of two response buttons (left for the lottery and right for offer choice). Participants had 2.5 seconds

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[30] The technical details of the fMRI data acquisition are described in Appendix 4.A.

to use one of three buttons to indicate which of the randomly hidden prize was to be removed from the lottery (Figure 4-2A). The evaluation screen was shown for 4 seconds, and it was separated from the other screens by jittered 1-2 second delay periods. These jittered time periods are necessary to disentangle the brain activities related to the outcome phase from the activities that are induced by the choice stages.

4.3.2. Participants

Twenty-nine healthy students from the local universities participated in the study. Ten participants were excluded from the analysis due to the following reasons: participant did not complete a sufficient amount of choices in an experimental condition for fMRI analysis, i.e., less than 12 successful repetitions of a condition (1 participant), technical problems during scanning (1 participant), a high bias towards risky or safe choices (5 participants[31]), and lack of attention (3 participants). A group of 19 participants (9 males; mean age, 22.1 years; SD 2.2) were included in the actual analysis. Additionally, one participant was partially excluded from the behavioral analysis (see Section 4.4.1).

4.4. Results

4.4.1. Behavioral Results

We model the behavior in the second choice stage by comparing sets of decision problems where the lottery-offer pairs are matched across conditions (same set of options after a prior gain, neutral, and loss outcome; Figure 4-2). Thus, we are able to measure how prior outcome history influences the risk attitude on the next choice independently from other variables in the choice problem. The data is modeled with a mixed logit model (a generalized linear mixed model for binomially distributed data; Jaeger, 2008). The explanatory variables included in the model are history, expected value, and risk (modeled as standard deviation / EV). The participants are treated as a random effect with varying intercept and effect sizes. Prior to running the generalized mixed linear model on the data, we excluded one outlier participant from the analysis, who rarely selected the lottery on the second stage across all trials (15% of the time) and never after a loss. The

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[31] One participant also showed insufficient attention on the task.

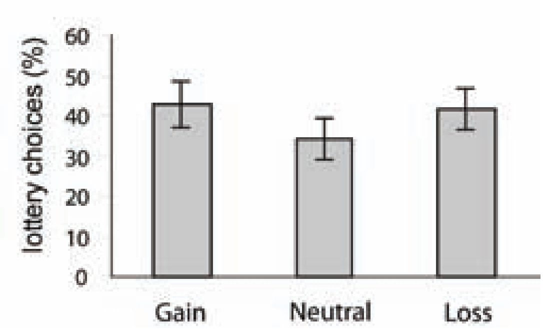

Figure 4-3. Percentage of lottery choices after each type of outcome history (including all 19 participants). The error bars depict the standard errors of the means.

inclusion of this participant in the model would cause an artificial increase in the estimate of variability in the BEE across participants. For HME estimates, there were no such outliers. To ensure that leaving out this one participant does not cause drastic effects on our analysis, we also compute another model containing all participants without the random slope in the model (i.e. fixed effects assumed for the history effects). The results of this analysis are very comparable to those reported below[32].

In agreement with the HME, participants' risk-appetite increases when the lowest prize is removed from the lottery, as compared to the removal of the intermediate prize, i.e., the amount of lottery choices increase significantly after a gain experience ($\beta = .45$; $z = 2.13$; $p = .034$). In addition, and in line with the BEE, we find a significant increase in lottery choices after the removal of the highest prize, again as compared to the removal of the intermediate prize ($\beta = .49$; $z = 2.15$; $p = .032$). Overall, the results indicate that gain and loss experiences, induced by

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[32] The conclusions on the behavioral data remain similar also when the data is analyzed with repeated measures ANOVA, probit model or structural equation model either including all trials with non-biased choices or matched trials-of-interest. Further evidence for the dependencies between the two choice stages is provided by prospect theory based analysis that indicates insufficient adaptation of the reference point after prior outcomes. Of all these additional models the linear probit model provides the best fit of the behavior data for 17 out of 19 participants. This supports the use of linear models also in the analysis of the fMRI data.

the removal of a prize from a lottery, increase risk-appetite in the future choices, in accordance with the house money and break even effect (Figure 4-3). We also tested whether there was a difference in the number of lottery choices between gain and loss experiences, but this comparison did not yield any significant results. The expected value and risk also do not significantly explain the choice behavior of the participants. Importantly, the current design allows for the induction of the HME and the BEE within-subject, which also enables the measurement of individual effect sizes for both behavioral biases.

4.4.2. fMRI Results: Outcome Phase[33]

To test whether the elimination of a prize from the initial three-prize lottery (leading to gain, neutral, and loss experiences) evokes activity in the affective salience and executive control networks of the brain, which potentially underlies the increase risk appetite after relative gains and losses, we compare the brain activities during the gain and loss experiences to those that occur during the more neutral outcomes. Note that in our setup the remaining lottery prizes are matched between the conditions (gain, neutral, and loss outcome), implying that reported brain activities are independent of EV and risk. Table 4-1 shows the results and the statistical details of all the contrasts in the outcome phase. The table provides statistical information on the significance of the activations both on a cluster level (strength and extent of the activation) and on a single voxel (measurement point in the brain) level. All clusters reported in the table are significant on the cluster level. The p-values are corrected for multiple comparisons problem by using random field theory. The table also reports peak coordinates indicating the location of the most strongly activated voxels in MNI coordinates.

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[33] Details of the fMRI data analysis are described in Appendix 4.B. Though not necessary for the understanding of the results, the appendix may be informative for those readers who are familiar with the fMRI method or who want to learn more in detail how the data is modeled in this experiment.

Table 4-1. Activated brain areas in the outcome phase.

Anatomical region	Cluster-level		Voxel-level		Peak coordinates			
	Cluster size	p (corr)	Z	p (corr)	x	y	z	
Gain > Neutral								
ACC	3715	0.000	5.85	0.000	-4	40	4	
L anterior insula	397	0.000	5.31	0.005	-32	20	-16	
R anterior insula	802	0.000	5.22	0.008	32	18	-16	
Midbrain, striatum, globus pallidus	564	0.000	5.93	0.013	8	-12	-12	
Loss > Neutral								
ACC	254	0.005	4.03	0.612	-2	38	4	
L anterior insula	189	0.021	4.05	0.586	-34	26	-12	
R anterior insula	155	0.046	4.14	0.478	34	18	-16	
L anterior insula	56	0.020	4.24	0.009	-36	8	0	+
Gain > Neutral & Loss > Neutral								
ACC	220	0.010	4.03	0.612	-2	38	4	
L anterior insula	156	0.044	4.05	0.586	-34	26	-12	
R anterior insula	70	0.013	4.14	0.013	34	18	-16	+
Neutral > Gain								
left IPL	130	0.013	4.30	0.049	-32	-48	40	+
right IPL	82	0.0496	4.28	0.052	44	-40	54	+
Neutral > Loss								
left IPL	1570	0.000	5.79	0.000	-16	-56	50	
right IPL	827	0.000	5.03	0.018	44	-40	54	
dorsal striatum	172	0.030	4.60	0.109	-14	22	8	
right DLPFC	242	0.006	4.21	0.392	58	14	38	
Occipital gyrus	348	0.001	4.26	0.349	30	-92	0	
Paracentral lobule	742	0.000	5.19	0.009	16	-32	62	
Precuneus	224	0.009	3.96	0.703	28	-68	38	
Neutral > Gain in areas activated by Neutral > Loss								
left IPL	130	0.003	4.30	0.009	-32	-48	40	+
right IPL	82	0.011	4.28	0.009	44	-40	54	+
dorsal striatum	64	0.019	4.24	0.011	-14	22	6	+

+ Significant only in ROI analysis (statistics from the ROI analysis; see Appendix 4.B.)

Increases in Affective Salience Network for Gains and Losses (Hypothesis 1)

We first test whether gain and loss experiences induce higher activity levels in the affective salience mechanisms than the neutral outcomes (Gain > Neutral). When we compare the differential activations between gain and neutral outcomes we find increased activity levels for gain outcomes in the left and right anterior insula, ACC, and in a cluster including parts of the striatum, midbrain, globus pallidus and amygdala. Hence, we find activity in the network of brain regions that has previously been related to affective processing.

Next, we test which brain areas have higher activity during loss outcomes than neutral outcomes (Loss > Neutral). We find significant activity in the left and right anterior insula and the ACC. Strikingly, these activated regions overlap with bilateral anterior insula and ACC activations that are observed in the gain versus neutral comparison: indeed, a strict conjunction analysis indicates that overlapping parts of the left and right anterior insula and the ACC are significantly activated in both contrasts (Gain > Neutral & Loss > Neutral), as shown in Figure 4-4. In line with our Hypothesis 1a, we find that gain and loss outcomes evoke activity in the affective salience network. Further, our data indicates that the affective mechanisms evoked by the two outcomes are partially overlapping.

Next, we test whether the activity in this common affective salience network during gain and loss experiences predicts the future lottery choices, as stated in Hypothesis 1b. To do this we categorize the trials into lottery and offer trials based on the choices made in the second choice stage, and extract the average data of each cluster for these trial types from the outcome phase which precedes the decision-making stage. The analysis indicates that the ACC has a significantly higher level of activity during the outcome phase of the task in trials where participants later on select a lottery than when they select a 'sure-thing' offer, as shown in Figure 4-4B. Thus, the ACC shows increased activity levels during gain and losses experiences, with this increased activity predicting subsequent lottery choices and hence increases in risk appetite. These results indicate that the ACC may be driving the behaviorally observed HME and BEE. In contrast, the activation cluster in the midbrain/striatum does not significantly predict future lottery choices ($p = 0.18$, n.s.), nor does the anterior insula ($p = 0.69$, $p = 0.84$ for left and right sides respectively).

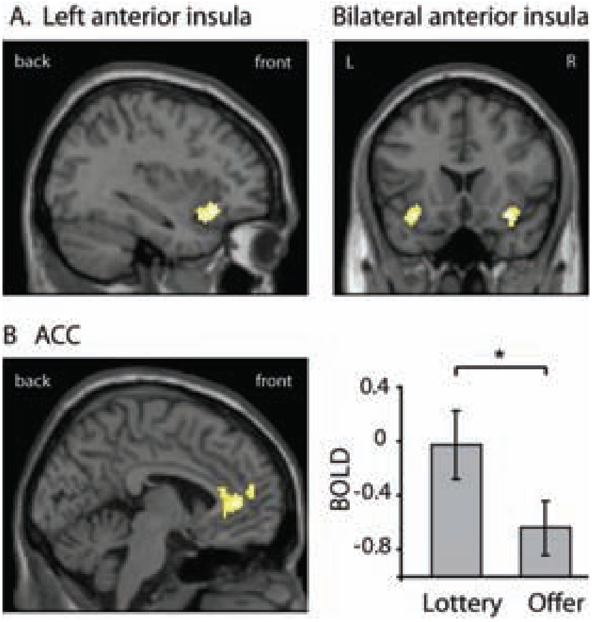

Figure 4-4. Affective salience network, consisting of the left and right (bilateral) anterior insula (A) and the ACC (B), activates for both gains and losses. B, The average activity of the ACC cluster is significantly higher for subsequent lottery choices than for offer choices. Note that at this time point participants know only the lottery option and not the riskless alternative of the following choice, thus this predictive activity for lottery choices is purely based on the evaluation of the lottery and the changes in it. * $p < 0.05$.

Decreases in Executive Control Network for Gains and Losses (Hypothesis 2)

We hypothesized that gain and loss experiences are associated with a decreased amount of activity in the executive control network relative to neutral outcomes. In other words, we expect that the neutral outcome has higher level of activity in the executive control regions than the gain and loss outcomes. First, relative to gain outcomes, the neutral outcomes (Table 4-1; Neutral > Gain) evoke higher activity in both the left and right intraparietal lobule (IPL; part of parietal cortices that are related to control). Second, when comparing neutral outcomes to loss

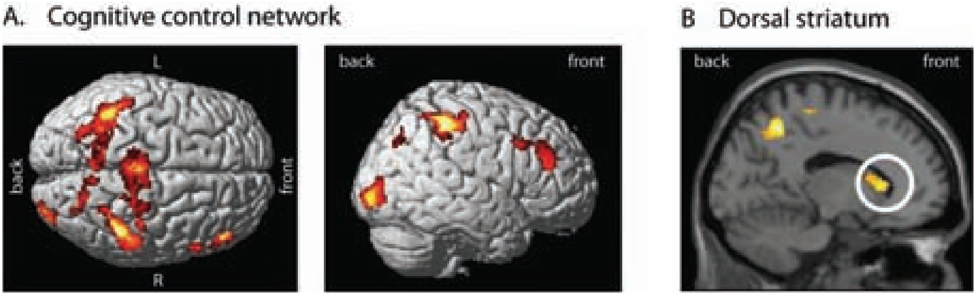

Figure 4-5. A, During neutral outcomes activity in the parietal cortices and in the right DLPFC increases relative to loss outcomes, reflecting the increasing executive control. B, Also the dorsal striatum is more activated for neutral outcomes than for losses.

outcomes (Neutral > Loss), we also find activity in the executive control network for the neutral outcomes (Figure 4-5A). More specifically, we find activation in the parietal cortices, including the left and right IPL, and in the right DLPFC. Additionally, we find increased activity in the dorsal striatum (Figure 4-5B) and in the occipital lobe. The activity in the occipital lobe (visual processing) may reflect the differences in the visual screens (even though it did not reach statistical significance in other comparisons regardless of similar differences in the screens), whereas the increased striatum activity may reflect satisfaction of receiving the neutral outcome relative to the loss outcome.

To test whether there is a network of brain areas that is specifically activated for neutral outcomes, we perform a region of interest analysis by testing whether the neutral outcome has higher activation than the gain outcome within those regions that are active in the neutral versus loss contrast (Neutral > Gain in areas activated by Neutral > Loss)[34]. Indeed, we find that the left and right IPL, and also the dorsal striatum, are significantly activated in this analysis, indicating that this set of regions has higher activity during neutral experiences when compared to both gains and losses. Consistent with Hypothesis 2a, we find increased activity in the executive-control network for neutral outcomes relative to both gain and loss outcomes. The striatum activity may relate to the expectation of

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[34] This test is less conservative than a strict conjunction analysis.

choosing, and receiving, a 'sure-thing' amount of money in the following choice stage, as the striatum is known to show anticipatory activity for future rewards.

Next, we test whether the activity in this executive control network predicts future sure-thing offer choices similarly to the analysis in the affective salience network (Hypothesis 2b). All the parietal clusters, besides for the left IPL that is activated in the neutral versus gain contrast ($p = 0.18$), show a trend towards having higher activity during the outcome phase when participants later on selected an offer than when they selected a lottery ($p < 0.10$). This suggests that high activity level in the cognitive control regions, which are more active during neutral outcomes than gain and loss outcomes, might be promoting future offer choices.

4.4.3. fMRI Results: Second Choice Stage

Next, we compare the brain activations after gain, neutral, and loss outcomes during the phase when the second-stage choices are actually made, and test our two hypotheses in this time window. That is, in this phase the decision-makers are already informed of the updated sure-thing choice option, and they are able to select between the sure-thing and the lottery with the remaining two prizes. Recall that the choice problems that participants face are equivalent across the comparisons, and only differ in the prior history of having a gain, neutral or loss experience. Table 4-2 provides an overview of the statistical information on the activated clusters in this time window (statistics reported similarly to Table 4-1).

Affective Salience Network for Choices after Gains and Losses (Hypothesis 1)

To test Hypothesis 1a, we compare the brain activations between choices that have a history of gain/loss and neutral outcomes. When we compare the decision-making stage after prior losses to the stage after a neutral outcome (Loss > Neutral), we find increased activity in the affective part of the ACC in line with our hypothesis. This activation is only slightly overlapping with the activation found in the outcome stage (overlap of 7 voxels based on a region of interest analysis within the activation maps of the outcome phase), indicating that the activity pattern is not similar between the two stages. In contrast to the findings in the outcome stage, the ACC activity does not differentiate between lottery and offer choices ($p = 0.16$), as suggested by Hypothesis 1b. The gain trials do not show any significant increases in activation in comparison to the neutral trials.

Table 4-2. Brain regions that are differentially activated during the decision making phase after prior gain, neutral, and loss outcomes.

Anatomical region	Cluster-level		Voxel-level		Peak coordinates			
	Cluster size	p (corr)	Z	p (corr)	x	y	z	
Loss > Neutral								
ACC	243	0.008	4.06	0.557	6	34	18	
Neutral > Gain								
Occipital	505	0.000	4.59	0.105	-6	-88	20	
left IPL	130	0.015	4.56	0.017	-36	-56	42	+
right IPL	119	0.020	4.38	0.034	34	-54	34	+
Loss > Gain								
Occipital	415	0.000	4.53	0.135	-6	-94	12	
ACC	186	0.027	4.51	0.141	8	34	18	
Right Thalamus	255	0.006	4.49	0.155	14	-18	6	
Left Thalamus	202	0.019	4.37	0.236	-26	-22	4	
Claustrum	228	0.011	4.25	0.334	-38	-4	0	
Insula	334	0.001	4.16	0.440	-48	4	10	
Ventrolateral PFC/ lateral OFC	415	0.000	3.95	0.696	30	58	10	
Superior temporal gyrus	191	0.024	3.91	0.736	58	-42	16	

+ Significant only in ROI analysis (statistics from the ROI analysis)

Executive Control Network for Choices after Gains and Losses (Hypothesis 2)

When we compare the brain activities during decision making after previous neutral and gain outcomes (Neutral > Gain), we find increased activity in the right and left IPL, and in the occipital cortex following neutral outcomes. While the IPL is known to be a part of the executive-control network, the occipital activity most likely reflects slight differences in the visual displays between conditions (history information). In contrast, when we compare the activities between choices following neutral and loss outcomes, we do not find any significant increases in activity for neutral trials. Thus, we find evidence for Hypothesis 2a in the gain

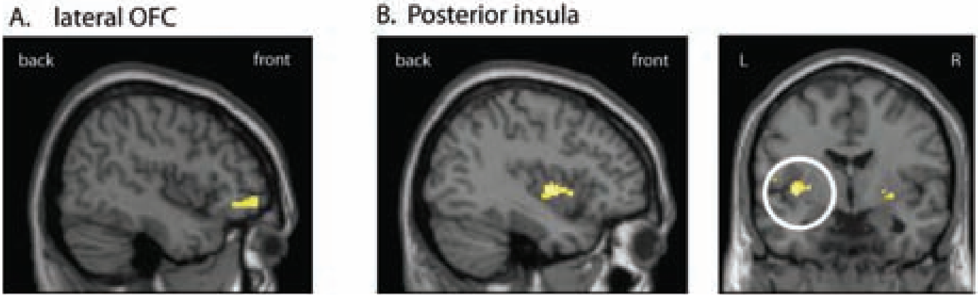

Figure 4-6. A, Differential activations during decision making after loss and gain outcomes. A, The lateral OFC, which is related to negative outcomes, is active after prior losses. B, The insula activates after losses.

trials, but not in the loss trials. When we compare the trials with lottery and offer choices in the activated IPL clusters, we do not find support for Hypothesis 2b.

Since one prior behavioral study indicates the importance of negative emotions during the decision making for increasing risk appetite (Andrade & Iyer, 2009), we also calculate an additional contrast in the decision-making stage. Instead of using the neutral trials as a reference level for loss trials, we compare the loss trials to the gain trials, in order to attain a maximum difference in the emotional valence across the comparison. In this analysis (Loss > Gain), we find increased activity in the affective salience network for loss trials, including the insula, thalamus, and ACC (Figure 4-6). Additionally, we find activity in a cluster that consists of the VLPFC and the lateral OFC. The lateral OFC has previously been related to experiencing negative outcomes (Kringelbach, 2005) while VLPFC is part of the executive control network. The comparison reveals no brain regions that are significantly more active following a gain outcome. In sum, during the decision-making phase, the affective brain regions are particularly strongly active after negative outcomes whereas executive control network shows significantly decreased activity only following positive outcomes. These findings suggest that, after similar affective and deliberative reactions in the outcome phase, the gain and loss trials employ the two mechanisms differentially during the subsequent decision-making phase.

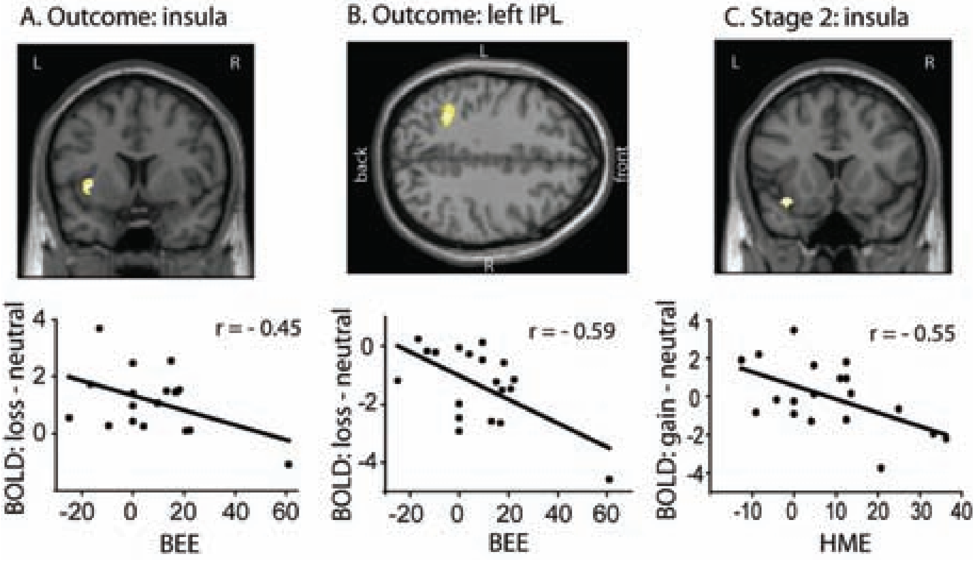

Figure 4-7. Correlations between brain activities and corresponding behavioral measures. The strength of the BEE is measured as the difference in percentage lottery choices after losses and neutral outcomes (loss – neutral). Similarly, the HME is measured as the difference in percentage lottery choices after gains and neutral outcomes (gain – neutral). The correlation in the insula (A) is marginally significant ($p<0.1$) and the other correlations (B, C) are significant at $p<0.05$ (2-tailed).

4.4.4. Brain Activity and Changing Risk Appetite

Overall the results indicate higher levels of affective processing in gain and loss trials than in neutral trials. In contrast, the neutral trials are associated with higher level of executive control activity. Next, we ask whether these affective and executive control networks can explain individual variability in the changes of risk appetite after gains and losses in line with Hypotheses 1b and 2b. To do this, we correlate the average brain activities of the affective and executive control regions with the sizes of corresponding behavioral effects[35]. We restrict our analysis to the

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[35] We measure the effect sizes as percentage changes in the amount of lottery choices between the conditions. The effect sizes could also be estimated with logistic regressions

affective salience and to the executive-control networks that have been activated in the previous analysis.

In the outcome phase, we find that a loss-specific part of the left anterior insula[36] has a marginally significant negative correlation with the behavioral increase in lottery choices after losses (Figure 4-7A), in line with previous findings by Paulus et al. (2003). This finding indicates that even though the anterior insula shows an overall increase in activity during loss experiences, participants with the strongest insula reactions for losses show the smallest increases (or even decreases) in risk-appetite after losses (i.e., opposite behavior to the BEE). Also the left IPL, a part of the executive control network that is specifically activated for neutral outcomes, correlates negatively with BEE (Figure 4-7B). That is, participants who have the largest decrease of activity in the cognitive control network during loss trials show the strongest behavioral BEE, in line with our expectation. Note however, that one participant demonstrates particularly strong BEE. If this participant is removed from the analyses, the direction of the correlation remains, but the correlations are longer significant.

In the second choice stage we find that the left anterior insula, which showed increased activity for gain and loss outcomes in the outcome phase, correlates negatively with the behavioral HME effects (Figure 4-7C). Thus, the participants who showed a high level of insula activity during the decision-making stage after a previously experienced gain tended to select the safe option. This opposes the general finding that affective reactions drive increases in risk appetite.

4.5. Discussion

4.5.1. Behavioral Findings

Previous theoretical accounts on the HME and the BEE suggest that the effects are driven by insufficient updating of a reference point, and thus by the integration of

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calculated separately for each participant. Due to the outlier participant in this analysis (see behavioral results), we use the more simple measure in order to include all participants in the analysis. The two effect-size measures are also highly correlated (0.93 and 0.98 for the HME and the BEE, respectively; 18 participants).

[36] Significantly active only in loss versus neutral contrast and not in the gain versus neutral contrast.

the previously received outcomes to the current choice problems. This occurs especially when the choices are processed within one mental account (Thaler & Johnson, 1990). In the present study, we encourage the integration of prior outcomes and the current choice problems by having a structure where two prizes of the first stage lottery proceeded to the second choice stage. Our experimental setup indeed leads to a clear path dependence of second stage choices, uniquely showing both HME and BEE in a controlled within subject design. Importantly, in the present study the choice problems are identical across the three different conditions (history of gain, neutral and loss outcomes), thus excluding the possibility that any other variability in the choice problems could be driving the behavioral results besides for the differing outcome history. Furthermore, by having multiple repetitions of all three conditions for each participant, we are able to measure the strength of the two effects for each individual decision-maker. These findings demonstrate the robustness of the HME and the BEE by showing that the two effects can be elicited within a reasonably short timeframe in a single within-subject design. The findings extend the prior studies on the HME and the BEE that use aggregate data across groups of decision-makers without concentrating on individual effects, and/or report only one of the effects and lack control over multiple variables in the decision problems.

4.5.2. Affect and Deliberation in Path Dependence

Affective Processing during Gains and Losses

We proposed that path dependence in risky choices is driven by increased affective processing and decreased deliberative processing related to gain and loss experiences. In other words, we expected that the amount of affective processing for positive (increase in EV) and negative (decrease in EV) outcomes is higher than for more 'neutral' (no change in EV) outcomes. When we compare the brain activities during the outcome phase of the task, we strikingly find increased activity in partially overlapping networks of brain areas for the gain and loss conditions compared to the neutral condition. These activated brain regions are known to be part of an interconnected affective salience network (Seeley, et al., 2007). Interestingly, a part of the common network has also higher level of activity when participants later on selected a lottery over a 'sure-thing' amount of money, indicating the relevance of this early affective reaction to the subsequent choice behavior. These findings provide evidence for the hypothesis that path dependence in risky choice is underlined by affective processing in the brain, and suggest that the affective processes related to gain and loss experiences share common mechanisms.

One might argue that the previous finding is not surprising because the gain and loss experiences are inherently emotional relative to a 'neutral' outcome, and thus experiencing gains and losses should naturally induce affective processing. Importantly, the 'neutral' condition in the present study is not affectively neutral, since in this condition the risk related to the lottery relatively increases after the removal of the middle prize whereas in the gain and loss conditions the risk becomes relatively smaller after the removal of the smallest and largest prizes, respectively. In general, the brain network which has higher activity for gains and losses than neutral outcomes is not purely related to positive and negative outcomes, but it is involved in a wide range of emotionally arousing situations (Craig, 2009). In fact, prior research indicates that the observed insula-ACC network has increased activity also for the arousal caused by uncertainty and risk. For instance, one early study indicates that the ACC and insula activities are modulated by the risk of receiving a reward or a punishment. In addition to correlating with the risk level, the ACC activity is also modulated by the related affective arousal as measured by galvanic skin conductance (Critchley, Mathias, & Dolan, 2001). More recently, in addition to replicating the earlier finding of insula activity reacting to risk, Preuschoff, Quartz, & Bossaerts (2008) show that the anterior insula also activates when participants make 'errors' in the prediction of risk. In fact, also in the current data set we find significant positive correlation between ACC activity and the risk level of each lottery during the second stage choice. Thus, one might expect that the relative increases in risk in the neutral outcome condition would drive increases in insula and ACC activity. Instead, we find an increase in this affective salience network for gains and losses which indicates that these two conditions with increasing risk appetite involve affective processing system more than the 'neutral' condition, irrespective of the emotional salience of all three conditions.

Decrease in Deliberation during Gains and Losses

The second half of our proposition claims that gain and loss experiences decrease the use of deliberation mechanisms. In line with this expectation, we find a decreased level of activity in the executive control network in the brain during gain and loss experiences. Similarly to the affective mechanisms, also here we find evidence for an overlap in the control areas between the gain and loss conditions, indicating that similar type of control processes might have a decreased level of functioning in the gain and loss conditions. Furthermore, a part of this common network also explains between-subject variability in the strength of the BEE: the decision-makers with the lowest level of control function have strongest tendency to select a lottery after losses. Additionally, in multiple parts of the executive control network we find a trend for a lower activity level in the outcome time window in trials where decision-makers later on selected a risky lottery. Taken together, these findings indicate that decreased activity in the cognitive control network increases lottery choices, and that both gain and loss outcomes induce decreased use of these control mechanisms.

Time Dynamics of Affect and Deliberation

So far we have discussed our findings concerning the outcome window of the task, i.e. the brain activities that occurred prior to the final decision-making stage. While in the outcome window we find overlapping activation in the affective system for gain and loss outcomes, as well as similar deactivation in the deliberative system, the subsequent choice stage with gain and loss histories have differential patterns of brain activation. In detail, the results indicate a higher level of affective salience network activity in the loss domain than in the gain domain. First, when we compare the decision-making stage after a loss experience to that after a neutral experience, we find increased activity in one region of the affective network which is not significantly present in the corresponding comparison for gain condition. Second, when we directly compare the loss and gain conditions we find that a large portion of the affective salience network is activated during the decision making after loss outcomes. In contrast, when we compare the gain condition to the neutral condition, the only significant activation is in an area that is part of the executive control network. In sum, the data seems to indicate more similar processing in the outcome stage for the gain and loss conditions whereas in the next choice stage the affective processes are more active after loss than gain experiences. The presence of affective processing during decision making after losses is well in line with prior behavioral research which indicates the importance of affect during decision making for inducing increasing risk appetite after prior losses in respect to prior plans (Andrade & Iyer, 2009). Together these findings suggest that especially after experiencing losses, it is important to first neutralize the emotional state before proceeding with further decision-making tasks in order to avoid excessive risk taking. To achieve this, the decision-maker could for instance employ cognitive reappraisal strategies which are known to decrease decision biases related to negative moods (Heilman, Crisan, Houser, Miclea, & Miu, 2010) and loss aversion (Sokol-Hessner, et al., 2009). As for the gain outcomes, the present data suggests that the decision-makers might use insufficient level of deliberation in the decision-making stage which may lead to carefree behavior in the form of increased risk taking. Increasing self-regulation by giving careful and thoughtful consideration to the decision problem might induce better control over behavior during emotional arousal (Leith & Baumeister, 1996), thus potentially reducing the HME.

In addition to indicating differential involvement of affective and deliberative systems in the outcome and choice stages, the data suggests that affective mechanisms explain individual choice behavior in different time windows for gains and losses. During the outcome phase, decision-makers with high activity in one part of the affective network, which is specifically activated for loss experiences, show decreased amount of risk taking in the subsequent choice stage[37]. Even though this finding seems contradictory to the general argument that the activity of affective mechanisms increase risk appetite after losses, it is in line with prior accounts suggesting that earlier losses may sensitize decision-makers to future losses (Thaler & Johnson, 1990), and create more negative expectations towards future outcomes (Monga & Rao, 2006). Similarly, in the following choice stage, decision-makers with high activity in a corresponding part of the affective network select more often safe choices after a prior gain outcome than decision-makers with smaller affective reaction. These seemingly contradictory results in respect to our prior findings might relate to a more general discrepancy in neuroeconomics literature, where it has been argued that emotions are necessary for rational decision making (Damasio, 1994; Shiv, Loewenstein, et al., 2005) and that affective processes bias decision making away from rationality (De Martino, et al., 2006; Roiser, et al., 2009). Possibly the influence of affective processes is somewhat context dependent. In the case of path dependence, our data suggests

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[37] Note however that this result was only marginally significant.

that generally gain and loss outcomes induce more affective processes and less deliberative evaluation which are related to increase in risk appetite. However, some decision-makers might be particularly sensitive to specific emotional reactions, such as particularly high negative arousal to a loss or a strong fear of losing a previous gain, which may decrease the risk appetite of these decision-makers against the general bias.

4.6. Conclusions

The present work indicates how neuroscience methodology can currently be used in testing hypothesis on economic behavior. The main contribution of the present study is to provide insights into the mechanisms that underlie path dependence in risky choice behavior which can inform future research in path dependence. The brain imaging findings clearly distinguish two separate networks that promote path dependence: increased affective processing and decreased deliberation during gains and losses are generally related to future tendency to select risky prospects. Interestingly, the fMRI data suggests different time dynamics for these processes for gain and loss outcomes. These findings indicate that emotion regulation might be particularly important after prior losses in order to prohibit excessive risk taking in future choices whereas after gain experiences decision-makers should pay special attention on sufficient deliberation. In contrast, individual sensitivity to negative loss experiences, as well as a fear of losing a previous gain during decision making, might lead to increasing risk aversion. In general, the data indicates that path dependence is promoted by emotional arousal, which suggests the possibility of reducing the biases with emotion regulation strategies, such as cognitive reappraisal. Additionally, especially after prior gain experiences, the decision-maker might benefit from careful, analytical considerations of decision problems.

The present study contributes to the theoretical basis of path dependence by indicating the role of affect and deliberation in respectively enhancing and decreasing the risk appetite after gains and losses. Moreover, the implied differences in the dynamics of these two mechanisms might promote differential susceptibility to external interventions in the house money and break even effects. Overall, the current findings suggest that the models of path dependence should also account for situational factors that promote or suppress affect and deliberation in sequential choice situations.

All the previous implications to path dependency in risky choice behavior which are ‘read’ from the pattern of brain activations are speculative by nature and they need to be verified and supported by behavioral experiments prior to claiming their practical relevance with high level of certainty. The prospects for future research are discussed more in detail in the general discussion of the dissertation in Chapter 7. We hope that these insights into the cognitive mechanisms that underlie path dependency will inspire future research and model development that considers the dynamics of affect and deliberation in sequential risky choice. Eventually this development may lead to better policies that help decision-makers to intervene in a chain of losses before the magnitude of the increasingly growing losses become too extensive and also to ascertain that the previously gained money is not spend too light heartedly.

Appendix 4.A. MRI Data Acquisition

We recorded functional MRI brain scans during the task performance, as well as a separate anatomical brain scan after the task. The functional brain scans, or blood oxygenation level dependent (BOLD) signals, were measured with ascending slice acquisition using a T2* weighted echo-planar imaging sequence (Avanto 1.5 T, Siemens, Munich) with the following imaging parameters: 32 axial slices; 2.34 s volume repetition time (RT); 35 ms echo time (TE); 90° flip angle; 64 x 64 slice matrix; 3.5 mm slice thickness; 0.35 mm slice gap; and 212 mm field of view. For the structural scan, we acquired a T1-weighted GRAPPA sequence: 176 sagittal slices; 2.25 s TR; 2.95 ms TE; 15° flip angle; 256x256 slice matrix; 1.0 mm slice thickness; 0.5 mm slice gap; and 256 mm field of view.

Appendix 4.B. fMRI Data Analysis

Image analysis was performed with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The first four EPI scans were discarded to allow for stabilization of magnetic properties (T1 equilibration). The remaining images were analyzed in two steps. First we performed the standard preprocessing steps necessary for fMRI data analysis, followed by modeling the design specific brain activations in the preprocessed data and performing statistical analysis.

When preprocessing the data we first corrected for the head motion of the participants and differences in the slice acquisition time across different parts of the brain. Next, we transformed the data to the standard Montreal Neurological Institute (MNI) coordinate system, first coregistering the functional data to the anatomical scan, and then spatially normalizing the anatomical scan to MNI T1 template. Finally, we resampled the data into 2x2x2 mm3 voxels, and spatially smoothed the data (Gaussian kernel of 8 mm full-width at half-maximum).

The statistical analysis was performed in an event-related manner using the general linear model approach (Friston, Frith, Turner, & Frackowiak, 1995), whereby a linear model consisting of expected data patterns was fitted to all brain locations where the data was measured (voxels). Before calculating group statistics, we first modeled the brain data on a single subject-level with expected activation patterns elicited by different phases and conditions of the task. The model included three regressors of interest for the outcome phase, where participants learned which prize was removed from the three-prize lottery. We modeled each type of outcome separately (gain, neutral, and loss outcomes), and included only the trials where the lotteries were matched across the conditions to allow a clear comparison of the conditions without any differences in the expected value (EV) and risk of the remaining two-prize lottery. Due to the similarity of the two-prize lotteries across the different conditions, the EV of the initial three-prize lotteries was different (gain trials: low EV; neutral trials: average EV; loss trials: high EV). To account for the possible confound of differential reaction to the initial three prize lotteries, we included one regressor for the EV of the three-prize lotteries. For the second-stage choice, we created similar regressors for each condition.

To account for additional fluctuations in the data, we included some regressors in the model that were not of interest to our analysis. The model included these regressors of no-interest for first stage choices, button presses, as well as for outcome screens and second stage choices that were not matched in the lottery prizes. We also included realignment parameters to model potential movement artifacts. To account for additional variance in the data, we also included EV and risk (modeled as standard deviation / EV) regressors in the model in the outcome and choice stages (outcome phase included only the first stage EV modulator which is highly correlated with the second stage EV, $r = 0.84$).

Before fitting the general linear model to the fMRI data, we first constructed each regressor based on the properties of the expected fMRI signal. The decision stages of the task were modeled with a boxcar function with the duration of 1.5 seconds starting at the time of the stimuli appearance (forced delay before responding) and the outcome screens and button presses were modeled at the time of onset with a peak function. The regressors were convolved with a canonical hemodynamic response function to model the delayed reaction in the fMRI signal.

After fitting the general linear model separately on each individual subject to each brain location, we entered contrast maps from different condition to a second level group analysis. On the group analysis, we used repeated measures ANOVA (3 levels: gain, neutral, loss) separately for the outcome and second stage choices. We also included the behavioral HME and BEE (difference in % lottery choices between conditions) in the models as covariates. Within the ANOVA we calculated planned contrasts between the different outcomes (gain > neutral, neutral > gain, loss > neutral and neutral > loss). To find possible common areas that were activated both by gains and losses relative to neutral outcomes, we used a conservative conjunction analysis with a conjunction null of the two separate contrasts (gain > neutral and loss > neutral). To account for multiple comparisons (due to the large number of voxels), we used the family-wise error correction on the basis of random field theory ($p<0.05$). We report activation that reached significance either on the voxel-level (with a ten voxel extent threshold) or on the cluster-level. In the cluster-level inferences the statistical maps were thresholded at $Z > 3.1$ (corresponding to $p < 0.001$ uncorrected). This same threshold is used when creating the illustrations of brain activations. In addition to a whole brain corrected analysis, we also run a region of interest (ROI) analysis where the search volume consisted of anatomically defined parts of the affective salience and executive control networks, such as the insula, ACC, parietal cortex, and DLPFC

(WFU PickAtlas), or activation maps from other contrasts (see results). All the results which are based on ROI analysis are indicated in the result tables. For additional analysis on the activation patterns, we extracted the mean data of the significantly activated clusters with MarsBar toolbox (the Marseille region of interest toolbox for Statistical Parametric Mapping).

In addition to the above model, we also calculated another fMRI model on the data where the trials were categorized into second-stage lottery and offer choices, instead of gain, neutral, and loss conditions. By using this model we were able to extract the data for the trials with lottery and offer choices, either from the outcome phase or from the second decision-making phase, and to test whether a region had a higher activity in trials where participants chose the lottery or the offer on the second stage.

Chapter 5

Path-Dependent Valuation of Risky Prospects

Abstract

Risky environments, such as financial markets, are often dynamic over time. Recent research in neuroeconomics has studied the valuation of risky prospects but largely ignored how the history affects the current valuation of the prospect. We conducted a functional magnetic resonance imaging (fMRI) study on the valuation of identical risky prospects resulting from different historical paths. Our results indicate that both the bilateral striatum and the medial orbitofrontal cortex (mOFC) value risky prospects relative to their prior states as opposed to their absolute values. Specifically, the mOFC and the striatum demonstrated sensitivity to perceived gains, with higher sensitivity to perceived gain observed in the ventral than in the dorsal striatum. Additionally, both the ventral and dorsal striatum discriminated perceived losses in the historical paths. These findings support the role of the striatum and the mOFC in reference dependent valuation, and suggest that path dependence may be important for generating different reinforcement signals for identical risky prospects.

5.1. Introduction

The previous chapter discussed the role of emotion and deliberation in path-dependency of risky choice. The findings in Chapter 4 support the hypothesis that increasing emotional reactions and decreasing level of cognitive deliberation are related to increasing risk appetite after gain and loss experiences. In addition to these affective and cognitive influences on the subsequent choice, the history may also bias the way we value the present risky choice options. As discussed in Chapter 2, the reference dependence of valuation posits that people evaluate achieved prizes in respect to the previously available options. The question arises whether people also value the current risky prospects in respect to the previously available prospects, i.e. evaluate how good the present prospect is in respect to the previous one.

Real-world decision-making environments are in many cases time dynamic, where both outcomes and their associated probabilities are continuously changing. In this type of changing environment risky prospects may be framed and valued relative to their prior states (Tversky & Kahneman, 1981), which can lead to the demonstration of differential preferences between economically identical prospects. For instance, imagine an investor who has two stocks in his portfolio that are currently considered to be equivalent, both in terms of their value and their future risk. Now assume that one day earlier, due to random noise in the market, one of these stocks had improved to the current value whereas the other had decreased in value to reach the present state. Even though the two stocks are currently equivalent, the investor might experience a more positive valuation of the improved stock and a more negative valuation of the stock that had recently declined. Thus, he might value the stocks in his portfolio differently, in a path-dependent manner, instead of according to their actual present value. The goal of this chapter therefore is to examine whether path dependence can influence the process underlying the evaluation of risky prospects.

It is well established that valuation is in many cases context dependent. Behaviorally, people do not value outcomes in an absolute manner but rather tend to evaluate outcomes relatively to some reference point (Kahneman & Tversky, 1979). Recent neuroimaging evidence has suggested that brain's reward circuitry, consisting of dopamine target regions such as the striatum and the orbitofrontal cortex (Delgado, 2007; Kringelbach, 2005), might also value outcomes in a relative manner in a variety of contexts, with the evaluation of outcomes shown to be influenced by other possible outcomes (Breiter, et al., 2001), the outcomes of others (Fliessbach, et al., 2007), and the scaling of the numerical representations of financial gains (Weber, et al., 2009)[38]. In particular, the striatum has been shown to process an outcome in respect to subjective expectation (Hare, et al., 2008) though the dorsal striatum has been shown to reflect also absolute value calculations (Tobler, Fletcher, Bullmore, & Schultz, 2007). Similarly, the mOFC has been implicated in relative value calculations (Elliott, Agnew, & Deakin, 2008) as well as in absolute valuation (Hare, et al., 2008).

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[38] See Section 2.3 for further details.

Research has also examined the neural reward circuitry as it computes a value for risky gambles. Some work has claimed that the striatum reflects the actual expected value of risky prospects (Preuschoff, et al., 2006; Tobler, O'Doherty, et al., 2007; Yacubian, et al., 2006), suggesting that the valuation network in this instance computes an absolute, non-relative value for a risky prospect. In contrast however, one experiment studying the influence of ownership on the pricing of lottery tickets found that the ventral striatum evaluated buying and selling prices of these tickets relative to the ownership status, thus reflecting context dependent valuation in the ventral striatum (De Martino, et al., 2009). Based on this experiment, the absolute expected value of the lottery is computed in the mOFC and the dorsal striatum. Therefore, there is still some disagreement on whether risky prospects are evaluated in an absolute or in a relative manner by the brain's reward system.

Here we extend the investigation into the nature of relative versus absolute evaluation of choices by examining historical path dependence in the evaluation of risky prospects. This question will allow us to answer whether people use the past to evaluate the present, and whether this is computed neurally. In particular, we test whether risky prospects are processed in a reference dependent or independent fashion in the striatum and the mOFC. More specifically, we will use our previous fMRI data set to study how participants react to changes in the set of possible prizes in a lottery, and whether numerically identical risky prospects are valued differentially depending on the prior set of available prizes. We hypothesize that

> Hypothesis 1a: Lotteries are evaluated in the context of prizes that were previously available, so that a lottery consisting of the highest prizes from a previous prize set activates the striatum and the mOFC more than an identical lottery that consists of the lowest prizes of a previous prize set.

Alternatively of course prospects may be evaluated via their objective values.

> Hypothesis 1b: Brain activation in the striatum and in the mOFC correlates with the expected value of the current lottery and there is

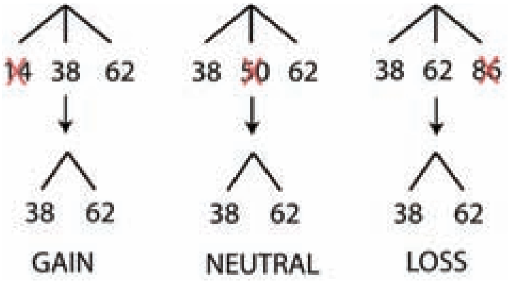

Figure 5-1. Experimental design.

no differential activation in these rewards areas when comparing identical prospects.

5.2. Experimental Data

We test the hypothesis with the fMRI data set described in Section 4.3. The current analysis concentrates on the outcome window of the task. That is, in this phase the participants were only informed of the two lottery prizes that remained in the lottery, and they were not able to make their next choice yet. Importantly, the choice problems in the sequential choice paradigm were designed so that participants faced 24 sets of two-prize lotteries in the evaluation phase, with each set seen three times, once after each type of prize removal (removal of low, medium and high prize options). Thus, this design enabled the comparison of two-prize lotteries in the evaluation phase that were identical in numerical value (and thus identical in expected value), but which had different historical paths (Figure 5-1).

Here we excluded six participants (out of the twenty-nine scanned participants) from the analysis due to the following reasons: too small a number of trials in one experimental condition (1 participant), technical problems during data acquisition (1 participant), and lack of attention to the task (4 participants). The behavioral criterion used in Chapter 4 is not critical for the current analysis because the present question concerns valuation mechanisms instead of behavioral

Table 5-1. Brain regions that are differentially activated during the outcome phase for relative gain and loss experiences. The table provides both voxel and cluster level information. The p-values are corrected for multiple comparisons problem by using random field theory. The table also reports peak coordinates indicating the location of the most strongly activated voxels in MNI coordinates.

Anatomical region	Cluster-level		Voxel-level		Peak MNI coordinates			
	Cluster size	p (corr)	Z	p (corr)	x	y	z	
R ventral striatum	500	0.000	6.35	0.000	14	6	-10	
L ventral striatum	378	0.000	5.69	0.001	-14	2	-10	
R dorsal striatum	178	0.025	4.97	0.022	18	16	10	
L dorsal striatum	72	0.003	4.86	0.001	-14	12	12	*
mOFC	157	0.041	4.40	0.217	6	38	-12	

* Significant only in ROI analysis (statistics from the ROI analysis)

All clusters were significant in the ROI analysis with FWE corrected voxel threshold of $p < 0.05$

changes[39]. Thus, a group of 23 subjects (13 males; mean age, 21.9 years; SD 2.1) were included in the final fMRI analysis.

5.3. Results[40]

The time window of most interest for the current study is the outcome phase (Figure 4-2A), that is, the point at which participants were informed which pair of prize options remained in the lottery. The primary comparison is computed between the neural evaluations of identical two-prize lotteries that differed only in the preceding three-prize lotteries (Figure 5.1). Our primary hypothesis was that identical two-prize lotteries are valued in the context of previously available prizes, that is, reference dependent as opposed to absolute valuation (Hypothesis 1a). Neuroimaging evidence supports this hypothesis, as analysis demonstrates that a two-prize lottery consisting of the highest prizes from the three-prize lottery ('*relative gain*') evokes higher activity in the bilateral striatum and mOFC than an

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[39] Results are effectively the same even though we would exclude four more participants based on the behavioral criterion of Chapter 4.

[40] Technical details of the data analysis are presented in Appendix 5.A.

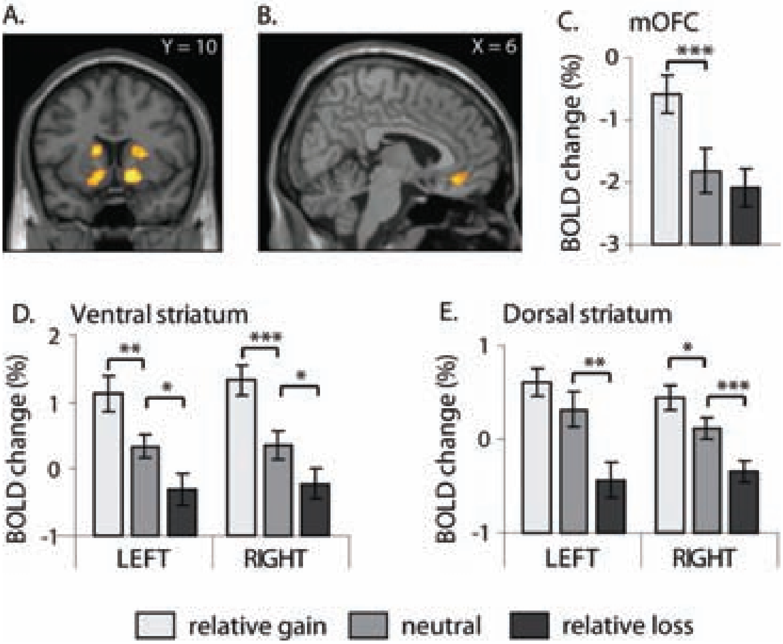

Figure 5-2. Striatum (A) and mOFC (B) activity increases on trials where the two prize lotteries consists of the two highest prizes of the three-prize lottery (relative gain) compared with trials where they have the two lowest prizes (relative loss). Maps are thresholded at $p < 0.001$ uncorrected; all displayed clusters reach the corrected threshold in cluster-level inference and/or in the ROI analysis (see Table 5-1). C, mOFC is specifically activated for trials where two highest prizes remain in the lottery (relative gain). D, E, Striatum differentiates between all three conditions (relative gain, neutral and relative loss). * $p < 0.05$, **$p < 0.01$, ***$p < 0.001$ (two-tailed paired T-test).

identical two-prize lottery consisting of the two lowest prizes from the previous three-prize lottery (‘*relative loss*’; Table 5-1 and Figure 5-2 A and B present the data of Gain > Loss contrast[41]). The opposite contrast does not reveal any significant activation.

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[41] Note, the analysis in Chapter 4 concentrated on finding similar activities in Gain and Loss conditions relative to Neutral condition, whereas here we are interested in finding relation Gain > Neutral > Loss. As a first step we compare the extremes Gain > Loss.

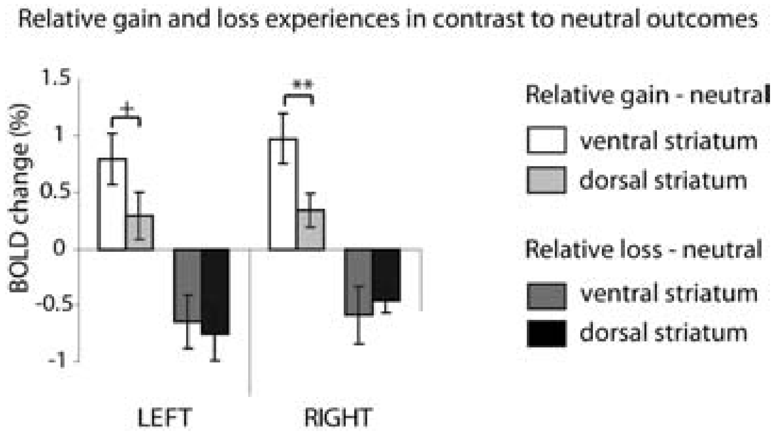

Figure 5-3. Ventral striatum activates more to relative gain experiences than dorsal striatum. $^{+}$ $p < 0.1$, **$p < 0.01$ (two-tailed paired T-test).

Next, we extract the average BOLD responses from the activated regions in the striatum and in the mOFC to study the activation patterns in respect to the exact composition of the two-prize lotteries. We find that the mOFC was particularly sensitive for the lotteries containing two highest prizes as compared to both the set containing the two lowest prizes and the set with the highest/lowest combination (relative gain > '*neutral*' outcome; relative gain > relative loss; p<0.001), but did not differentiate between the lotteries with extreme and lowest prizes (neutral vs. relative loss; p = 0.51, n.s.; Figure 5-2C). Also the activity level in the striatum reflects reference dependent valuation of lotteries. The greatest activity is observed for the lotteries containing the two highest prizes from the previous stage, followed by the combination of highest and lowest, followed by the two lowest prizes (relative gain > neutral > relative loss; p<0.05; except for the left dorsal striatum that does not reach significance in highest vs. extreme prizes contrast p = 0.18 n.s.; see Figure 5-2 D and E). Furthermore, a repeated measure ANOVA analysis (dorsal/ventral striatum x hemisphere (2 levels) x historical path (3 levels)) reveals a significant interaction effect between the dorsal/ventral striatum and historical path (F(2, 44) = 3.55, p<0.05), reflecting a higher sensitivity for relative gain experiences in the ventral striatum (relative gain − neutral) than in the dorsal striatum (Figure 5-3).

Finally, we directly test the alternative Hypothesis 1b, that is, whether the expected value of the remaining two prizes is encoded in an absolute, reference-independent fashion. Our model included one 'parametric' regressor whose amplitude for each trial was based on the expected value of the lottery. This parametric analysis did not demonstrate any significant activation in the whole brain nor in the ROI analysis.

5.4. Discussion

Results from the study confirm the hypothesis that risky prospects are valued in a path-dependent manner in a dynamically changing environment, with this activation pattern evident specifically in the striatum. When evaluating identical two-prize lotteries, striatal activity differentiates between trials in which the two-prize lottery consisted of either the two highest, the two lowest, or the highest and lowest prizes of the preceding three-prize lottery. In contrast, the mOFC shows increasing activity only for trials with the two highest prizes remaining in the lottery, in line with previous findings of specificity to positive rewards in the mOFC (Kringelbach, 2005).

Some previous studies have suggested the role of the striatum in the calculation of an absolute expected value of a risky prospect (Tobler, O'Doherty, et al., 2007; Yacubian, et al., 2006), though these studies have attracted criticism for their potentially confounded differentiation between reference dependent calculation (value relative to an expected prospect) and absolute valuation of expected value (Hare, et al., 2008). The unique feature of our study design is that the sequential structure of the paradigm and the large variation in prize amounts across lotteries enables the differentiation of reference dependent reward-signals and absolute expected value signals from each other. We find strong evidence for reference-dependent valuation of risky prospects, and the data does not support the hypothesis of absolute expected value calculation in the striatum. The current results additionally provide support for relative value calculation in the mOFC, an area also previously proposed to compute either absolute (De Martino, et al., 2009; Hare, et al., 2008) or relative value (Elliott, et al., 2008).

Furthermore, our data suggests a distinction in the sensitivity to relative positive and negative experiences in the striatum, most prominently along the dorsal-ventral axis. Comparison of the activated clusters indicates that the dorsal striatum is less sensitive to relative gain experiences than the ventral striatum (extending to globus pallidus). The dorsal-ventral distinction in the striatum has previously been linked to actor-critic models of reinforcement learning, with suggestions that the ventral striatum reacts to outcomes in active and passive stimulus-reward tasks (critic), whereas the dorsal striatum contributes only to stimulus-response learning (actor) (O'Doherty et al., 2004). The presence of both the dorsal and ventral striatum in the current active task is in accordance with this model. Indeed, the current results provide some further evidence for specific sensitivity to relative gains along the dorsal-ventral axis, with decreased sensitivity to gains in the dorsal striatum. An earlier report showed higher sensitivity in the ventral/dorsal striatum for actual losses than for actual gains, and linked this activation pattern to behavioral aversion for losses (Tom, et al., 2007). Together with these results of Tom et al. and the actor-critic model, the current findings suggest that with respect to decreased sensitivity to gains in the dorsal striatum, participants are less sensitive to gain experiences in active than in passive tasks, giving relatively more weight to the negative loss experiences and loss aversion.

In addition to valuation, there are at least two alternative theoretical accounts that may be related to the current data. First, the evaluation phase might involve feelings of regret and rejoicing related to the previous choice. Interestingly, the mOFC has consistently been activated by experienced and anticipated regret (Coricelli, Dolan, & Sirigu, 2007; Sommer, Peters, Gläscher, & Büchel, 2009). However, the mOFC has shown positive correlation with the level of regret, in contradiction with the current data where the mOFC has increased activity for trials with positive outcomes, which more likely evoke rejoicing rather than regret. Second, even though a few recent studies disentangle reward-specificity of striatum activity from behavioral errors and prior expectations (de Bruijn, de Lange, von Cramon, & Ullsperger, 2009), the striatum is generally considered to reflect reinforcement learning signals (Hare, et al., 2008; Schultz & Dickinson, 2000). We suggested that the striatum computes a path-dependent value for risky prospects, but instead the observed activity pattern may well be interpreted as a prediction error signal, i.e. a difference between the value of the two-prize lottery and the expectations created by the preceding three-prize lottery. Overall, the results indicate that the striatum evaluates the prospects relative to their prior states, which can be interpreted both as calculation of prediction error signals as well as path-dependent valuation. However, the striatum activation does not predict here the behavioral pattern in line with reinforcement learning hypothesis[42].

To conclude, the main contribution of this study is that risky prospects are valued path-dependently instead of in an absolute manner. That is, after a removal of a potential outcome from a lottery, the remaining possible prize options are evaluated relative to the initial lottery. This is associated with differential activation in the striatum and in the mOFC when comparing numerically identical lotteries, with these areas responding to the relative gains or losses depending on the historical path. This is important, as it suggests that corresponding valuation on a behavioral level may lead to suboptimal evaluation of choice situations. Indeed, behavioral research indicates that the historical path of risky lotteries does influence later choice behavior (Post, et al., 2008). Reconsider the example of our hypothetical private investor, who holds two stocks in his portfolio, one of which has previously improved to the current value whereas the other has recently decreased in value. Having experienced the random changes in these stocks, the investor might be tempted to evaluate these stocks in a path-dependent fashion leading to retaining the stocks for too long or selling them too early, thus displaying path-dependent behavior which is common among his peers in the stock market ('disposition effect'; Odean, 1998; Shefrin & Statman, 1985), especially when concentrating on the gain and loss history of one stock at a time (Kumar & Lim, 2008).

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[42] After a risk related negative reinforcement the risk appetite should decrease instead of increasing (see Section 4.4.1). Trial-based striatum activation also does not predict the behavior on that particular trial in line with reinforcement learning models.

Appendix 5.A. fMRI Data Analysis

Image analysis was performed with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). Preprocessing steps were identical to the analysis presented in Appendix 4.B.

Statistical analysis was performed in an event-related manner using the general linear model approach (Friston, et al., 1995). In the subject-level model, events in the evaluation phase were modeled as peaks at the time of screen onset and the regressors were convolved with the canonical hemodynamic response function. We run two separate first-level models on the data. The first model was quite identical to the model that was run in Chapter 4, and thus the analyses differ mainly in the second level comparisons that are described in the results section. The model included three regressors of interest for evaluation of identical two-prize lotteries in three different path conditions. In each condition the lottery consisted of two of the three initial prizes: medium and high prize (relative gain); low and high prize (neutral); or low and medium prize (relative loss). The non-matched trials were modeled with an additional regressor. Due to the matching of the lottery prize options in the evaluation phase across history conditions, the three history conditions differed in the EV of the initial three-prize lotteries (relative gain: relatively low first stage EV; neutral: average first stage EV; relative loss: relatively high first stage EV). To account for the possibility that the comparisons between history conditions could reflect a difference in the valuation of the first stage gambles, we included one parametric regressor that models the expected value of the three-prize lottery. In order to test reference independent valuation of the two-prize lottery in the evaluation phase, we also ran a second, otherwise identical model, where this three-prize expected value regressor was replaced by a two-prize expected value regressor (the two EV regressors could not be used within one model due to a high correlation, corr = 0.84). In addition, both models included regressors of no-interest for button presses and decision stages, and the realignment parameters were also included to model potential movement artifacts.

The second level group analyses were performed with one-way ANOVA (three levels), and with one-sample T-tests for parametric modulation. To account for multiple comparisons, we used the family-wise error correction on the basis of random field theory ($p<0.05$). We report activation that reached significance either on the voxel-level and/or on the cluster-level. In the cluster-level inferences the statistical maps were thresholded at $Z > 3.1$ (corresponding to $p < 0.001$ uncorrected). In addition to a whole brain analysis, we also ran one region of interest (ROI) analysis where the search volume consisted of anatomically defined putamen, caudate, medial parts of bilateral superior frontal gyrus (incl. orbitofrontal cortex), and bilateral gyrus rectus (WFU PickAtlas). These areas were chosen *a priori* as they have been well-established as showing activity for reward-related processes. For additional analysis between the activated regions, we extracted the mean data of the clusters with MarsBar (the Marseille region of interest toolbox for Statistical Parametric Mapping).

Part III

Social Conformity

Chapter 6

Conflict with Others Modulates Judgments through Basic Reinforcement Learning Mechanisms

Abstract

Not only our choices but also the current judgments are influenced by contextual factors. For instance, we often change our judgments to conform to normative group behavior. Here we show, using functional magnetic resonance imaging, that these changes in judgment are based on mechanisms that comply with principles of reinforcement learning. We found that individual judgments of facial attractiveness are adjusted in line with group opinion. Conflict with group opinion triggered a neuronal response in the rostral cingulate zone and the ventral striatum similar to the 'prediction error' signal suggested by neuroscientific models of reinforcement learning. The amplitude of the conflict-related signal predicted subsequent conforming changes in judgment. Furthermore, the individual amplitude of the conflict-related signal in the ventral striatum correlated with differences in conforming behavior across participants. These findings, together with results of control studies, provide evidence that the social environment influences our future judgments via learning mechanisms reflected in the activity of the rostral cingulate zone and ventral striatum.[43]

6.1. Introduction

Subjective values and attitudes that guide human behavior are not constant in time, but instead they are influenced by the surrounding environment. For instance, we adjust our behaviors and judgments by the perceived behavior of others, in particular by social norms (Cialdini & Goldstein, 2004). The persuasive

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[43] An adapted version of this chapter was published in *Neuron* by Klucharev, Hytönen, Rijpkema, Smidts, & Fernandez (2009).

power of the social environment also directs consumer behavior. For instance, it has been known already for a long time that the purchase choice of products and brands is influenced by reference group behaviors (Bearden & Etzel, 1982). Also more recent research indicates the role of normative group opinion in consumer behavior and how even simple information about the behavior of reference group members can be used as a tool to guide consumption choices. For instance in hotels, informing the guests that the other people who have previously stayed in the room reused their towels, increases the towel reuse rate significantly (from 37.2% to 49.3%) in comparison to standard environmental motivators (Goldstein, Cialdini, & Griskevicius, 2008). People conform to group opinion even when it is financially harmful for them: when consumers learned that other people in their neighborhood used more energy than they did, they increased their own energy consumption (Schultz, Nolan, Cialdini, Goldstein, & Griskevicius, 2007). Consumers who learned that others used less energy indeed decreased their own energy use. Trespassing on the social norms and on the legitimate rules can also spread disorderly behavior to other related social norms. For instance, when people observe inappropriate behaviors like graffiti or parking bikes in prohibited areas, they are more likely to conduct disorderly behaviors, such as stealing or littering (Keizer, Lindenberg, & Steg, 2008). These examples indicate that very simple messages about the behavior of others can guide consumer choices in economically and environmentally profitable direction—or to the opposite unprofitable behaviors.

Conformity refers to the act of changing one's behavior and opinions to match the responses of others (Cialdini & Goldstein, 2004). The behavior and judgment of other people provides information on the normal and expected behavior in these circumstances and what is typically approved or disapproved. The effect of group opinion on individual judgments and decisions have been robustly replicated (Cialdini & Goldstein, 2004) since Solomon Asch's pioneering work on the line-judgment conformity experiments in which a third of the participants conformed to the erroneous majority opinion of the confederates, even when the majority claimed that two lines different in length by several inches were the same length (Asch, 1951). Conformity has been extensively studied in social psychology and three central motivations for conforming behavior are suggested: a desire to be accurate by properly interpreting reality and behaving correctly, to obtain social approval from others, and to maintain a favorable self-concept (Cialdini & Goldstein, 2004). Whereas psychological studies emphasize the rewarding value of social approval or affiliation with others (Cialdini & Goldstein, 2004), behavioral economics focuses more on the effects of punishment for violation of the norm (Fehr & Fischbacher, 2004). In fact, both approaches may suggest that conforming changes in judgment are underlined by reinforcement learning, i.e. social norms selectively reinforce certain behaviors. Here we utilize the cognitive neuroscience approach (Phelps & LeDoux, 2005) to provide a useful framework for studying reinforcement learning mechanisms of conformity effects in judgment.

This chapter is organized as follows. Section 6.2 outlines the theoretical background information on the principles of reinforcement learning and the corresponding neural correlates. Section 6.3 describes the experimental design and Section 6.4 presents the results of the conducted behavioral and fMRI experiments. The general discussion on the results is presented in Section 6.5. Appendix 6.C elaborates on the possibility of range effects and on the effects of stimulus properties in conformity. Since social studies have robustly demonstrated that social influence is most effective in an ambiguous situation (Cialdini & Goldstein, 2004), we test how the categorization ambiguity related to the stimulus influences the tendency to change judgments.

6.2. Theoretical Framework and Hypotheses

Recent neuroscientific and computational models assume that goal-directed behavior requires continuous performance monitoring (Montague, King-Casas, & Cohen, 2006). Successful behavioral patterns are reinforced while errors call for adjustments of behavior. Many reinforcement learning models include a 'prediction error'—a difference between the expected and obtained outcome (Schultz, 2006). Reward prediction error guides decision making by signaling the need for adjustment of behavior. Importantly, a conflict with social norms is not a usual behavioral error, i.e. it is not a typical behavioral mistake but rather any action that deviates from the behavior of the majority. Conformity with social norms requires neural signals related to deviations from it (Montague & Lohrenz, 2007). Here we propose that a perceived deviation from group norms triggers a neural response that is similar to prediction error in reinforcement learning, indicating a need to change individuals' future judgment in line with group norms.

Event-related brain potential and fMRI studies suggest that the rostral cingulate zone (RCZ; sometimes referred to as the ACC in the literature), has a specific role in reinforcement learning and generation of feedback- and error-related responses (Gehring, Goss, Coles, Meyer, & Donchin, 1993). The RCZ is the region on the border of Brodman areas 6, 8, 24 and 32 (Picard & Strick, 1996). Cognitive neuroscience provides strong evidence to imply that activity of the RCZ, the region in the posterior medial frontal cortex, indicates the need for adjustments both when the action goal was not achieved and when the likelihood of failure is high (Cohen & Ranganath, 2007; di Pellegrino, Ciaramelli, & Ladavas, 2007; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuiss, 2004). The magnitude of the RCZ activity has also been shown to predict the strength of subsequent behavioral adjustments during simple choice decisions (Cohen & Ranganath, 2007; Kerns et al., 2004). The reinforcement learning theory of performance monitoring suggests that the RCZ activity is modulated by a midbrain dopaminergic signal which indicates whether an action outcome is worse or better than expected, regardless of the primary cause of the deviation from the prediction (Holroyd & Coles, 2002). The RCZ is not alone in monitoring behavioral outcomes. In fact, a growing body of research has identified a distributed neural network involved in this process which includes the ventral striatum, i.e. the nucleus accumbens[44] (NAc). Indeed, unpredictable reward modulates the activity of the human NAc (Berns, et al., 2001; McClure, Berns, & Montague, 2003; O'Doherty, 2004). The NAc has also been implicated in social learning (Rilling, et al., 2002). Overall, previous studies have demonstrated that the NAc is involved into gain prediction in response to reward cues (Knutson & Wimmer, 2007). Importantly, the cell bodies of the majority of dopamine neurons that show an actual prediction error signal are located in the midbrain (substantia nigra and ventral tegmental area; Schultz, 2006). These midbrain neurons project heavily to the NAc and the RCZ. Thus, assuming that the BOLD signal may primarily reflect inputs (and local computation), it is possible that with human fMRI such a full prediction error signal would show up primarily in the NAc and the RCZ rather than in the midbrain where it originates.

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[44] NAc is a subpart of the ventral striatum. See also Chapter 2 for a general discussion on the role of striatum in valuation.

In line with our proposition that conformity is based on reinforcement learning, we form the following hypotheses:

> Hypothesis 1: A conflict with group opinion triggers a ′prediction error′ response manifested in activity of the RCZ and the NAc.
>
> Hypothesis 2: When conflict occurs, RCZ and NAc activity predicts the subsequent adjustment of the behavior, i.e. social conformity.

6.3. Experimental Setup for the Main Experiments

To test our hypothesis, we designed a paradigm in which the participant's initial judgments of facial attractiveness were open to influence by group opinion. Facial attractiveness is a highly important social characteristic (Langlois et al., 2000) and an everyday target of normative influence, for example by fashion magazines and cosmetics commercials. During fMRI female participants rated the attractiveness of female faces and after each rating they were informed of an 'average European rating' of the face—group rating (Experiment N1). Actual group ratings were systematically manipulated during the experiment. We assumed that group opinion (group ratings) signaled the normative opinion (a 'descriptive norm' representing typical behavior; Cialdini & Goldstein, 2004) about the attractiveness of each individual face. Thus, with our procedure, we introduced a conflict between the participant's own judgment and the normative group opinion. To identify subsequent conforming changes in judgment, participants rated the same set of faces again after the fMRI session. We also conducted an fMRI control experiment (Experiment N2) to examine the relevance of social environment by using a non-social version of the task in which group normative opinion was replaced with computer-generated ratings. Before reporting the fMRI results, we first present behavioral pilots on the design indicating the social nature of the task.

6.3.1. Detailed Description of the Experiment

Participants were informed that they were participating in a pan-European project "Seeing Beauty" to study human perception of attractiveness. They were told that the project team was conducting the same studies in France (Paris), Italy (Milan) and Netherlands (Nijmegen). The logos of European 'collaborators' (Milan School of Design, French Institute of Beauty, and Dutch Royal Academy of Art) were included at the bottom of the written instructions. During the fMRI session[45] participants were exposed to a series of 222 photographs of female faces (stimuli duration=2 s, inter-trial interval (ITI)=3-5 s, see Figure 6-1). Participants were instructed to rate the face on an 8-point scale, ranging from very unattractive (1) to very attractive (8). Participants indicated their rating by pressing the appropriate button. Eight buttons were used, four for each hand. The participant's rating (initial rating, green rectangle frame) was visualized on screen immediately after the face stimulus. Three to five seconds later, at the end of each trial, the participant was informed (by red rectangle frame) of the rating of the same face given by an 'average European female participant from Milan and Paris' (Group rating). The difference between the participant's and the group rating was also indicated by a score shown above the scale (0, ±2 or ±3 points). Importantly, the frame and the number indicating the conflict with group opinion were present during both 'conflict' and 'no-conflict' trails. Actual group ratings were programmed using the following criteria: in 33% of trials, group ratings agreed with participant's ratings, whereas in 67% of trials group ratings were pseudo-randomly above or below participant's rating by ±2 or ±3 points, i.e. using an adaptive algorithm that kept the overall ratio of 'more negative' or 'more positive' group ratings approximately equal during the experiment. Participants were told that group ratings which matched with their own rating to within ±1 points produced the frame of the group rating visually overlapping with the frame of the participant's own rating. Participants were not informed about the real purpose of the experiment and the manipulation of the group ratings. All photographs were randomized across participants and conditions. Importantly, the sign of the difference between individual and group ratings does not play a role similar to positive and negative prediction error. In our experiment any difference between individual and group ratings (positive or negative) indicated a deviation of the individual opinion from the group norm irrespective of the sign, i.e. the prediction error was always negative. Otherwise, those trials where group gave a more positive attractiveness rating for the stimulus than the participant should be rewarding, whereas group's more negative rating should be punishing.

Thirty minutes after the fMRI session in an unexpected (unannounced) subsequent behavioral session participants were instructed to rate again—at their

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[45] fMRI scanning parameters are described in Appendix 6.A.

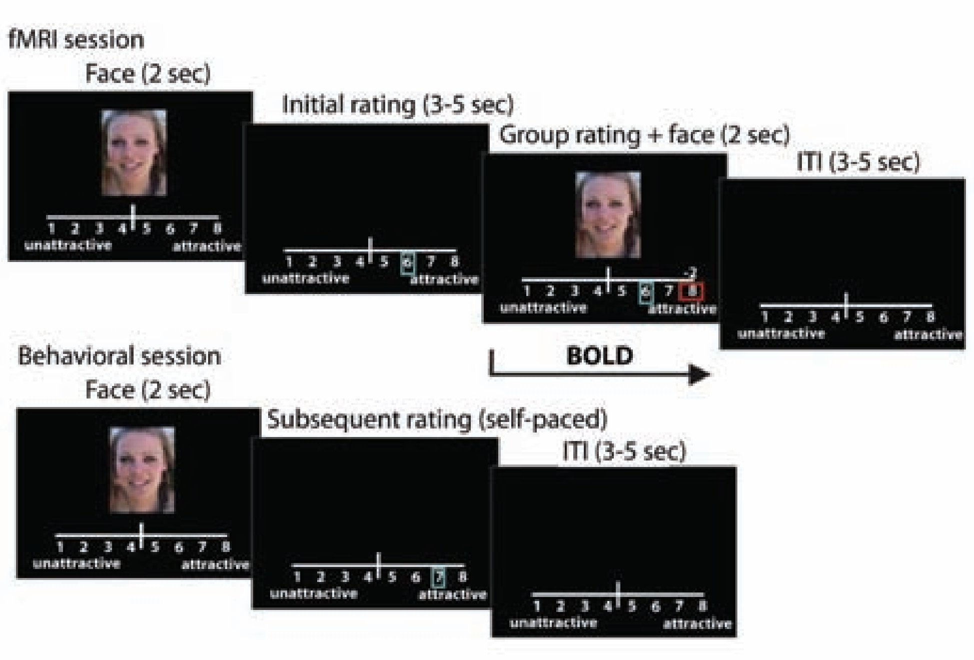

Figure 6-1. The task (fMRI session) evoking a conflict with group ratings followed by the behavioral session. The sequence of the events within a trial is shown. During the fMRI session (Experiment N1), participants rated the attractiveness of female faces and were subsequently presented with the group ratings that could be similar (no conflict with group ratings), below or above (as is shown in the figure) participants' rating (conflict with group ratings). Thirty minutes after the fMRI session participants rated again the same faces during the Behavioral session in order to identify the subsequent conformity effects. The control experiment (Experiment N2) had the same trial structure, but a different cover story.

own pace—the attractiveness of the same faces presented in a new randomized order without the normative ratings (subsequent rating, Figure 6-1). At the end of the experiment participants were questioned using the Self-Monitoring scale on interpersonal influence (Snyder & Gangestad, 1986).

Our set-up imitates social psychological studies investigating persuasion, where participants are informed of a dominant behavior in a group (Cialdini & Goldstein, 2004). Social psychology suggests two types of social norms which can influence judgment (Cialdini & Goldstein, 2004): (1) injunctive norms have a moral tone and characterize what people should do, whereas (2) descriptive norms represent typical behavior or what most people actually do, regardless of its appropriateness. In the current study we investigated the descriptive social norms that send out the message, “If a lot of people are doing this, it's probably a wise thing to do”. It is also important to note that in our study participants were not involved in a standard reinforcement task, i.e. they could not learn correct answers or a correct evaluation criteria because there was no correct answer, the normative feedback was pseudo-random.

6.3.2. Stimuli

A set of 222 digital photos of European females (aged 18–35 years, from free internet sources) were used as stimuli. Color portraits of moderately attractive (mean 4.2, SD=1.2 of the 8-point scale) females and moderate smile (rated AU6A/C+AU12B/C in accordance with the Facial Action Coding System (FACS) by a certified FACS coder; Ekman & Friesen, 1978) were selected from a set of 1000 stimuli, all made with a highly similar photographic style and appearance. Attractiveness is a socially important facial feature (Langlois, et al., 2000); judgments of facial attractiveness are fast, effortless and consistent across participants (Willis & Todorov, 2006). Therefore, a mismatch of individual judgments of facial attractiveness with group opinion should create a strong normative conflict. Social standards of female facial attractiveness are also constantly influenced by social norms, e.g. via fashion magazines and cosmetics commercials. Previous studies showed that individuals adjust their judgments of attractiveness in various situations (Geiselman, Haight, & Kimata, 1984; Kenrick & Gutierres, 1980). Ratings of facial attractiveness are modulated by social environment (Jones, DeBruine, Little, Burriss, & Feinberg, 2007; Little, Burriss, Jones, DeBruine, & Caldwell, 2008) and thus it makes them an optimal and important model for studying social conformity.

Only female portraits and female participants were selected. Cross-gender rating of attractiveness is related to mate selection that has very specific neural mechanisms (Cloutier, Heatherton, Whalen, & Kelley, 2008). In contrast, within-gender ratings of attractiveness can be generalized to other types of conforming behavior. One participant was excluded from the analysis due to reported homosexual orientation and motion artefacts.

6.3.3. Participants

A total of 46 young right-handed women participated in the social (Experiment N1) and non-social control (Experiment N2) neuroimaging experiments with two experimental sessions: an fMRI session and a behavioral session, separated by approximately 30 minutes. None of the participants reported a history of drug abuse, head trauma, neurological or psychiatric illness. Twenty-four healthy students (aged 19–27 years, mean 21.8 years) participated in the social version of the experiment (Experiment N1). Two participants were rejected from the study due to large head motions exceeding 3 mm, one participant was excluded due to her reported suspicion about the cover story of the experiment. Twenty-two healthy students (aged 19–29 years, mean 22.1 years) participated in the non-social control study (Experiment N2). The average age of participants was not significantly different from those in experiment N1 ($t(1,20)=1.6$, $p=0.1$). One participant was rejected from the study due to large head motions exceeding 3 mm.

6.4. Results

6.4.1. Behavioral Pilot Test: Group Saliency and Conformity

Before reporting the fMRI results, we present the data of a pilot behavioral experiment testing whether the paradigm described in Section 6.3.1 is truly social in nature. One might question whether the behavior and brain reaction in the design are indeed the result of social conformity instead of being simple error reactions. The participant could for instance interpret the group opinion on the screen as a ‘correct’ attractiveness rating. That is, participants could perceive the task so that the feedback rating on the screen is an objectively correct attractiveness rating that they should also be able to report themselves (similarly than people can learn to categorize animals to different species based on correcting feedback). Thus to test the social nature of the task, we first report a behavioral study to demonstrate the relevance of the social environment in our experimental task.

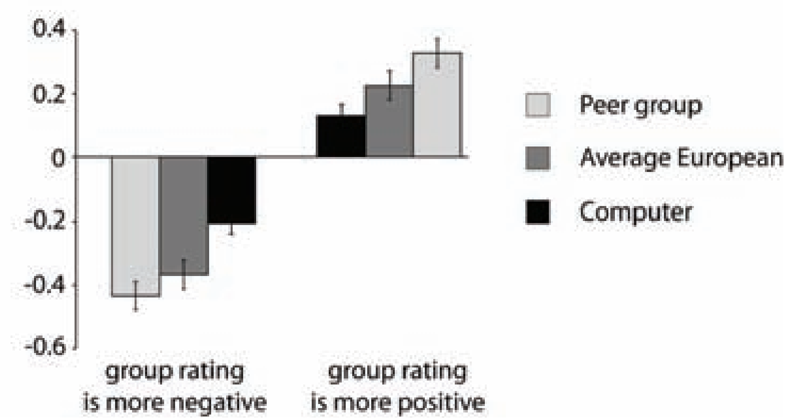

Figure 6-2. Behavioral control study: conformity effects (adjustments of ratings after a positive or negative conflict relative to no-conflict trials) for normative information coming from (1) peer group of fellow students attending the same session; (2) average European female; (3) computer script. See the text for the details of the statistical analyses.

For this behavioral test we recruited 62 young female participants (age=19-26; mean=22.7; SD =3.2). The participants were divided into three groups. Each group received a different cover story. The feedback on the screen was told to be: (1) average rating of the peer group (fellow students from the same university, attending the same experimental session and present in the same lab room); (2) average rating of European females from Milan and Paris, as described in the main fMRI design; (3) output of a computer script. Participants performed the task in separate cubicles in the behavioral lab. All other aspects of the paradigm and experimental set-up were identical to the fMRI design (instructions, task design and analysis).

In this data we find a significant interaction effect*: social task* (peer group, averaged European and computer) x *conformity* (MANOVA, F(2,61)=3.8, p=0.001) due to a stronger conformity in social conditions (see Figure 6-2). Moreover, we find a significant correlation between the conformity effects and the level of externally manipulated social relatedness (r=0.68, n=128, p=0.001). Overall, participants change their opinion more after a conflict with a social group than after a conflict with a computer. Thus, these results demonstrate the social nature of the fMRI design using 'average European ratings'. We also find weak conformal adjustments of judgments after a conflict with computer feedback. Previous social psychological studies reliably demonstrate that individuals mindlessly apply social rules and expectations to computers (see Nass & Moon, 2000 for a review): for example, individuals apply gender stereotypes, show politeness towards computers, demonstrate reciprocity to computers, show ingroup/outgroup effects and even ethnically identify with computer agents. Therefore, it is not surprising to find a weak behavioral adjustment to computer rating but, importantly, the effects are stronger with social feedback and become even stronger with higher social relatedness.

6.4.2. Experiment N1: Behavioral Results

In agreement with our expectations, participants change their ratings of attractiveness, aligning themselves with group ratings (Figure 6-3): On average, participants decrease their attractiveness ratings when group ratings have been more negative than their own initial rating, whereas more positive group ratings are associated with more positive re-evaluation of faces. Participants do not change their ratings significantly if group ratings match their initial ratings (no-conflict trials). One-way ANOVA analysis (three-level factor of *group ratings*) reveals a significant main effect of the factor *group ratings* on changes in attractiveness ratings (F(2,20)=31.1 p=0.0001). Therefore, group opinion effectively modulates judgments of individuals even when the group is not physically present and so cannot directly affect participants[46]. The conformity effect was especially strong for highly ambiguous faces: for faces whose initial ratings varied most across participants (standard deviation ≥ 1.621, see Appendix 6.C and Figure 6-12 for details).

To establish an even closer relationship between group ratings and individual behavior, we perform a correlation analysis between the magnitude of the conflict (i.e., the difference value between participants' own and group ratings during the fMRI session) and the subsequent change in the perceived facial attractiveness separately for each participant. We find a significant correlation among all participants (mean values: r=0.21, n=222, p=0.005, SD=0.06, min value: r=0.13, max value: r=0.33), except for one participant who shows a correlation that

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[46] See also Appendix 6.C for a discussion on the possibility that the results are driven by different scale use in the fMRI and behavioral sessions.

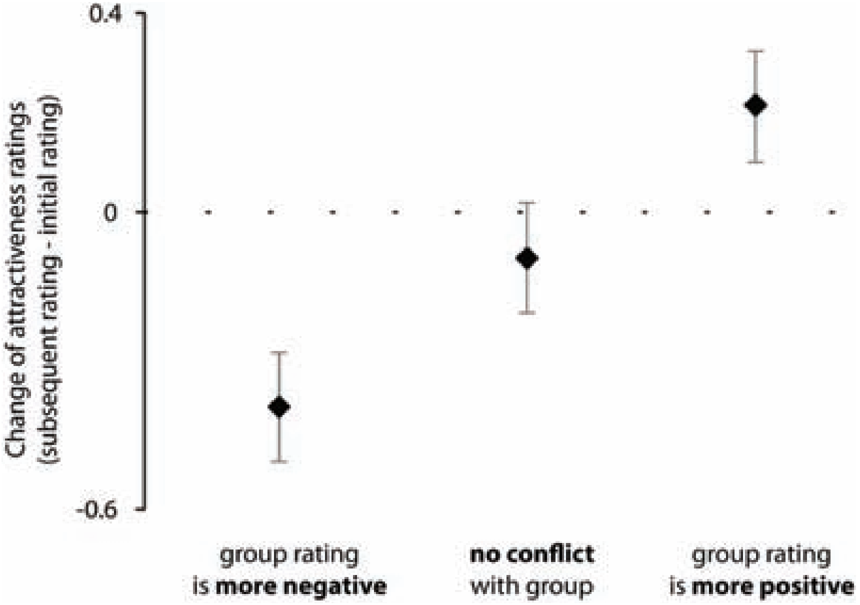

Figure 6-3. Mean behavioral conformity effects. On average the attractiveness ratings changed in line with the group ratings. The picture illustrates the change of the faces' attractiveness measured during the behavioral session as compared to the initial ratings during the fMRI session. Bars indicate the standard error of the mean.

just failed to reach statistical significance (r=0.126, p=0.07). The larger the conflict with group opinion, the more pronounced the conformity effect is, even at the level of individual participants. We later use the individual correlation coefficients as conformity scores (i.e., a measure of the individual tendency to conform, thereby distinguishing conformists from nonconformists), and correlate them with individual fMRI conformity effects.

To test whether inter-individual differences in a trait measure of self-monitoring are associated with experimental behavior as assessed by changes in attractiveness ratings, we conducted an additional correlation analysis. The self-monitoring scale explains individual differences in the (self-)control of expressive behavior and refers to a person's ability to adjust his or her behavior to external situational factors (Snyder & Gangestad, 1986). High self-monitors are 'social chameleons', adjusting their behavior to social situations. We did not find a significant correlation between the size of subsequent change in the perceived facial attractiveness (i.e. persuasive effect) and the self-monitoring index.

Our study therefore reveals that conformity leads to the transmission of facial preferences from the group to the individual. Overall the behavioral results indicate that the manipulation of social normative influence is successful in inducing conformity effects in the judgment of facial attractiveness.

6.4.3. Experiment N1: fMRI Results[47]

To identify the neural activity related to 'social (normative) conflict' we first compare the brain responses in all trials in which the group rating differed from the participant's rating (conflict trials) with all no-conflict trials. To model subsequent conformity effects in judgment we then calculate a contrast within conflict trials: conflicts with group ratings followed by conformity (i.e. where perceived facial attractiveness subsequently changes in line with group ratings) vs. conflicts with group ratings not followed by conformity (where perceived facial attractiveness does not change).

Neural Correlates of Social Conflict (Hypothesis 1)

To study brain activity associated with the perception of 'social conflict', we compare neural activity occurring during all trials in which the group rating conflicts with the participant's rating with all trials in which the group rating does not conflict with the participant's rating—the *conflict contrast*. As expected, the conflict with group opinion activates the RCZ (Figure 6-4). The location of the cluster maximum (x=-3, y=14, z=48) matches closely the results of a previous meta-analysis on error monitoring (x=1, y=15, z=43, for details see Ridderinkhof, et al., 2004). In addition, conflict trials activate more strongly than no-conflict trials (Table 6-1) the insular cortex, the precuneus, the cerebellar tonsil and the middle frontal gyrus, all areas known to be engaged in general error processing (Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Ridderinkhof, et al., 2004). Furthermore, the conflict deactivates (i.e., more activity for no-conflict than conflict trials) the ventral striatum (NAc) and the posterior cingulate cortex, brain areas that are known to be involved in reward processing and error detection

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[47] Details on the fMRI data analysis are described in Appendix 6.B.

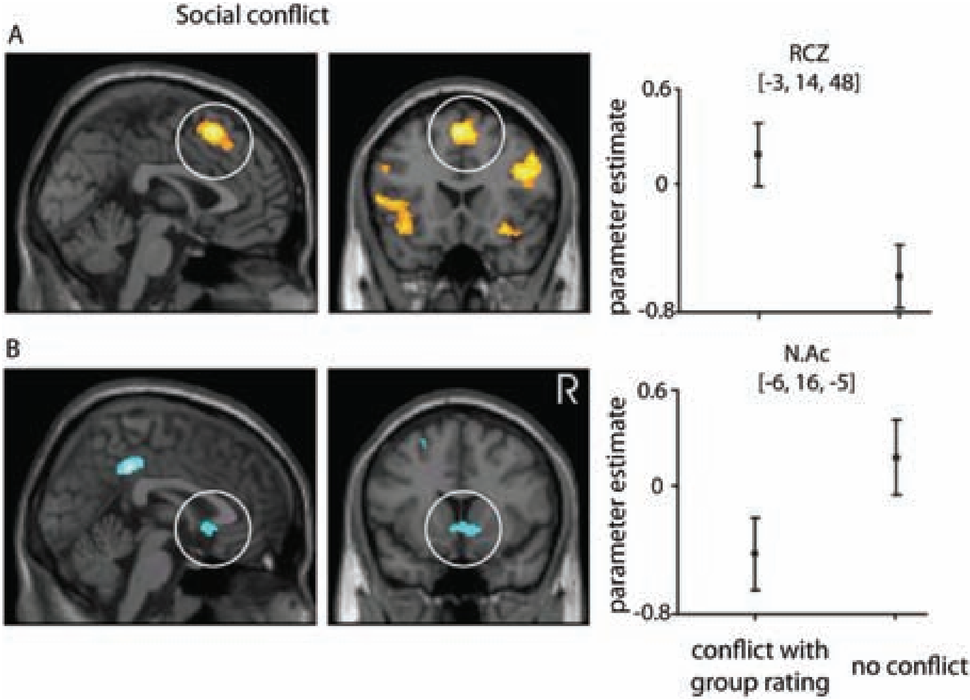
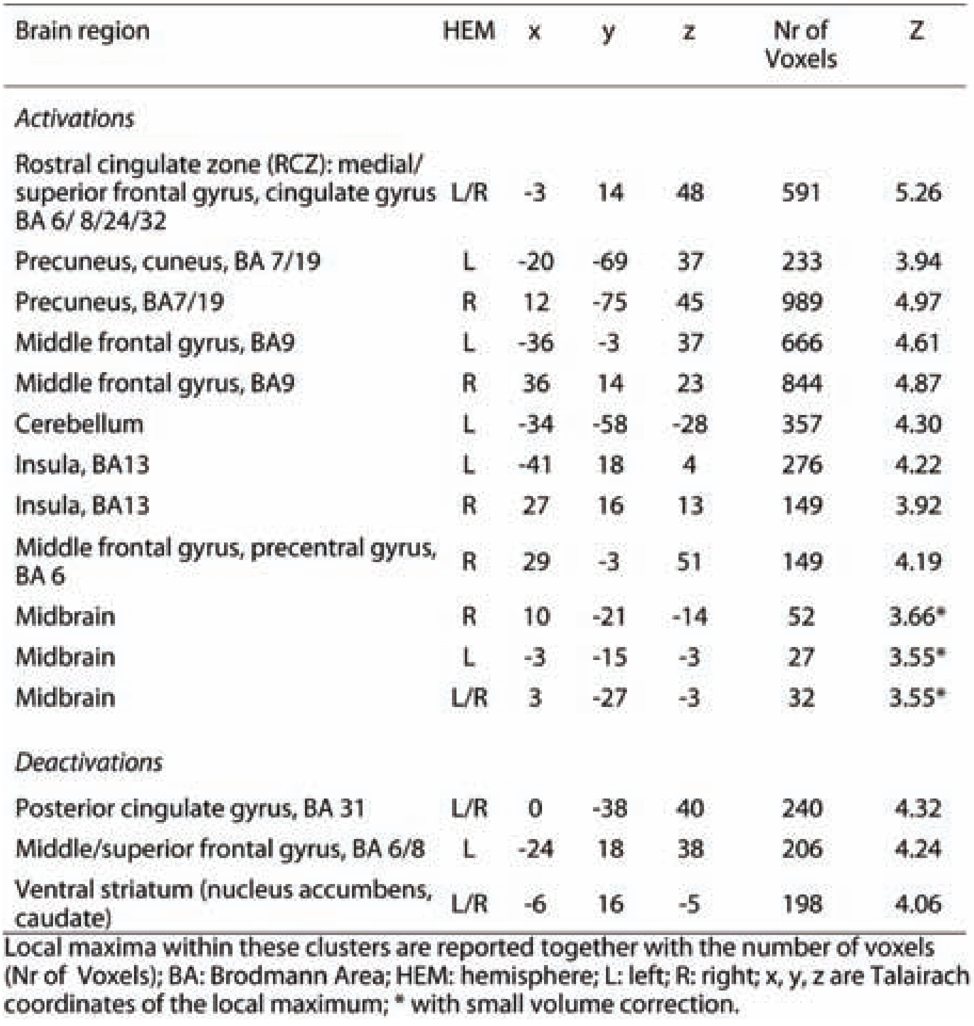


Figure 6-4. Social conflict effects: neural response to group ratings in conflict vs. no-conflict trials. Left: z-maps of activations (A) and deactivations (B) induced by a conflict with group ratings. Right: the signal change of the hemodynamic response for conflict and no conflict trials. RCZ – rostral cingulate zone; N.Ac. – nucleus accumbens; R – right hemisphere. All maps are thresholded at $p<0.001$, the clusters are significant at $p<0.05$ (FDR corrected). Bars indicate standard error of the mean.

(McCoy & Platt, 2005; Schultz, 2006). Our results thus indicate that a mismatch with group opinion triggers a neural response in the RCZ and the NAc that is similar to prediction error signal.

Table 6-1. Significant activation clusters for social conflict contrast.



Brain region	HEM	x	y	z	Nr of Voxels	Z
Activations						
Rostral cingulate zone (RCZ): medial/ superior frontal gyrus, cingulate gyrus BA 6/ 8/24/32	L/R	-3	14	48	591	5.26
Precuneus, cuneus, BA 7/19	L	-20	-69	37	233	3.94
Precuneus, BA7/19	R	12	-75	45	989	4.97
Middle frontal gyrus, BA9	L	-36	-3	37	666	4.61
Middle frontal gyrus, BA9	R	36	14	23	844	4.87
Cerebellum	L	-34	-58	-28	357	4.30
Insula, BA13	L	-41	18	4	276	4.22
Insula, BA13	R	27	16	13	149	3.92
Middle frontal gyrus, precentral gyrus, BA 6	R	29	-3	51	149	4.19
Midbrain	R	10	-21	-14	52	3.66*
Midbrain	L	-3	-15	-3	27	3.55*
Midbrain	L/R	3	-27	-3	32	3.55*
Deactivations						
Posterior cingulate gyrus, BA 31	L/R	0	-38	40	240	4.32
Middle/superior frontal gyrus, BA 6/8	L	-24	18	38	206	4.24
Ventral striatum (nucleus accumbens, caudate)	L/R	-6	16	-5	198	4.06

Local maxima within these clusters are reported together with the number of voxels (Nr of Voxels); BA: Brodmann Area; HEM: hemisphere; L: left; R: right; x, y, z are Talairach coordinates of the local maximum; * with small volume correction.

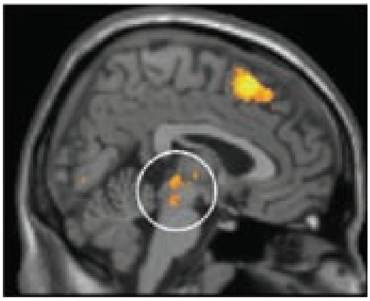


Figure 6-5. Midbrain activity: the effects of social conflict. Z-map of activations. The midbrain activations with three local maxima (x,y,z: 10, -21, -14; -3, -15, -3 and 3, -27, -3). The map is thresholded at $p<0.001$.

The posterior cingulate cortex has been implicated into the ‘default’ network (Buckner, Andrews-Hanna, & Schacter, 2008)—a specific, anatomically defined brain system preferentially active when individuals are not focused on the external environment. The deactivation of the cingulate cortex in the current study could therefore indicate an additional cognitive demand triggered by the conflict with the group opinion. Interestingly, a recent study showed that the posterior cingulate cortex is affected by dopamine depletion (Nagano-Saito et al., 2008). Furthermore, animal studies have demonstrated that neurons of the posterior cingulate monitor the omission of expected reward, suggestive of a prediction error-like signal (see McCoy & Platt, 2005 for a review).

Prediction error signals are intimately associated with dopamine neurons in the midbrain (Schultz, 2006). We therefore conduct an ROI analysis in the midbrain dopaminergic region covering the entire area, including substantia nigra, ventral tegmental area (VTA) and other structures. The spherical ROI has a radius of 15 mm and is centered at the coordinate -1, -18, -9 (x, y, z) (Aron et al., 2004). We find significant clusters of activity in the midbrain triggered by conflict with the group opinion (see Figure 6-5) and no significant deactivations. The activity of the midbrain, the RCZ and the NAc could reflect a degree of the social conflict with normative group opinion or a degree of reward participants experienced when their ratings match the normative ratings in no-conflict trials.

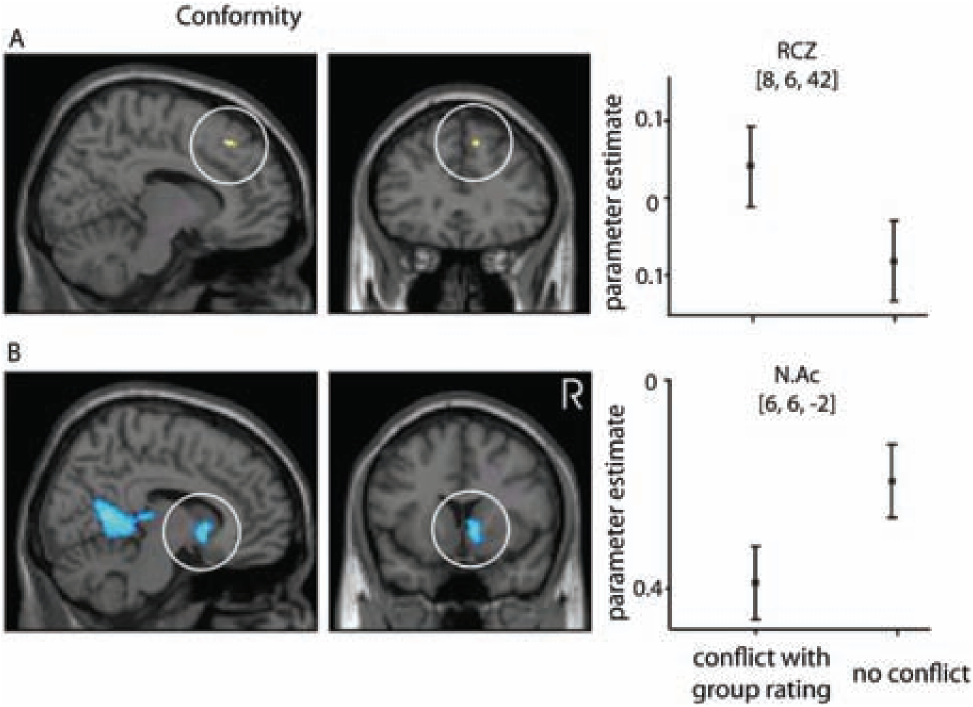
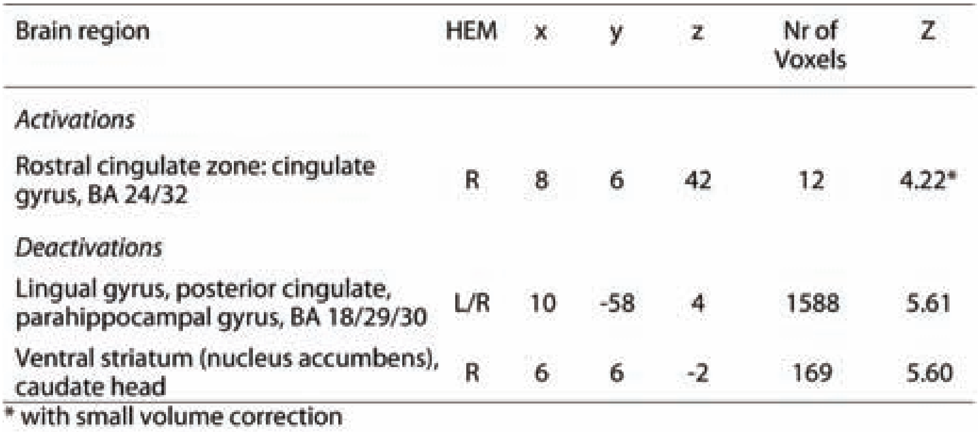


Figure 6-6. Conformity effects: the social conflicts followed by the subsequent change of facial attractiveness in line with group ratings (i.e. conformity) vs. the normative conflicts that were not followed by changes in attractiveness ratings (i.e. no conformity). Left: z-maps of activations (A) and deactivations (B) predicting the conformity with group ratings. Right: the signal change of the hemodynamic response for trials followed by conformity and by no conformity. RCZ – rostral cingulate zone; N.Ac. – nucleus accumbens. All maps are thresholded at $p<0.001$. Bars indicate standard error of the mean.

Conforming Adjustment in Judgment (Hypothesis 2)

Given the fact that no-conflict trials are not followed by behavioral changes in judgment we focus our further analysis on conflict trials that triggered conformity. We hypothesize that the social conflict response in the RCZ and the NAc is predictive of changes in participants' opinions on facial attractiveness. The activation of the RCZ and deactivation of the NAc should therefore be particularly

Table 6-2. Significant activations clusters for the social conformity contrast.



Brain region	HEM	x	y	z	Nr of Voxels	Z
Activations						
Rostral cingulate zone: cingulate gyrus, BA 24/32	R	8	6	42	12	4.22*
Deactivations						
Lingual gyrus, posterior cingulate, parahippocampal gyrus, BA 18/29/30	L/R	10	-58	4	1588	5.61
Ventral striatum (nucleus accumbens), caudate head	R	6	6	-2	169	5.60

* with small volume correction

strong during those conflict trials that effectively change participants' judgments, i.e. are followed by conformity. To test this hypothesis we compare brain activity during those conflict trials that are followed by changes in perceived attractiveness of faces in line with group ratings with conflict trials where there are no such changes—the *conformity contrast*. Indeed, the activation of the RCZ region of interest predicts subsequent conformity: the activity in the RCZ elicited by the conflicts with group opinion that are followed by conformity is stronger than that elicited by conflicts that are not followed by conformity (Figure 6-6A). Furthermore, the deactivation of the NAc region of interest during the perceived conflict with group opinion also predicts conformity (Figure 6-6B). In addition, we conduct a whole-brain analysis of conformity effects and find that the conformity-related suppression of activity in the NAc is significant, even without small volume correction. In the global search we find that conformity is also predicted by a deactivation of extrastriate visual cortex (BA 18,19) and parahippocampal cortices (Figure 6-6B, Table 6-2). We also check conformity effects in the fusiform gyrus, a region implicated in face and attractiveness processing (Iaria, Fox, Waite, Aharon, & Barton, 2008). We do not find statistically significant effects in the selected ROIs (for fusiform gyrus: spheres of radius 10 mm, x, y, z: 34,-54,-21 and -32,-42,-25, based on a previous study by Iaria, et al., 2008). These null-findings might indicate that observed conformity effects are not triggered by an immediate

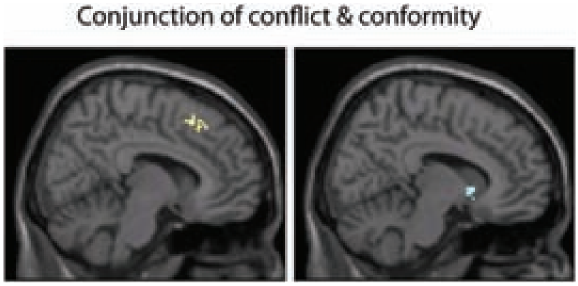


Figure 6-7. Results of the conjunction analysis of social conflict and conformity effects. Both the conflict with group ratings and the subsequent conformity activated RCZ (left part of the figure: local maxima at x=6, y=16, z=46) and deactivated the NAc (right part of the figure: local maxima at x=6, y=6, z=-2). Maps are thresholded at p<0.001, clusters are significant at p<0.05 (FDR corrected).

perceptive re-evaluation of facial attractiveness. ROI analysis of conformity effects in the midbrain also do not reveal effects reaching the level of statistical significance. Thus, the midbrain shows a nonspecific conflict-related signal in contrast to the neural signal at the RCZ and the NAc that is predictive of conformity effects.

To control the specificity of conformity effects in the RCZ and the NAc for conformal changes in judgment we conduct an additional analysis by calculating subsequent 'anti-conformity' effects—contrasting conflict trials followed by changes against the group vs. conflict trials followed by unchanged ratings. However, we do not find any significant effect (thresholded at p<0.001), even using an ROI analysis centered in the RCZ and the NAc. Furthermore, a direct contrast of conflict trials followed by changes in line with the group vs. conflict trials followed by changes against the group show significant activation of the RCZ (x, y, z: 8,5,40) and deactivation of the NAc (x, y, z: 1,4,-5) ROIs. These results indicate that observed conformity effects are specific for conformal adjustments in judgment and not related generally to changes in behavior.

To support more directly the hypothesis that adjustment in judgment in social environment are indeed triggered by social conflict-related neural activity in the RCZ and the NAc, we conduct a conjunction analysis (testing the conjunction null hypothesis, see Nichols, Brett, Andersson, Wager, & Poline, 2005, for details), aiming to identify those brain regions that are activated in both the *conflict* and the *conformity* contrast. The conjunction analysis reveals the activation of the RCZ and the deactivation of the NAc in both contrasts (Figure 6-7). Thus the very same brain regions in the medial prefrontal cortex and the ventral striatum are sensitive for social conflict and predict conformity with group opinion.

To link individual performance differences to individual differences in brain activity we compare neural responses of conformists (i.e., people conforming easily to group opinion) with nonconformists (see Section 6.4.2 for details). We split participants in two groups using a median split on conformity scores: conformists (mean r=0.26, n=11) and nonconformists (mean r=0.16, n=10). We hypothesize that individual differences in levels of conformity are based on variability in response to social conflict, e.g. conformists generally show a greater degree of conflict-related activity than nonconformists, and for that reason the conflict-signal of the conformists reaches more easily the hypothetical threshold that triggers conformity. The current view on the functional role of the neural prediction error signal seems to suggest a threshold for error-related activity (Schultz, 2006; similar to perceptual and motor decision-making models, e.g. Schall, Stuphorn, & Brown, 2002 that triggers the adjustment of future behavior). Only an activity that crosses such a threshold evokes a change of behavior.

This mechanism of conformity predicts that (1) the neural conflict-related signal is stronger in conformists than nonconformists and (2) the difference in conflict-related signal in trials that are and are not followed by conformity (conformity effects) has to be weaker in conformists due to a higher chance of any conflict-related response crossing the hypothetical threshold, assuming that the threshold is similar across participants. Figure 6-8A shows that the conflict-related response in the NAc is stronger for conformists than for nonconformists (prediction 1). This observation is supported by a MANOVA (*conformists/ nonconformists* as a between-subject factor, subsequent *conformity* as a within-subjects factor): we find a significant effect of the *conformists/nonconformists* factor (F(1,20)=19.9, p=0.0003). Furthermore, the neural conformity effect is weaker for conformists than for nonconformists (prediction 2). We find a significant interaction between *conformists/nonconformists* and *conformity* factors (F(1,20)=6.1, p=0.023), due to the smaller difference in the conflict-related signal in trials that are and are not followed by conformity for conformists in comparison to

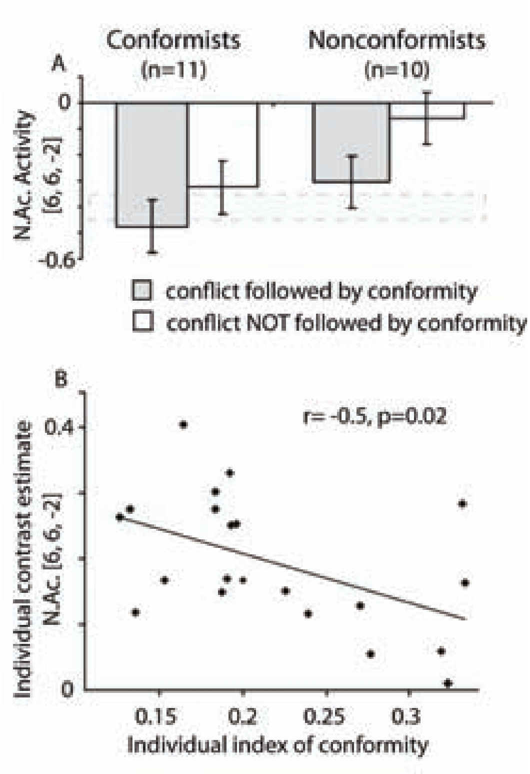
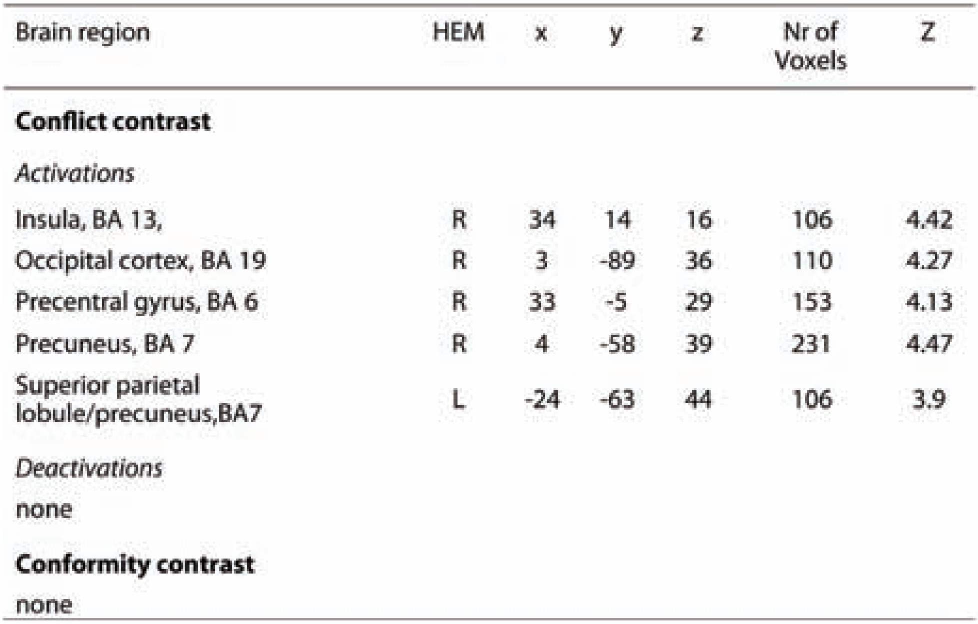


Figure 6-8. Nucleus accumbens (NAc) recruitment during a conflict with group opinion predicts individual differences in conformity. A, Conformists (participants easily conforming to group ratings) showed the stronger conflict-related deactivation of the nucleus accumbens. Error bars indicate standard error of the mean. Grey rectangular area indicates a putative threshold of conformity. B, Significant correlation of the neural *conformity* effect with the individual level of conformity. Due to a higher probability of any conflict to trigger conformity, conformists showed a smaller difference (conformity effect) between neural responses to the conflicts with group ratings followed by conformity and those that were not followed by conformity.

Table 6-3. Significant activations clusters for the non-social control study.



Brain region	HEM	x	y	z	Nr of Voxels	Z
Conflict contrast						
Activations						
Insula, BA 13,	R	34	14	16	106	4.42
Occipital cortex, BA 19	R	3	-89	36	110	4.27
Precentral gyrus, BA 6	R	33	-5	29	153	4.13
Precuneus, BA 7	R	4	-58	39	231	4.47
Superior parietal lobule/precuneus,BA7	L	-24	-63	44	106	3.9
Deactivations						
none						
Conformity contrast						
none						

nonconformists (see Figure 6-8A). Moreover, Figure 6-8B illustrates the significant negative correlation of the neural *conformity* effect (*conformity* contrast) with the individual level of conformity (r=-0.5, n=21, p=0.021). The NAc has been previously linked to individual differences (Cohen, 2007; Schonberg, Daw, Joel, & O'Doherty, 2007; Tobler, Fletcher, et al., 2007) in reinforcement learning and thus could also mediate individual differences in conforming behavior.

6.4.4. Experiment N2: Assessment of the Social Relevance of the Results

Even though the data reported in Section 6.4.1 indicates that behaviorally the task is sensitive to the social relatedness of the reference group, the brain reactions might still reflect standard error reactions without a social dimension. To assess the social relevance of our fMRI findings, we employ a non-social version of the experimental paradigm in which the normative group ratings are replaced with computer ratings—a method commonly used in social cognitive neuroscience (e.g. Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007; Zink et al., 2008). All other

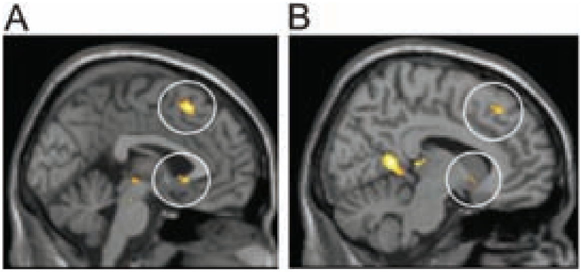


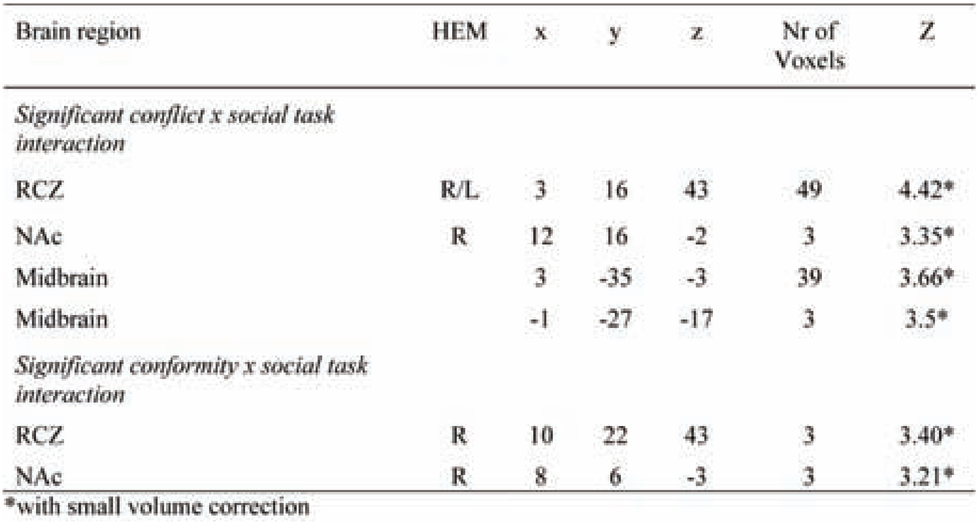
Figure 6-9. Comparison of social and non-social (control) fMRI studies. A, Conflict x social task interaction. White circles indicate RCZ (local maxima at x=3, y=16, z=43) and NAc (local maxima at x=12, y=16, z=-2). B, Conformity x social task interaction. White circles indicate RCZ (local maxima at x=10, y=22, z=43) and NAc (local maxima at x=8, y=6, z=-3). The maps are thresholded at p<0.001.

aspects of the paradigm and experimental set-up are identical to the original fMRI design (task design and analysis).

The primary analysis of the control experiment shows that the mismatch with the computer activated the right insula, precuneus and precentral gyrus, in a similar way to the conflict with social group opinion (Table 6-3). We find conflict-related effects in the RCZ (x, y, z: 3,12,44) and the NAc (x, y, z: 18,14,-6 and -10,12,-7), only using a looser statistical threshold for the SPM analysis (p<0.006). In statistical comparisons of data from both the original and control fMRI experiment we find an interaction between the *conflict* factor (within group factor: conflict vs. non conflict) and the *social task* factor (between group factor: social vs. computer feedback) at the RCZ, NAc and midbrain region (see Table 6-4 and Figure 6-9A). Thus, the activity of the RCZ, NAc and midbrain is significantly more strongly affected by a conflict with social group opinion than by a conflict with a computer. The conflict-related effects are thus strongly attenuated in the non-social experiment.

To explore further these results we study the *conformity* x *social task* (between-group: social vs. computer feedback) interaction. We find a significant *conformity* x *social task* interaction in the RCZ and the NAc (see Table 6-4 and Figure 6-9B). Our results indicate that conformity-related neural effects in the RCZ

Table 6-4. Comparison of social (Experiment N1) and non-social (control Experiment N2) experiments.



Brain region	HEM	x	y	z	Nr of Voxels	Z
Significant conflict x social task interaction						
RCZ	R/L	3	16	43	49	4.42*
NAc	R	12	16	-2	3	3.35*
Midbrain		3	-35	-3	39	3.66*
Midbrain		-1	-27	-17	3	3.5*
Significant conformity x social task interaction						
RCZ	R	10	22	43	3	3.40*
NAc	R	8	6	-3	3	3.21*

*with small volume correction

and the NAc are particularly strong for the social version of the task. Overall, the behavioral and fMRI results confirm that the observed effects in the RCZ and the NAc (sites receiving substantial dopamine inputs) are related to social conformity and are modulated by social factors.

Next, we study the main effect of congruent behavioral adjustments in the control study by comparing neural responses for all conflict trials that are followed either by congruent behavioral changes (i.e. facial attractiveness subsequently changed in accordance with the computer rating) or by no behavioral changes (facial attractiveness ratings not changed). We find activation predicting adjustments in accordance with computer ratings (RCZ; x, y, z: 1,4,49 and NAc; x, y, z: 8,3,-7 and -10,8,-5) only with a decreased threshold ($p<0.003$). Thus, the reinforcement mechanisms in both experiments are rather similar but the effects are strongly modulated by the social context. By and large, social descriptive norms of facial attractiveness are stronger and more effective reinforcers than computer-generated 'norms'.

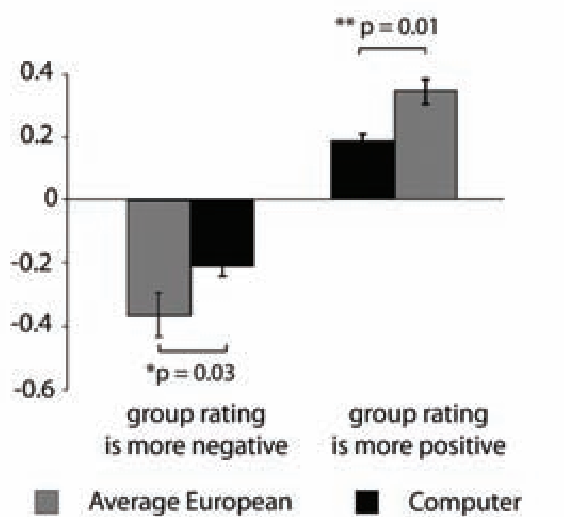


Figure 6-10. Behavioral conformity effects (adjustments of ratings after a positive or negative conflict relative to no-conflict trials) for normative information coming from average European female (N1) or computer script (N2).

In addition to distinct neural results, the social and non-social conditions are also dissociable behaviorally (see Figure 6-10). Overall, participants change their opinion more after a conflict with a social group than after a conflict with a computer (MANOVA, F(3,38)=5.5, p=0.004), both when group opinion is more negative and more positive than participants' opinion (t(1,20)=2.23, p=0.03 and t(1,20)=2.46, p=0.01). To establish an even closer relationship between computer ratings and individual behavior, we performed a correlation analysis between the magnitude of the conflict and the subsequent change in the perceived facial attractiveness separately for each participant. We find a weak correlation (mean values: r=0.15, n=222, p=0.05, SD=0.02, min value: r=-0.01, max value: r=0.28). Importantly, 12 out of 21 participants do not show a significant correlation. Moreover, the correlation is significantly weaker in the computer condition than in the social one (t(1,20)=3.8, p=0.001). Thus the results demonstrate the social nature of the experimental paradigm.

Overall, the results of all studies support the hypothesis that social conformity is based on neural mechanisms similar to those implemented in reinforcement learning. A conflict with social normative opinion triggers a conflict-related response at the RCZ and the NAc that is similar to prediction error in reinforcement learning; if the conflict-related signal exceeds a 'learning' threshold then social conformity is triggered. Furthermore, the NAc activity shows a correlation with individual levels of conformity that indicates a close link of observed neural effects with actual behavior. The observed effects were particularly strong in the social context.

6.5. Discussion

6.5.1. Behavioral Results

We found a robust behavioral effect of group opinion on perceived facial attractiveness. A conflict with a normative opinion triggered a long-term conforming adjustment of participants' own rating. This result is in line with a recent study that demonstrated the social influence of others on an individual's face preferences (Jones, et al., 2007). Furthermore, our results could explain the finding that there is considerably greater agreement in attractiveness ratings between individuals who share a close relationship (Bronstad & Russell, 2007): the ratings are homogenized within groups due to the strong conformity that is known to exist within social groups.

One might argue that the present behavioral findings are driven by intentional behavioral strategies aiming to match the judgments of others. During the debriefing participants did not report any specific strategy such as a matching strategy (an attempt to predict group ratings). It is also important to note that during the fMRI session participants could not learn correct answers or a correct evaluation criterion[48] because the normative feedback was pseudo-random. Furthermore, a matching strategy cannot explain why participants subsequently changed their own opinion about facial attractiveness in a systematic way. A matching strategy during the fMRI session should lead to random (nonsystematic) subsequent changes of participants' initial ratings due to the pseudo-random algorithm of normative rating generation in our study. In contrast, our results

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[48] For instance, learn to pay attention on particular facial features that are associated with a high or low score.

indicate systematic adjustments of participants' opinion between the fMRI and the subsequent behavioral sessions. Finally, ratings during the first and second session were highly correlated (r=0.73, SD=0.06), clearly indicating that responses were not simply random predictions of normative scores.

A demand effect in the current study is also highly unlikely. The instructions stressed that the study focused on participants' own opinion. All participants were debriefed after the experiment. Only one participant reported any suspicion about the cover story and was excluded from the study. The large number of stimuli (n=222) and a long break between sessions ensured that ratings during the second session were indicative of participants' own opinion, because contamination by explicit memory is extremely unlikely. Overall, a demand effect would suggest that during the two hours of the experiment, a participant remembered 222 faces with their associated ratings and the conflict with group opinion. Taking into account that the participants were not forewarned of the second session, we can conclude that a simple demand effect cannot be entirely excluded but is nevertheless highly unlikely.

6.5.2. Neural Correlates of Conflict and Conformity

Social norms prescribe behaviors that a member of a group can enact, and norms are thought to exist "if any departure of real behavior from the norm is followed by some punishment" (Homans, 1950). Indeed, social norms reward or punish people (Bendor & Swistak, 2001) and can be seen as positive or negative reinforcers for socially appropriate or inappropriate behaviors. In other words, a conflict with social norms indicates an error that is similar to a reinforcement learning signal calling for an adjustment of the behavior. In the present study, we examine neural activity during a conflict with group opinion to test the hypothesis that the reinforcement learning signal guides conforming changes in judgments in a social environment. Our results are consistent with the reinforcement learning hypothesis of social conformity.

We find that a conflict with group opinion activates the RCZ and deactivates the NAc, both of which are known to be involved in the computation of the prediction error. Human neuroimaging studies consistently implicate the RCZ in monitoring response conflicts and errors and in differential processing of unfavorable outcomes such as monetary losses, abstract performance feedback, primary negative reinforcers (see Ridderinkhof, et al., 2004 for an extensive review). Overall, the RCZ is engaged when the need for adjustments of the behavior becomes evident. It has been shown that the RCZ is activated by an unfair offer in an ultimatum game (Sanfey, et al., 2003), by social exclusion (Eisenberger, Lieberman, & Williams, 2003) and by the incorrect prediction of social rejection (or acceptance) by others (Somerville, Heatherton, & Kelley, 2006). Furthermore, RCZ has been found to predict attitude change in times when prior attitudes conflict with own actions ('cognitive dissonance'; Izuma et al., 2010; van Veen, Krug, Schooler, & Carter, 2009). RCZ activity is also modulated by the moral character of the partner in the trust game (Delgado, Frank, & Phelps, 2005) and by moral judgments (Greene, Nystrom, Engell, Darley, & Cohen, 2004). Furthermore, a recent study by (Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008) indicates a role of the RCZ in situations of choice difficulty: greater RCZ activation is found when participants choose between alternatives of similar desirability (indicating a high decision conflict) than when they make easier (low decision conflict) decisions. Our findings suggest a new interpretation of the role for the RCZ in social cognition: the RCZ is monitoring the incongruence of our judgments with social descriptive norms that are normally negatively reinforced by social rejection, exclusion, and moral or even physical punishment.

Activity of the NAc represents the value of the expected reward (Knutson, et al., 2005; Knutson & Wimmer, 2007) and thus decreases for aversive stimuli (Besson & Louilot, 1995; Singer et al., 2006). In line with the previously reported inhibitory response to aversive stimuli, we find that the NAc activity during a conflict with group opinion is deactivated relative to a no-conflict situation. We investigate the social relevance of conflict-related effects in the RCZ and the NAc using a non-social control experiment. These effects are modulated by the social context, suggesting a social nature of the conflict. By and large, our findings indicate that the NAc, together with the RCZ, participates in the generation of the neural response indicating a conflicting judgment with group descriptive norms.

Recent learning theories have revealed the role of error monitoring in subsequent performance adjustments: errors indicate a need for behavioral changes (Schultz, 2006). Even though the present experimental paradigm with random feedback prohibits us from analyzing the data with the formal reinforcement learning model, the present study shows that the amplitude of the conflict-related responses in the RCZ and the NAc predicts the subsequent conforming change in judgment in line with learning theories. We demonstrate that the conflict-related activity in RCZ in the trials that are followed by conformity is stronger than in trials that are not followed by conformity. The pattern is reversed in the NAc. Our finding indicates that when the conflict-related signals are strong enough, the performance is adjusted and participants conform to the group normative opinion. These results establish a link between conflicts with descriptive norms and conformity. In addition, conjunction analysis reveals the clear spatial overlap of the neural activity underlying the conflict-related signal and conformity. Importantly, the effects predicting behavioral changes are strongest for the social version of the experiment. In accordance with our hypothesis, the conflict and conformity effects found may be enhanced by social situations rather than representing a specific social mechanism.

A previous study demonstrated that the magnitude of feedback-related negativity (FRN), whose neural generators are located in the RCZ (Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004), predicted whether participants would change decision behavior on the subsequent trial of a simple computer strategic game (Cohen & Ranganath, 2007). Other studies have linked the magnitude of FRN to overall learning or decision making (Frank, Woroch, & Curran, 2005; Yeung & Sanfey, 2004) and to changes in reaction time on the subsequent trial (Gehring, et al., 1993). Cingulate lesions in monkeys impair their ability to use previous reinforcements to guide decision-making behavior (Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006). The role of the RCZ in behavioral adjustment is also consistent with the 'conflict-monitoring hypothesis' (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). This hypothesis suggests that the cingulate cortex is activated by the occurrence of response conflict during the so-called Stroop or Simon tasks. The monitoring of response conflict by the RCZ serves as a signal that aims to minimize the amount of conflict on subsequent performance. Indeed, the RCZ activity during response-conflict tasks predicted the adjustment of behavior (Kerns, et al., 2004). Importantly, in our study the behavioral task does not evoke a response conflict, because the participants responded before the conflicting group ratings were presented. Therefore, in the present study the RCZ activity does not indicate a response conflict but a neural signal similar to prediction error calculated as a perceived difference of own judgments from group opinion.

Our results extend the functional role of the NAc to social learning underlying conformity. We find that deactivation of the NAc during conflict with group opinion robustly predicts subsequent conformity and correlates with individual differences in conforming behavior. The NAc is often viewed as an integrator of memory, motivation and goal-directed behaviors (Carelli, 2002). Thus, the individual variability of conformity could also be based on individual differences in the amplitude of the NAc conflict-related responses evoked by conflict with group opinion. The error signal at the ventral striatum, of which the NAc is part, has been previously correlated with individual differences (e.g. Tobler, Fletcher, et al., 2007). A recent study reported that individual behavioral differences predicted the variability of the prediction error activity, particularly in the ventral striatum (Cohen, 2007). We find that conformists demonstrate stronger deactivation of the NAc during conflict with group opinion, indicating a stronger prediction error. We also find that differences in conflict-related responses in trials that are and are not followed by conformity (conformity effects) are weaker in conformists, indicating a higher probability of conformity after any social conflict. Previous studies demonstrated that the social context modulated the activity of the NAc, for example, the perceived fairness of a person seen in pain affected the activity of the ventral striatum (Singer, et al., 2006), the opinion of others modulated the future valuation of objects in the striatum (Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010), and social comparison modulated the activity of the ventral striatum during the processing of rewards (Fliessbach, et al., 2007). We suggest that the social comparison of the obtained reward could also be based on a prediction error mechanism that is similar to that reported in the current study.

Our findings expand the knowledge of the neuronal mechanisms of social norms. Previous studies probing the neural mechanism of conformity or social norms have focused on the differences in neural responses to normative feedback delivered by a social group versus a computer (Berns et al., 2005), on the pathology of norms (King-Casas et al., 2008) and on a modulation of neural activity related to decision making by the possibility of punishment for violation of the norm (Spitzer, et al., 2007). These studies uncovered the effects of the normative context (a prior group opinion Berns, et al., 2005, or the possibility of punishment Spitzer, et al., 2007) on decision making but did not investigate closely the mechanism predicting conforming adjustments in judgment on trial-by-trial basis. The current study has for the first time revealed that the same regions are activated when there is a conflict with group opinion and predict subsequent adjustments of judgments. Our result provides evidence that behavioral conformity to descriptive group norms is triggered by the social conflict monitoring mechanism that is similar to the reinforcement learning signal (Holroyd & Coles, 2002). It is important to note here that there can be different mechanisms underlying conformity (Cialdini & Goldstein, 2004). Informational conformity (in contrast to normative conformity) serves an informational function in helping to be accurate, especially if normative information is provided before the actual decision (e.g. study Berns, et al., 2005). From a neuroscience perspective, informational conformity assumes an attention-related neural mechanism, i.e. an activation of sensory cortices by normative information. In contrast, we find that neural activity predicting conformity to group norm is similar to a reinforcing learning signal. Therefore, conforming adjusted in judgment investigated in the current study are most probably normative and based on reinforcing social approval. In other words, group opinion works as a reinforcer for the individual's judgments. Both reward for being aligned with the group and aversion to being non-aligned may have acted as reinforcers. Further studies will help to generalize the observed mechanisms to the male population and other social situations (including injunctive or moral norms) leading to conformity.

6.5.3. Conclusion

The present study shows that group opinion affects our judgments of facial attractiveness, which play a critical role in human social interaction (see Langlois, et al., 2000 for a review). Our results support the view in social psychology and economics that conformity is based on reinforcing social feedback, and we go on to propose a neural mechanism of conformity that agrees with the concept of reinforcement learning from animal learning theory. The fMRI results suggest that social conformity is based on mechanisms that comply with reinforcement learning. This process starts when a deviation from group opinion is detected by neural activity in the paracingulate region and in the ventral striatum. These regions then produce a neural signal similar to the prediction error signal in reinforcement learning that indicates a need for social conformity: a strong conflict-related signal in the RCZ and the NAc triggers adjustment of judgments in line with group opinion. In fact, a follow-up TMS experiment indicates that the relation between activity in the RCZ and behavioral conformity is causal by nature (Klucharev, et al., 2011). Both the NAc and the RCZ receive midbrain dopaminergic innervations (Schultz, 2006). Moreover, animal studies robustly demonstrated that prediction error signal is dopamine-mediated (Schultz, 2006). Our results suggest that a phasic change in presumably dopamine-related activity occurs when individual judgments differ from normative group opinion. Dopamine-dependent synaptic plasticity is thus a potential cellular mechanism for long-term conforming adjustments of judgments (Schultz, 2006). Since the present results suggest that social conformity is underlined by such fundamental learning principles, for marketing purposes one can rely on conformity and expect a behavioral effect that lasts over long periods of time. Overall, our results suggest that social conformity is underlined by the neural error-monitoring activity which signals probably the most fundamental social mistake—that of being ‘too different’ from others.

Appendix 6.A. MRI Data Acquisition

Functional MRI was performed with ascending slice acquisition, using a T2*-weighted echo-planar imaging sequence (Sonata 1.5 T, Siemens, Munich; 33 axial slices; volume repetition time (TR), 2.28 s; echo time (TE), 35 ms; 90° flip angle; slice matrix, 64 x 64; slice thickness, 3.5 mm; slice gap, 0.5 mm; field of view, 224 mm). For structural MRI, we acquired a T1- weighted MP-RAGE sequence (176 sagittal slices; volume TR, 2.25 s; TE, 3.93 ms; 15° flip angle; slice matrix, 256x256; slice thickness, 1.0 mm; no gap; field of view, 256 mm).

Appendix 6.B. fMRI Data Analysis

Image analysis was performed with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The first three EPI volumes were discarded to allow for T1 equilibration, and the remaining images were realigned to the first volume. Images were then corrected for differences in slice acquisition time, spatially normalized to the Montreal Neurological Institute (MNI) T1 template, resampled into 3x3x3 mm^3 voxels, and spatially smoothed with a Gaussian kernel of 8 mm full-width at half-maximum. Data were high-pass filtered (cut-off at 1/128 Hz).

Statistical analysis was performed within the framework of the general linear model (Friston, et al., 1995). Conflict and no-conflict trials were modeled separately, as were no-conflict trials (mean number of trials 73, SD=0.8), conflict trials (mean number of trials 148, SD=1.5), conflict trials followed by conformity (as tested during the behavioral session, mean number of trials 61, SD=7.8), conflict trials that were not followed by conformity (mean number of trials 52, SD=8.7). The regressors were convolved with the canonical hemodynamic response function of SPM5. In addition, the realignment parameters were included to model potential movement artifacts. In a whole-brain analysis, statistical tests were family-wise error rate corrected for multiple comparisons across the entire brain. For the regions of interest, a small volume correction was used for the analysis of the conformity effects to correct for multiple comparisons across the search volume. For the RCZ and the NAc the search volumes were defined as a sphere with 10 mm radius around the center (x=4, y=15, z=43 and x=±11, y=11, z=-2, respectively) based on the results of a previous study (Knutson, et al., 2005) and meta-analysis (Ridderinkhof, et al., 2004).

The individual contrasts were submitted to group-level random effects analysis. The main effect of social conflict was estimated by contrasting the group ratings in conflict and no-conflict trials. The main effect of conformity was investigated by comparing neural responses for all conflicting group ratings followed by conformity (i.e. facial attractiveness subsequently changed in accordance with the group rating) and all conflicting group ratings that were not followed by conformity (facial attractiveness not changed). In addition, a conjunction analysis was performed to confirm the regional overlap between the main effects of social conflict and conformity by testing the conjunction null hypothesis using the minimum T-statistic as implemented within SPM5 (Nichols, et al., 2005). To assess the relationship between neural activity and individual level of conformity across participants, individual contrast estimates within the RCZ and the NAc local maxima were extracted and entered in correlation analyses (2-tailed).

Image preprocessing and data analysis of Experiment N2 was identical to that of Experiment N1. Differences of neural responses in Experiments N1 and N2 were investigated by two-sample t-test.

Appendix 6.C. Range Effect and Stimulus Properties in Conformity

The Use of Attractiveness Scale in the Consecutive fMRI and Behavioral Sessions

Given the fact that group ratings were often 'more extreme' than participants´ initial ratings, one may argue that the behavioral effect of conformity is simply caused by an increase in variance of the scale used, i.e. variation in ratings of faces is greater in the subsequent behavioral session than in the initial fMRI session. Similarly, the behavioral effect could also be due to a decrease in variance of the scale used if decision-makers initially (during the fMRI scanning) have a tendency to use the extreme ratings more and then learn to use middle range ratings by the subsequent behavioral session. To exclude this simple 'range' effect, we compare variances of ratings for the first (fMRI) session and the second (behavioral) session. We calculated the percentage of extreme ratings (ratings 1, 2, 7 and 8) as an index of extreme responding. In contrast to the alternative range effect hypothesis, Figure 6-11 demonstrates that participants with a central tendency (with a low percentage of extreme ratings) show a smaller variance in the second session, whereas participants with higher portion of extreme ratings do not have this tendency. We also split participants in two groups by a median split on percentage of extreme ratings: participants with the low score (= 0.297) show a significant decrease of variance across sessions (t(1,23)=2.3, p=0.04); participants with a high score did not show any significant difference (t(1,23)=0.1,p=0.34). We did not therefore find any support for the alternative range hypothesis.

Effect of Stimulus Ambiguity on Conforming Changes in Judgment

Social studies have robustly demonstrated that social influence is most effective in an ambiguous situation (Cialdini & Goldstein, 2004). Therefore, the conformity effects should be especially strong for highly ambiguous faces, i.e. for faces whose initial ratings vary a lot across participants. We thus have the following expectation:

Hypothesis 3: The size of the conformity effect (the absolute change in attractiveness judgments due to a conflict with social norms) is lower for non-ambiguous faces than for highly ambiguous faces.

To determine the ambiguity level of each face stimulus, we analyze the variability (standard deviation—SD) of ratings during the fMRI session for each face across all participants: in our sample the SD varies within the range 0.72-1.83. Faces with the lowest (SD = 1.042, n=26) and with the highest SD (SD = 1.621, n=26) are selected for further analysis as non-ambiguous and ambiguous faces, respectively. The hypothesis 3 is supported by the results of a 2-way ANOVA (two-level factor of ambiguity and three-level factor of group ratings): the interaction ambiguity x group ratings is significant (F (2,21)=4.87, p=0.018). A planned comparison shows the size of the conformity effect to be greater for highly ambiguous faces than for non-ambiguous ones (t(1,23)=1.71, p=0.003; see Figure 6-12). This finding thus

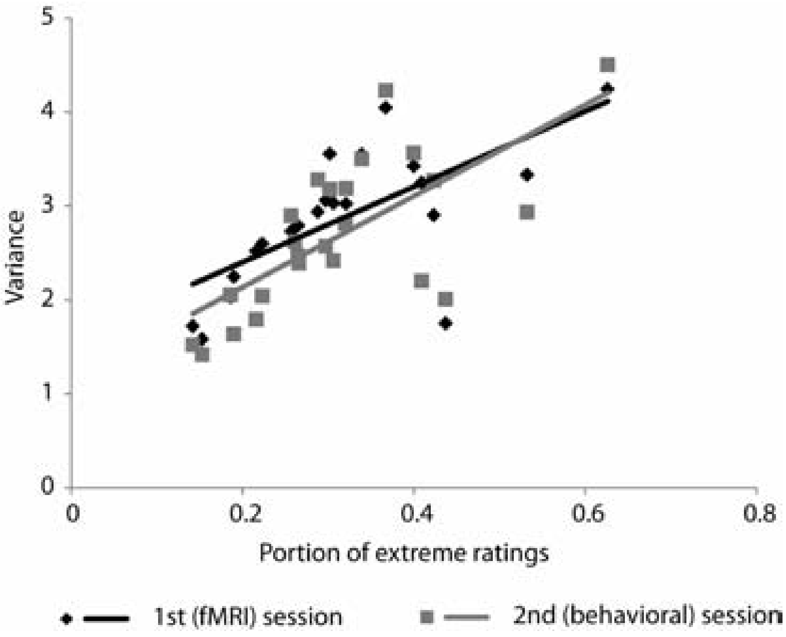

Figure 6-11. Overall distribution of ratings' variance (Experiment N1) for the first (fMRI) session (black) and the second (behavioral) session (grey) as a function of a behavioral tendency. Lines represent trend-lines for each session.

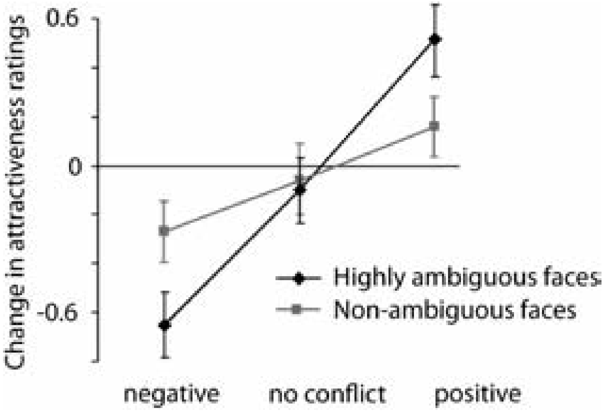

Figure 6-12. Persuasive behavioral effects for highly ambiguous and non-ambiguous stimuli as a function of conflict. In the 'no conflict' condition participants and groups responses are similar. In the other two conditions group's ratings are more positive (negative) than the participant's ratings.

indicates that when there is a high consensus on the initial judgments of a particular stimulus, possibly indicating less ambiguous face stimuli and stronger confidence in the judgment, the participants are not as prone in adjusting their judgment based on social environment.

Chapter 7

General Discussion

This dissertation has introduced the current stage of neuroeconomics literature on valuation and choice and utilized fMRI methodology to investigate the biological mechanisms that underlie contextual effects in valuation, judgment and choice. Section 7.1 summarizes the main insights of the dissertation, giving most weight to the experimental work. Section 7.2 discusses the advantages and limitations of the methodological choice. The following two sections highlight the contributions of this dissertation to literature and practice respectively, and in Section 7.5 the dissertation concludes with prospects for future research.

7.1. Summary of the Main Findings

The first part of the dissertation provided an introductory overview of neuroeconomic studies and methods. In particular, Chapter 2 discussed the role of brain's valuation network in encoding multiple dimensions of risky decision making: outcome magnitude, probability and even the combined expected value are all represented in the valuation network. Also multiple nonlinearities in valuation, such as reference dependence and loss aversion, are present in the brain signal. We also discussed the role of higher cognitive mechanisms (affect and deliberation) in behavioral framing effects. After introducing these basic findings on valuation and choice, Chapter 3 introduced fMRI which is a common method in neuroeconomics and also used in the experiments reported in the dissertation. The next two sub-sections summarize the main findings of the fMRI experiments.

7.1.1. Path Dependence in Risky Choice

Prior behavioral research indicates that decision-makers show increased risk appetite both when they gamble with previously won money (house money effect) and when they have a chance to win back a prior loss (break-even effect). Previously these effects have been explained by insufficient updating of a reference point: after a positive outcome, the reference point is low, decreasing the influence of loss aversion in future choices, whereas after a negative outcome the reference point is high, leading to a risk-seeking attitude which is predominate in a loss domain. In Chapter 4 we proposed and tested another explanation: the changes in appetite for risk after gains and losses may be driven by increasing affective processing and by decreasing deliberation. We recorded the brain activities of decision-makers while they made choices in a novel sequential risky-choice task. Importantly, we found that house money and break-even effects persist even in a single within-subject experiment. The brain imaging findings clearly distinguish two networks that promote path dependence: in line with our expectations, increased affective processing and decreased deliberation during gains and losses are generally related to the future tendency to select risky prospects. Moreover, the strength of activation in these brain networks explains the strength of behavioral effects in individual participants. Interestingly, the fMRI data suggests different time dynamics for affective and deliberative processes for gain and loss outcomes: while both increasing affect and decreasing deliberation were observed in gain and loss trials during feedback information (outcome phase), in the decision making phase that followed we observed increased affect only after losses and decreased deliberation only after gains. Overall, the results support the role of affect and deliberation in path dependence of risky choice.

In Chapter 5 we tested whether risky prospects are evaluated in absolute terms or in a history-dependent fashion. In our novel paradigm, we were able to compare identical risky prospects with different historical background while accounting for a high variability in the absolute expected value of individual gambles. Results from the study confirm the hypothesis that risky prospects are valued in a path-dependent manner in a dynamically changing environment: both the bilateral striatum and the medial orbitofrontal cortex (mOFC) value risky prospects relative to their prior states as opposed to their absolute values. The mOFC was found to be particularly sensitive to relative gains whereas the striatum differentiated both relative gains and losses from neural states. These findings provide strong support for the role of the striatum and the mOFC in reference to dependent valuation of risky prospects.

7.1.2. Social Feedback Modulates Future Judgments

In Chapter 6 we studied how the social environment modifies judgments. In detail, we tested how participants' initial judgments of facial attractiveness were influenced by group opinion. We found that the perceived difference of individual ratings from group ratings triggers long-term conforming behavioral adjustments in judgment, i.e. participants change their attractiveness ratings to align them with group ratings. As we expected, a conflict with group opinion activates RCZ and deactivates the NAc, which implies that conflict with normative group opinion triggers neuronal signals similar to the prediction error signal of reinforcement learning. Subsequent conformity in judgment is predicted by larger conflict-related responses. Conjunction analysis revealed a spatial overlap between the conflict-related activity and activity which predicts subsequent conformity. Furthermore, the individual strength of the conformity-related activity in the ventral striatum correlates with differences in conforming behavior across participants. Finally, we conducted behavioral and fMRI control experiments (a pilot behavioral experiment and Experiment N2) to examine the relevance of the social environment for our results. In these experiments we used a modified social version and/or a non-social version of the task by replacing group normative opinion with other social feedback (behavioral pilot) or computer-generated ratings (behavioral pilot and Experiment N2). We found that conforming behavior and related effects in the RCZ and the NAc are particularly strong in the social condition, and that social relatedness is correlated with the degree of conformity in the task. Overall, this data provides novel evidence that social conformity effects in judgment are based on basic and automatic brain mechanisms similar to reinforcement learning: a conflict with group opinion triggers a prediction error signal, indicating a need for adjustment of judgments.

7.2. Methodological Considerations: Limitations and Advantages

7.2.1. Inverse Inference Fallacy and Lack of Causality

Ideally, using neuroscientific methods could enhance decision theory by providing process-level information on the calculations that lead to observed behavior, thus giving better possibilities to understand and forecast decision behavior in experimental and real life circumstances. The status of neuroimaging technologies and the current level of knowledge on the functioning of the human brain set some restrictions on reaching this goal. Here we discuss some prominent problems in the context of this dissertation work, one that is created by the level of knowledge on brain function and the others are specific for fMRI. The first problem is the inverse inference fallacy, i.e. the problem of inferring mental states from observed brain activation sites. Second, we discuss some typical features of fMRI data set: the lack of causality and absolute measure of brain activation[49].

In the studies reported in this dissertation we have attempted to circumvent, or at least minimize, the problem of inverse inference by basing our interpretations on larger networks of brain regions that are simultaneously activated in tasks instead of relying on an interpretation that is based only on one activated brain region. In the risk experiment we used knowledge of interconnected brain networks that are known to have at least some level of specificity to affective salience and executive control processes (Seeley, et al., 2007). In Chapter 5 we tested a hypothesis on path-dependent valuation of risky prospects. We found differential activation in two distinct reward-sensitive brain regions when comparing identical prospects with different historical paths. Similarly, when studying the effects of social feedback on judgment, we based our interpretations on the simultaneous effects in the RCZ and the NAc (striatum), both of which have previously been reported to reflect prediction error signals in reinforcement learning (Gehring, et al., 1993; Hare, et al., 2008). However, the discussion on the exact role of brain regions in affective salience, executive control, valuation, and learning processes is still continuing. For instance, Craig (2009) argues that parts of the salience network are related to the feeling of awareness, instead of indicating the presence of affective content.

Due to the correlative nature of fMRI research, most of the findings reported in this dissertation lack causality between brain and behavior, and instead indicate correlation between events and brain activation. However, some of the findings do implicate causality in the sense that brain activations which occurred in an earlier time point explained later behaviors. For instance in Chapter 4, the affective and deliberative brain networks that activate for gain and loss experiences also correlated with subsequent choices, so that high affective activation indicates future risky choices and high control network activation correlates with subsequent safe choices. Similarly, in Chapter 6, error-related brain regions, which reacted to conflicts in judgment with the group opinion, also showed stronger responses in those conflict trials where decision-makers

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[49] See also Section 3.3.1 for further elaboration on the limitations of fMRI.

subsequently conformed to the group opinion than where they did not. This 'predictive power' of fMRI signals for subsequent behaviors implies the possibility of a causal relation between the brain processes and behavioral patterns. Additionally, fMRI research gives a good basis for further experimentation on the causal link between brain and behavior. As an example, the implied causality from RCZ to behavioral social conformity has been later confirmed with TMS (Klucharev, et al., 2011).

In addition to the lack of causality, fMRI does not provide an absolute measure of brain activity. The relative nature of the signal leaves room for interpretation: the same statistical results can be found when the activity level of a brain region increases in some conditions or when it decreases in opposing conditions. For instance, in the risk experiment (Chapter 4), the difference in the executive control activity between gain (loss) and neutral conditions can be interpreted as increased use of the executive control network during neutral outcomes or as reduced use of the network during gain (loss) experiences.

7.2.2. What Does Neuroimaging Provide Beyond Behavioral Studies?

Based on the present studies and other research in neuroeconomics, we argue that using neuroscientific tools can contribute to the process-level understanding of human decision making, which may facilitate future research on the topic. For instance, the results of the risk study in Chapter 4 suggest the role of affective and deliberative systems in path dependence of risky choice, and provide information on the timing and the behavioral influence of these two processes. Specifically, the results indicate that, after negative events, emotional arousal activity continues during the subsequent choice whereas after a positive event the next choice is accompanied by decreased levels of activation in the executive control regions of the brain. One could thus hypothesize that controlling for affective reactions during decision making is especially important after negative events in order to prevent excessive risk taking whereas after positive events decision-makers might resist the increasing appetite for risk by deliberating carefully on the choice situation. Thus, even though the neuroimaging findings do not necessarily provide conclusive evidence of the underlying psychological processes, fMRI does provide a direct, objective measure of the reactions to the task and gives insightful exploratory perspectives on choice behavior which can inspire future research. Naturally it may be possible to attain similar information on decision-making processes also by behavioral means, for instance by manipulating either the affective network or the deliberative network in multiple time points of the decision-making task. Without a clear hypothesis, however, this type of behavioral approach might require extensive effort due to the large number of possible influencing variables.

7.3. Contribution to Literature

Due to the interdisciplinary nature of neuroeconomics and neuromarketing, this dissertation aimed to contribute to multiple lines of literature: scientific contributions to economic and consumer decision making as well as to neuroscience were of importance. One of the basic principles when planning the research was to design fMRI experiments with the potential to provide high quality data and insightful results which shed light on both the functioning of the brain and the biological underpinnings of risky choice behavior and social conformity. The rest of this section discusses the contributions of each part of the dissertation in turn.

Chapter 2 explored the existing literature on neuroeconomics, giving a neuroscience perspective on preference formation and dual process models in decision making. The main contribution of this work was to summarize the biological mechanisms underlying choice behavior and indicate how different processes relate to behavioral deviations from utility maximization. In detail, the chapter indicated how some behavioral deviations, such as reference dependence of valuation and nonlinear probability weighting, are reflected in the brain's valuation network whereas other phenomena, such as framing effects, are more driven by the balance between emotion and deliberation. The chapter concludes with a speculation on how different deviations could be reduced. Since valuation is related to reasonably automatic neurotransmitter mechanisms it is argued that deliberately suppressing valuation-driven deviations in behavior is more challenging than suppressing deviations driven by emotion.

Considering that consumers make their choices as a part of ongoing sequence of experiences, it is relevant to understand what kind of dependencies there are between past experiences and current choices. This dissertation addressed path dependency in risky choice from two different perspectives. First, the findings of Chapter 4 contribute to the theoretical basis of path dependence in risky choice by indicating the role of affect and deliberation in respectively enhancing and decreasing the risk appetite after gains and losses. Previously path dependence has been accounted for by assuming insufficient updating of a reference point, but our findings suggest that higher-level affective and cognitive functions may also play a role. Interestingly, the data also indicates that these affective and deliberative reactions correlate with the individual strength of the behavioral effects. This finding suggests that variability in the behavioral path-dependency might be related to differential functioning of emotional and executive control mechanisms between decision-makers. This study contributes to the neuroscientific literature on risky choice by paying special attention to the effects of prior outcomes and events on the current performance. Often neuroscientific studies concentrate more on individual choices, ignoring possible carry-over effects in trial sequences (see, for example, Chapter 2 for a review of some of the neuroeconomics studies). Second, Chapter 5 expanded knowledge on reference-dependent valuation. Previously it has been shown that outcomes are valued in respect to the other possible outcomes. Here we show that risky prospects are also valued relative to the previously available risky prospects. This history-dependence in valuation may also bias the evaluation of decision problems in sequential choice situations.

Chapter 6 of the dissertation presented fMRI data on social conformity. The experimental paradigm captured the neural mechanisms underlying compliance to descriptive social norms. The results support the hypothesis suggested in social psychology and economics that conforming adjustments in judgment are based on the reinforcing nature of social feedback. The findings indicate that the very same basic neural mechanisms that indicate erroneous responses in simple tasks are activated when decision-makers' judgment differs from a group opinion, and that these basic 'error' reactions guide future judgments towards the group opinion. Furthermore, behavioral conformists and non-conformists differ in the strength of their 'error' reactions, explaining individual sensitivity to group pressure. These findings contribute to the theoretical understanding of social conformity and extend the neuroscience literature on error detection to social conflicts where there are no absolute 'correct' and 'incorrect' answers.

7.4. Managerial Relevance

Reconsider the scenario of consumer who enters a casino with a group of friends without any intention of investing money on gambling. As discussed in the introduction, the consumer's attitude towards playing might be adjusted in response to her social surroundings, and once she begins playing the win and loss history can affect her subsequent risk appetite. The behavior of consumers in such environments has significant financial and societal consequences. First, gambling is a large-scale business with substantial revenues. For instance, in the Netherlands the revenues of the state-owned lottery, *Staatsloterij*, were 889.7 million Euros in 2009 (Staatsloterij, 2009) and those of Holland Casino were 595.6 million Euros (De Nationale Stichting tot Exploitatie van Casinospelen, 2009). Second, gambling is a public health issue, raising health, social and economic problems in a community (Korn & Shaffer, 1999). On a personal level, gambling behavior can become compulsive and develop into a pathological gambling disorder. Compulsive gambling can have serious adverse effects on personal and family life and finances, similar to other compulsive consumption behaviors such as compulsive buying (Korn & Shaffer, 1999; Oguinn & Faber, 1989).

This dissertation addressed the mechanisms that influence path dependence in risk-taking behavior and how social environment influences our judgments. The dissertation adopted an exploratory approach by studying the brain networks that are activated during choices and judgments. In general, the findings suggest that increasing risk appetite after gains and losses is driven by increasing emotional arousal and decreasing deliberation. The addictive nature of gambling might be decreased by providing services that prohibit consumers from overspending. Such services could be based on activities that help consumers to 'cool down' emotionally after they have lost significant amounts of money or mechanisms that remind consumers to consider their actions carefully after they have made large gains. These types of policies would be in line the fMRI findings from Chapter 4 which imply a role for emotion regulation in preventing excessive risk-taking in future choices particularly after earlier losses. The results also suggest that after gain experiences decision-makers should pay special attention to deliberation. In fact, helping consumers to cope with their emotional arousal might even increase consumer satisfaction and the likelihood that the customer will revisit the site after a pleasant experience. Previous behavioral research indicates that when decision-makers reduce their emotional arousal after losses, they continue gambling at their previously planned level of risk and avoid the excessive gambling that otherwise occurs after losses, and such 'cooling-down' services after losses have successfully been provided for consumers at casinos (Andrade & Iyer, 2009). In addition to such interventions, consumers might also benefit from training on emotion-regulation skills: therapeutic tools for improving emotion regulation have been successfully used with patient groups suffering from emotion regulation deficits and as a preventive tool for people who experience high emotional strain on a daily basis (Berking, Meier, & Wupperman, 2010; Shearin & Linehan, 1994).

In Chapter 6 we report that social environment influences our judgments through similar neural 'error responses' to those that induce learning in simple trial-and-error tasks. An important detail in the findings is that the judgments did not only change short term in the presence of other people, but instead the social context altered the subjective attractiveness ratings over a longer time period, indicating a change in opinion beyond temporary social gratification. Since the results indicate that the conforming adjustments to group opinion are driven by quite basic learning mechanisms, social conformity might be difficult to control intentionally. It is even possible that people are not always aware of these adjustments in their judgment. Such automatic mechanisms can have a very strong effect in guiding consumer behavior. Indeed, descriptive social norms have been found to be more effective in adjusting behavior than, for instance, environmental or financial motivators (Goldstein, et al., 2008; Schultz, et al., 2007). This indicates the strength of social norms in adjusting behavioral patterns of consumers and the potential for using social norms in social marketing. If social marketing campaigns can successfully create a perception that the majority of the salient others enjoy healthy food, support environmental values by recycling, quit smoking or protect themselves against direct sunlight, this could lead to reduced obesity and pollution of the environment and it could also decrease the number of lung and skin cancer patients. When designing such social marketing campaigns, one should also bear in mind the possibility of 'boomerang effects'. If the consumers realize that they are being persuaded, this can reverse the intended effects, bringing about the opposite behaviors: people act against the promoted behavioral patterns to demonstrate their freedom of choice. The strength of social norms in adjusting consumer behavior might also create a challenge: all real-world examples influence consumer behavior as well. Promoting healthy diets with the slogan “everyone loves healthy food!” next to a fast food restaurant might belie the campaign message.

7.5. Prospects for Future Research

This dissertation investigated path dependence and environmental effects in valuation, judgment, and choice by using fMRI, a modern neuroscientific method. The experiments suggest that context dependence can be driven by multiple mechanisms: for instance affect, deliberation, and basic learning mechanisms. In particular, the results suggest that increasing affect and decreasing deliberation drive increases in risk appetite after prior gain and loss experiences, that prospects are valued in a path-dependent manner, and that conforming judgments in line with group opinion are driven by basic learning mechanisms. Future research is needed to study the neuronal underpinnings of other important factors that influence sequential consumer choices. An example of such factor is goal fulfillment and how prior experiences might influence goal target levels. Previously it has been shown that prior positive experiences increase consumers’ goal target levels which motivate increasing risk appetite (Novemsky & Dhar, 2005), but there is limited information on what type of processes could drive these changes in target levels.

Another interesting line for future research is to test behaviorally the hypotheses that can be derived from the process-level information described in this dissertation and from neuroeconomics literature in general. For instance, one could test whether consumers remain at their normal level of attitude to risk if they are instructed to pay special attention to deliberation during decision making after prior positive experiences, and whether this instruction would have similar effects on decision making after negative experiences. Taking that further, one could use the process-level knowledge provided by these fMRI experiments as one information source for further development of behavioral models. This theoretical work could provide more accurate forecasts of behavior in novel settings and also give useful rules of thumb for understanding behavior in real-life circumstances. In general, combining information from behavioral and neuroscience research could provide interesting insights and avenues for future research and practical applications.

So far, the neuroeconomic research program has provided valuable information on the brain processes involved in valuation and choice but the direct practical implications, which could not be gained without neuroimaging, are less clear. Increasing understanding of these basic processes and technological advances in neuroimaging provide a fruitful set of tools for higher-level applications, but more consideration is still needed to find the proper tools and questions for which neuroimaging can provide unique information. For instance, new approaches to neuroscientific data, such as multi-voxel pattern analysis, may increase the sensitivity of fMRI research and improve the quality of neuromarketing research. In the field of marketing one potential avenue which remains largely unexplored in neuroscientific terms is early product design (Ariely & Berns, 2010). In addition to the related studies described in the introduction (Chua, et al., 2011; Falk, et al., 2011; Knutson, et al., 2007; Tusche, et al., 2010), some recent findings suggest that neuroimaging tools might be useful in predicting a product's future success prior to commercial breakthrough: listening to songs by unsigned or independent artists evokes brain activity that correlates with the realized sales of the coming three years (Berns & Moore, 2011). In conclusion, brain imaging can provide predictions of future success, indicating the great potential of these tools for market research.

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Summary

This dissertation investigates economic behavior in risky and social settings with neuroscientific tools. The recent expansion of knowledge in human brain function has created unprecedented prospects for studying human behavior directly at its source—the brain. These new possibilities have also motivated the development of consumer neuroscience and neuromarketing by providing insights on the relevant brain processes that drive consumer decision making. The research reported in this dissertation utilizes modern functional magnetic resonance imaging (fMRI) technology that is currently one of the most popular methods in cognitive neuroscience.

The first part of the dissertation gives a theoretical and methodological introduction to neuroeconomics and fMRI. The chapter discusses relevant background literature on valuation and risk, as well as on the influence of emotion and cognitive deliberation in decision making. The literature review indicates that the valuation (reward) network, including the striatum and the orbitofrontal cortex, encodes multiple dimensions of risky prospects, i.e. the outcome magnitude, probability and expected value. The striatum also accounts for nonlinearities in valuation: both reference dependence and loss aversion are reflected in the striatum activity. In respect to the role of higher cognitive mechanisms (affect and deliberation) in decision making, the prior research findings suggest that affect, as reflected in the amygdala activity, is related to strong framing effects whereas cognitive conflict related activity in the anterior cingulate cortex reflects resistance to context effects. Overall the literature review indicates the relevance of valuation mechanisms and higher cognitive functions in decision making.

The second part of the dissertation investigates risk behavior in sequential choice situations. Prior research indicates that decision-makers may increase their risk appetite after gains and losses. Here we show that this increase in risk appetite is driven by affective brain reactions and by insufficient use of cognitive control mechanisms. In detail we found that gain and loss experiences induce activity in an affective brain network consisting of insula and affective parts of anterior cingulate cortex, and that this activity predicts future risky choices. Simultaneously, activity in a cognitive control network, especially in the lateral parietal cortices, decreases and predicts future risk avoidance. During the

subsequent choice after an outcome revelation, we found brain evidence for an increased level of affective processing only after loss experiences whereas after gain experiences we found decreased level of cognitive control activity. Overall, these results contribute to the literature by indicating the role of affect and deliberation in path dependency. On a practical level these results suggest that decision-makers might be able to reduce path dependence in risky choice by 'cooling down' after negative experiences before committing to a new choice. In contrast, after positive events the decision-makers should deliberate on new choices carefully to avoid careless risk taking. Policies that help consumers in achieving these goals may lead to more consistent choice behavior and long-term satisfaction. In the context of the sequential choice task, the dissertation also discusses reference dependence in valuation. Prior literature indicates that decision-makers value outcomes relatively to the other possible outcomes instead of in an absolute manner. Here we show that the striatum values also risky lotteries in a reference dependent manner, suggesting that risky choice problems are evaluated in the brain in a path-dependent manner.

The third part of the dissertation discusses social conformity, i.e. the tendency of adjusting one's opinion in line with the observed group opinion. We found that disagreement with others activates learning mechanisms and induces an 'error reaction' in the participant's brain. In detail, a conflict with the group evoked responses in two brain regions which have previously been related to conflict detection and error processing: we found increased activity level in the rostral cingulate zone, an area which is sometimes also labeled as the anterior cingulate cortex, and decreased activity in the nucleus accumbens (ventral striatum). The stronger these learning signals are the more likely participants change their own judgment to conform to the group opinion. Overall, these results indicate that the brain mechanisms of social conformity comply with the fundamental and automatic brain processes of reinforcement learning. These findings support the effectiveness of social marketing campaigns that make use of social norms (descriptive norms). Public's attitude towards promoted behavioral patterns may change through basic learning mechanisms on a long term basis when people perceive the promoted behaviors to be common among their peers.

In the final chapter we conclude that regardless of the current challenges that neuroscientific research methods encounter when studying high level cognitive functions such as decision making, neuroimaging has its place in the palette of research tools in economics and marketing. When the neuroimaging tools are used for appropriate research questions, the directness of the measure and its exploratory power can provide great advantage in respect to other available research methods.

Nederlandse samenvatting (Summary in Dutch)

Dit proefschrift onderzoekt economisch keuzegedrag in risicovolle en sociale situaties met behulp van methoden uit de neurowetenschappen. De huidige groei van kennis over het brein heeft geleid tot de ontwikkeling van 'neuroeconomics' en 'neuromarketing', onderzoeksgebieden waarin de neurale processen worden onderzocht die van belang zijn bij consumentenbeslissingen. Dit proefschrift maakt gebruik van een populaire onderzoeksmethode in de cognitieve neurowetenschappen, 'functional magnetic resonance imaging' (fMRI).

Het eerste deel van het proefschrift bestaat uit een inleiding over de theoretische en methodologische achtergrond van 'neuroeconomics' en fMRI. Dit deel introduceert de relevantie van emoties, hogere cognitieve functies en zogenaamde waarderingsmechanismen bij besluitvorming.

Het tweede deel van het proefschrift onderzoekt risicogedrag in situaties waarin deelnemers sequentiële keuzes maken. Uitkomsten van een risicobeslissing blijken grote gevolgen te hebben voor de daaropvolgende keuze. Mensen blijken meer risico's te nemen zowel na een grote winst als na een groot verlies in vergelijking met een gemiddelde uitkomst. Onze resultaten laten zien dat deze neiging tot het nemen van risico's na winst en verlies wordt gedreven door de ervaring van emoties in het brein in combinatie met een onvoldoende gebruik van systemen die een rol spelen bij cognitieve controle. De resultaten suggereren dat emoties en zorgvuldige rationele overwegingen een rol spelen bij padsafhankelijkheid ('path dependency'). In hetzelfde experiment vinden we ook dat het brein risicovolle keuzeproblemen waardeert op een padsafhankelijke, relatieve manier. Het beloningssysteem in het brein kijkt bij het beoordelen van risicovolle keuzes (loterijen) ook naar de voorgaande situatie. Oftewel, de waardering van een loterij is relatief: een loterij wordt positief gewaardeerd als in de voorgaande situatie minder goede loterijen aanwezig waren en dezelfde loterij wordt negatief gewaardeerd als in de eerdere situatie betere loterijen aanwezig waren .

Het derde deel van het proefschrift gaat over de neiging om je mening aan te passen aan die van de groep (de neiging tot conformisme). Dit werd onderzocht door proefpersonen gezichten te laten beoordelen op aantrekkelijkheid en ze vervolgens het oordeel van hun 'peer' groep te laten zien over datzelfde gezicht. Wij vonden dat wanneer iemands mening verschilt met die van de groep er in het brein een zogenaamd foutsignaal wordt gegenereerd. De sterkte van het foutsignaal bepaalde de mate van aanpassing van het oordeel in de richting van de groepsmening. De resultaten suggereren dat de neurale processen die een rol spelen bij sociale aanpassing dezelfde zijn als de fundamentele processen die van belang zijn bij het leren door middel van beloning en straf. Deze bevinding ondersteunt het gebruik van sociale normen in sociale marketing campagnes.

Het laatste hoofdstuk concludeert dat ‘neuroimaging’ een toegevoegde waarde heeft binnen de verschillende onderzoeksmethoden die gebruikt worden in economie en marketing. Vergeleken met andere methodes levert de neurowetenschappelijke methode een directe en exploratieve manier om de processen te meten die een rol spelen bij besluitvorming.

Tiivistelmä suomeksi (Summary in Finnish)

Tämä väitöskirja tutkii taloudellista käyttäytymistä sekä riskipitoisissa että sosiaalista kanssakäymistä sisältävissä tilanteissa aivokuvantamisen avulla. Viime aikoina lisääntynyt tieto ihmisaivojen toiminnasta on luonut pohjaa kuluttajien päätöksentekoprosessien tutkimiseen aivokuvantamismenetelmillä neurotaloustieteen ja neuromarkkinoinnin aloilla. Tämä väitöskirja tutkii päätöksentekoprosesseja toiminnallisella magneettikuvauksella, joka on tällä hetkellä yksi suosituimmista aivokuvantamismenetelmistä.

Väitöskirjan ensimmäinen osa käsittelee neurotaloustieteen teoriaa ja menetelmiä. Erityisesti tässä osassa keskitytään korkeiden kognitiivisten toimintojen ja tunteiden rooliin päätöksenteossa sekä arvottamiseen liittyviin aivomekanismeihin.

Väitöskirjan toinen osa tutkii riskikäyttäytymistä toistuvissa päätöksentekotilanteissa. Aikaisempien kokeiden perusteella tiedetään, että koehenkilöt ottavat enemmän riskejä sekä voittojen että tappioiden jälkeen. Tuloksiemme perusteella nämä muutokset riskikäyttäytymisessä voivat johtua aivojen tunnereaktioista sekä vähenevästä kognitiivisesta harkinnasta. Tulokset viittaavat siihen, että tunnereaktiot ja rationaalinen harkinta ovat merkittäviä tekiöitä peräkkäisten päätösten välisiin riippuvuuksiin eli polkusidonnaisuuteen ('path dependency'). Mittausaineisto osoittaa myös että aivot arvottavat riskipitoisia tilanteita polkusidonnaisesti: riskitilanteet arvotetaan suhteessa aikaisempiin riskivaihtoehtoihin.

Väitöskirjan kolmas osa käsittelee laumakäyttäytymistä, eli miten ihmiset muuttavat mielipidettään ryhmän mielipiteen mukaiseksi. Tuloksemme osoittavat, että ryhmän mielipiteestä eroaminen herättää aivoissa oppimiseen liittyvän virheestä ilmoittavan reaktion. Tämä löydös viittaa siihen, että laumakäyttäytymistä ohjaavat samat aivojen oppimismekanismit, jotka liittyvät myös hyödyn ja haitan kokemisen kautta tapahtuvaan vahvistusoppimiseen. Ihmiset siis oppivat melko automaattisesti käyttäytymään samoin kuin kaikki muutkin käyttäytyvät.

Väitöskirjan viimeinen kappale pohtii aivokuvantamismenetelmien roolia taloudellisen päätöksenteon tutkimuksessa. Verrattuna muihin saatavilla oleviin menetelmiin aivokuvantaminen tarjoaa suoran ja eksploratiivisen mitan ihmisten päätöksentekoprosesseihin.

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About the Author

Kaisa Hytönen was born in Kuopio, Finland on August 12, 1981. In her undergraduate studies at the Helsinki University of Technology she majored in Biomedical Engineering with a minor in Systems and Operations Research. In 2005, she received her master's degree in Engineering Physics with a distinction. Soon after her graduation she started her Ph.D. research in neuroeconomics at the department of Marketing Management, Rotterdam School of Management. Due to the interdisciplinary nature of her Ph.D. project, Kaisa conducted most of her research in Nijmegen at the Donders Institute for Brain, Cognition and Behaviour, Centre for Cognitive Neuroimaging. She has presented her work at several international conferences, such as the annual meetings of the Society for Neuroeconomics in Park City (UT), Nantasket Beach (Hull, MA) and Evanston (IL). Currently, she works as a post-doctoral researcher at the Aalto University in Finland.

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CONTEXT EFFECTS IN VALUATION, JUDGMENT AND CHOICE
A NEUROSCIENTIFIC APPROACH

It is well known that our choices and judgments depend on the context. For instance, prior experiences can influence subsequent decisions. People tend to make riskier decisions if they have a chance to win back a previous loss or if they can gamble with previously won money. Another example of context is social environment. People often change their judgments to conform to observed group behavior. Since the reasons driving such context effects are less clear, this dissertation explores the mechanisms behind behavioral patterns with the help of a modern neuroscience technique, functional magnetic resonance imaging. The dissertation concentrates particularly on choice and judgment in risky and in social settings. It consists of three parts. The first part provides a primer on the methodology of neuroeconomics and a synthesis of the body of knowledge on the brain mechanisms of valuation and choice. The second part investigates risk behavior in sequential choice situations. The findings suggest that decision makers tend to take excessive risk after both wins and losses, due to increasing affective arousal and decreasing control. The third part of this dissertation focuses on the influence of social context on judgment. Results indicate that people automatically learn to behave as others do—being different from others is processed in the brain in a similar way to behavioral errors. This indicates the great power of relevant social groups in influencing our behavior. Overall, this dissertation highlights the reasons behind context dependency and demonstrates the power of modern neuroscientific methods for understanding economic behavior.

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