Neuroeconomic Foundations of Reward, Loss, and Risk Processing

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„Wenn ein Mensch mit aller Anstrengung lernt und forscht, so wird ihm mit jeder neuen Erkenntnis, die er auf sich nimmt, die Welt größer und weiter.“

- Willi Graf

Mitglied der Widerstandsgruppe Weiße Rose
Alumnus der Rheinischen Friedrich-Wilhelms-Universität Bonn

„When a person fully commits themselves to learning and exploring, their world grows larger and broader with each new discovery.“

- Willi Graf
Member of the German resistance movement White Rose
Alumnus of the University of Bonn

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List of Abbreviations

AI	Anterior Insula
AIM	Affect-Integration-Motivation framework
AOI	Areas Of Interest
BAS	Behavioral Activation System
ß-value	Weight attached to a regressor x in a GLM
BIS	Behavioral Inhibition System
BOLD response	Blood-Oxygen-Level Dependent response
DTI	Diffusion Tensor Imaging
EEG	Electroencephalography
EU	Expected Utility
EV	Expected Value
FFFS	Fight Flight Freeze System
FFM	Five-Factor Model of personality
FWE	Family Wise Error
fMRI	functional Magnetic Resonance Imaging
GARP	Generalized Axiom of Revealed Preference
GLM	General Linear Model
Hb	Hemoglobin
HEXACO-PI-R	“Honesty-Humility”, “Emotionality”, “eXtraversion”, “Agreeableness”, “Conscientiousness”, and “Openness to Experience” Personality Inventory – Revised
HH	Honesty-Humility scale assessing egoism in the HEXACO-PI-R
IST 2000R	Intelligence-Structure-Test 2000 Revised
LP	Loss Prediction
LPE	Loss Prediction Error
LR	Loss Reception
MEA	Munich Center for the Economics of Aging
MFG	Middle Frontal Gyrus
MNI	Montréal Neurological Institute
MRI	Magnetic Resonance Imaging
MR signal	Magnetic Resonance signal
NEO-O	Openness to Experience, measured using the NEO-FFI
NEO-C	Conscientiousness, measured using the NEO-FFI
NEO-E	Extraversion, measured using the NEO-FFI
NEO-FFI	The Neuroticism-Extraversion-Openness to experience Five Factor Inventory
NEO-A	Agreeableness, measured using the NEO-FFI

NEO-N	Neuroticism, measured using the NEO-FFI
PCA	Principal Component Analysis
PCC	Posterior Cingulate Cortex
PT	Prospect Theory
ROI	Risk Optimism Index
RP	Reward Prediction
RPE	Reward Prediction Error
RR	Reward Reception
rRST-Q	Reuter and Montag's revised Reinforcement Sensitivity Theory Questionnaire
RST	Reinforcement Sensitivity Theory
RTI	Risk Tolerance Index
SN	Substantia Nigra
SVO	Social Value Orientation questionnaire
T	Tesla
VS	Ventral Striatum
VTA	Ventral Tegmental Area
vmPFC	ventromedial Prefrontal Cortex
WARP	Weak Axiom of Revealed Preference

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Preface

Please note that as part of this cumulative doctoral thesis and with the help of my co-authors, I was able to publish three studies in peer-reviewed journals. The first one, entitled “Goal or gold: Overlapping reward processes in soccer players upon scoring and winning money”, was published in April 2015 in the journal *PLOS ONE* and is referred to as “study one” (Häusler et al., 2015). The second study, entitled “Gain- and loss-related brain activation are associated with information search differences in risky gambles: An fMRI and eye-tracking study”, was published in September 2016 in the journal *eNeuro* and is referred to as “study two” (Häusler et al., 2016). The third study, entitled “Preferences and beliefs about financial risk taking mediate the association between anterior insula activation and self-reported real-life stock trading” was published in July 2018 in the journal *Scientific Reports* and is referred to as “study three” (Häusler et al., 2018).

Additionally, please note that the materials and methods described in chapter two only include the ones used in these three studies and not the ones used in the other four that I additionally worked on during the time of my doctoral studies (chapters 8.1.2 and 8.1.3).

Summary

Together with neuroscientific inventions such as functional magnetic resonance imaging (fMRI), economic and psychological developments in the study of human decision making have led to the formation of neuroeconomics. As part of this research, several aspects of reward, loss, and risk processing have been related to (sometimes irrational) human decision making. The three studies that form the foundation of this doctoral thesis integrated techniques from neuroscience, psychology, and economics to answer specific questions about this relationship.

The first study provides evidence for a common neural currency of reward processing and shows that it exists in the context of money and soccer. The second study implemented fMRI and eye-tracking in two separate experiments to show that reward- and loss-related brain activation is associated with attention distribution (e.g. winning amount vs. winning probability) in risky gambles. The third study presents the neuroeconomic (i.e. neuroscientific, psychological, and economic) associations of real-life stock purchase and extends previous findings of financial risk taking from the laboratory to real life. Using the framework of reward, loss, and risk processing to answer detailed research questions about human decision making, all three studies show the strength of the neuroeconomic approach and add valuable information to our understanding of human behavior.

In the first chapter, the thesis provides background information on the field of neuroeconomics and describes the benefits of the neuroeconomic approach. The second chapter describes the materials and methods used in the three studies. It is followed by chapter three, which summarizes and links the three main publications that I worked on during my doctoral studies. Finally, chapter four consists of a conclusion, as well as an outlook and possible applications of the research findings.

Zusammenfassung

Zusammen mit neurowissenschaftlichen Erfindungen wie der funktionellen Magnetresonanztomographie (fMRT) haben ökonomische und psychologische Entwicklungen bei der Untersuchung von menschlichem Verhalten zu der Entstehung der Neuroökonomie geführt. Als Teil dieser Untersuchungen wurden Aspekte der Belohnungs-, Verlust- und Risikoverarbeitung in Relation zu (teilweise irrationalem) menschlichem Verhalten gesetzt. Die drei Studien, welche Teil dieser Doktorarbeit sind, haben Techniken der Neurowissenschaften, Psychologie und Ökonomie verwendet, um bestimmte Fragen über diese Zusammenhänge zu beantworten.

Die erste Studie zeigt, dass eine gemeinsame neuronale Währung bei der Belohnungsverarbeitung im Kontext von Geld und Fußball verwendet wird. In der zweiten Studie wurden in jeweils unterschiedlichen Experimenten Daten mit Hilfe von entweder fMRT oder Blickregistrierungstechniken gesammelt, um einen Zusammenhang zwischen der Belohnungs- und Verlustverarbeitung und der Aufmerksamkeitsallokation (e.g. Gewinnbetrag vs. Gewinnwahrscheinlichkeit) in risikobehafteten Lotterien festzustellen. Die dritte Studie stellt die neuroökonomischen (i.e. neurowissenschaftlichen, psychologischen und ökonomischen) Zusammenhänge des Aktienkaufs (im echten Leben) fest und überträgt bisherige laborbasierte Untersuchungen auf das echte Leben. Alle drei Studien verwendeten das Gerüst der Belohnungs-, Verlust-, und Risikoverarbeitung, um die Stärke des neuroökonomischen Ansatzes zu veranschaulichen. Dadurch konnten wertvolle Informationen zu unserem Verständnis des menschlichen Verhaltens gewonnen werden.

Das erste Kapitel dieser Doktorarbeit komprimiert unser Hintergrundwissen der Neuroökonomie und erläutert die Bedeutung des neuroökonomischen Ansatzes. Das zweite Kapitel beschreibt die Techniken, welche in den drei Studien verwendet wurden. Im dritten Kapitel werden die drei Veröffentlichungen, an denen ich während meiner Promotion gearbeitet habe, zusammengefasst und verknüpft. Das abschließende vierte Kapitel besteht aus einem Fazit, Ansätzen zu möglichen Folgestudien sowie denkbaren Anwendungen der Studienergebnisse.

1. Introduction

Humans make thousands of decisions every day. These can range from small decisions (e.g. what to order in a restaurant) to larger, more life-changing ones (e.g. what career to pursue after graduating high school). In simple terms, making a decision can be defined as choosing one option over another or several others. Henceforth, "decision making" research studies the processes associated with making a certain choice and the response to its subsequent outcomes.

As far as we know, Blaise Pascal (1623-1662) was the first researcher to express theories on the processes of decision making (Pascal, 1941). What followed were approximately 200 years of neoclassical economic research that produced ideas ranging from marginal value to expected utility theory. During this time, humans were seen as rational agents who constantly aim to maximize their overall utility (also referred to as satisfaction or personal happiness). However, the Nobel Prize winners Daniel Kahneman and Amos Tversky provided several examples that challenged the belief that humans are completely rational decision makers (Kahneman and Tversky, 1979). Their revolutionary findings are seen as one of the cornerstones of behavioral economics and sparked off a great wealth of studies investigating different aspects of human decision making. Additionally, it brought the fields of economics and psychology closer together. Then, after a decade of mostly behavioral research, functional magnetic resonance imaging (fMRI) was invented and introduced into the study of human decision making (Ogawa et al., 1990; Blamire et al., 1992; Frahm et al., 1992; Kwong et al., 1992).

This made it possible for researchers to use an interdisciplinary approach to study the underlying brain activation patterns of human decision making. This new research field, now consisting of theories and methods from economics, psychology, and neuroscience, was named neuroeconomics. Since 1990, the number of studies in the field of neuroeconomics (here defined as studies using the terms "brain" and "decision making") has greatly increased (Figure 1). In the course of this endeavor, it has become clear that reward, loss, and risk processing play an essential part in human decision making.

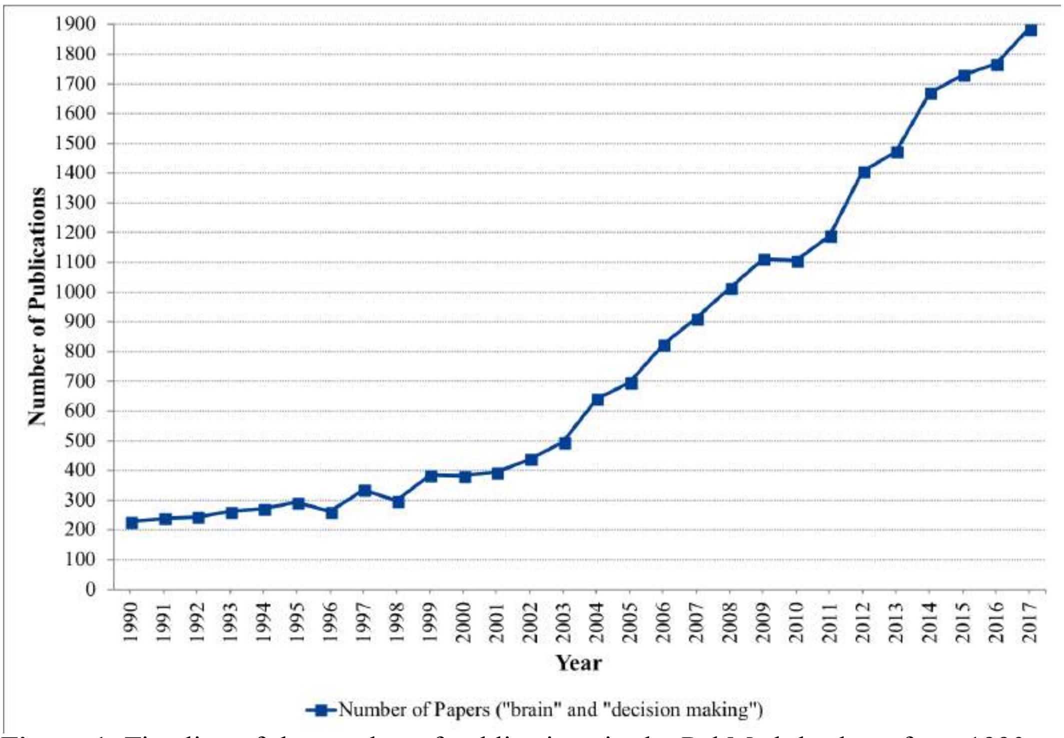

Figure 1. Timeline of the number of publications in the PubMed database from 1990 to 2017, including the terms "brain" and "decision making" (data obtained via www.pubmed.gov, accessed on June 28th, 2018).

The first part of this introduction starts off by providing a brief history of neoclassical economic theories. It continues with a description of prospect theory and shows how it led to the establishment of neuroeconomics. This is then followed by a summary of findings in reward, loss, and risk processing research, which shows why understanding these processes is essential for our comprehension of human decision making. The chapter ends with an explanation of why further neuroeconomic research is necessary in order to improve our understanding of human decision making.

1.1 Economic Theories of Human Decision Making

1.1.1 Neoclassical Economic Theories

The first theories regarding choice behavior can be traced back to the middle of the 17th century, when Blaise Pascal suggested that decision makers should choose the option with the highest expected value (EV; Pascal, 1941). Since the EV is made up of the probability of winning multiplied by the amount to be won, decision makers are considered risk neutral if they are indifferent between two options with the same EV, risk-seeking if they choose a risky option over a sure payment with the same or higher EV, and risk averse if they choose a sure payment over a risky payment with an equal or higher EV. In this context, it is important to define risk and distinguish it from the associated concept of uncertainty. While in decisions under risk, decision makers know the probability distributions of the possible outcomes (e.g. 50/50 in a coin flip), they have no such information in decisions under uncertainty (Knight, 1921).

Almost two centuries after Pascal, David Ricardo (1772-1823) worked on the determination of prices and suggested a “labor theory of value” (Ricardo, 1817). This theory states that a good’s value is determined by the hours of labor put into the creation of the product. Even though several flaws were attached to that theory (put into modern terms: It is just as hard to barbecue a perfect rump steak from American beef as it is from Kobe beef, even though the latter is almost five times as expensive), a solution was only suggested during the marginal revolution (middle and late 19th century). There, it was emphasized that a second quantity of a product is of higher value to an individual than a 10,000th quantity of the same product (Glimcher and Fehr, 2014). The economists during that time reasoned that this is the case, because the 10,000th quantity does not elicit as much utility (or satisfaction) as the second quantity. A commonly used example for such an argument is (e.g. 500ml) bottled water, in which, especially when an individual is thirsty, the 10,000th bottle does not elicit as much utility as its second counterpart. Then, Daniel Bernoulli (1700-1782) went one step further and introduced the total wealth of an individual into the EV formula (Bernoulli, 1954). This implied that individuals should make choices that maximize the expected utility (EU), and the associated concave logarithmic function showed that the wealth of an individual was an important factor in decision making (Figure 2).

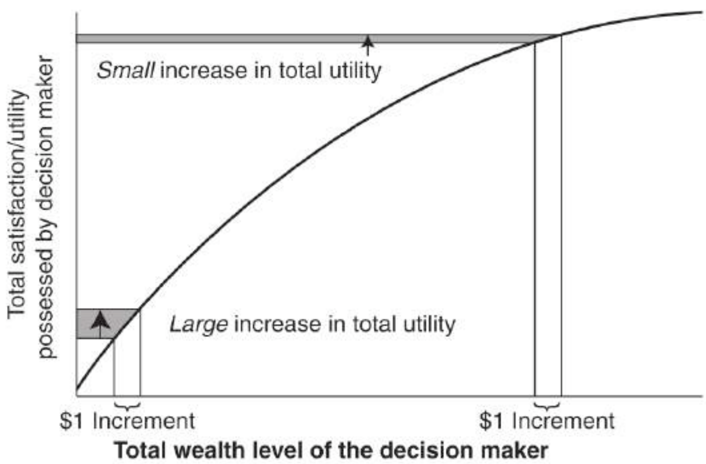

Figure 2. The logarithmic expected utility function by Daniel Bernoulli, which shows how the increments in utility decrease with each additional quantity of a product (here in US $, adapted from Glimcher and Fehr, 2014).

In 1906, Vilfredo Pareto (1848-1923) started the ordinal revolution by arguing that the exact absolute numbers or values of different options cannot be exactly quantified and that the preference of choices can thus only be ordered (Aspers, 2001). In line with Pareto's suggestion that choices should be used to study preferences, Paul Samuelson (1915-2009) established the revealed preference approach. Using this empirical (and for the first time non-normative) approach, he established the Weak Axiom of Revealed Preference (WARP). Importantly, Samuelson and his colleagues pointed out that while choices can be used to assume utilities, it is the choices that are directly observed, not the utilities (Samuelson, 1938). Hendrik Houthakker (1924-2008) subsequently suggested a Generalized Axiom of Revealed Preference (GARP), which was seen as an advanced version of the WARP. It states that decision makers who constantly follow a similar ordering of preference can be called transitive (Houthakker, 1950). Only then can an ordinal ranking of preferences for goods be made, and the conclusion drawn that a decision maker is maximizing utility. Otherwise, the decision maker is said to be irrational (in an economic sense).

Considered as the final part of neoclassical economics, John von Neumann (1903-1957) and Oskar Morgenstern (1902-1977) established EU theory (von Neumann and Morgenstern, 1953). As part of this theory, they introduced four axioms that made it possible to test whether or not an individual is a rational decision maker. First, the completeness axiom assumes that the individual has predefined preferences and can always decide between two options (either A over B or B over A (leaving the issue of indifference between the options aside)). Next, the transitivity axiom states that a rational individual makes consistent decisions (if A over B and B over C, then A over C). Third, the continuity axiom assumes that there must be a lottery between two of the products that has the same subjective value as the third product. Finally, the independency axiom states that when the same factor is added to two gambles, then a rational decision maker will maintain the same preference order as when the two gambles are presented without the additional factor.

1.1.2 From Prospect Theory to Neuroeconomics

In 1979, Daniel Kahneman and Amos Tversky presented empirical evidence that led to the discredit of EU theory and the establishment of prospect theory (PT; Kahneman and Tversky, 1979). Using choice problems and thus data from behavioral economics, they showed that humans violate the axioms described in EU theory and show irrational (i.e. not utility maximizing) decision making behavior. As one of these choice problems, the Allais paradox was used to counter the independency axiom (Allais, 1953). In the Allais paradox, individuals are asked to make choices between two gambles in two separate experiments (Table 1). In these experiments, it was found that individuals tend to choose gambles A and D, which is in stark contrast with the independency axiom of EU theory. This becomes clear when the paradox is depicted in a different manner (Table 2), which specifically shows that in each experiment a third factor (1000€ in experiment 1 and 0€ in experiment 2, depicted in bold, italicized letters in Table 2) is added to each gamble.

Table 1. First depiction of the Allais paradox.

Experiment 1				Experiment 2			
Gamble A		Gamble B		Gamble C		Gamble D	
Amount	Chance	Amount	Chance	Amount	Chance	Amount	Chance
1000€	100%	1000€	89%	0€	89%	0€	90%
		0€	1%	1000€	11%		
		5000€	10%			5000€	10%

According to EU theory, the individual should choose either A and C or B and D, since they can be seen as the same choice. However, empirical data showed that human decision makers consistently violate the independency axiom of EU theory, thus showing irrational human behavior.

Table 2. Second depiction of the Allais paradox. The third factors are depicted in bold, italicized letters and the gamble amounts and chances are colored to emphasize their similarities.

Experiment 1				Experiment 2			
Gamble A		Gamble B		Gamble C		Gamble D	
Amount	Chance	Amount	Chance	Amount	Chance	Amount	Chance
1000€	***89%***	***1000€***	***89%***	***0€***	***89%***	***0€***	***89%***
1000€	11%	0€	1%	1000€	11%	0€	1%
		5000€	10%			5000€	10%

As one of the main pillars, PT replaced the utility function with a value function. This value function showed that individuals have a reference point relative to gains and losses and that individuals exhibit loss aversion (Kahneman and Tversky, 1979). This becomes particularly clear when the steep convex shape in the loss domain is compared to the more gradual concave shape in the gain domain (Figure 3A). It emphasizes that “losses loom larger than gains”, because a loss is related to a more negative value when compared to its relative gain and the associated positive value. Besides the value function, Kahneman and Tversky used PT to additionally provide evidence that individuals overweight low probabilities and underweight large probabilities, thus resulting in an inverse-S shaped weighting function (Figure 3B).

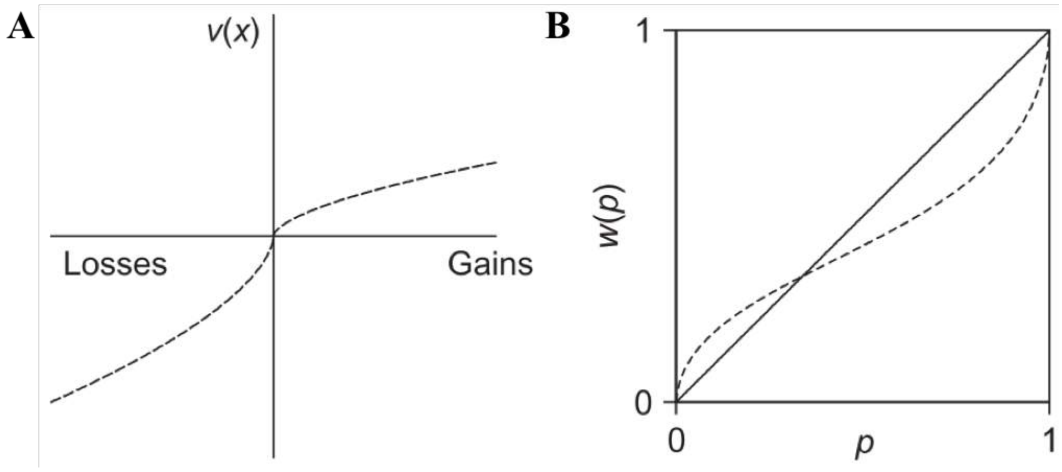

Figure 3. Functions of prospect theory (adapted from Glimcher and Fehr, 2014). A. Value function, showing a steeper and convex shape for losses. B. Weighting function (inverse "S" shape), depicting an individual's tendency to overweight low and underweight high probabilities.

Therefore, by incorporating the idea of subjective weighting during the decision process, PT provided researchers with a more accurate model of human decision making (Civai and Hawes, 2016). Ever since, several phenomena in psychology, such as the endowment effect (people value things more if they own them) or the framing effect (behavioral differences when the same question is asked in terms of losses or gains), have been explained using PT. With respect to individual stock market behavior, the disposition effect (holding losing stocks too long while selling winners too early) and the equity premium (irrational risk and loss aversion leading to a high premium demand for buying stocks instead of bonds), have both been shown to be consistent with PT and not EU theory (Camerer, 2004). Additionally, research using real-life financial data has shown that PT can explain systematic trading biases and loss aversion of individual investors (Benartzi and Thaler, 1995; Barberis, 2013; Barberis et al., 2016).

The idea of humans as irrational decision makers was so revolutionary that it brought the fields of economics and psychology closer together and, collectively with the invention of fMRI in the beginning of the 1990's (Ogawa et al., 1990; Blamire et al., 1992; Frahm et al., 1992; Kwong et al., 1992), led to the formation of neuroeconomics. Nowadays, almost all research that includes economics, psychology, and neuroscience to study the processes of human decision making can be considered neuroeconomic research.

1.2 The Neuroscience of Reward, Loss, and Risk Processing

1.2.1 Processing of Rewards, Losses, and Subjective Value

Based on a great wealth of neuropsychological decision making research, several frameworks have recently been suggested to explain voluntary economic decision making (O'Doherty, 2011; Padoa-Schioppa, 2011; Schultz, 2015). These frameworks agree on four major steps (listed here chronologically): choice perception (sensory detection), choice comparison and decision (including valuation, value comparison, and action choice), decision implementation (action), and a final learning step.

In this context, reward-based learning mechanisms have been identified as a crucial component for the survival of a species (Schultz, 2015). Without rewards, no organism would survive, since the inherent beneficial properties of a reward (such as obtaining a nutrient-rich fruit or successful sexual reproduction) are essential for survival. In a meta-analysis involving 206 fMRI studies, two regions (among others not mentioned for sake of simplicity) were identified as playing a major role in reward processing (Bartra et al., 2013); namely, the ventromedial prefrontal cortex (vmPFC, Figure 4A) and the ventral striatum (VS, also termed nucleus accumbens, Figure 4B). In line with these findings, neurochemical studies have shown that the neurotransmitter dopamine, produced in neuronal cell bodies of the ventral tegmental area (VTA) and the substantia nigra (SN, also seen in Figure 4B), is released in the vmPFC and the VS (excellent overviews can be found in Haber and Knutson, 2010 and in Schultz, 2015). Here, the reward prediction error (RPE) has been established as an explanation of learning processes (Glimcher, 2011; Schultz, 2016, 2017). The RPE is implemented via dopamine and makes it possible for humans to learn from correct and incorrect choices by comparing the outcome of a decision to its previous reward prediction (further explanations and a detailed implementation can be found in section 2.1.4). A long line of research has identified the VS as the main center for RPE computations (Schultz et al., 1997; Schultz and Dickinson, 2000; Hare et al., 2008; Fliessbach et al., 2010; Rohe et al., 2012; Schultz, 2015, 2016, 2017).

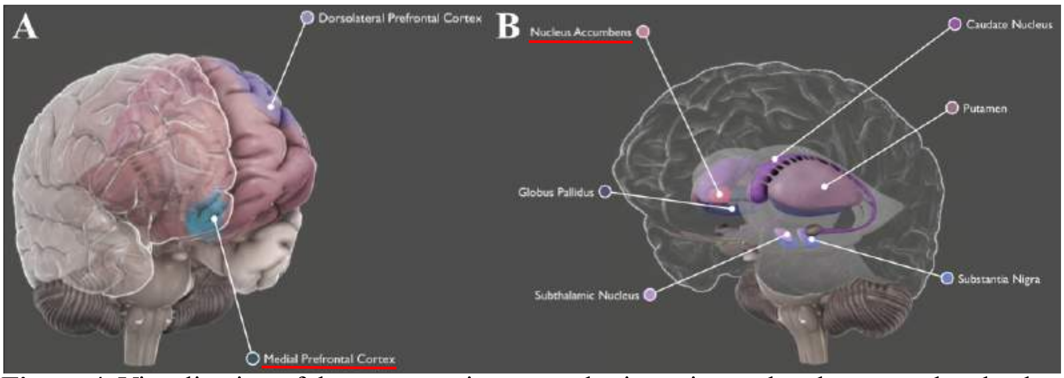

Figure 4. Visualization of the two most important brain regions related to reward and value processing (underlined in red). A. The ventromedial prefrontal cortex (vmPFC), here labeled as the “Medial Prefrontal Cortex”. B. The ventral striatum (VS), here labeled as the “Nucleus Accumbens”. Both images were adapted from 3D Brain.

Besides rewards, loss avoidance plays an important role in decision making. Since a loss entails a negative impact on the organism’s state, its natural goal must be to avoid it. Both the vmPFC and the VS have been shown to be involved in loss processing (Seymour et al., 2007; Tom et al., 2007; Cooper and Knutson, 2008), but the brain region that has primarily been linked (again, amongst others that are not mentioned here for sake of simplicity) to both the processing and avoidance of losses has been the anterior insula (AI, Figure 5; Samanez-Larkin et al., 2008; Fukunaga et al., 2012).

In the light of evolution, the human decision making process is thus based on pursuing rewards and avoiding losses. Amongst other factors (e.g. motivation, delay, and risk, last of which is discussed in the next section; Padoa-Schioppa, 2011), these two aspects are weighted against each other to assign a value to each option. Importantly, in the valuation and outcome phase of a decision, all three regions (i.e.

the AI, VS, and especially the vmPFC) have been shown to be active (Bartra et al., 2013; Clithero and Rangel, 2014).

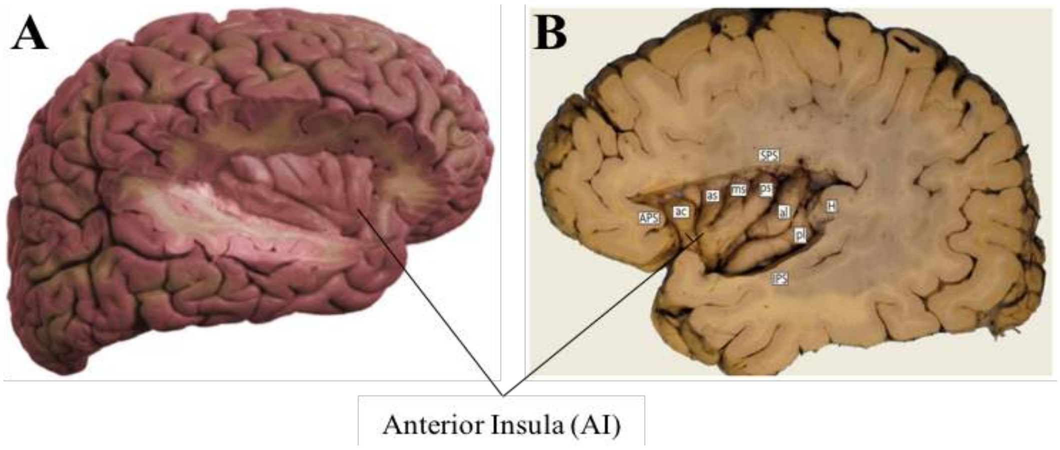

Figure 5. Neuroanatomy of the anterior insula (AI), A. Illustration of the insula cortex (adapted from Singer et al., 2009). B. Photograph of a human left insular cortex, with both ac (anterior long insular gyrus) and as (anterior short insular gyrus) being part of the anterior insula (adapted from Craig, 2009).

1.2.2 Risk Processing

In decisions under risk, the probability distributions of the possible outcomes are known. Notably, all three previously mentioned regions (i.e. the AI, VS, and the vmPFC) have been shown to play important roles in risky decision making (Figure 6). Especially the risk seeking signals in the VS and risk aversion signals in the AI have been the focus of a great line of previous laboratory-based studies (Kuhnen and Knutson, 2005; Knutson and Greer, 2008; Preuschoff et al., 2008; Bossaerts, 2010; Rudorf et al., 2012; Smith et al., 2014; Knutson and Huettel, 2015; Leong et al., 2016). In a recent seminal study investigating brain activation in market bubbles, VS activation (in the region of interest shown in Figure 6B) was linked to a higher propensity to buy risky assets, while AI activation (in the region of interest shown in Figure 6C) was associated with selling such assets in time before the market crashed (Smith et al., 2014). Henceforth, the AI activation acted as a warning signal and individuals with more AI activation and less VS activation earned more money in the experiment (Smith et al., 2014).

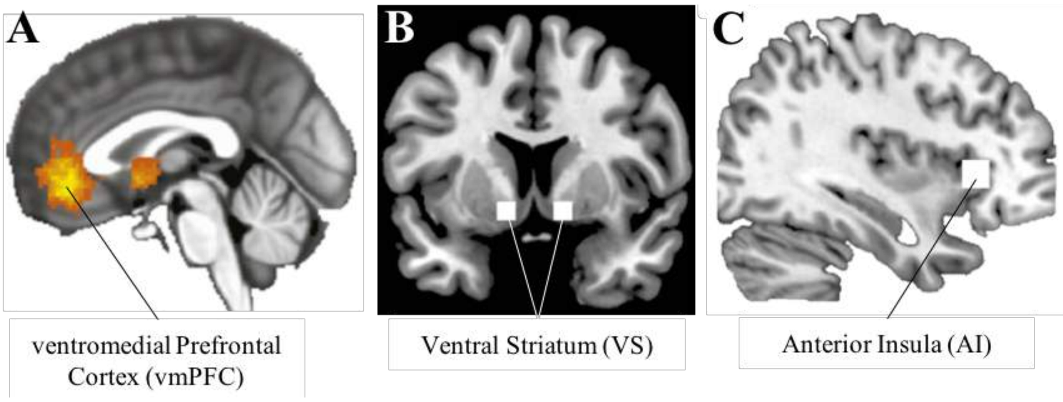

Figure 6. Three brain regions of interest from the literature that are known to be involved in risky decision making. A. The modality-independent subjective value signal in the ventromedial prefrontal cortex (vmPFC; adapted from Bartra et al., 2013). B. The 6 mm-radius sphere centered on the ventral striatum (VS; adapted from Smith et al., 2014). C. The 6 mm-radius sphere centered on the right anterior insula (AI; adapted from Smith et al., 2014, who created it by taking the peak coordinates from the peak "risk prediction" signal from Preuschoff et al., 2008).

1.3 Benefits of the Neuroeconomic Approach

Since its inception in the 1990s, the field of neuroeconomics has significantly advanced. The inclusion of neuroscientific techniques made it possible for economists to understand the neural processes of certain economic decisions. Neural processes from prospect theory, such as loss aversion (Tom et al., 2007) and framing effects (Gonzalez et al., 2005), were mostly investigated in the beginning of the 21st century. On top of the basic and exploratory research, each neuroeconomic subfield (e.g. risky choices or intertemporal discounting) now integrates additional scientific tools (e.g. personality tests) and includes studies with more applied questions. In this process, more accurate and comprehensive models of human decision making have been developed, and some analyses that include brain activation have even gone so far as to predict real-life outcomes, such as the cultural success of music (Berns and Moore, 2012) or the success of public health campaigns (Falk et al., 2015c). Both basic and applied neuroeconomic research is important for the field, as one can drive the other and strengthens the collaboration between science and funding agencies (especially from the industry). This thesis contains aspects from both basic and applied research. Study one describes the basic research of a common neural currency in context with two applied topics: soccer and money. Study two is a basic research study that analyses the correlation between attention distribution in risky gambles and reward- and loss-related brain activation. Study three is the most applied study and presents the first neuroeconomic model of real-life stock trading.

Avenues of both basic and applied research are necessary to improve and build newer and better models of human behavior, which in turn reveal previously hidden gaps of knowledge. This precept guided the studies included in this thesis. In particular, study three demonstrates that a combined neuroeconomic (neuroscience, psychology, and economics) approach is better at filling one of many knowledge gaps found in relation to real-life household financial behavior (Frydman and Camerer, 2016), namely real-life financial risk taking.

2. Materials and Methods

This chapter describes the materials and methods that I used throughout my doctoral studies. It gives an overview of how brain activation can be measured using functional magnetic resonance imaging (fMRI) and how risk-, reward-, and loss-related brain activation can be analyzed. This is then followed by a description of further neuroeconomic techniques, including risk assessments (behavioral and self-assessments), eye-tracking, personality measurements, as well as the assessment of household and cognitive characteristics.

2.1 Functional Magnetic Resonance Imaging

2.1.1 From Atomic Flips to Whole-brain Analysis

First published in the early 1990s, fMRI is a neuroimaging technique that provides researchers with the ability to create brain activation images based on the metabolic changes found in relation to brain activity (Ogawa et al., 1990; Blamire et al., 1992; Frahm et al., 1992; Kwong et al., 1992). In fMRI, a very strong and static magnetic field (quantified in Tesla (T)) is used to align atoms along the axis of the magnetic field (Huettel et al., 2014). A specialized electrical coil then uses radio waves to deliver pulses of energy to these atoms, which causes them to jump from a low- to a high-energy state and back, thus resulting in a measurable energy release (the magnetic resonance signal (MR signal; Huettel et al., 2014)). Red blood cells contain the molecule hemoglobin (Hb), for which the degree of oxygenation varies. Oxygenated Hb is diamagnetic, whereas deoxygenated Hb is paramagnetic. The MR signal reflects this ratio.

In this context, it is important to understand the blood-oxygen-level dependent (BOLD, or hemodynamic) response (Figure 7), seen as the physiological response to neuronal activation (Siero et al., 2013).

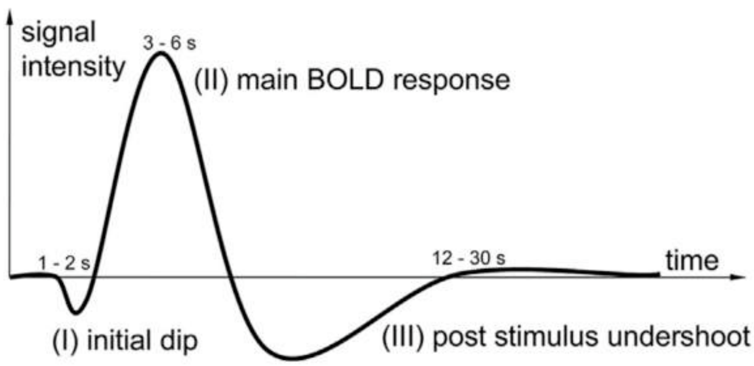

Figure 7. A typical blood-oxygen-level dependent (BOLD) response, divided up into three phases (adapted from Siero et al., 2013).

In a typical BOLD response, a firing of neurons in a certain brain area leads to local oxygen extraction and increase of deoxygenated blood concentration, represented as the “initial dip” (Siero et al., 2013, Figure 7). This is then followed by the main BOLD response, which is a major boost in cerebral blood flow and results in an oversupply of oxygenated blood to the area associated with the neuronal activity (Siero et al., 2013, Figure 7). The change in the ratio of oxygenated to deoxygenated blood is used to create parametric maps of the brain, thus indicating brain activation associated with a specific task. Since the brain is reconstructed using three-dimensional 3 x 3 x 3 mm cubic spatial units called “voxels”, the BOLD time course of each voxel can be investigated (Markett, 2016). However, before any investigations can take place, artifacts are removed in a series of computational procedures, called preprocessing. These usually include slice time correction, motion correction, spatial normalization, reslicing, and a final smoothing step. After preprocessing, a general linear model (GLM) is used to predict the BOLD time course variation of each voxel using a combination of several regressors (Penny et al., 2011). A basic GLM formula is as follows:

Equation 1:

$$\mathbf{y = x * ß + n}$$

Here, **y** stands for the dependent variable (in our case the observed BOLD signal), **x** for the regressor, **ß** for the weight attached to the regressor (ß-value), and **n** for the intercept, which is a constant value added to the equation (Penny et al., 2011). The regressors are defined by the researcher and according to the experimental paradigm used in the fMRI task.

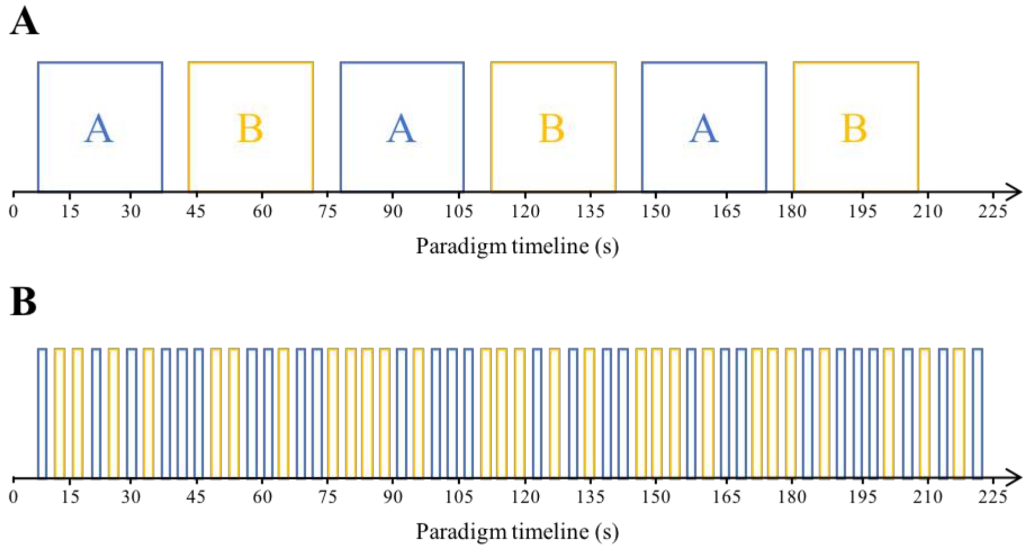

Figure 8. Two types of fMRI paradigm designs. A. Example of a block-related design, showing the stimuli of conditions A (light blue) and B (light orange) as part of three predefined alternating blocks each. B. Event-related design, randomly showing stimuli from condition A (light blue) and condition B (light orange).

The design of an fMRI paradigm that is shown to the participant can be either block- or event-related[1]. In a block-related design, two or more different conditions are variantly shown to the participant in a pre-defined sequence (Figure 8A). This is done to study the brain activation differences between the conditions. However, due to the limitations of block-related designs (e.g. habituation effects), researchers developed the event-related design (Figure 8B; Josephs et al., 1997). In event-related fMRI tasks, the presentation of certain stimuli is not collectively shown as part of a

[1] Or a mixture of the two (mixed design). Its description is omitted here for the sake of simplicity.

block. Instead, the presentation of trials belonging to a certain condition (e.g. condition A vs. B in Figure 8B) is randomized. Even though an event-related design needs more trials per condition than a block-related design, it is better at estimating the shape of the hemodynamic response function and allowing the estimation of brain activation in response to single events (D'Esposito et al., 1999). The invention of event-related designs led to a whole new genre of fMRI experiments, because researchers could from thereon use fMRI to study the brain activation patterns associated with more complex tasks (Josephs et al., 1997; D'Esposito et al., 1999). In the studies presented as part of my dissertation, we exclusively used event-related fMRI designs.

An example of a regressor (**x** in Equation 1) that my colleagues and I defined in one of our event-related fMRI tasks is the choice of stock or bond in the gain domain in the stock learning task of study three (for all regressors of each fMRI study please see pages 6 and 7 in study one, Table 1 in study two, and Supplementary Tables S1 and S2 in study three). Depending on the research question, a duration (e.g. the reaction time until stock or bond selection in study three) and parametric modulators (e.g. the reward prediction in Table 2 of study two, further explained in chapter 3.14) can be defined for each regressor, as well. Once the regressors (**x**) are defined and used to estimate the ß-values (**ß**), t-tests can be calculated to look for differences between two experimental conditions (e.g. stock > bond choice, study three) or between a regressor and baseline activation (e.g. parametrically modulated reward prediction error > 0, all three studies). To look at such differences, contrasts are established (e.g. $\boldsymbol{ß}_1 > \boldsymbol{ß}_2$) at the individual subject level (first-level, also later used in the weighted ß-value extraction). The specific contrasts of all participants can then be combined at a group-level to make statistical inferences across participants. This is usually referred to as the second-level analysis. However, since one fMRI volume consists of more than 10,000 voxels, the whole-brain activation cannot simply be looked at without a statistical threshold and should be corrected for multiple comparisons. In our studies, we attempted to minimize the alpha (false-positive) error by using a conservative family wise error (FWE) rate correction using the Bonferroni procedure. Additionally, we used a cluster correction of larger than ten voxels ($k > 10$) to eliminate isolated voxels that exceeded the FWE-threshold.

2.1.2 Further Brain Analysis

On top of the now-standard whole-brain analysis, we used three additional techniques in our studies: covariate and region of interests[2] analysis, as well as weighted ß-value extraction. In covariate analysis, a variable (e.g. a personality trait score such as egoism in study one) is included as a covariate in a certain contrast (e.g. scoring a goal after a shot > scoring after a pass, study one) to test for the association between the variable and the estimated brain activation. In region of interest analysis, masks can be taken from established previous studies to test for locally specific brain activation. Alternatively, researchers can create their own regions of interest using their own contrasts (considered the least acknowledged option since the regions of interest are created from and analyzed with the same data set) or by creating spheres around coordinates taken from the literature or a reverse-inference database (e.g. Neurosynth). For each participant, mean weighted ß-values can then be extracted for each mask. Importantly, these values can be used for further statistical procedures, such as correlation analysis with eye-tracking fixations (study two) or as independent variables in regression analysis of real-life financial risk taking outcomes (study three).

2.1.3 Measuring Financial Risk-related Brain Activation

Financial risk-related brain activation can be measured in several different ways (Häusler and Weber, 2017). While paradigms such as the Balloon Analogue Risk Task (BART, Lejuez et al., 2002) and the certainty equivalent (CE) task (Christopoulos et al., 2009) represent more abstract paradigms, we used an established (Kuhnen, 2015) and more applied stock learning paradigm that specifically asked participants to decide between a stock (risky) and a bond (riskless). More specifically, participants were asked to make 96 choices between a stock (risky) and a bond (riskless) option in a gain or a loss context (Figure 1 in study three) and we used this task to compare brain activation during a risk seeking versus a risk aversive choice (stock > bond). Additionally, we extracted ß-values from these choice

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[2] Please note that the usual abbreviation for region of interest (i.e. ROI) is not used throughout this thesis, because of possible confusion with the Risk Optimism Index (ROI, see chapter 2.2.1 for details)

contrasts using regions of interest taken from the neuroeconomic literature (study three) and subsequently associated them with real-life financial risk taking.

2.1.4 Measuring the Components of Reward and Loss Processing

In 1997, researchers used single dopamine neuron recordings in monkeys to find the neural basis of reward processing (Schultz et al., 1997). Since then, many studies have investigated reward processing (for an excellent review see Schultz, 2016) and have identified its main components, namely reward prediction (RP), reward reception (RR), and reward prediction error (RPE). The RP represents the probability of obtaining a reward (e.g. 33.33% for selecting the correct symbol out of three (Figure 2B in study one)). Since the RR can either be a win (represented as a "1") or no win (represented as a "0"), the RPE can be calculated as the difference between the RR and the RP (RPE = RR – RP). In this context, paradigms with financial incentives can be very useful, because the specific values of the above-named components can be introduced as parametric modulators in the first-level analysis. Our research group has therefore developed several such paradigms to investigate the neural activations of each reward processing component (Fliessbach et al., 2010; Rohe et al., 2012).

We chose one of the previously established paradigms to be part of our research (studies one and two). In this monetary guessing paradigm, the participant is asked to make a choice between either one, two, three, or four symbols. A correct choice results in a win of 10€ cents, while a wrong choice results in no monetary gain. In study one, we used the exact same version of the paradigm as in a previous study (Rohe et al., 2012). This paradigm contained 150 trials, since in fMRI research multiple trials of the same manipulation are necessary to improve the functional signal-to-noise ratio (signal averaging; Huettel et al., 2014). Before the second study, we performed a small (n = 20) fMRI pre-testing study in which we used modified versions (with fewer trials) of the monetary guessing paradigm to identify the number of trials necessary to elicit robust reward-related brain activation. As a result, we were able to decrease the trial number down to 48 (while keeping an appropriate signal-to-noise ratio and reliable reward processing activation), thus making the paradigm less time-consuming. Importantly, this modification made it possible to additionally include a loss and a neutral domain. In the loss domain, we introduced the processing components of loss prediction (LP: the probability of obtaining a loss), loss reception (LR: either no loss (represented as 0) or loss (represented as -1)), and loss prediction error (LPE = LR – LP). By using each of these components as parametric modulators during either the choice or the feedback phase of the paradigm (see Table 2 in study two for an overview), we were able to study both reward and loss activation using a single paradigm.

In addition to investigating monetary reward and loss processing, we applied the reward processing logic to a social context, namely two-versus-one situations in front of a soccer goal (soccer paradigm, Figure 1 and 2 in study one). By pre-testing these situations via the online survey tool, we were able to obtain the average likelihood of scoring a goal (with 38.6 ±3.44 ratings per situation). We then implemented this probability as the RP modulation. Since the result was either scoring a goal (represented as 1) or not (represented as 0), the RPE could be calculated. These three parametric modulators where then included in the first-level analysis and made it possible to compare money- and soccer-related reward activation (study one).

In study three, we used the stock payoff feedback phase of the stock learning task to compare good with bad outcomes (i.e. high stock payoff feedback after stock choice > low stock payoff feedback after stock choice) and to study reward and loss reception in a risk-related context (Supplementary Tables S3 and S4 in study three, see chapter 2.2.2 for further details).

2.2 Risk Taking and Further Risk-related Assessments

2.2.1 Self-assessments of Financial Risk Taking

In study three, several self-assessment scales from financial institutions and from the German Socio-Economic Panel (SOEP; Wagner et al., 2007) were used to measure self-ratings pertaining to either risk tolerance or risk optimism (please see Supplementary Table S5 in study three for a full overview). Additionally, risk taking in a hypothetical lottery question was assessed by asking how much of 100,000€ (previously won in a lottery) a participant would re-invest into a 50:50 chance of another lottery. Here, the amount invested was taken as another measure of financial risk taking. Importantly, all the behavioral (except for the stock estimation error) and self-assessments were grouped into either the risk tolerance or risk optimism category. Each category then underwent a principal component analysis (PCA), which resulted in two indices representing risk optimism (ROI) and risk tolerance (RTI). Notably, the creation of more general risk factors using both behavioral and self-assessment measures has recently been shown to be appropriate, since behavioral and propensity measures assess specific risk components and correlate only weakly (Mamerow et al., 2016; Frey et al., 2017).

2.2.2 Behavioral Measurements

In the stock learning task of study three (Figure 1 in study three), participants were asked in 96 trials to decide between a risky (stock) and a riskless (bond) choice. The 96 trials were split up into 16 blocks containing either a good or a bad stock. A good stock was programmed to present a good outcome in 70% of the trials, while a bad stock was programmed to present a good outcome in only 30% of the trials. Over the course of a block (containing six trials each), subjects used the stock payoff feedback to learn about a stock being either good or bad. To exclude a learning-effect on the risk-related choice, we calculated the ratio of risky (stock) to riskless (bond) choices, but only using the choice of the first trial out of every block. Besides this behavioral measure of financial risk taking, we used the stock estimation after each stock payoff feedback to obtain two measurements relating to risk learning. As one of these, the stock assessment error was taken as the absolute difference between the objective and subjective probability of the stock being good, while behavioral risk optimism was measured as the same, but non-absolute difference.

Another behavioral paradigm assessing financial risk taking was the stock allocation task, used in study three (Supplementary Figure S4 in study three). Here, participants were asked to make ten independent decisions, in which they had to split up 23€ into either a risky (stock) or riskless (bond) asset. The average amount of money allocated to the stock was taken as a measurement of financial risk taking.

2.2.3 Eye-tracking

In eye-tracking research, a participant's eye is illuminated with an infrared light source (Holmqvist et al., 2011). Together with a corneal reflection, the pupil position is tracked and the point of regard is thus calculated (Holmqvist et al., 2011). Being the most popular eye-tracking method since the early 1990s, the pupil-corneal reflection system is used to track the eye while compensating for small head movements (Holmqvist et al., 2011). Several types of eye movement events (saccades, smooth pursuits, microsaccades etc.) can be measured this way. We were specifically interested in fixation numbers (i.e. gaze stability > 50 ms in prespecified areas of interest (AOI); study two), since these were previously used in financial risk-related research (Brandstätter and Körner, 2014) and are known to represent attention.

To measure attention patterns in a gambling task (Figure 2 in study two), two colleagues and I designed and set-up a laboratory with an eye-tracking and behavioral testing area (Figure 9). On the participant table (Table #1 in Figure 9) of the eye-tracking area, a chinrest, a display, and a keyboard were used to fixate the participant's head, show the paradigm, and let the participant make decisions. Together with an adjacent infrared light illuminator, an Eyelink 1000 (SR Research) eye-tracker was positioned below the display.

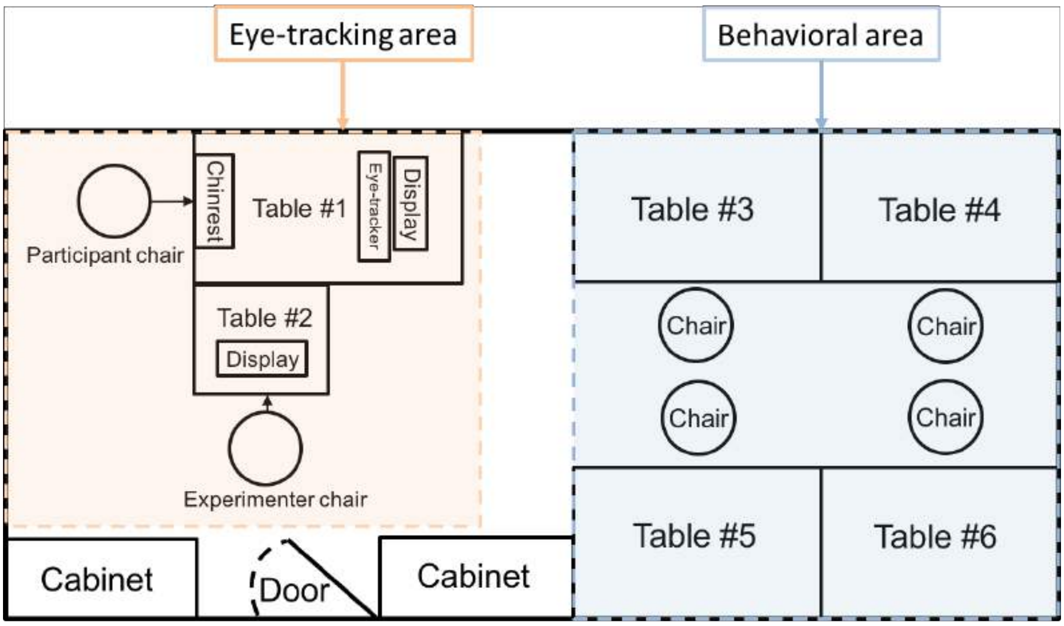

Figure 9. Setup scheme of the laboratory, which included an eye-tracking area (light orange) and a behavioral area (light blue).

Using the pupil and corneal reflection of the infrared illumination to reconstruct a point of regard, we measured the number of fixations in predefined AOIs (Figure 2C in study two). We used these to calculate attentional differences between monetary values (f(v)) and their respective probabilities (f(p)) in risky gambles in the win (Df win = f(v) – f(p)) and in the loss (Df loss = f(v) – f(p)) domain (Figure 2 and Table 7 in study two). These attentional differences (Df win and Df loss) were then associated with the reward and loss-related brain activation measured in a separate paradigm (Figure 1 in study two). Since a choice between a high- and a low-risk gamble (A and B, Figure 1B in study two) had to be made additionally, we used the percentage of high-risk choices in each domain as a behavioral measurement of financial risk taking.

2.3 Personality

During my PhD, I used four questionnaires to assess personality traits: the NEO Five Factor Inventory (NEO-FFI, study three), the HEXACO Personality Inventory - Revised (HEXACO-PI-R, study one), the social value orientation (SVO, study one) questionnaire, and Reuter and Montag's revised Reinforcement Sensitivity Theory Questionnaire (rRST-Q, study three). In study one, we used to the HEXACO-PI-R and the SVO questionnaire due to their relevance to our research question concerning egoism, while the widely employed NEO-FFI and rRST-Q were used in study three to study the correlates of financial risk taking.

The NEO-FFI is a 60-item inventory that is based on the Five-Factor Model (FFM) of personality and was developed to measure the personality traits of "Neuroticism" (NEO-N), "Agreeableness" (NEO-A), "Extraversion" (NEO-E), "Conscientiousness" (NEO-C), and "Openness to Experience" (NEO-O, (Costa and McCrae, 1992). A decade later, the HEXACO model was developed to measure six personality scales: "Honesty-Humility", "Emotionality", "eXtraversion", "Agreeableness", "Conscientiousness", and "Openness to Experience" (Lee and Ashton, 2004, 2006). Even though the HEXACO model is based on the Five-Factor model, it importantly contains the additional HH scale, which has been shown to lie beyond the Big Five and measure egoism (Ashton and Lee, 2005; de Vries et al., 2009; Hilbig and Zettler, 2009; Lee and Ashton, 2012; Ashton, 2013). In study one, we thus used the HH score to study the association between brain activation in soccer situations and egoism. We furthermore used the SVO questionnaire, which uses financial decisions in a social context to distinguish between prosocial and proself choices (van Lange et al., 1997).

While the FFM was developed using a lexical approach (Cattell, 1947; Tupes and Christal, 1992; Ashton, 2013), the first RST was developed on the basis of brain structures (Gray, 1981, 1987; Ashton, 2013). It was initially designed to measure the mesolimbic behavioral activation system (BAS: formerly the "go" system), septo-hippocampal behavioral inhibition system (BIS: formerly the "stop" system), and the Fight-or-Flight system. Later, it was first revised by the original authors (Gray and McNaughton, 2000) and then also recently (Reuter et al., 2015) to include revised versions of the BAS and BIS, as well as a new Fight Flight Freeze System (FFFS). We used the most recent version (i.e. the rRST-Q in study three) to assess approach and goal-directed behavior (BAS), responses to situations of uncertainty (or wary behavior, BIS), as well as defensive responses (low fight, high flight and high freezing behavior, FFFS) in relation to financial risk taking.

2.4 Sociodemographic Characteristics

We used several scales and questions from the German Socio-Economic Panel (SOEP) study (Wagner et al., 2007) and the Munich Center for the Economics of Aging (MEA) to assess household characteristics (Table 1 in study three) pertaining to the personal (e.g. age and years of education) and family situation (e.g. marital status and number of people in household). Questions regarding financial matters (e.g. income and having financial liabilities) and financial knowledge (financial literacy, numeracy, and debt literacy) were assessed (Christelis et al., 2006; Lusardi and Tufano, 2009; Mitchell and Lusardi, 2011), as well. Importantly, the dependent variable of study three ("Do you trade stocks yourself?") was specifically created to study financial risk taking in a real-life context.

Since the measurement time of each participant in the experiment of study three was already approximately three to four hours, we decided to include only three sub-scales of the Intelligence-Structure-Test 2000 Revised (IST 2000R). These cognitive measures assessed verbal, numerical, and figural intelligence (Liepmann et al., 2007).

3. Summary of Research Findings

3.1 Study One: Comparing Reward Processing upon Winning Money and Scoring a Soccer Goal

Häusler AN, Becker B, Bartling M, Weber B (2015) Goal or gold: overlapping reward processes in soccer players upon scoring and winning money. *PLOS ONE* e0122798:1–16.

The idea of a "common neural currency" was first introduced in 2002 and defined as a necessity in reward-guided behavior "to value diverse behavioral acts and sensory stimuli" (Montague and Berns, 2002). To enable a comparison between diverse goods (e.g. 2€ (money) and 100g of blueberries (food)), neuroeconomists deemed it crucial for the brain to transform the values of goods into one neural currency. Ever since, many studies have shown similarities in neural processing of dissimilar goods (Chib et al., 2009; Hare et al., 2010; Bartra et al., 2013; McNamee et al., 2013; Clithero and Rangel, 2014). In relation to social rewards and in line with social exchange theory (Homans, 1958), only two studies had previously investigated common reward processing upon positive monetary and social outcomes. Izuma et al. (2008) studied brain activation in response to monetary gains and good reputation, while Lin et al. (2012) examined brain activation in relation to monetary gains and positive social feedback. However, no study had examined, whether a common reward-related brain activation would also be found in situations of positive social reward in the context of sports. For this purpose, we used arguably one of the most common reward-related sport situations, i.e. scoring a goal in the world's most popular team sport: soccer (in 2006, 270 million people were active in soccer (FIFA, 2007)).

We invited 33 soccer players (24.4 ±3.2 years, all male) to the study and used the three components of reward prediction error (RPE) processing (reward prediction (RP), reward reception (RR), and RPE, see chapter 2.1.4 for details) to compare brain activation upon winning (or not winning) money and scoring (or not scoring) a soccer goal (Figure 2 in study one). We found that reward-related structures (specifically the ventromedial prefrontal cortex (vmPFC) and the ventral striatum (VS)) were activated during RR and RPE processing of both reward types (Table 1 and Figure 3 in study one). These major findings supplied a possible reward-guided explanation for the popularity of playing soccer and team sports in general. They provided further evidence for a common neural currency, which has recently been additionally extended using another neuroscientific method, namely electroencephalography (EEG) (Distefano et al., 2018).

We additionally studied egoism, because it is seen as a motive for allegedly selfish behavior in sport situations. We used the ratio of shooting versus passing in a newly invented soccer paradigm (Figure 2A in study one) and two personality scales (the Honesty-Humility (HH) scale of the HEXACO-PI-R, as well as the social value orientation questionnaire (SVO); see chapter 2.3 for details) as indices of egoism. We hypothesized that more egoistic individuals would have higher reward-related activation upon scoring after having decided to shoot the ball versus scoring after having decided to pass it to a teammate. This would then indicate a reward-guided motivation for seemingly egoistic behavior on the soccer pitch. We did not find evidence supporting this theory, but discovered that activation in the left middle frontal gyrus (MFG) upon scoring after a pass versus a shot is positively correlated with egoism (Figure 4 in study one). We were therefore able to draw two additional minor conclusions. In soccer, more egoistic individuals do not act egoistically due to a reward-related motive. Furthermore, they require more self-reflective spatial and reasoning neural effort upon observing success after a selfless act (Belger et al., 1998; Goel et al., 1998; Taylor et al., 1998; Prohovnik et al., 2004; Addis et al., 2007).

3.2 Study Two: Correlating Reward- and Loss-related Brain Activation to Attention in Risky Gambles

Häusler AN, Artigas SO, Trautner P, Weber B (2016) Gain- and loss-related brain activation are associated with information search differences in risky gambles: An fMRI and eye-tracking study. *eNeuro* 3:1–13.

After having completed study one and while collecting the data for study three, I reviewed the literature to find out whether individuals – when confronted with a lottery – pay more attention to the probability of winning or to the associated monetary amount. Additionally, I was interested in whether such differences had previously been associated with brain regions responsible for reward, loss, and risk processing. I found that studies had demonstrated individual differences in attention (Fiedler and Glöckner, 2012; Brandstätter and Körner, 2014) and risk-related brain activation (Samanez-Larkin et al., 2008; Rudorf et al., 2012; Smith et al., 2014). Additionally, in the context of human decisions involving rewards, losses, and risks, an "affect-integration-motivation" (AIM) framework had been suggested, thus providing a framework for the study of brain activation and attention (Samanez-Larkin and Knutson, 2015). Along with the AIM framework, many previous studies involving reward, loss, and risk processing (Schultz et al., 1997; Knutson et al., 2000; Kuhnen and Knutson, 2005; Tom et al., 2007; Seymour et al., 2007; Cooper and Knutson, 2008; Samanez-Larkin et al., 2008; Fliessbach et al., 2010; Fukunaga et al., 2012; Bartra et al., 2013; Clithero and Rangel, 2014) led to our hypothesis that gain- and loss-related brain activation in the ventromedial prefrontal cortex (vmPFC), the ventral striatum (VS), and the anterior insula (AI) would be associated with attention (measured via number of fixations; see chapter 2.2.3 for details) to probabilities or their respective monetary outcomes in an eye-tracking task involving risky gambles.

We used a similar fMRI paradigm to the monetary paradigm in study one, but additionally included a loss domain (Figure 1 in study two; see chapter 2.1.4 for details). Even though eye-tracking had been used in relation to event-related fMRI paradigms and inside the fMRI scanning environment before (Ettinger et al., 2008; Lim et al., 2011; Meyhöfer et al., 2015; Kasparbauer et al., 2016), we collected the eye-tracking data outside of the fMRI environment. For this purpose, we created an eye-tracking task with risky gambles (Figure 2 in study two) based on a previously established binary lottery choice task (Fiedler and Glöckner, 2012; Glöckner et al., 2012; Fiedler et al., 2013).

We invited 50 healthy adult males (25.9 ±4.6 years, all male) to participate in both experiments and found that individual differences in vmPFC activation during RPE processing were associated with paying more attention to the monetary outcomes compared to the respective probabilities in the gain domain (Figure 4A and B in study two). Additionally, individual differences in the VS and the posterior cingulate cortex (PCC) during loss prediction error (LPE) processing (see chapter 2.1.4 for details) were associated with paying more attention to the probabilities of risky gambles in the loss domain (Figure 4C and D in study two). This study therefore provided evidence that individual differences in monetary reward and loss processing are associated with individual differences in risk-related attention to either probabilities or their respective outcomes. Additionally, this study was the first to show a correlation between fMRI brain activation and eye-tracking data, as measured via two independent experiments using either method. Our RPE and LPE findings have recently been strengthened by the inclusion in an fMRI meta-analysis on prediction error valence and surprise (Fouragnan et al., 2018), in which similar brain regions were found to be responsible for each processing type (e.g. vmPFC in reward domain and insula in the loss domain). Furthermore, a recent study on the brain activation mechanisms of risky vs. secure e-payments (Casado-Aranda et al., 2018) has extended our brain activation findings to a more applied context. Here, the researchers linked the brain activation, which was found in our study in relation to reward prediction (e.g. the middle frontal gyrus), to brain activation in response to secure e-payments (Casado-Aranda et al., 2018).

3.3 Study Three: Neuroeconomic Correlates of Real-life Financial Risk Taking

Häusler AN, Kuhnen C, Rudorf S, Weber B (2018) Preferences and beliefs about financial risk taking mediate the association between anterior insula activation and self-reported real-life stock trading. *Scientific Reports* 8:1-13.

In Germany, ownership of direct shares amongst private households amounts to an estimated 158 billion Euros (Deutsche Bundesbank (German National Bank), 2016). However, in comparison to other countries, the German population is financially risk averse and invests fewer of its assets into stocks (von Lüde, 2013; Campbell, 2016; OECD, 2017). Since this behavior can be costly for households (Calvet et al., 2007) and the neuroscientific correlates of real-life financial risk taking are unknown, we invited 210 participants (39.0 ±6.7 years, all male) to partake in a 3.5h long neuroeconomic experiment. Participants underwent extensive neuroscientific, psychological, and economic measurements to find the correlates of individual differences in financial risk taking.

We used the real-life financial risk taking question of active stock trading ("Do you trade stocks yourself?") to group individuals into active stock traders and non-active stock traders. We then adapted a previously established stock paradigm (Kuhnen, 2015) to a functional magnetic resonance imaging (fMRI) setting. By extracting brain activation during risky (stock) versus safe (bond) choice from regions of interest (taken from three seminal neuroeconomic studies (Preuschoff et al., 2008; Bartra et al., 2013; Smith et al., 2014)), we examined whether the previously found association between financial risk taking and the ventral striatum, ventromedial prefrontal cortex, and the anterior insula (AI; Kuhnen and Knutson, 2005; Singer et al., 2009; Mohr et al., 2010; Wu et al., 2011; Rudorf et al., 2012; Bartra et al., 2013; De Martino et al., 2013; Clithero and Rangel, 2014; Smith et al., 2014; Knutson and Huettel, 2015; Leong et al., 2016) would transfer to financial risk taking in real life.

We found that individuals who trade stocks in real life show a lower risk aversion signal in the AI when choosing the stock versus the bond in the fMRI task. The study therefore advanced the neuroeconomic research agenda by discovering the brain activation correlates of real-life stock trading. Because evidence of the association between household variables and neuroscience had been scarce (Frydman and Camerer, 2016), the study was able to fill this important gap in the field of neuroeconomics (i.e. relating laboratory measures to real-life behavior). Additionally, we showed that not economic variables (i.e. financial constraints, education, the understanding of financial matters, and cognitive abilities), but two separate indices of risk tolerance and risk optimism explain the association between brain activation and real-life financial risk taking behavior. To formally test this, we used mediation analysis and found that the association between the risk aversion signal in the AI and real-life financial risk taking was mediated through both indices of risk tolerance and risk optimism.

3.4 Linking the Three Studies

The three studies presented in this thesis all used fMRI to provide new scientific evidence on the neuroeconomic foundations of reward, loss, and risk processing (Figure 10). Study one compared brain activation from a monetary and a social (sports) context, but only in the reward domain. Study two built on these findings by using a similar paradigm that additionally included a loss domain. This made it possible to further analyze loss-related brain activation. Finally, study three investigated the brain activation when participants were in both the reward and loss domain, and were asked to make risk-related decisions ((risky) stock vs. (safe) bond). The extracted reward-, loss-, and risk-related brain activation (VS, vmPFC, and AI) was then associated with financial risk taking behavior.

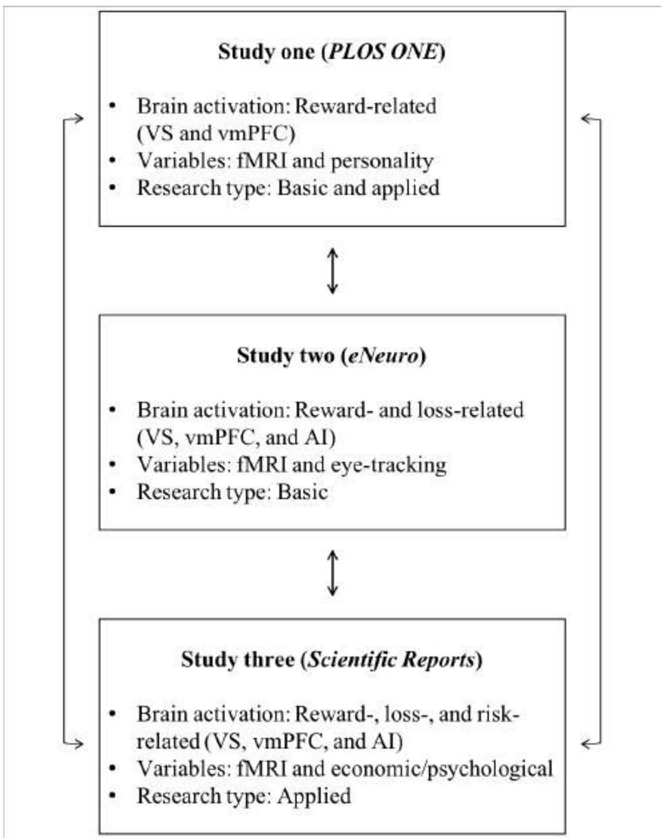

Figure 10. Diagram depicting the relation between the three studies presented in this thesis. This overall scheme shows the use of neuroeconomic (neuroscientific, economic, and psychological) methods to investigate both basic and applied research questions.

All three studies show the benefit of the neuroeconomic approach to answer both basic and applied research questions about individual and group differences in human decision making (Figure 10). Studies one and two both unveiled individual differences in brain activation and found the respective associations with personality traits (egoism in study one) and behavioral outcomes (attention in study two). Study one investigated the basic research question of a common neural currency in monetary and social contexts. It additionally combined fMRI with personality questionnaires to answer a more applied research question that investigated egoism in sports. The analysis of the monetary-relevant brain activation in study one was then extended in study two. Here, the reward- and loss-related brain activation was placed into context with attention (eye-tracking) patterns to answer the basic research question of whether these two measures are significantly correlated. Finally, study three investigated the applied research question of stock trading in real life. To fully show the benefit of the neuroeconomic approach, it included a comprehensive methodology that combined fMRI with research methods from economics and psychology. This extensive approach unveiled the group differences between individuals who trade stocks in real life and those who do not.

4. Conclusion, Outlook, and Applications

In this thesis, I presented three major findings. First, reward activation in social activities such as sports and reward activation elicited via financial wins share a common neural currency. Second, individual differences in attention distribution to either the values or the associated probabilities of risky gambles are related to individual differences in monetary reward and loss processing. Third, differences in neural activation patterns of regions associated with risk aversion help to explain real-life financial risk taking.

As an outlook for study one, decision making in other sports (e.g. basketball) and sport contexts (e.g. risky (dribble) vs. safe (pass) choices) could be investigated. This would clarify whether or not there is a general common neural currency across different sports and sport situations that could pose as an explanation for its worldwide success. The brain activation in these decision making processes could additionally be compared to financial decision making (e.g. the stock exchange paradigm from study three that also includes risky (stock) versus safe (bond) choices) to investigate whether the common neural currency can likewise be seen in relation to risk-, and not only reward-related decision making. From an application point of view, the egoism findings should find their way into the training books of soccer coaches to help them understand that individuals do not decide to shoot the ball themselves due to a reward-related motive, which is often seen as the driver for the seemingly greedy and egoistic behavior of shooting the ball yourself.

Since the study design in study two prohibits any interpretation regarding causality, future studies could try to investigate the fundamental question of whether the identified brain activation differences observed during reward and loss processing lead to individual differences in attention distribution, or vice versa. Taking it one step further, it could be explored whether fMRI and eye-tracking measures can be used as early indicators of excessive financial risk taking and gambling addiction. Better understanding the causal dynamics of decision making processes behind lottery choices could lead to the development of appropriate measures and policies to protect potential gambling addicts from financial ruin.

As an outlook for study three, follow-up studies could include assessments of the financial choices of family and friends, genetic information, and structural brain data (e.g. diffusion tensor imaging (DTI), which we are currently investigating, see chapter 8.1.3). Such variables are likely to improve the model of active stock trading and lead to an even better understanding of this real-life human behavior. On a more global scale and considering recent evidence of risk taking dissimilarities between different parts of the world (Falk et al., 2015b, 2015a; Becker et al., 2016), the same study could be performed in other countries (e.g. USA) to unveil the neuroeconomic foundations of this internationally heterogeneous behavior (OECD, 2017). Such an approach could uncover why German citizens are more financially risk averse than their US counterparts (Campbell, 2016; OECD, 2017). Additionally, the two risk indices developed in study three could be used to assess two important features that relate to financial risk taking. These measures of risk tolerance and risk optimism (RTI and ROI) could then help policy makers and financial institutions. Policies could be established to protect individuals with low financial means (but very high RTI and ROI scores) from taking too many financial risks. Furthermore, individuals with a very low RTI score could be protected from a significant decrease in quality of life as a consequence of taking too many financial risks. From a financial institution point of view, individuals with a very low ROI score could be educated from a third party on the financial market and its associated products, thus possibly encouraging more financial risk taking.

The findings from all three studies advance our understanding of reward, loss, and risk processing and bring us closer to comprehending the complex processes associated with human decision making. Methods from neuroscience (neuroimaging), psychology (behavioral data, personality, and eye-tracking), and economics (lotteries and household assessments) were used in all three studies and demonstrate the success of the interdisciplinary neuroeconomic approach. The prime example of this is study three, in which we compare separate and combined models to show that combining measurements from all three fields is essential for an apt analysis of real-life human decision making. Since human behavior is usually determined by many different variables, the goal of future neuroeconomists should be to identify these variables to create more comprehensive models of human behavior. With this interdisciplinary approach, the independent findings of each field can be connected and complex human behavior can be better understood. Finally, these more comprehensive models of human behavior can be used to improve individual choices by creating policies that steer individuals away from irrational decisions.

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6.2 Publications

7. Copies of Peer-reviewed Publications

7.1 Study One (PLOS ONE)

PLOS | ONE

RESEARCH ARTICLE

Goal or Gold: Overlapping Reward Processes in Soccer Players upon Scoring and Winning Money

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Abstract

Social rewards are important incentives for human behavior. This is especially true in team sports such as the most popular one worldwide: soccer. We investigated reward processing upon scoring a soccer goal in a standard two-versus-one situation and in comparison to winning in a monetary incentive task. The results show a strong overlap in brain activity be-tween the two conditions in established reward regions of the mesolimbic dopaminergic system, including the ventral striatum and ventromedial pre-frontal cortex. The three main components of reward-associated learning i.e. reward probability (RP), reward reception (RR) and reward prediction errors (RPE) showed highly similar activation in both con-texts, with only the RR and RPE components displaying overlapping reward activity. Passing and shooting behavior did not correlate with individual egoism scores, but we observe a positive correlation be-tween egoism and activity in the left middle frontal gyrus upon scoring after a pass versus a direct shot. Our findings suggest that rewards in the context of soccer and monetary incentives are based on similar neural processes.

Introduction

Seen as a driving force of human behavior and decision making, reward has previously been de-scribed as an operational concept for the positive value animals, including humans, ascribe to a behavioral act, object, or internal physical state [1]. While a lot of previous research has been dedicated to processing of primary rewards such as food, liquid, and sexual stimuli [2–4], sec-ondary rewards of monetary and social nature are also very important motivators for human be-havior [5–7]. Only two studies compared monetary and social reward processing in the form of positive social feedback and good reputation [8, 9]. In these studies, reward-related areas, i.e. the ventral striatum (VS) as well as the ventromedial prefrontal cortex (vmPFC), showed overlap-ping brain activity in response to monetary and social rewards [8, 9]. Results of these studies concurred with social exchange theory [10], which states that in social interactions not only materialistic goods such as money, but also non-materialistic goods such as social help are traded for other social goods as e.g. improved reputation.

Three major components are important in reward processing and reward-based learning: the probability, i.e. expectation of reward size and magnitude, the actual reward reception, and their difference: the reward prediction error [11, 12]. Previous studies comparing reward processing in a social and monetary context failed to investigate these different components in an active decision-making paradigm. We therefore developed a paradigm which allowed disentangling these different components in a social sport context by using reward in the form of goal-scoring in the most popular sport worldwide: soccer, which is played by about 265 million people around the globe (FIFA Communications Division (2007)—FIFA Big Count 2006: 270 million people active in football).

Our paradigm presents standard two-versus-one (2v1) situations in front of a goal in which subjects decide to either shoot to the goal directly or pass the ball to a team mate. By varying the situations and having them pre-rated by soccer experts, we manipulated the perceived probabilities of scoring the goal. The participant has a choice between a socially modest choice (pass) and a socially self-serving choice (shoot). The choice to pass to a teammate implies a more social, possibly team-oriented decision, while the decision to directly aim at the goal may add a personal on top of the social benefit. This is explained by pointing out that scoring a goal directly has an additional benefit to the goal scorer: while the team benefits from the goal, the scorer's social reputation increases as well by directly becoming the focus point for celebration and social approval. This emphasizes that the decision to either pass or shoot is not solely influenced by the perceived probability of scoring the goal—but also by personality factors such as egoism, that determine whether social (prosocial) or personal (proself) benefits will be given greater weighting.

Two types of egoism have been previously identified: a hostile and derogatory kind, as well as a narcissistic and self-enhancement kind [13]. The Dutch Personality Questionnaire (DPQ) and Supernumerary Personality Inventory (SPI) egoism tests measure these two different kinds of egoism, which have been shown to converge on the Honesty-Humility (HH) scale of the HEXACO Personality Inventory—Revised (PI-R) [13]. The abbreviation HEXACO stands for the six dimensions of the PI-R: "Honesty Humility", "Emotionality", "eXtraversion", "Agreeableness", "Conscientiousness", and "Openness to Experience", with the test being freely accessible online (hexaco.org). It is based on the Five Factor Model and it is the HH scale which has been established as a sixth dimension which lies beyond "the Big Five" [13]. Specifically, the HH assesses egoism on a behavioral dimension ranging from sincere, modest, and fair (when scoring low) to insincere, greedy, and boastful (when scoring high) [13–17]. It might therefore be ideally suited to assess the personality trait egoism in the context of the present research question. Another well-established measure to explain social behavior by distinguishing between prosocial and proself orientations is the social value orientation (SVO) questionnaire [18]. Using this questionnaire, previous studies were able to identify a correlation between it and the HH scale of the HEXACO PI-R [15].

By means of an active decision making soccer paradigm and a well-established monetary incentive task, we examined overlapping brain activation during monetary and soccer-specific social reward processing, including reward probability, reward reception and reward prediction errors. Additionally, we hypothesize egoism to correlate with stronger reward related signals upon scoring a goal after a direct shot versus after a pass to a teammate. On the behavioral level we expect to find more egoistic players to shoot the ball significantly more than to pass it.

Materials and Methods

Pre-testing

Pre-testing stimuli for the soccer paradigm were created by taking screenshots (1400x1050 pixels, 4:3 format, window mode, rendering quality: high, MSAA option: off, frame rate: no limit) of 200 different 2v1 situations from the soccer simulation FIFA 13 (Electronic Arts Inc., Redwood City, CA, USA). Screenshots displayed standardized 2v1 situations involving two attacking players with ball possession and a defending goalkeeper from the opposing team (Fig 1 and S1 Supporting Information). Pre-testing was performed using the online survey tool Qualtrics

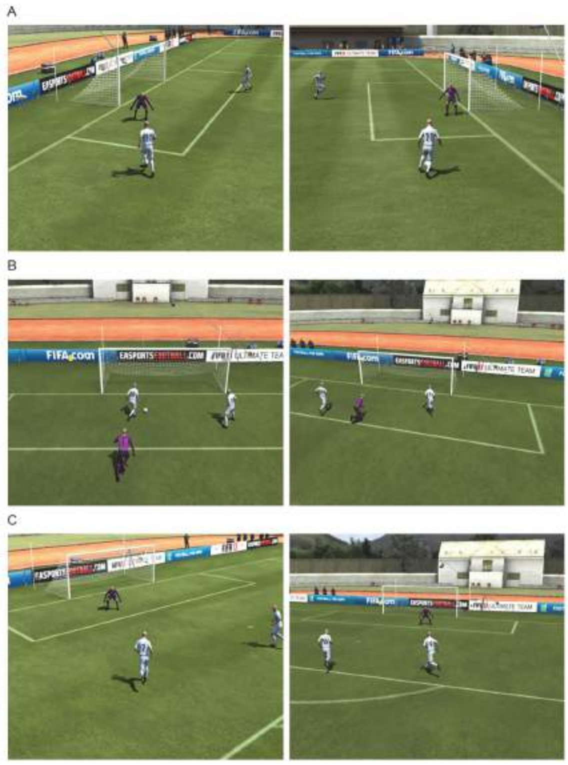

Fig 1. Soccer situations. Six exemplary images of the different soccer situations presented in the soccer paradigm. The player in ball possession approaches the goal from either the left or the right side of the penalty spot. A. Clear situation (pass). B. Clear situation (shoot). C. Unclear situation.

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(Provo, UT, USA). For each image, participants were asked three randomly presented questions:

1. How likely is it that you shoot the ball yourself, rather than passing it to your teammate, in order to score?
2. How likely is it for you to score upon shooting the ball?
3. How likely is it for your teammate to score after having received a pass?

377 German soccer players rated the situations. These soccer players were recruited by distributing the Qualtrics online link via Email to all of the 262 German regional soccer associations, while the Berlin and Hamburg soccer clubs were written to individually. Only teams and officials from the Middle Rhine soccer association were not contacted to keep this pool of participants for the fMRI part of the experiment. Furthermore, the link was posted online in local soccer blogs and social platforms. Each situation was rated an average of 38.63 (± 3.44) times. Question one ratings were used to categorize the situations into the 40 most unclear and 20 clearest situations (10 for shot and pass, respectively) and question two and three ratings were used to determine the scoring probabilities.

Soccer Paradigm

The fMRI paradigm was programmed using in-house software. Upon being confronted with the situation, participants decided to either pass or shoot the ball via button press (Fig 2A). Each situation was randomly shown twice and half of the feedbacks were preset to be positive (GOAL!) and the other half negative (MISS!), thus leading to 60 goals and 60 misses, respectively. The stimuli had an interstimulus interval (ISI) and intertrial interval (ITI) of 3000–6000 ms programmed for randomization using the "randint" function of Python 2.7 (Python Software Foundation, Beaverton, OR, USA). The feedbacks were preset in reference to the ratings of pre-testing questions two and three, thus making the feedback as realistic as possible.

Monetary Paradigm

In the previously published monetary incentive paradigm [19, 20], participants guessed under which out of one to four randomly shown boxes a circle was hidden, leading to winning probabilities ranging from 25% to 100% (Fig 2B). In each of the 150 trials, a correct guess led to a positive monetary feedback (win) of 10 euro cents and a wrong guess to no monetary win (no win), while no guess led to a monetary loss of 10 euro cents. The ISI and ITI were also programmed for a randomization of 1500–4500 ms using Python 2.7.

Participants

33 male (age: 24.39 ± 3.20 years) participants were recruited from local soccer teams via internet advertisements, flyers, word of mouth, and personal recruitment sessions at local soccer clubs. Exclusion criteria were a history of neurological or psychiatric disorders, involvement in the online pre-testing questionnaire, as well as conditions prohibiting the participation in an MRI setting. Additionally, participants had to be right-footed and actively playing at a soccer club. The participants received a show-up fee of 10 euro as well as additional monetary compensation depending on the results of the monetary paradigm and the monetary incentivized SVO test. All participants gave written informed consent according to the Declaration of Helsinki (BMJ 1991; 302; 1194) and the experiment was approved by the ethics committee of the University of Bonn.

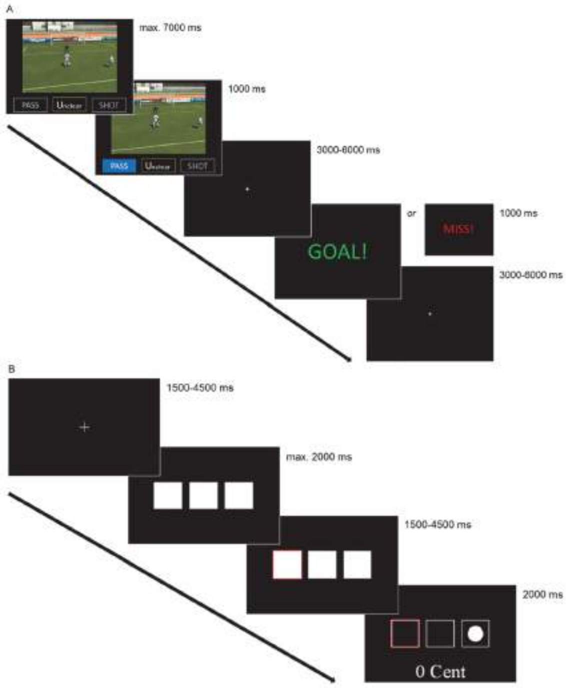

Fig 2. The soccer and monetary paradigm. Timeline for an exemplary trial out of the 120 trials shown in the soccer paradigm and the 150 trials shown in the monetary paradigm.

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Experimental Procedure

Personality Questionnaires. Each participant handed in the completed personality questionnaires (HEXACO PI-R 200 and SVO, previously distributed) at the scanning appointment. Additionally, a questionnaire regarding personal data and soccer experience was filled out by the participants on site (S1 Table). They subsequently received detailed instructions about the experimental procedure as well as ethical and medical implications. As part of an oral briefing procedure taking place directly ahead of entering the scanning room, each subject was instructed to not view the scenes as being from a video game, but rather as real-life situations with the teammate and opposing goalkeeper possessing real-life flaws.

fMRI Experiment. In total the experiment took two hours, consisting of three parts: a psychological questionnaire (~30 minutes), scanning preparation (~30 minutes), and scanning session (max. 90 minutes). The scanning session consisted of the soccer paradigm (max. 34 minutes), monetary paradigm (max. 32 minutes) and the final structural T1 measurement (~9 minutes). Participants were scanned on a 1.5 T Avanto Scanner (Siemens, Erlangen, Germany). Instructions were given regarding the emergency ball, the use of OHROPAX Classic ear protection (OHROPAX GmbH, Wehrheim, Germany), and the correct button pressing via the respective response grips (Nordic NeuroLab, Bergen, Norway). An 8-channel head coil was placed above the participant's face and video goggles (Nordic NeuroLab, Bergen, Norway) used to present the stimuli were installed on the head coil. Each paradigm was presented using Presentation v14.9 (NeuroBehavioural Systems Inc., Albany, CA, USA). Following the scanning sessions, participants were debriefed with regard to the preset soccer feedbacks and the study objective concerning egoism.

Imaging Protocol

Acquisition of the functional data was done using EPI-sequences with a repetition time (TR) of 2.5 s, echo time (TE) of 45 ms, and a flip angle of 90 degrees. The image resolution was 64 x 64 pixels and the field of view 192 x 192 mm. 31 slices covering the brain from the superior part of the cerebellum to the top of the cerebrum including the midbrain were obtained in an axial fashion and an interslice gap of 0.3 mm. This resulted in a voxel size of 3 x 3 x 3.3 mm.

fMRI Analyses

Data sets of five participants were excluded due to one participant not fully understanding the monetary paradigm, one scanning session being cancelled because of technical problems, one participant having a metal plate inside his knee, and data sets of two participants showing excess head motion (translational: >3 mm, rotational: >2.5 degrees). Statistical Parametric Mapping 8 (SPM8, Wellcome Department of Imaging Neuroscience, London, UK) was used to analyze the data sets of the remaining 28 participants (age: 24.57 ± 3.21 years).

Pre-processing steps included slice time correction, motion correction, spatial normalization to the T1 image of each participant, reslicing to a 3 x 3 x 3 mm voxel size, and a final smoothing step using a Gaussian kernel with full-width at half-maximum (FWHM) of 8 mm. Creating an identical GLM for both paradigms was technically not possible due to the necessity of combining the positive and negative feedback as well as the combined parametrically modulated (via the reward prediction error (RPE)) feedback in one regressor each. Therefore, brain activation was estimated using a total of four general linear models (GLM): two soccer and two monetary GLMs with GLM-specific regressor combinations.

GLM1 (soccer paradigm):

1. Choice
2. Choice (parametrically modulated via reward probability (RP))
3. Positive feedback (goal) after a pass
4. Positive feedback (goal) after a shot
5. Negative feedback (miss)
6. Missed response

7.-12.: Movement regressors

GLM2 (monetary paradigm):

1. Choice
2. Choice (parametrically modulated via RP)
3. Positive feedback (win)

4. Negative feedback (no win)
5. Missed response
6.-11.: Movement regressors

GLM3 (soccer paradigm) and GLM4 (monetary paradigm):

1. Choice
2. Feedback
3. Feedback (parametrically modulated via reward prediction error (RPE))
4. Missed response
5.-10.: Movement regressors

The RP parameter in the soccer paradigm was calculated based on the scoring probabilities assessed in the pretest; the reward probabilities in the monetary paradigm were directly related to the number of boxes shown in each trial (i.e. 0.25, 0.33, 0.5 or 1). The RPE parameter was computed as the difference between the outcome (i.e. 1 or 0) and the given RP. All of the regressors were convolved with the canonical hemodynamic response function (HRF) as implemented in SPM8. First-level contrasts were then established for each of the four GLMs and used for the second-level random effects analyses ($p<0.001$, uncorrected). These included one sample t-tests for the "RP versus zero' (one for each paradigm), 'goal versus miss'/'win versus no win' (reward reception), 'goal after a shot versus goal after a pass', 'goal after a pass versus goal after a shot', as well as 'RPE versus zero' (one for each paradigm) contrasts. A whole brain search was performed for each contrast and activities were listed accordingly (S4 and S5 Tables). The coordinates and T values of the peak voxels were determined in SPM8 and the relevant regions were then resolved using the automatic anatomic labeling (aal) atlas [21], as implemented in the xjView toolbox (available via http://www.alivelearn.net/xjview). By using this atlas, brain regions were inspected individually and labeled according to the terms used in the literature. The exact procedural description and an abbreviation overview can be found in the supplementary information (S8 Table). All of the beta and contrast images for each of the 28 subjects are freely accessible via the Harvard Dataverse Network website at "http://thedata.harvard.edu/dvn/dv/ANH".

The differential activation was statistically compared using the second-level specification feature of SPM8. For this purpose, each of the three specific reward contrast images (RP versus 0, RR, and RPE versus 0) were compared via paired t-tests. After subsequent estimation, the contrasts of soccer versus monetary reward activity were compared on a whole-brain level ($k>10$, $df = 27$, S6 Table).

The egoism analysis was performed by using the egoism values from the Honesty-Humility scale of the HEXACO 200 PI-R as covariates in the contrasts "scoring after a shot versus a pass" and "scoring after a pass versus scoring after a shot". Additionally, behavioral egoism values were calculated by taking the proportion of shots in the clear situations normalized by the number of total shots and integrating them as covariates in the same contrasts described above. All behavioral data was analyzed using IBM SPSS Statistics 21 (IBM Corp., Armonk, NY, USA).

ROI Analyses

In line with a previous study investigating overlapping brain activation [8], regions of interest (ROI) masks were created from the monetary reward contrasts 'RP versus 0', 'win versus no win', and 'RPE versus 0' using the xjView toolbox ($p<0{,}001$, $k>10$, Fig 3 (yellow color)). More

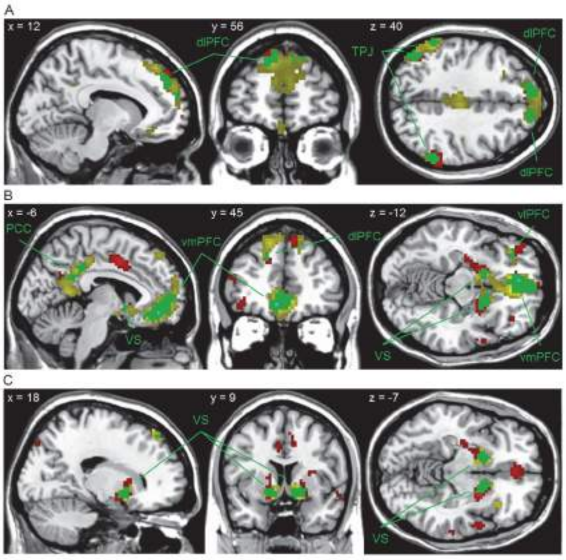

Fig 3. Masks of the reward processing regions activated in each and both paradigms (k > 10, df = 27). A. Reward Probability (RP) versus 0. B. Reward Reception (RR): Win/Goal > NoWin/Miss. C. Reward Prediction Error (RPE) versus 0. Yellow: monetary, p<0.001, uncorrected. Red: soccer, p<0.001, uncorrected. Green: areas activated in both paradigms, p<0.001, uncorrected. Turquoise: areas activated in both paradigms, p<0.05, FWE-corrected. Abbreviations: dlPFC: dorsolateral prefrontal cortex, PCC: posterior cingulate cortex, TPJ: temporal parietal junction, vlPFC: ventrolateral prefrontal cortex, vmPFC: ventromedial prefrontal cortex, VS: ventral striatum.

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details of the regions included in the monetary ROI masks and the results of the whole brain search for each of paradigms can be found in the supporting information (S4 and S5 Tables, as well as S2 Supporting Information). The monetary masks were then applied to the respective soccer brain activation contrasts ($p<0.001$, $k>10$, relevant masks can be seen in Fig 3 (red color) and S2 Supporting Information).The results were small volume corrected ($p<0.05$, familywise error (FWE)-corrected) and checked for significantly overlapping active regions (Table 1). Additionally, four ROI masks were obtained from the authors of the previously published paper involving the monetary paradigm [20]. These were based on the Oxford-Harvard cortical and subcortical atlases and included the bilateral ventral striatum, the ventral midbrain, and the medial orbitofrontal cortex. These ROI masks were however only used to check for the independent activation robustness of the monetary paradigm and are considered irrelevant for the main part of the analysis.

Results

Participants and Personality Test Results

The most competitive player was active in the 5th German league (Mittelrheinliga), while most participants (n = 10) played in the 9th German league (Kreisliga B; S1 Table). The HEXACO PI-R 200 was analyzed on each domain and facet-level scale (S2 Table), resulting in only four participants being categorized as egoistic. Using the data from the SVO questionnaire, 21 prosocials, five proselfs, and no competitors were identified (mean = 1.19, SD = 0.40), while two were not classified due to inconsistent responses. Only one participant was characterized as egoistic and proself. Subsequent analysis using the SVO scores was refrained from due to lack of statistical power.

Behavioral Results

Behavioral data from the soccer paradigm was grouped into four categories. For each of the clear and unclear categories, pass and shoot choices were analyzed (S3 Table). Out of the 3360 situations, only five situations were not responded to. Overall, soccer players did not decide to shoot significantly more or less than to pass the ball (S3 Table). In order to identify individual soccer players that chose to either shoot or pass more than others, one SD above/below the average ratio was used as a threshold. This resulted in five participants having chosen to shoot directly significantly more than the rest.

fMRI Results

Reward Probability. Overlap analysis using inclusive masking revealed overlapping brain activity modulated by reward probability in the bilateral temporal parietal junction (TPJ), bilateral dorsolateral prefrontal cortex (dlPFC), and right postcentral gyrus (POG) (Table 1 and Fig 3A, green color). No differential activation was observed.

Reward Reception. The very medial posterior cingulate cortex (PCC), bilateral ventral striatum (VS), left dlPFC, left ventrolateral prefrontal cortex (vlPFC) and left vmPFC were all found to be significantly active in both types of reward reception (Table 1 and Fig 3B, green color). The vmPFC activation was found to extend into the subgenual and rostral anterior cingulate cortex (sgACC and rACC, respectively), as well as into the medial orbitofrontal cortex (mOFC). Only scoring a goal versus missing led to additional significant brain activity (S6 Table). This was found in the bilateral TPJ, as well as in areas of the left vlPFC.

Reward Prediction Error. Overlapping activation during reward prediction error processing was observed in the bilateral VS (Table 1 and Fig 3C, green color) and no differential activation was observed.

Correlation to Egoism. Contrasting scoring a goal after a shot versus a pass and vice versa led to no significant activation. Furthermore, the behavioral egoism covariate analyses did not show significant brain activation. No correlating brain activation was observed between egoism scores (Honesty-Humility scale of the HEXACO PI-R 200) and brain activation due to "scoring after a shot versus scoring after a pass". However, a negative correlation was found between the Honesty-Humility scale of the HEXACO PI-R 200 and brain activation (i.e. positive correlation of egoism) upon "scoring after a pass versus scoring after a shot" (S7 Table and Fig 4A) in the left middle frontal gyrus (MFG; p(FWE-corr.) = 0.002; S7 Table and Fig 4B).

Discussion

Using the combination of a standard monetary incentive and a newly developed soccer-related task, we were able to investigate different computational aspects in reward-based learning in a

Table 1. Overlapping activity in both tasks: Small volume corrected brain activation upon soccer and monetary reward probability (RP), reward reception (RR), and reward prediction error (RPE) (k >10, df = 27).

Contrast	Region	Laterality	MNI coordinates			Cluster size	T
			x	y	z		
Reward probability	TPJ***	L	-51	-70	34	192	6.26
	dlPFC*	L	-15	50	37	65	5.53
	TPJ*	R	60	-52	43	37	5.36
	POG*	R	45	-25	64	55	5.01
	TPJ**	L	-60	-49	43	48	4.70
	dlPFC*	R	18	50	40	25	4.54
Reward reception	vmPFC***	L	-3	47	-8	310	6.57
	VS**	R	24	5	-11	61	6.13
	VS**	L	-12	11	-5	42	5.69
	PCC***	L/R	0	-46	28	189	5.54
	dlPFC**	L	-18	32	52	52	5.09
	vlPFC*	L	-36	38	-8	20	4.73
Reward prediction error	VS***	R	21	2	-11	58	7.20
	VS**	L	-18	2	-11	45	5.33

ROI masks were created from the monetary contrasts 'RA versus 0', 'win versus no win', and 'RPE versus 0', respectively. The activity during soccer reward processing was then corrected for by small volume using the respective masks. Abbreviations: dlPFC (dorsolateral prefrontal cortex), PCC (posterior cingulate cortex), POG (postcentral gyrus), TPJ (temporal parietal junction), vlPFC (ventrolateral prefrontal cortex), vmPFC (ventromedial prefrontal cortex), VS (ventral striatum).

*** p(FWE-corr.)<0.001,

** p(FWE-corr.)<0.01,

* p(FWE-corr.)<0.05.

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soccer-specific social in comparison to a monetary context, i.e. reward probability, reward reception, and reward prediction errors. Our data does not only show a strong overlap of the neural substrates involved in monetary and soccer-specific social feedback in different aspects of reward processing, but also differential activation during reward reception.

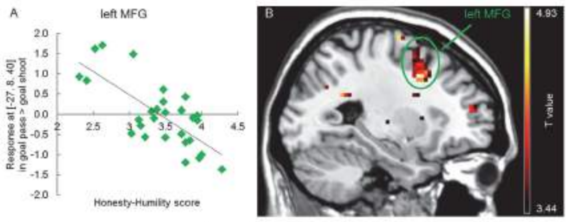

Fig 4. Positive correlational activity between egoism and scoring after a pass versus a shot at the left middle frontal gyrus (MFG, k >10, df = 27). The negative correlation of brain activity and Honesty-Humility depicts a positive correlation with egoism. A. Correlational analysis of Honesty-Humility scores and contrast values at the left MFG cluster. B. left MFG (green circle) activation in correlation to egoism upon scoring after a pass versus a shot.

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Reward Probability

The bilateral dorsolateral prefrontal cortex (dlPFC), temporal parietal junction (TPJ), and right postcentral gyrus (POG) were shown to be active during anticipation of both reward types. The dlPFC has been associated with social judgment and decision making, specifically in relation to behavioral control of social strategic behavior [22], implementation of fairness-related behavior [23], and social norm compliance [24, 25]. The TPJ has been shown to be involved in spatial working memory tasks [26] as well as social contexts such as apology and forgiveness [27], as well as attention and social cognition [28, 29]. Additionally, right POG activation was observed during the reward anticipation in both paradigms, a region that has identified as the primary somatosensory cortex [30].

Reward Reception

The ventromedial prefrontal cortex (vmPFC), bilateral ventral striatum (VS), posterior cingulate cortex (PCC), as well as the left dorsolateral prefrontal cortex (dlPFC) and left ventrolateral prefrontal cortex (vlPFC) were involved in reward reception in both paradigms. The largest cluster peaking in the vmPFC and extending into the subgenual and rostral anterior cingulate cortex (sgACC and rACC, respectively), and medial orbitofrontal cortex (mOFC), as well as the activation of the VS have been associated with social and monetary reward processing in other previously mentioned studies comparing social and monetary reward [8, 9]. Besides the ventral parts of the striatum having long been known to be part of the reward circuit [31–33], the sgACC and rACC could have played a role in the attention circuit regulating cognitive and emotional processing [34, 35]. This is also relevant in pointing out that similar activation in these two regions was observed in another soccer reward processing study that contrasted goal and miss, as well as goal versus open play [36]. To our knowledge this is the first study showing evidence for a direct overlap in the vmPFC and VS with respect to monetary and soccer-specific social rewards, even though other studies have shown involvement in social reward processing as well [5, 8, 9, 37, 38]. The PCC has been previously shown to be linked to value association in connection with reward processing [39], as well as episodic memory retrieval [40], and visuospatial attention [41, 42]. It is therefore difficult to interpret the exact role in our paradigm. Specifically, activations of the left dlPFC have been linked to behavioral control of strategic social behavior [22] and attention control during task preparation [43], while left vlPFC activation has been related to cognitive control of current relevant memory [44], and selection between competing active representations as used in goal-selection [45, 46].

The direct comparison of reward-related activity in both tasks revealed more activation in the soccer as compared to the monetary paradigm. Of these, the TPJ has been associated with spatial working memory tasks [26], suggesting a stronger involvement possibly occurring due to expertise of the soccer players with these standard situations and therefore implicit spatial memory retrieval. Additionally, the TPJ has been associated with social contexts, such as social cognition in relevance to attention [28], apology and forgiveness [27], and parochial punishment [29]. The differential activation of the TPJ only existing in relevance to the soccer paradigm could therefore be suggested to represent the sport's implicit social context as shown in the form of 2v1 situations. Additionally, activation only found upon scoring a goal was also located in the left vlPFC. As mentioned before, this region is especially activated during cognitive control of current relevant memory [44] and selection between competing active representations as used in goal selection [45, 46]. It can henceforth be suggested that processing these features of the soccer situations require greater neural effort than simpler guessing situations such as shown in the monetary paradigm. It is important to note however that such a suggestion can only be finalized following a same study procedure involving "non-experts".

Reward Prediction Error

The bilateral VS was significantly activated during reward prediction error processing in the soccer game as well as in the monetary domain. It is well known for its role in reward prediction error processing [19, 20, 37, 47–49], but this is the first time a sport-related context has been shown to elicit this type of activity.

Egoism

The whole HEXACO test was handed out to the participants to prevent the soccer players from recognizing the egoism component of the study and thus influencing the decision making process of the individuals. This was especially important since egoism is known to be associated with negative personal features such as antisocial behavior [13]. Even though no correlation between egoism and brain activation upon scoring a goal after an own shot and scoring after a pass was observed, we did find a positive correlation between egoism and activation in the middle frontal gyrus (MFG) in response to scoring a goal after a pass versus after a shot. This region has been linked to many different higher cognitive processes such as image recognition [50], spatial working memory tasks [26], emotional processing of happiness [51], reasoning [52], as well as future event construction and elaboration [53], but has not been shown to be involved in reward processing, specifically. This rather counterintuitive finding might be explained by suggesting that more egoistic soccer players do not require any neural effort to process scoring a goal after a shot since these individuals value this as a rather normal situation, while scoring after passing the ball to a teammate requires self-reflective spatial and reasoning neural effort in regions such as the MFG. By not finding significant activation in the previously mentioned reward areas, our data does not support the hypothesis of egoism correlating with stronger reward related signals upon scoring a goal after a direct shot versus after a pass to a teammate. Additionally, our behavioral observations do not show a correlation between passing and shooting behavior in 2v1 situations in front of goal and egoism. These results can be seen as a first step towards dealing with individuals in team sports who thus far have been labeled by the public and media as 'egoistic'. Even though we did not find any correlation between egoism scores and passing versus shooting behavior, it is too far-fetched to suggest the personality trait egoism to not guide the oftentimes labeled selfish decisions on a soccer pitch. Future studies involving other in-game soccer situations (e.g. in the middle of the pitch decisions: 'dribble versus pass') and other team sport decision making paradigms should therefore be done in order to determine the personality and social aspects guiding such behavior. Determining these aspects could be crucial in developing guidelines for coaches and teammates to deal with mistakenly labeled 'egoistic' individuals in social activities such as team sports.

Limitations

Even though we think that a soccer-related task such as the one implemented in the experiment has an inherent social context, it is important to point out that there are several possibilities for improving the social aspect of the experimental setup. Since the participant in the scanner does not interact with other participants directly, creating an avatar of the participant and one of his teammates could serve as an idea for a future study. With the participant then lying in the scanner, the teammate could observe the decisions made by the participant from the scanner operating room and respond accordingly, thus giving social feedback, or two players could directly interact in a hyperscanning experiment. As recently published in relation to social feedback processing, another idea would be to implement a camera in the scanner in order to emphasize the social aspect of the soccer-specific social experimental procedure even further [54].

Conclusion

Our results suggest strong overlapping neural processes underlying reward probability, reward reception, and reward prediction error processing during highly motivating team sport situations and monetary incentives. While reward reception and reward prediction error processes overlap in reward related regions, reward probability processing requires higher cognitive effort in both domains. Besides extending this research to other reward-related sport activities and to different levels of sport expertise, future research could investigate the differences and similarities of reward paradigms in order to decipher the exact processing components of decision making during reward anticipation and probability. Our results furthermore suggest that the role of the term egoism in team sports should be further researched on in order to possibly support the finding of egoism failing to be shown as a driving force of on-pitch soccer behavior.

Supporting Information

S1 Supporting Information. Screenshot specifications.
(DOCX)

S2 Supporting Information. Detailed region of interest specifications relevant to the mask created via the monetary paradigm ($p<0.001$, $k>10$, uncorrected).
(DOCX)

S1 Table. Physical, soccer, and video game attributes of 28 soccer players.
(DOCX)

S2 Table. HEXACO PI-R 200 domain and facet-level scale values of 28 soccer players.
(DOCX)

S3 Table. Behavioral data from the soccer paradigm, displaying number of shots and passes in the given 80 unclear and 40 clear situations.
(DOCX)

S4 Table. Brain activity related to soccer reward probability, reward reception, and reward prediction error ($k>10$. $df = 27$).
(DOCX)

S5 Table. Brain activity related to monetary reward probability, reward reception, and reward prediction error ($k>10$, $df = 27$).
(DOCX)

S6 Table. Differential Brain activity upon contrasting soccer versus monetary reward reception (paired t-test, $k>10$, $df = 27$).
(DOCX)

S7 Table. Negative correlation between the HEXACO PI-R 200 Honesty-Humility scale and brain activity at scoring after a pass versus scoring after a shot ($k>10$, $df = 27$).
(DOCX)

S8 Table. Brain region name abbreviations.
(DOCX)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: ANH BB MB BW. Performed the experiments: ANH. Analyzed the data: ANH BB BW. Wrote the paper: ANH BW.

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7.2 Study Two (eNeuro)

eNeuro

New Research

Cognition and Behavior

Gain- and Loss-Related Brain Activation Are Associated with Information Search Differences in Risky Gambles: An fMRI and Eye-Tracking Study

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Abstract

People differ in the way they approach and handle choices with unsure outcomes. In this study, we demonstrate that individual differences in the neural processing of gains and losses relates to attentional differences in the way individuals search for information in gambles. Fifty subjects participated in two independent experiments. Participants first completed an fMRI experiment involving financial gains and losses. Subsequently, they performed an eye-tracking experiment on binary choices between risky gambles, each displaying monetary outcomes and their respective probabilities. We find that individual differences in gain and loss processing relate to attention distribution. Individuals with a stronger reaction to gains in the ventromedial prefrontal cortex paid more attention to monetary amounts, while a stronger reaction in the ventral striatum to losses was correlated with an increased attention to probabilities. Reaction in the posterior cingulate cortex to losses was also found to correlate with an increased attention to probabilities. Our data show that individual differences in brain activity and differences in information search processes are closely linked.

Key words: decision-making; eye-tracking; fMRI; information search; reward

Significance Statement

The processing of gains and losses has been thoroughly investigated in the field of decision-making using different methods, such as eye tracking and neuroimaging. Even though previous studies have combined both of these methods in single tasks before, this is the first study that correlates the results from two separate tasks using either method. Using this approach, we show for the first time that individual differences in neural gain and loss processing relate to individual differences in the information search phase of risky gambles. These results emphasize the functional interplay between attention and the neural circuits of reward and loss processing.

Introduction

When individuals are confronted with risky decisions, they have to choose between options that entail different outcomes with known probabilities of realization. Risk-averse individuals prefer a safe over a risky gamble of equal expected value (EV), with the opposite being true for risk-seeking individuals. Even though risk preferences are mostly investigated using self-assessments or behavioral tasks in an experimental setting, they have been shown to relate to important real-life social and economic out-

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comes. Risk-seeking individuals are, for example, more likely to migrate (Jaeger et al., 2010) and to have higher-earning occupations (Bonin et al., 2007). Since attention differences measured via eye tracking (Brandstätter and Körner, 2014) and individual differences in neural processing of risk (Rudorf et al., 2012) have both been shown to relate to risk preferences, the investigation of the relation between attention and neural processing is an important and necessary step to enhance our understanding of human decision-making under risk.

Functional magnetic resonance imaging (fMRI) and eye tracking have widely been used to investigate the neural correlates and behavioral aspects of decision-making under risk. Recently, an "affect-integration-motivation" framework has been presented as a model that integrates the affect, integration, and motivational aspects of decisions that involve gains, losses, and risks (Samanez-Larkin and Knutson, 2015). This cognitive-processing framework is based on several studies that unveil the neural circuits involved in the processing of rewards, losses, and risks. One of these brain areas is the ventral striatum (VS), which has long been known as a key region in reward and risk processing (Schultz et al., 1997; Knutson et al., 2000; Kuhnen and Knutson, 2005; Fliessbach et al., 2010; Bartra et al., 2013; Clithero and Rangel, 2014; Samanez-Larkin and Knutson, 2015). The ventromedial prefrontal cortex (vmPFC) is another region that has been found to play a role in reward processing through its role in valuation (Fliessbach et al., 2010; Bartra et al., 2013; Clithero and Rangel, 2014). Both regions have also been related to processing losses (Seymour et al., 2007; Tom et al., 2007; Cooper and Knutson, 2008), which has been interpreted as a representation of a gain–loss continuum (Tom et al., 2007). Besides these two areas, the anterior insula (AI) has been shown to play a major role in loss processing (Samanez-Larkin et al., 2008; Fukunaga et al., 2012), with its activation also preceding risk-averse choices (Kuhnen and Knutson, 2005). Even though it has been shown that many different cortical and subcortical regions are involved in processing positive and negative outcomes (Vickery et al., 2011), we are focusing on the three mentioned brain regions, because the individual activation differences in the VS and AI have been related to risk preferences and even to financial success in a stock market experiment (Samanez-Larkin et al., 2008; Rudorf et al., 2012; Smith et al., 2014) and the vmPFC has been robustly linked to valuation (Bartra et al., 2013; Clithero and Rangel, 2014).

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Behavioral results have noted for a long time the tendency of individuals to place more weight on outcomes compared with probabilities (Daston, 1995; Arnauld and Nicole, 1996; Loewenstein et al., 2001; Sunstein, 2003). More recently, studies involving eye tracking have been aiming to dig deeper into the underlying causes of such tendencies by measuring information search processes in risky gambles. Information search processes are behaviorally expressed through eye movements that can be traced and recorded. Especially attention, measured through the number of fixations, has been studied in this context, and attention differences to values and probabilities of risky choices in both the gain and loss domain have been found (Brandstätter and Körner, 2014). Even though individual differences in attention have been shown (Fiedler and Glöckner, 2012), it is unclear up to now whether and how they relate to individual differences in neural gain and loss processing.

Taking into account the findings from each of these studies using different techniques, we propose that information search in risky choices is related to the neural processing of gains and losses. Using two independent experiments that involve fMRI and eye tracking, we describe the link between individual attention differences and activation during reward and loss processing in the VS, vmPFC, and AI.

Materials and Methods

Over the course of 2 months, 50 healthy adult males (25.9 ± 4.55 years) participated in a study consisting of two independent parts measured on the same day: an fMRI and an eye-tracking session. Exclusion criteria were a history of neurological or psychiatric disorders, conditions prohibiting the participation in an MRI setting, and imperfect eyesight. Upon arrival and prior to the tasks, a thorough instruction was handed out, explained, and discussed. The study was approved by the Ethics Committee of the University of Bonn, and all subjects gave written informed consent according to the Declaration of Helsinki (World Medical Association, 2004).

fMRI acquisition and paradigm

Participants underwent a structural T1 measurement (160 slices; voxel size, $1 \times 1 \times 1$ mm; repetition time (TR), 1660 ms; echo time (TE), 3.09 ms; and flip angle, 15°) in a 1.5 T Avanto Magnetom scanner (Siemens) using a standard eight-channel matrix head coil. Afterward, participants completed an fMRI paradigm (Fig. 1), which was an extended version of a previously established choice task (Fliessbach et al., 2010; Rohe et al., 2012; Häusler et al., 2015). In this task, participants were asked to guess under which of one, two, three, or four symbols a ball was hidden (Fig. 1). Our task was thus related to the popular shell game, with the difference being that ours was a pure guessing task excluding deception and including varying probabilities of guessing correctly due to the varying number of symbols (e.g., 100% in case of one symbol, 50% for two symbols). The nondeception aspect was made especially clear to the participants to avoid inconsistent brain responses due to possible biases coming from deception experienced during observation of the real-life

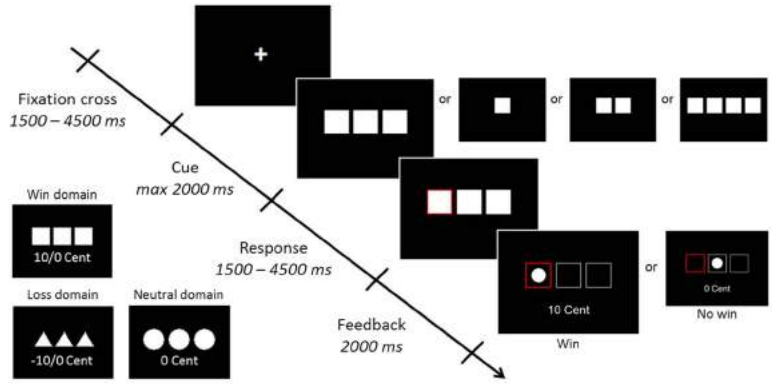

Figure 1. The fMRI paradigm timeline and symbol explanation for each of the three domains. Each subject completed 48 win, 48 loss, and 24 neutral trials, and the symbol–domain relationship was counterbalanced.

shell game, in which participants are often deceived. Furthermore, whereas the original paradigm used in previous studies was composed of situations with different probabilities in only the win domain, the new paradigm was adapted to also involve monetary loss and neutral situations. The paradigm consisted of 120 total trials: 48 in the win, 48 in the loss, and 24 in the neutral domain. Each of the three domains (win, loss, and neutral) was represented by a different symbol, namely squares, triangles, and circles (Fig. 1). The mapping between a domain and its specific cue symbol was counterbalanced across subjects. The sequence of trials was randomized with the condition in order for a trial of a specific domain to not be followed by a trial of the same domain. The paradigm was programmed using in-house software based on Python (version 3.4; RRID:SCR_008394). Images were displayed via video goggles, and participants made decisions via response grips (both from Nordic NeuroLab) using the index fingers and thumbs of both hands.

First, a fixation cross was shown with a randomized duration between 1500 and 4500 ms. In the second phase (the cue phase), each participant saw one, two, three, or four symbols, all from the same domain (either win, loss, or neutral). Subjects were told that selecting one specific symbol would lead to a win, a loss, or nothing, depending on the domain. Subjects had up to 2000 ms to choose the respective target symbol. The number of items (one, two, three, or four) were shown next to each other and represented the chances of winning (reward probability: 100%, 50%, 33%, and 25%) or losing (loss probability: 0%, 50%, 66%, and 75%) 10 € cents. Guessing incorrectly in the win domain led to no win, and guessing incorrectly in the loss domain led to a loss of 10 € cents. The participants did not win or lose any money in the neutral domain.

After pressing one of the four buttons, the selected option was highlighted for a randomized time between 1500 and 4500 ms. Last, the result was presented in an outcome feedback phase during which the participants found out whether they won or lost 10 € cents, or did not win or lose any money. Functional data were acquired using a TR of 2.5 s, a TE of 45 ms, and a flip angle of 90°.

Each volume contained 31 slices with a voxel size of 3 × 3 × 3 mm, covering the whole brain, including midbrain but sparing part of the cerebellum. A total of 800 scans were acquired. At the end of the scanning session, each subject was informed about the total amount of money won (outcome of each task plus a 15 € participation fee) during the first part and that this monetary win was independent of subsequent results in the eye-tracking session.

Eye-tracking acquisition and paradigm

The participants took a 5–10 min break between both experiments in the non-laboratory-related waiting room of our institute. They were then accompanied to the eye-tracking laboratory and asked to sit comfortably while resting the head on a chinrest. They were instructed to make a total of 80 decisions while undergoing eye-tracking recordings from the left eye at 1000 Hz using an Eyelink 1000 eye-tracker (SR Research; RRID:SCR_009602). The eye-tracking experiment was programmed using in-house software based on Python 3.4, and each participant completed a nine-point calibration and a practice phase before starting with the experimental trials.

Each trial consisted of a blank screen (3000 ms) to rest the eye, a fixation cross (500 ms), and a decision phase with no time limit showing two lotteries (Fig. 2A). The participants were asked to opt for lottery A or B during the decision phase, as indicated by the respective letters "A" and "B" positioned next to the two lotteries (Fig. 2B). White horizontal and vertical lines were used to divide the lottery options in order to make the decision process more intuitive for the participants. The participants were then able to press one of two keyboard letters to enter

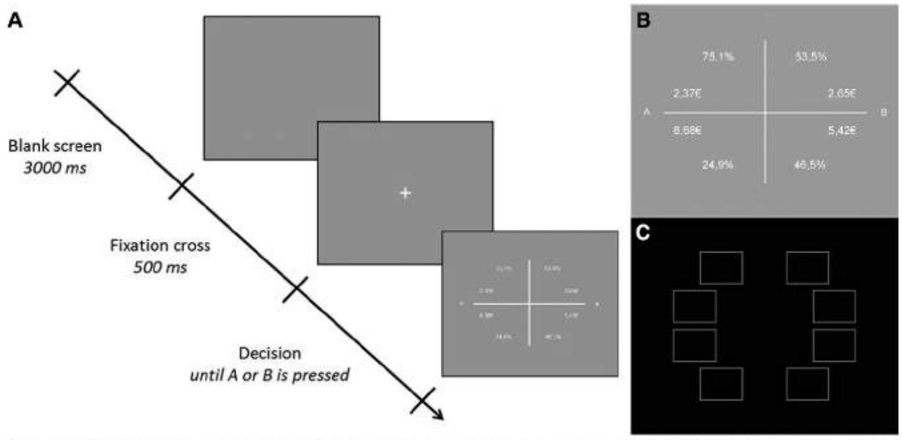

Figure 2. The eye-tracking experiment. ***A***, Paradigm timeline. ***B***, Exact display of the eye-tracking stimulus shown during the decision phase. ***C***, The eight areas of interest used to extract the number of fixations.

their decisions for options A or B, respectively. In each lottery (Fig. 2*B*, lottery A), two different monetary amounts were presented as possible outcomes to the subject. Both amounts of money were associated with respective probabilities, and the number of digits was identical for both amounts and percentages. The stimuli were shown as white writing on gray background, a color scheme used in a previous eye-tracking study (Fiedler et al., 2013). The areas of interest (AOIs; size, 200 × 150 pixels) centers were positioned at the same distance from the total image center (Fig. 2*C*).

A script in MATLAB R2014a (MathWorks; RRID: SCR_001622) was used to create gambles in which the domain, winning/losing probabilities, and winning/losing values were pseudo-randomized. Different ranges of values (Vs; Fig. 2) and probabilities (Ps) were used to create a high-risk and a low-risk lottery. The EVs for both the high-risk and the low-risk options in our experiment were chosen to be within a range of 3–5 € and always similar between the two lotteries. This was done because a previous study by Fiedler and Glöckner (2012) found the decision time and the number of fixations to increase with mean EV. The riskiness of a lottery was defined as the difference between the two monetary amounts (i.e. the possible variance of the outcomes). In Figure 2, the high-risk lottery would therefore be "A" and the low-risk lottery would be "B," even though the EV of both gambles is 3.94 €. The locations of the two lotteries were randomized between left and right, and the locations of the values and probabilities (upper or lower) varied between subjects and were counterbalanced.

For each domain, 30 value and probability combinations were pseudorandomly chosen from a list of 175,000 generated combinations containing all of the mentioned parameters. None of the probabilities were used more than once. Additionally, 10 distractors for each domain (random values and probabilities with the same amount of digits) were generated in order to mix up the paradigm and thus require each subject to concentrate in every trial. Hence, each domain (win and loss) contained 30 experimental and 10 distractor trials, summing up to the total of 80 trials. At the end of the experiment, one trial from each domain was randomly selected and paid to the participant on top of the participation fee (15 €). This amount was added to the amount won in the first part of the experiment and transferred to the participant's bank account.

fMRI analysis

Datasets of two participants were excluded due to both participants not having understood the fMRI task correctly. None of the participants exceeded head motion limits (translational, >3 mm; rotational, >2.5°), thus leading to an fMRI analysis of 48 participants. The fMRI analysis was performed using Statistical Parametric Mapping software version 12 (SPM12, Wellcome Department of Imaging Neuroscience; RRID:SCR_007037) through scripts written in MATLAB. Preprocessing included slice time correction, motion correction, spatial normalization to the canonical template from the Montreal Neurological Institute (MNI), reslicing to a 3 × 3 × 3 mm voxel size, and spatial smoothing using a Gaussian kernel with full-width at half-maximum of 8 mm. In the first-level analysis, a general linear model (GLM) was created (Table 1) with the aim of analyzing the prediction and prediction error in both the reward and loss domain [reward prediction (RP), loss prediction (LP), reward prediction error (RPE), and loss prediction error (LPE); Table 2]. The following four parametrical contrasts were defined: "RP > 0" and "LP >

Table 1: Overview of the GLM used for estimating brain activation

Regressor	Parametrical modulation	Contrasts of interest
Onset of choice, win domain	Yes: RP	RP > 0
Onset of choice, loss domain	Yes: LP	LP > 0
Onset of choice, neutral domain	Yes: RP	
Onset of result, win domain	Yes: RPE	RPE > 0
Onset of result, loss domain	Yes: LPE	LPE > 0
Onset of result, neutral domain	Yes: RPE	
Six movement regressors	NA	

NA, not applicable.

0" (both at anticipation phase, Table 1), as well as "RPE > 0" and "LPE > 0" (both at feedback phase, Table 1). The first-level contrasts were used for the second-level analysis.

In order to investigate individual differences and relate brain activity to behavioral and eye-tracking measures, activations from three independent and previously defined 6 mm spherical regions of interest (ROIs) were used. These included the VS and AI using coordinates from a recent study by Smith et al. [2014; MNI coordinates (*x*, *y*, *z*): AI, ±36, 24, 2; VS, ±12, 8, −8]. Additionally, vmPFC coordinates were obtained in a manner similar to that of Smith et al. (2014) by entering the brain term ("ventromedial prefrontal") into the "Neurosynth.org" database (accessed on February 17, 2016) and obtaining the peak MNI coordinates [of 250 studies (*x*, *y*, *z*): ±4, 42, −8]. We additionally included the oral area of the somatosensory cortex (OSS; *x*, *y*, *z*: ±64, −13, 14; Miyamoto et al., 2006).

The AFNI (Analysis of Functional Neuroimages; RRID: SCR_005927) program 3dClustSim, which is based on Monte Carlo simulations, was used to obtain cluster-size threshold information to correct for multiple comparisons (http://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html). After observing that the posterior cingulate cortex (PCC) was also associated with reward processing in our experiment, we decided to include this activation cluster in an explorative analysis. An ROI mask of the PCC was created using the second-level contrast "RPE > 0" at a cluster size FWE-corrected *p* value of 0.05 (MNI coordinates *x*, *y*, *z*: 0, −16, 44). Beta values from all of the ROIs were extracted using the MarsBaR (MARSeille Boîte À Région d'Intérêt, RRID:SCR_009605) ROI toolbox for SPM (Brett et al., 2002).

Eye-tracking analysis

Datasets of six participants had to be excluded. These exclusions arose due to the loss of one dataset, unfeasible calibrations of four participants, and one participant having fixated only one of the options in too many trials (±2 SDs outside of the mean). Eye-tracking fixations of the remaining 44 participants were furthermore checked for a gaze stability of at least 50 ms, with fixations <50 ms subsequently being excluded. Data viewing, and the corresponding fixation extraction for each of the AOIs was performed using the Eyelink Data Viewer version 1.10 (SR Research), while reaction times and choice results were extracted using in-house software based on Python version 3.4. Descriptive overviews were performed using IBM SPSS Statistics 22 (IBM; RRID:SCR_002865). Correlation analysis of only the eye-tracking data was performed using Pearson correlations in STATA version 13 (StataCorp LP; RRID:SCR_012763).

Correlation analysis of fMRI and eye-tracking data

After previous exclusions of both eye-tracking and fMRI data, analyses of the remaining 43 datasets were performed using STATA version 13. To test our initial hypotheses of brain activation correlating with attention patterns, we created the two variables "Df win" [difference in fixations between values (*f*[*v*]) and probabilities (*f*[*p*]) in the win domain] and "Df loss" [difference in fixations between values (*f*[*v*]) and probabilities (*f*[*p*]) in the loss domain].

Both are defined as the difference of fixations between values and probabilities in such a way that a positive value reflects more fixations on values compared with probabilities. Additionally, the variable "Df high risk" for both the win and the loss domain represent the difference in fixations between the high-risk [*f*(*h*)] and low-risk [*f*(*l*)] lotteries, with a positive value reflecting more fixations on the high-risk versus the low-risk gambles. After creating these variables, all extracted fMRI β values from the gain and loss domain were correlated with Df win and Df loss, respectively. These estimated Pearson correlations were

Table 2: Overview of the parametric modulator calculations used for estimating brain activation

	Number of symbols shown	RP	RPE in case of win (1): RPE = 1 − RP	RPE in case of no win (0): RPE = 0 − RP
Win domain	1	1	1 − 1 = 0	0 − 1 = −1
	2	1/2	1 − 1/2 = 1/2	0 − 1/2 = −1/2
	3	1/3	1 − 1/3 = 2/3	0 − 1/3 = −1/3
	4	1/4	1 − 1/4 = 3/4	0 − 1/4 = −1/4
	Number of symbols shown	LP	LPE in case of loss: LPE = −1 − LP	LPE in case of no loss: LPE = 0 − LP
Loss domain	1	0	−1 − 0 = −1	0 − 0 = 0
	2	−1/2	−1 − (−1/2) = −1/2	0 − (−1/2) = 1/2
	3	−2/3	−1 − (-2/3) = −1/3	0 − (−2/3) = 2/3
	4	−3/4	−1 − (−3/4) = −1/4	0 − (−3/4) = 3/4

Table 3: Whole-brain activity related to RP and RPE

Contrast	Region	Laterality	MNI coordinates x	y	z	Cluster size	t	Cluster P (FWE corrected)
RP > 0	MTG	R	66	−49	2	1368	7.01	<0.001
	oMFG	L	−57	29	−10	2017	6.70	<0.001
	vmPFC	L	−9	38	−7	2017	5.64	<0.001
	MTG	L	−63	−55	29	1337	6.17	<0.001
	PCUN	L	3	−52	20	671	6.07	<0.001
	POG	R	39	−19	56	175	5.05	0.011
RPE > 0	VS	L	−12	5	−10	1805	7.95	<0.001
	VS	R	12	5	−10	1805	7.84	<0.001
	vmPFC	L	−6	44	−1	1094	6.87	<0.001
	vmPFC	R	3	47	−1	1094	6.35	<0.001
	MTG	L	−60	−46	5	189	4.35	0.004
	VIS	L	−3	−76	2	235	4.33	0.001
	MCC	L/R	0	−16	44	317	4.26	<0.001

Cluster size FWE-corrected, voxel threshold = 0.005; df = 47. L, Left; R, right.

subsequently bootstrapped (seed set at 10; repetitions, 10,000) and reported.

Results

Whole-brain fMRI

Brain regions corresponding to the reward and loss processing cluster peaks shown in Tables 3 and 4 are reported in the following two paragraphs and can also be seen in Figure 3. The reported activations are thresholded at a cluster size FWE-corrected p value of 0.05.

Reward domain

The bilateral middle temporal gyrus (MTG), orbital part of the left middle frontal gyrus (oMFG), vmPFC as well as the left precuneus (PCUN), and right postcentral gyrus (POG) were all activated during the reward anticipation phase with increasing reward prediction (RP > 0; Table 3; Fig. 3, magenta, first row). The PCUN cluster also included activation in the midcingulate cortex (MCC) and the PCC. The reward prediction error parameter (RPE > 0) correlated, among others, with activity in the bilateral VS, vmPFC, and MCC (Table 3; Fig. 3, green, first row). Notably, a large portion of the MCC cluster was located in the PCC.

Loss domain

During the loss anticipation phase (LP > 0), the temporal parietal junction (TPJ), MTG, and vmPFC were all activated bilaterally (Table 4; Fig. 3, blue, third row). Additionally, the right PCUN and dorsomedial prefrontal cortex (dmPFC) were activated as well. Brain areas correlating with the loss prediction error parameter (LPE > 0) included the visual cortex (VIS) and the AI (Table 4; Fig. 3, yellow, third row).

ROI fMRI

In the following paragraph, we report brain activation in three a priori determined ROIs: the vmPFC, VS, and AI. The activations sustained a whole-brain correction of 0.05 and custom 3dClustSim thresholds (Tables 5, 6). Activation in these regions is also shown as part of the whole-brain fMRI activation depicted in Figure 3. The reward prediction parameter "RP > 0" correlated with activity in the vmPFC (Table 5), while the opposite contrast only showed activation of the left AI (Table 5). Investigating activity correlating with the RPE during the outcome phase resulted in bilateral activation in all of the ROIs (Table 5), while the opposite contrast showed no significant activation (Table 5). Contrasting loss prediction to baseline, we observed the bilateral vmPFC to be activated (Table 6), while the opposite contrast resulted in activation of the left AI and the bilateral VS (Table 6). Only the bilateral AI was correlated positively with the LPE parameter (Table 6), while the bilateral vmPFC and VS correlated negatively (Table 6).

Table 4: Whole-brain activity related to LP and LPE

Contrast	Region	Laterality	MNI coordinates x	y	z	Cluster size	t	Cluster p (FWE corrected)
LP > 0	dmPFC	R	3	50	35	392	6.06	<0.001
	TPJ	L	−57	−67	29	647	5.76	<0.001
	MTG	R	60	−43	5	159	5.68	0.015
	PCUN	R	6	−55	35	139	5.19	0.028
	MTG	L	−63	46	−1	174	4.90	0.001
	TPJ	R	57	−58	35	447	4.68	<0.001
	vmPFC	L/R	0	26	−16	158	4.49	0.015
LPE > 0	VIS	R	9	−79	−1	4845	14.54	<0.001
	AI	R	42	20	−1	129	5.47	0.038

Cluster size FWE-corrected, voxel threshold = 0.005, df = 47. L, Left; R, right.

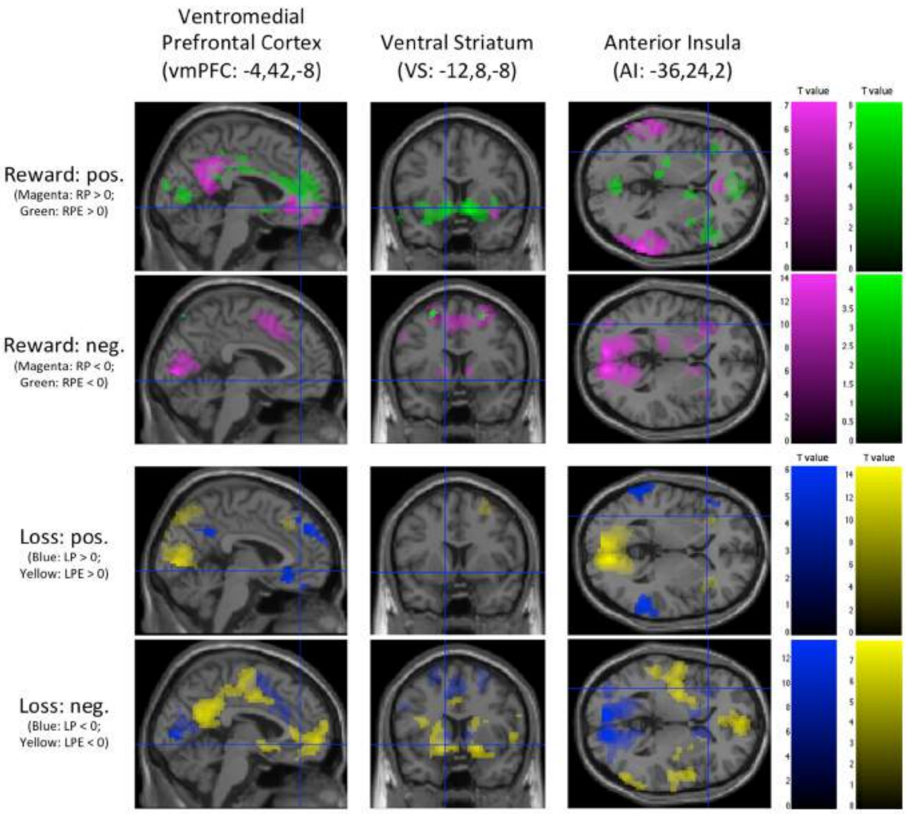

Figure 3. Whole-brain activation during the different parts of reward and loss processing (whole-brain corrected $p < 0.05$, based on 3dClustSim correction [$k > 33$, $p < 0.005$], df = 47) and obtained using the fMRI paradigm. Color coding: magenta, RP; green, RPE; blue, LP; yellow, LPE. The first and the third row represent the positive contrasts vs baseline (>0), and the second and fourth row represent the negative contrasts vs baseline (<0) in the reward and loss domains, respectively. Respective t value color bars are shown on the right side.

Eye tracking

Analysis of the eye-tracking data revealed that subjects differed neither in the number of total fixations in both domains, nor in fixation differences between values and probabilities (Table 7). However, subjects paid slightly more attention to values compared with probabilities in both the win (one-sample t test; mean, 2.51 ± 4.959; $p = 0.002$; df = 43) and the loss domain (one-sample t test; mean, 2.73 ± 4.521; $p < 0.001$; df = 43). The two variables Df win and Df loss were highly correlated (Table 8), and the participants did not show differences in fixations on high-risk and low-risk gambles between the gain and loss domains (Table 7). The behavioral results of the eye-tracking task revealed that in both domains subjects made high-risk choices slightly more often than low-risk choices, and that the average reaction time did not differ with regard to domain or choice type (Table 7).

In both domains, higher reaction times correlated with more fixations on probabilities compared with values (Table 8). Additionally, more fixations on high-risk gambles compared with low-risk gambles correlated with more high-risk gamble decisions, but only in the win domain (Table 8).

Correlation of fMRI and eye tracking

Bootstrapping the results of the fMRI and eye-tracking data correlations showed that higher activation in the bilat-

Table 5: ROI analysis results for the win domain (df = 47)

Contrast	*k* threshold+	Contrast direction	Region	Laterality	Peak MNI coordinates *x*	*y*	*z*	Cluster size (*k*)	Peak *t*
RP > 0	34	Positive	AI	Left	n.s.	n.s.	n.s.		
				Right					
			vmPFC	Left	−9	47	−13	556	4.60
				Right	6	50	−10	556	4.80
			VS	Left	n.s.	n.s.	n.s.		
				Right					
		Negative	AI	Left	−33	23	5	105	5.26
				Right	n.s.	n.s.	n.s.		
			vmPFC	Left	n.s.	n.s.	n.s.		
				Right					
			VS	Left	n.s.	n.s.	n.s.		
				Right					
RPE > 0	32	Positive	AI	Left	−33	17	−7	371	5.29
				Right	30	20	−7	697	7.37
			vmPFC	Left	−3	47	5	583	6.34
				Right	3	47	−1	583	6.35
			VS	Left	−12	5	−10	371	7.95
				Right	12	5	−10	697	7.84
		Negative	AI	Left	n.s.	n.s.	n.s.		
				Right					
			vmPFC	Left	n.s.	n.s.	n.s.		
				Right					
			VS	Left	n.s.	n.s.	n.s.		
				Right					

+Whole-brain corrected, $p < 0.05$ (based on 3dClustSim correction: $k > 33$, $p < 0.005$). n.s., Not significant.

eral vmPFC during reward prediction error (RPE > 0) processing correlated with a higher number of fixations on values versus probabilities in the eye-tracking task (Table 9). In the loss domain, left VS activation during loss prediction error (LPE > 0) processing correlated with more fixations on probabilities versus values (Table 9).

Additionally, PCC activation during LPE processing was found to correlate with decreased Df loss (i.e. increased

Table 6: ROI analysis results for the loss domain (df = 47)

Contrast	*k* threshold+	Contrast direction	Region	Laterality	Peak MNI coordinates *x*	*y*	*z*	Cluster size (k)	Peak T
LP > 0	34	Positive	AI	Left	n.s.	n.s.	n.s.		
				Right					
			vmPFC	Left	−6	29	−10	52	4.43
				Right	0	26	−16	52	4.49
			VS	Left	n.s.	n.s.	n.s.		
				Right					
		Negative	AI	Left	−30	26	−4	114	3.77
				Right	n.s.	n.s.	n.s.		
			vmPFC	Left	n.s.	n.s.	n.s.		
				Right					
			VS	Left	−18	11	−1	114	6.60
				Right	12	8	5	95	5.26
LPE > 0	33	Positive	AI	Left	−30	26	2	47	4.61
				Right	33	29	−1	74	4.26
			vmPFC	Left	n.s.	n.s.	n.s.		
				Right					
			VS	Left	n.s.	n.s.	n.s.		
				Right					
		Negative	AI	Left	n.s.	n.s.	n.s.		
				Right					
			vmPFC	Left	−12	47	−4	390	3.86
				Right	6	41	−13	390	5.58
			VS	Left	−15	11	−10	733	7.95
				Right	24	−1	−13	178	5.26

+Whole-brain corrected $p < 0.05$ (based on 3dClustSim correction: $k > 33$, $p < 0.005$).

Table 7: Descriptive overview of the eye-tracking task variables

Variable	N	Minimum	Maximum	Mean	SD
Total fixations, win domain	44	7.90	65.23	29.32	12.726
Total fixations, loss domain	44	7.50	61.17	28.94	11.720
Df win domain: $[f(v) - f(p)]$	44	−9.13	12.20	2.51	4.959
Df loss domain: $[f(v) - f(p)]$	44	−7.77	11.07	2.73	4.521
Df high risk, win domain: $[f(h) - f(l)]$	44	−5.00	2.07	−0.35	1.395
Df high risk, loss domain: $[f(h) - f(l)]$	44	−3.97	4.37	0.34	1.495
Percentage of high-risk choices, win domain	44	26.67	100.00	66.59	20.466
Percentage of high-risk choices, loss domain	44	30.00	100.00	77.27	18.584
Average reaction time, all trials	44	3.02	17.99	8.51	3.544
Average reaction time, win domain	44	2.92	21.63	8.68	3.935
Average reaction time, win domain, high-risk choices	44	2.92	22.68	8.74	3.958
Average reaction time, win domain, low-risk choices	41	3.23	19.76	8.96	4.058
Average reaction time, loss domain	44	3.12	16.38	8.56	3.471
Average reaction time, loss domain, high-risk choices	44	3.12	15.59	8.37	3.363
Average reaction time, loss domain, low-risk choices	44	3.57	38.20	10.33	6.309

attention toward probabilities $[f(p)]$ compared with values $[f(v)]$ in the loss domain (Table 9). Neither the AI nor the control region OSS correlated significantly with fixation differences in any of the two domains (Table 9). Plotting the correlations revealed individual differences in attention and brain activation (Fig. 4).

Discussion

We show that individual differences in neural reactions to gains and losses relate significantly to differences in information search over risky gambles. Activity in the vmPFC during gain processing correlated positively with attention to the monetary amounts of risky gambles in the gain domain, while activity in the VS and PCC during loss processing correlated positively with subjects' attention to the probabilities of gambles in the loss domain. Our results concur with previous findings in the reward domain, in which the vmPFC, VS, and PCC were identified as regions involved in reward and loss processing, and crucially important for value computations and salience (Fliessbach et al., 2007; Seymour et al., 2007; Tom et al., 2007; Bartra et al., 2013; Clithero and Rangel, 2014).

There are a number of studies with a wide array of topics that have previously successfully combined eye tracking and fMRI (Kang et al., 2012; Paschke et al., 2012; Tylén et al., 2012; Meyhöfer et al., 2015). The study of highest relevance for this experiment investigated the relation of attention to value signals (Lim et al., 2011). In the experiment, participants first performed a liking–rating task, which was followed by a binary choice task, during which the subjects were instructed to fixate on the food item and were then asked to make a selection for one of the two food items shown (Lim et al., 2011). During both tasks, fMRI and eye-tracking data were simultaneously recorded, and the researchers found out that activation in the vmPFC and the VS represented a relative value code between the items, which was in turn guided by visual attention measured via eye tracking (Lim et al., 2011). It is important to note here that despite the fact that these findings somewhat overlap with our results, there has been neither a study that has combined eye-tracking and fMRI data collected in two separate experiments, nor a study that has investigated the neural relations of attention patterns in a monetary gambling task. We henceforth add to previous studies by relating individual differences in neural reactions to gains and losses to differences in information search processes, as measured by an independent eye-tracking experiment using risky gambles.

Individual brain activation differences have previously been shown to correlate with behavioral risk preferences. Specifically, risk averters were shown to exhibit higher VS and AI activation during high-risk gamble anticipation (Rudorf et al., 2012). Further correlations of individual brain activation differences using two separate assessment techniques have been described using the behavioral inhibition scale (BIS) and behaviorial activation scale (BAS), and an fMRI task involving monetary gains and losses (Kim et al., 2015). People with higher BIS scores exhibited higher activation of the left striatum during avoidance anticipation, while individuals with higher BAS scores showed higher activation of the bilateral striatum

Table 8: Additional significant Pearson correlations (uncorrected) of the variables from the eye-tracking task

Variable 1	Variable 2	r	P	N
Df win	Df loss	0.94	<0.001	44
	Average reaction time, win domain	−0.39	0.009	44
	Average reaction time, win domain, high-risk choices	−0.38	0.011	44
	Average reaction time, win domain, low-risk choices	−0.38	0.016	41
Df loss	Average reaction time, loss domain	−0.46	0.002	44
	Average reaction time, loss domain, high-risk choices	−0.48	0.001	44
	Average reaction time, loss domain, low-risk choices	−0.36	0.023	44
Df high risk win	Percentage of high-risk choices, win domain	0.31	0.039	44

Table 9: Main bootstrapped Pearson correlation results (uncorrected, seed set at 10 with 10,000 repetitions) of the fMRI and eye-tracking data (df = 42)

Eye-tracking variable	ROI	fMRI contrast variable	
		RP > 0	RPE > 0
Df win	Left AI	−0.05 (0.169)	0.14 (0.142)
	Right AI	0.11 (0.122)	−0.02 (0.145)
	Left OSS	−0.03 (0.189)	0.01 (0.125)
	Right OSS	−0.08 (0.210)	0.02 (0.148)
	PCC	0.11 (0.151)	0.10 (0.129)
	Left vmPFC	0.22 (0.156)	0.31 (0.150)*
	Right vmPFC	0.18 (0.150)	0.40 (0.138)*
	Left VS	0.09 (0.135)	0.23 (0.140)
	Right VS	0.17 (0.140)	0.02 (0.131)
		LP > 0	LPE > 0
Df loss	Left AI	0.10 (0.144)	−0.20 (0.127)
	Right AI	0.13 (0.116)	−0.12 (0.151)
	Left OSS	0.17 (0.129)	−0.12 (0.145)
	Right OSS	0.03 (0.157)	−0.21 (0.142)
	PCC	−0.02 (0.129)	−0.28 (0.134)*
	Left vmPFC	−0.16 (0.159)	−0.17 (0.143)
	Right vmPFC	0.01 (0.156)	−0.15 (0.152)
	Left VS	−0.01 (0.152)	−0.32 (0.152)*
	Right VS	−0.08 (0.163)	<0.01 (0.138)

*$p < 0.05$.

during reward reception. In the eye-tracking domain, individual differences of attention were previously shown in a study involving similar financial gambles (Fiedler and Glöckner, 2012). With these individual differences having previously been found using fMRI or eye tracking, our study is the first to show their relation in a financial decision-making context and is thus able to add an important piece to how attention and value computations are linked.

We have to note obviously that the exclusion of a controlled intervention in our study design inherently limits causal conclusions. Hence, one interpretation is that paying more attention to either monetary amounts or probabilities may cause differences in activation in the vmPFC, VS, and PCC. This hypothesis is supported by previous studies, which showed that exogenous manipulation of attention can successfully change brain activation patterns and ultimately influence behavioral choices, as shown, for example, using cues in the context of food choices (Hare et al., 2011a; Milosavljevic et al., 2012). In an eye-tracking experiment implementing everyday supermarket decisions, manipulation of product salience led to participants making incoherent, "wrong," product choices, with individuals displaying a visual saliency bias and thereby depicting the strong influence of attention manipulation on decision-making (Milosavljevic et al., 2012). Furthermore, results from a behavioral binary-choice experiment using electroencephalography showed that the additional presentation of a value-associated distractor was associated with making more incorrect decisions and differences in the P300 brain activation amplitude (Itthipuripat et al., 2015).

Another interpretation of the detected correlation is that the vmPFC acts as a driver and guides attention during the information search in risky gambles. This can be placed into the context of a very recent model by Schultz (2016). He describes reward as having inherent sensory and value components, thus leading from object detection to its identification; from there to its valuation; and finally to the decision, action, and reinforcement. Placing our results into the context of this model, the vmPFC can be described as a possible modulator guiding object detection, identification, and valuation. The VS has previously been identified to play a role in risk and prediction error computation, thus leading to the idea that already during the information search phase, the VS could be involved in the perception of risks by guiding information search processes. The laterality of only the left VS being significantly associated with attention patterns is surprising, considering that Lim et al. (2011) found the bilateral VS to be associated with attention, Smith et al. (2014) associated activation from a bilateral VS mask with success in a stock exchange paradigm, and both the left and the right VS have been associated in a meta-analysis investigating the neural basis of subjective value (Clithero and Rangel, 2014). Since reward and loss processing in our study was found in the bilateral VS as well, we are not able to systematically determine why this laterality occurred. Previous studies have investigated such laterality differences in the dopamine response to reward in the VS (Martin-Soelch et al., 2011), but the decision-making field is lacking a comprehensive meta-analysis of especially VS laterality in reward and loss processing, which would greatly help the understanding of such incidental findings.

We did not expect a priori that the PCC would also be associated with attention patterns during risky choices. Finding this correlation, however, points toward the PCC playing an important role in guiding attention more toward the probabilities of risky gambles compared with their values in the loss condition. Notably, the PCC cluster used in our analysis included the location of the PCC previously shown to be associated with attention toward relative value (Lim et al., 2011). Additionally, a meta-analysis by Clithero and Rangel (2014) found that both ventral and dorsal areas of the PCC (both included in the cluster used here) were associated with processing value during the decision phase. A review article by Leech and Sharp (2014), investigating the role of the PCC in relation to disease and cognition, sheds even more light onto our findings. Besides showing the role of the PCC in regulating the focus of attention that concurred with our findings, the authors also introduce an "Arousal, Balance, and Breadth of Attention" (ABBA) model pertaining to the PCC. This model highlights the sensitivity of the PCC to arousal, internal/external thought, as well as attentional focus. In light of this model, the individual differences seen in our PCC results can be interpreted as brain activation related to these dimensions. Another study on the PCC (Studer et al., 2015) presented evidence that lesions in the PCC are detrimental to optimal risky decision-making. Importantly, PCC damage was inversely related to risk adjustment, thus showing the importance of the PCC in risky decision-making. Taking our findings and the previous literature into account, we believe that the role of

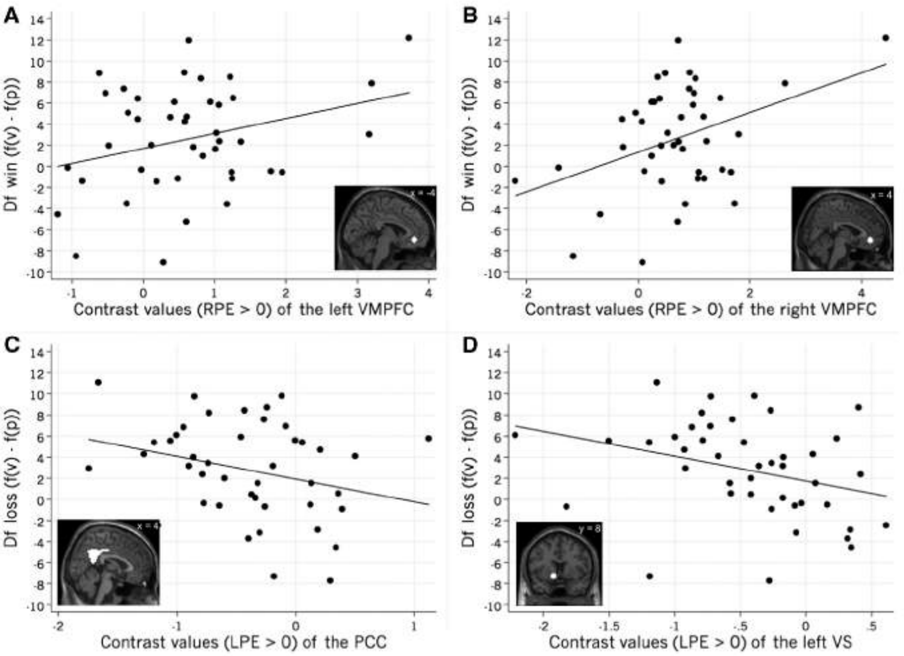

Figure 4. Correlation of fMRI and eye-tracking data, showing individual data points and the respective ROIs used for the contrast value extraction. ***A***, Contrast values of the left VMPFC during RPE processing correlate with higher values of Df win [i.e., increased attention toward values ($f[v]$) compared with probabilities ($f[p]$) in the win domain; $r = 0.306$, $p = 0.046$, df = 42]. ***B***, Contrast values of the right VMPFC during RPE processing correlate with an increased attention toward values [$f(v)$] compared with probabilities [$f(p)$] in the win domain ($r = 0.397$, $p = 0.008$, df = 42). ***C***, Contrast values of the PCC during LPE processing correlate with an increased attention toward probabilities [$f(p)$] compared with values [$f(v)$] in the loss domain ($r = -0.284$, $p = 0.065$, df = 42). ***D***, Contrast values of the left VS during LPE processing correlate with an increased attention toward probabilities [$f(p)$] compared with values [$f(v)$] in the loss domain ($r = -0.316$, $p = 0.039$, df = 42).

the PCC in financial decision-making has been somewhat underestimated in the past and should be further investigated in future studies of financial decision-making.

Despite our data not being able to determine causality, we believe that our results are essential to advance the knowledge of decision-making processes, and to lay the basis for future decision-making studies that are aiming to combine fMRI and eye-tracking data in a behavioral economic context. Leaving the causality discussion aside, the correlation depicted by our data can also be seen as evidence for the previously noted bidirectional relationship of eye movements and decision-making (Gottlieb et al., 2014). This relationship is described as values of different environmental stimuli influencing eye movements, with eye movements in turn influencing decision-making due to selecting the sensory input that impacts a person's decision. In this context, our results provide evidence that the bilateral vmPFC, left VS, and PCC represent three regions responsible for this interaction, henceforth playing a very important role in financial decision-making involving risks. Despite finding these results, a lack of a significant correlation between activation in the AI and attention patterns was noted as well. A reason for this might be that the fMRI paradigm did not specifically elicit brain activation related to risk, but in relation to reward and loss processing. It could therefore be of interest in future studies to check whether the AI activation is related to attention patterns in a risk-specific fMRI paradigm.

Peak activation in the VS was highly correlated to the RPE parameter, a finding that concurs well with previous discoveries (Schultz and Dickinson, 2000; Hare et al., 2008, 2011b; Fliessbach et al., 2010; Glimcher, 2011; Rohe et al., 2012; Häusler et al., 2015). As hypothesized based on the findings of previous studies (Kuhnen and Knutson, 2005; Izuma et al., 2008; Lin et al., 2012), activation of the vmPFC during all parts of reward processing was observed. Besides the vmPFC, other areas were found to be activated during both reward prediction and reward prediction error processing. This could have been the case because the reward prediction phase can also be seen as a time point of reward prediction error processing. The cue shown during reward prediction can elicit a prediction error response in that the probability of possible wins or losses may deviate from previous predictions.

With regard to the eye-tracking findings, the high correlation of the fixation differences in both domains (Df win and Df loss) shows the attention consistency of individuals during the information search phase, irrespective of being in a win or loss context. We observe a rather risk-seeking behavior in our experiment, possibly due to the fact that the gambles were performed with money that was additionally earned on top of the “safe” participation fee. It could be of interest to run the same experiment again without such a participation fee, thus having the subjects complete the eye-tracking experiment without a safe payment in the back of their mind. Finally, more fixations on high-risk compared with low-risk gambles correlated with more high-risk gamble decisions. This concurs with previous findings identifying choice as a function of attention (Brandstätter and Körner, 2014).

By combining fMRI with eye tracking using two separate tasks, our study shows that information search in risky gambles is related to neural reward and loss processing in the vmPFC, VS, and PCC. Higher reward processing activity in the vmPFC was correlated to paying more attention to the monetary values compared with their respective probabilities in risky gambles. Additionally, higher loss processing activity in the left VS and the PCC was correlated to paying more attention to the probabilities compared with the monetary values of risky gambles. Future studies will need to dig deeper into the causality of this link.

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7.3 Study Three (Scientific Reports)

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Preferences and beliefs about financial risk taking mediate the association between anterior insula activation and self-reported real-life stock trading

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People differ greatly in their financial risk taking behaviour. This heterogeneity has been associated with differences in brain activity, but only in laboratory settings using constrained behaviours. However, it is important to understand how these measures transfer to real life conditions, because the willingness to invest in riskier assets has a direct and considerable effect on long-term wealth accumulation. In a large fMRI study of 157 working age men (39.0 ± 6.4 SD years), we first show that activity in the anterior insula during the assessment of risky vs. safe choices in an investing task is associated with self-reported real-life active stock trading. We then show that this association remains intact when we control for financial constraints, education, the understanding of financial matters, and cognitive abilities. Finally, we use comprehensive measures of preferences and beliefs about risk taking to show that these two channels mediate the association between brain activation in the anterior insula and real-life active stock trading.

Functional magnetic resonance imaging (fMRI) has been used extensively to study financial risk taking in the laboratory, but less work has connected brain activation to financial risk taking choices in real life[1–6]. Here, we use data from a non-student sample to study a self-reported real-life indicator of financial risk taking that has a significant impact on wealth accumulation, namely, whether people trade stocks. In addition, we measure brain activation during an investing task and study the differences in the estimated mean activation of these brain regions between active stock traders and non-active stock traders (our binary dependent variable "active stock trading" was assessed using question 21 in the Supplementary Document "Do you trade stocks yourself?", see Supplementary Information). Previous studies have consistently linked the neural implementation of decisions under risk and, more broadly, value based choices to activity in brain regions such as the ventral striatum (VS), the anterior insula (AI), and the ventromedial prefrontal cortex (vmPFC)[1–12]. Even though these studies have greatly improved our knowledge of the neural mechanisms underlying risky choices[13], it is unknown how the observed heterogeneity in individual brain activity and behaviour in laboratory tasks transfers to financial risk taking in real life[12,14].

More specifically, studies of financial decision making under risk have linked risk seeking behaviour to VS activation, while risk averse choices have been shown to relate to increased activation in the AI[1,2,4–6]. Recent efforts have additionally shown that the interaction between these two regions plays a role in making financial choices under risk[11,12]. In our investing task, participants are repeatedly asked to choose between a risky option (stock) and a safe option (bond) while being in either a gain or loss domain. We expect that individuals who trade

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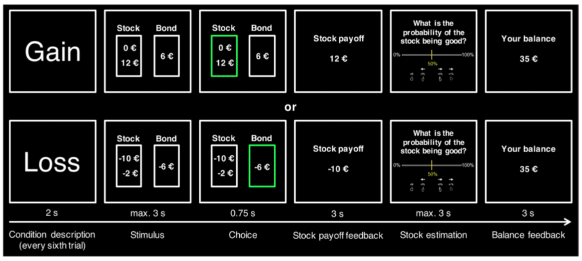

Figure 1. The investing paradigm and regions of interest. There were eight blocks in each domain (gain and loss), consisting of eight trials each (thus 96 total trials, one trial of each domain is shown here). In the beginning of a block, participants were shown in which domain they were. They chose between a risky (stock) or non-risky (bond) option and the choice implementation (button press) was highlighted with a green frame. Next, participants saw the stock payoff feedback, regardless of the previous choice. The participants then estimated the probability of the stock being good and finally, a balance feedback was shown.

stocks in real life show higher VS and lower AI activation during a risky versus a safe option. Furthermore, we believe that the chance to find these differences in VS and AI activation between active and non-active stock traders is higher in the gain domain, due to this part of the investing paradigm being more similar to stock trading in real life (in the gain domain of the investing task participants try to win money, while in the loss domain they try to avoid losses). With regard to the established role of the vmPFC in subjective value and reward processing[3,9,10,15], we hypothesize that individuals who trade stocks show higher vmPFC activation upon choosing the stock versus the bond and receive higher reward-related vmPFC activation upon getting the feedback to have made the correct choice after having chosen the risky versus the safe option. In a sample of 157 working age men, we find that, out of the three candidate regions (VS, AI, and vmPFC), only activation in the AI when choosing a risky over a safe option in the gain domain of an investing task is significantly lower in participants who actively trade stocks in real life, compared with those who do not.

Next, we investigate possible economic mechanisms by which the AI activation may influence real-life financial risk taking. Due to the fact that stock market participation has been associated with financial constraints[16,17], we assess whether higher AI activation in people who do not trade stocks may simply reflect these individuals' financial constraints and their interest to avoid further financial risk. We do not find this to be the case, because AI activation continues to be associated with real-life stock trading, even after we control for participants' household income and financial liabilities. We then inquire whether AI activation could be a proxy for education, as well as a general understanding of financial matters and cognitive abilities, because all these factors have been found to relate to stock market participation[16–22]. We do not find that these individual characteristics influence the association between the AI activation and real-life active stock trading. Next, we assess whether people's preferences and beliefs about risk taking[14,23,24] are captured by the AI activation differences between active and non-active stock traders. We use a combination of self-assessment questions and behavioural data from decisions under risk to create two comprehensive characteristics that evaluate people's beliefs regarding the outcomes of risky choices (risk optimism index (ROI)) and the willingness to bear risk (risk tolerance index (RTI)). Here, we find that the association between real-life active stock trading and AI activation is mediated by both of these channels.

Our paper contributes to the neuroeconomics literature by showing that brain activation measured in the laboratory is associated with financial risk taking in real life, thus lending external validity to previous laboratory studies. We show this by using brain regions of interest from previous neuroeconomic landmark studies[1,6,9] to identify differences in brain activation between groups of active stock traders and non-active stock traders during a stock investing task. Our paper then additionally contributes to the field of neuroeconomics by showing that differences in brain activation do not capture differences in terms of financial or cognitive constraints between these two groups of individuals, but that the association between real-life financial risk taking and AI activation is significantly mediated by comprehensive, independent measures of people's beliefs about risk taking, as well as their risk tolerance. Hence, our results provide novel evidence that this specific brain area shown previously to relate to financial taking risk in the laboratory plays a central role for risk taking in real-life by aggregating individuals' optimism and risk preferences.

Results

The fMRI paradigm is reliable from both a neuroscientific and behavioural point of view. To measure heterogeneity in brain activity across 157 working age participants (39.0 ± 6.7 SD years), we adapted a recently established investing paradigm[25] to a functional magnetic resonance imaging (fMRI) setting (Fig. 1). In this paradigm, we asked participants repeatedly to choose between a risky option (stock) and a safe option (bond) while being in either the gain or the loss domain (please see Experimental Design in the Methods section for more details). After each choice and regardless of the chosen option, the payoff of the stock was shown. To assess the reliability of this fMRI stock investing paradigm in relation to previous literature[2,9,10,15,26–30], we first

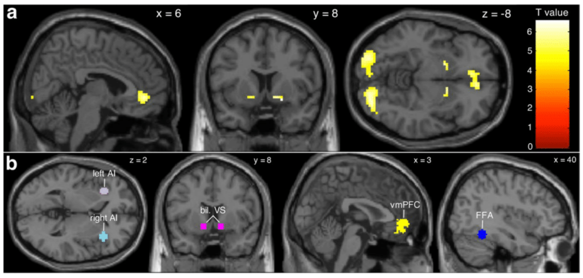

Figure 2. Group-level brain activation and regions of interest. (**a**) Whole-brain reward prediction error (RPE) activation (whole-brain corrected p(FWE) <0.05, $k > 10$, $n = 165$). (**b**) Regions of interest used to extract weighted beta estimates (see Figs 2–4, as well as Supplementary Figs S1, S2, and Supplementary Table S4). The right (turquoise) and left (pink) anterior insula (AI) masks, as well as bilateral ventral striatum (VS, magenta) masks were obtained from previous neuroeconomic studies on risk processing[1,6]. The ventromedial prefrontal cortex (vmPFC) mask (yellow) and the fusiform face area (FFA) mask (blue, used as a control region) were obtained from meta-analyses of valuation[9] and emotional face processing[31], respectively.

created a general linear model (GLM) that specifically included a parametric reward prediction error (RPE) analysis (see Supplementary Table S1). Here, we found RPE-related brain activation in the VS and the vmPFC (Fig. 2a). We then grouped participants into active stock traders and non-active stock traders according to their self-reports (see question 21 in the Supplementary Document "Do you trade stocks yourself?", see Supplementary Information) and found that active stock traders chose the stock in the task significantly more often than non-active stock traders (first trial of each block, two-sample t-test, $p = 0.029$, mean choice of stock versus bond, active stock traders: $63.0 \pm 27.1\%$ SD, non-active stock traders: $53.0 \pm 25.7\%$ SD, $n = 157$).

Brain activation is associated with real-life active stock trading. We then investigated whether the risk-related brain activation would help to explain real-life stock trading. Extending prior literature[1–3,6,9,12,14], we discovered that activation in an area that was previously linked to risk averse behaviour in the lab[1,6] – namely, the anterior insula (AI) – is a strong and significantly associated explanatory variable of people's reluctance to trade stocks in real life. To study this association, we created a GLM (see Supplementary Table S2) that was designed to assess individual brain activation during the decision process and payoff feedback in the gain and the loss domain, separately (an overview of the whole-brain analysis is given in Supplementary Table S3). Using this GLM, we extracted the individual mean brain activation (beta estimates) in the brain regions of interest (AI, VS, and vmPFC) with masks from previous landmark studies on risk processing and valuation (Fig. 2b[1,6,9]). Additionally, we included another area with no obvious relation to valuation or risk taking (fusiform face area (FFA; Fig. 2b)) to control for specificity of effects[31]. The weighted beta estimates from these regions of interest were henceforth extracted from brain contrasts in both the choice and the payoff feedback phase (e.g., stock vs. bond choice in the gain domain, see Supplementary Table S4; distribution plots are shown in Fig. 3 and Supplementary Figs S1 and S2). Two-sample t-tests were then performed to test for brain activation differences between active and non-active stock traders. We found that activity in the VS, vmPFC, and FFA in the choice and the payoff feedback phases were not significantly different between the two groups. However, activity in the bilateral AI when participants opted for the stock vs. the bond in the gain domain was significantly associated with real-life financial risk taking (for the right AI: $p = 0.0264$; for the left AI: $p = 0.0072$; see Supplementary Table S4). Specifically, when participants opted for the stock vs. the bond in the gain domain, the AI showed lower activity in real-life active stock traders compared with non-active stock traders, consistent with the notion of a lower risk signal[1,5–7].

Economic variables do not explain the link between AI activation and real-life stock trading. Next, we assessed whether previous aspects that have been related to stock market participation, namely, financial constraints[16,17], education[16,17,22], the understanding of financial matters[20,21], and cognitive abilities[18,19], would explain the association between the AI activation and real-life stock trading (Tables 1 to 3; distribution plots are shown in Fig. 3). We did not find evidence for this. We first tested whether economic financial adversity would impact the association between AI activation and real-life stock trading (Tables 2 and 3), because previous studies have suggested a link between adversity[32,33] and neural activation. When we included the value of participants' household income and an indicator for whether they have financial liabilities (e.g. outstanding credit card debt or a mortgage) as additional explanatory variables of active stock trading, we found that this did not influence the association between AI and real-life stock trading (Tables 2 and 3). Next, we assessed whether participants' education, understanding of financial matters, as well as their cognitive abilities could explain the link between AI activation and active stock trading. We therefore added measures of participants' education level, as well as their financial literacy, debt literacy, numeracy, and intelligence to our model (Tables 1 to 3). To assess intelligence, we used a measure of fluid intelligence[34] that included questions on analogies (verbal intelligence), numerical series (numerical intelligence), and matrices (figural intelligence). When we included all these measures as possible

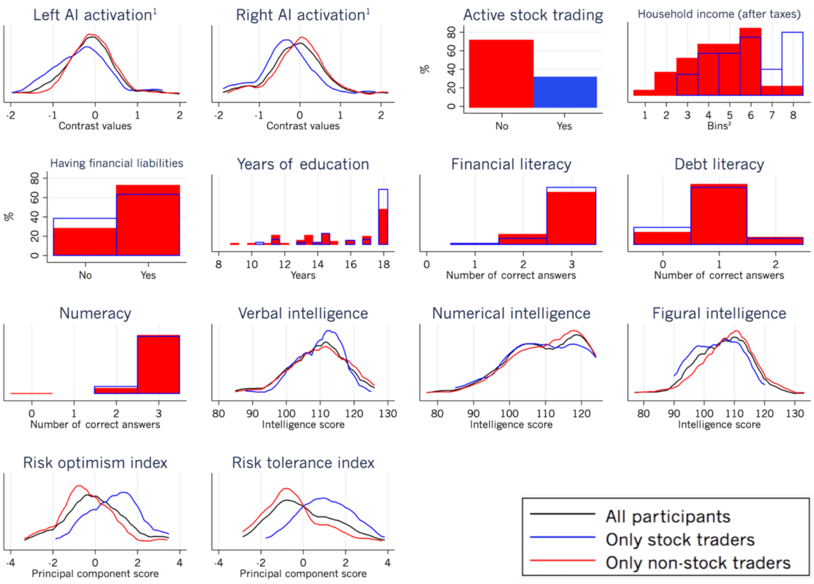

Figure 3. Data distribution of all variables used in the analysis (all n = 157, Tables 1–3). Kernel density graphs are shown for continuous variables, histograms for ordinal and interval variables, and bar graphs for binary variables. [1]During stock versus bond choice (gain domain). [2]Bins: 1 (<500€), 2 (500€–1000€), 3 (1000€–2000€), 4 (2000€–3000€), 5 (3000€–4000€), 6 (4000€–5000€), 7 (5000€–6000€), 8 (>6000€).

	Mean	Median	SD	N	Q#
Active stock trading	0.3	0	0.5	157	21
Household income (after taxes)	5.0	5	1.7	157	14
Having financial liabilities	0.7	1	0.5	157	23
Years of education	15.9	17	2.5	157	5, 6
Financial literacy	2.8	3	0.4	157	39, 40, 41
Debt literacy	0.9	1	0.5	157	42, 43
Numeracy	2.9	3	0.3	157	45, 46, 47
Verbal intelligence	109.8	110	7.8	157	n.a.
Numerical intelligence	110.3	111	10.0	157	n.a.
Figural intelligence	106.8	109	8.7	157	n.a.
Risk Optimism Index (ROI)	−0.009	−0.1	1.4	157	n.a.
Risk Tolerance Index (RTI)	−0.003	−0.3	1.5	157	n.a.

Table 1. Descriptive statistics of the variables included in the regression analysis. Q# = number in financial, risk preference, and personality questionnaire, provided as the Supplementary Document, see Supplementary Information. n.a. = not applicable.

explanatory variables, we did not find that they explained the association between AI activation and real-life trading.

To rule out a lack of significant results due to measurement issues, we additionally tested group differences within each economic variable and found that in concurrence with previous literature[16,17,22], participants' household income (two-sample t-test, $p < 0.001$, active stock traders: 5.9 ± 1.7 SD, non-active stock traders:

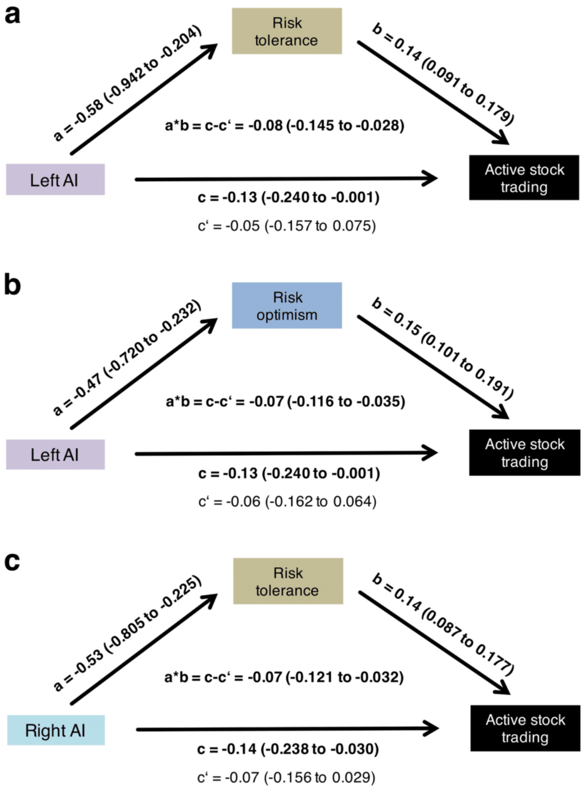

Figure 4. The association between the activation in the anterior insula (AI, independent variable, when choosing between a stock and a bond) and active stock trading (dependent variable) is mediated through risk tolerance and risk optimism (mediator variable, see Supplementary Table S10). The Sobel-Goodman (SG) Mediation test was used with subsequent bootstrapping of the effect (all n = 157, seed set at 10, 10,000 repetitions). Observed coefficients are shown with 95% (bias-corrected and accelerated) confidence intervals in parentheses. An effect is considered significant if the confidence interval does not include the null hypothesis (i.e. zero is not included) and is visualized in bold. (**a**) Mediation of left AI activation and active stock trading through risk tolerance (at least 17.7%). (**b**) Mediation of left AI activation and active stock trading through risk optimism (at least 22.9%). (**c**) Mediation of right AI activation and active stock trading through risk tolerance (at least 25.0%).

4.6 ± 1.6 SD, n = 157) and the years of education (two-sample t-test, $p = 0.014$, active stock traders: 16.7 ± 2.2 SD, non-active stock traders: 15.6 ± 2.5 SD, n = 157) were significantly different between the two groups.

Beliefs (risk optimism) and preferences (risk tolerance) explain the association between AI activation and real-life stock trading. Previous studies have found that experimentally-elicited beliefs and preferences about risk taking influence financial choices in laboratory settings[23,24]. Additionally, single measures of beliefs and preferences have been linked to real-life outcomes[35] and specifically portfolio decisions[36,37]. However, recent evidence suggests that risk preference reflects the structure of a multifaceted psychological trait and should henceforth be studied with a more comprehensive approach[38]. We therefore created two independent, aggregate measures related to beliefs regarding the outcomes of risky choices (risk optimism index (ROI)) and to the willingness to bear risks (risk tolerance index (RTI)). Here, we found that that the association of the AI

	Active stock trading				
Left AI (stock > bond choice, gain domain)	−0.13 (−2.24)**	−0.13 (−2.39)**	−0.10 (−1.93)*	−0.03 (−0.62)	−0.0001 (−0.00)
Household income (after taxes)		0.10 (4.72)***	0.09 (4.54)***	0.07 (3.48)**	0.06 (3.57)***
Having financial liabilities		−0.11 (−1.54)	−0.12 (−1.60)	−0.09 (−1.24)	−0.11 (−1.60)
Years of education			0.03 (1.78)*	0.02 (1.79)*	0.02 (1.66)*
Financial literacy			0.04 (0.41)	−0.08 (−0.92)	−0.05 (−0.60)
Debt literacy			−0.01 (−0.16)	−0.08 (−1.15)	−0.09 (−1.49)
Numeracy			−0.10 (−0.81)	−0.06 (−0.57)	−0.06 (−0.57)
Verbal intelligence			0.003 (0.64)	0.002 (0.39)	0.003 (0.68)
Numerical intelligence			0.0003 (0.07)	0.002 (0.45)	0.001 (0.33)
Figural intelligence			−0.01 (−1.99)**	−0.01 (−2.63)**	−0.01 (−2.22)**
Risk Optimism Index (ROI)				0.14 (5.70)***	0.10 (3.78)***
Risk Tolerance Index (RTI)					0.09 (3.95)***
N	157	157	157	157	157
Adjusted R^2	0.03	0.15	0.16	0.31	0.37

Table 2. Linear probability models with possible explanatory variables of real-life active stock trading. Left AI activation is included as an independent variable of interest. Coefficients are shown with t-statistics in parentheses. Significance levels: *$p < 0.1$, **$p < 0.05$, ***$p < 0.001$.

	Active stock trading				
Right AI (stock > bond choice, gain domain)	−0.14 (−2.72)**	−0.15 (−3.14)**	−0.14 (−2.85)**	−0.10 (−2.32)**	−0.07 (−1.58)
Household income (after taxes)		0.10 (4.84)***	0.09 (4.68)***	0.07 (3.65)***	0.07 (3.72)***
Having financial liabilities		−0.13 (−1.83)*	−0.14 (−1.87)*	−0.10 (−1.42)	−0.11 (−1.69)*
Years of education			0.03 (1.90)*	0.02 (1.91)*	0.02 (1.77)*
Financial literacy			0.03 (0.39)	−0.08 (−0.93)	−0.05 (−0.62)
Debt literacy			−0.01 (−0.12)	−0.07 (−1.04)	−0.08 (−1.34)
Numeracy			−0.08 (−0.69)	−0.04 (−0.39)	−0.04 (−0.40)
Verbal intelligence			0.004 (0.76)	0.002 (0.43)	0.003 (0.66)
Numerical intelligence			0.0004 (0.11)	0.002 (0.44)	0.001 (0.32)
Figural intelligence			−0.01 (−1.96)*	−0.01 (−2.50)**	−0.01 (−2.11)**
Risk Optimism Index (ROI)				0.14 (5.78)***	0.10 (3.82)***
Risk Tolerance Index (RTI)					0.08 (3.60)***
N	157	157	157	157	157
Adjusted R^2	0.04	0.17	0.19	0.34	0.39

Table 3. Linear probability models with possible explanatory variables of real-life active stock trading. Right AI activation is included as an independent variable of interest. Coefficients are shown with t−statistics in parentheses. Significance levels: *$p < 0.1$, **$p < 0.05$, ***$p < 0.001$.

	Left AI (stock > bond choice, gain domain)			Right AI (stock > bond choice, gain domain)		
Risk Optimism Index (ROI)	−0.10 (−2.83)**		−0.06 (−1.56)	−0.05 (−1.31)		0.01 (0.12)
Risk Tolerance Index (RTI)		−0.11 (−3.23)**	−0.08 (−2.18)**		−0.12 (−3.20)**	−0.12 (−2.90)**
N	157	157	157	157	157	157
Adjusted R^2	0.04	0.06	0.07	0.005	0.06	0.05

Table 4. Linear regression models showing the effects of risk tolerance and risk optimism on activation in the left and right anterior insula. Coefficients are shown with t-statistics in parentheses. Significance levels: $^{*}p < 0.1$, $^{**}p < 0.05$, $^{***}p < 0.001$.

activity with active stock trading is mediated through both ROI and RTI. For the creation of ROI and RTI, we first classified all self-assessment and behavioural measures into either the risk optimism or the risk tolerance category (see Supplementary Table S5) and then used regression analyses of active stock trading to assess which variables should be used for a subsequent Principal Component Analysis (PCA; see Supplementary Tables S6 and S7). With PCA, we then computed a primary factor for each category, which we labeled as ROI and RTI (see Supplementary Tables S8 and S9). When we added these primary factors to the model that controlled for the previous factors (i.e., financial and cognitive constraints) we found that both ROI and RTI impacted the association between the left AI and real-life stock trading (Table 2) and that RTI influenced the association between the right AI and real-life stock trading (Table 3). We formally tested the association between AI activation and ROI and RTI in a linear regression framework (Table 4), and then conducted a mediation analysis with subsequent bootstrapping of the effects (see Fig. 4 and Supplementary Table S10). Our evidence indicates that the association between AI activation and real-life stock trading is mediated by individuals' ROI and RTI, rather than by financial or cognitive constraints.

Additional self-reported and behavioural results. We found significant associations between our a priori determined self-reported active stock trading variable and two independent self-reported real-life financial outcome variables. These were the binary variables of having financial investments (Pearson's Chi-squared = 20.14, $p < 0.001$, Cramér's V = 0.32, n = 198) and stock market participation (having a fraction of financial investments invested into stocks and/or mutual funds; Pearson's Chi-squared = 63.01, $p < 0.001$, Cramér's V = 0.56, n = 198). Additionally, we found that the mean self-assessment of financial risk taking was significantly lower in active stock traders compared with non-active stock traders ($p < 0.001$, active stock traders: 4.63 ± 1.27 SD, non-active stock traders: 2.96 ± 1.05 SD, n = 194). For the self-assessment of financial risk taking, we also found that when considered separately (rather than as part of the RTI), the self-assessment of financial risk taking was significantly correlated with the extracted bilateral AI brain activation (left AI: $r = -0.21$, $p = 0.007$; right AI: $r = -0.25$, $p = 0.002$, both n = 163). In the investing paradigm, we found that the reaction time for choosing the stock vs. bond did not differ between the two groups (first trial of each block, $p = 0.483$, active stock traders: 1.89 s ± 0.97 SD, non-active stock traders: 1.93 s ± 0.98 SD, n = 157) and that the reaction time of participants in both groups decreased throughout the experiment (both $p < 0.001$, active stock traders: $r = -0.17$, non-active stock traders: $r = -0.22$, n = 157). Furthermore, participants were asked to estimate the probability of the stock being good in each trial (Fig. 1). This allowed us to obtain the participants' average stock assessment error (i.e. the difference between objective and subjective estimation), which was negatively correlated with measures of fluid intelligence (see Supplementary Table S11). Additionally, we found a significant correlation between ROI and RTI (see Supplementary Fig. S3).

Outcomes of a data-driven approach. To address the concern that our hypothesis-driven creation of ROI and RTI might have influenced the results, we performed a purely data-driven approach. To this end, we combined all individually significant variables (see Supplementary Tables S8 and S9) into one PCA and used the primary factor as an index of financial risk seeking and preference (RSPI, see Supplementary Table S12). We then performed the same analysis as previously done with ROI and RTI. For both the left and right AI, the RSPI significantly influenced the association between brain activation and real-life stock trading (see Supplementary Tables S13 and S14). Furthermore, it also mediated this association (see Supplementary Table S10). However, a comparison with the ROI and RTI results revealed that the data-driven approach resulted in a loss of qualitative information due to concealing differences in the mediation of the neural data (left and right AI differences with respect to ROI and RTI). We therefore refrained from using RSPI, and instead decided to use the two hypothesis-driven[14] indices RTI and ROI.

Discussion

In our study, we do not only extend the association between brain activation and active stock trading to behaviour in the real world, but additionally identify the mechanisms that underlie this association. We first show that brain activation in the AI during financial decision making under risk is associated with financial risk taking in real life. We then find that this association is not explained by individual differences in financial constraints, education, the understanding of financial matters, or cognitive abilities. However, we find evidence that the association between AI activation and real-life stock trading is explained by comprehensive measures of individuals' risk tolerance and beliefs about financial risk taking.

We examine the connection between activation in several brain areas (VS, AI, and vmPFC) previously associated with financial risk taking in the laboratory. We find that only one of these brain areas, namely, the AI, is associated with real-life financial risk taking as measured by a self-reported question of directly trading individual stocks. Our results extend previous research by demonstrating that activation in exactly those AI regions that have been associated with risk prediction[6] and a higher propensity to sell risky assets[1] in laboratory tasks transfers to financial risk taking in real life. Participants who show a stronger AI signal when choosing a risky over a safe asset in the gain domain are less likely to trade stocks in real life. In conjunction with the previously demonstrated role of the AI in risk aversion[2,4,7,8,11], as well as its function as a warning signal that differentiates high from low earners in a stock market bubble experiment[1], our findings indicate that these signals are decisive for behaviour in real life as well. From a clinical perspective, studies with insular-lesioned patients have unveiled an association with atypical financial risk taking behaviour[39,40]. Additionally, insula dysfunction has previously been shown to be part of the pathology of several neurological disorders[41–43]. This suggests that future research could investigate the financial decision-making behaviour of different clinical populations and find out whether atypical financial decision-making of such populations translates to similar behaviour in real life.

Notably, we find an association between real-life financial risk taking behaviour and AI activation in only the gain and not the loss domain. In our investing paradigm (Fig. 1), the motivation in the gain domain is to win money, while in the loss domain it is to avoid losses. In real life, investments in equities are characterized by positive expected returns. It is therefore possible that investing in stocks in real life is more similar to investing in the "stock" that is available during our lab experiment in the gain condition, where that asset promises positive outcomes. The "stock" in the loss condition is not a natural equivalent of real-life equity markets during normal economic conditions, in that during such times investors expect a positive return – not a loss, which is what our experimental condition promises.

In spite of our results being in line with previous studies of risk aversion signals in the AI, the findings could additionally be interpreted the other way around, thus implying that active stock traders who choose the safe (bond) over the risky (stock) option show higher AI activation in comparison to non-active stock traders. Although this interpretation could tentatively be placed in context with previous findings of regret[44], in our investing paradigm (Fig. 1) the stock outcome is not known at the time of making the choice (the participant does not know whether he made the right or wrong choice) and we therefore abstain from any further interpretations in this context. Even though we do not find evidence that activation in the VS and vmPFC explains real-life stock trading, it is possible that activation in these regions relates to other aspects of financial choices, for example, how individuals respond to new information about investment options[44,45]. Although beyond the scope of this article, it would be interesting to incorporate additional regions of interest from studies that used different approaches to quantify risk and uncertainty[46–48] and to investigate the exact neural mechanisms underlying stock trading from a computational perspective. Lastly, whereas our design included only male participants, future work should study female participants, as well.

We do not find that financial constraints, education, the understanding of financial matters, or cognitive abilities explain the interaction between active stock trading and AI activation. However, our comprehensive measures of preferences and beliefs about risk taking explain this interaction. Importantly, we included both self-assessments and behavioural data in the creation of these two aggregate measures, because it was previously demonstrated that behavioural and self-report measures of risk taking are weakly correlated, which suggested that they assess specific features of a complex construct[38,49]. The role of risk tolerance and risk optimism as mediators between brain activation and real-life financial behaviour leaves the question of whether the understanding of the mechanisms behind other real-life financial decisions such as stock market participation or portfolio choices in general[21,50] could likewise be better understood with a combination of self-assessment, behavioural, and especially neuroscientific analysis.

Although economic indicators of real-life stock trading have previously been identified, self-assessment, behavioural, and neuroscientific research on individual investors has been scarce and mostly confined to the laboratory[14]. This is remarkable considering that individual differences in risk preferences have important consequences for many life domains[14,51,52]. Additionally, understanding the characteristics of real-life stock traders is crucial considering the large number of individuals participating in asset markets and their impact on trading volume and prices. In Organisation for Economic Co-operation and Development (OECD) countries, roughly 23% of households hold shares and other equities[53]. In Germany alone, private households directly own stocks with an estimated total net worth of 158 billion Euros[54]. Here, we provide several explanatory variables of stock trading, which may help policy makers assess why certain households participate in equity markets, as well as help providers of financial services to tailor their advice and products to individuals in accordance with these investors' characteristics. Furthermore, stock market non-participation can imply welfare losses for households[55] and understanding the underlying mechanisms of this behaviour might therefore help to support individuals in more efficient ways. For example, consumers who are unduly pessimistic about stock investments, and thus have a weak risk optimism as measured by the ROI, could be educated with respect to the historical performance of equity markets worldwide. Also, consumers could be offered products by financial institutions that have appropriate risk-return profiles given these individuals' risk preferences, as captured by their RTI.

Concurring with recent suggestions regarding the study of individual brain activation differences[56], we use fMRI data from a large sample and base our analysis on strong prior hypotheses. Brain activation correlates have been previously documented in the context of economic decisions such as consumer choices and monetary donations[57–60], but not in the context of financial risk taking. This study extends our knowledge of financial risk taking from the laboratory to the real world, which is an important next step in understanding individual heterogeneity in real-life financial decisions and in helping individuals to make better financial choices.

Methods

Experimental Design. 210 men were invited to the Life & Brain Center at the University Clinic in Bonn (Germany) to participate in an experiment investigating the underpinnings of financial risk taking. Before coming to the appointment, participants underwent screening for the absence of neurologic, psychiatric, and cardiovascular diseases. Other exclusion criteria were ages below 29 and above 50, having a student status, unemployment longer than three months, very bad eyesight (more than ± 5 diopters), excessive smoking (more than ten cigarettes per day), as well as large tattoos above the waist. We asked only men to participate in the experiment, because previous studies have shown that the menstrual cycle impacts both financial risk seeking[61] and reward-related brain activation[62] in women. The experiment involved no deception and was approved by the ethics committee of the University of Bonn. Each participant gave informed written consent according to the Declaration of Helsinki[63] and the participants were made aware of the nature and consequences of the study. The experimental session consisted of the following parts: introduction and training, structural magnetic resonance imaging (MRI) with a concurrent behavioural task (stock allocation task, see Supplementary Fig. S4), functional MRI (fMRI) with an investing paradigm (Fig. 1), diffusion tensor imaging (DTI), intelligence tests, a financial questionnaire (Supplementary Document, see Supplementary Information), two personality tests (NEO-FFI[64] and rRST-Q[65]), and blood collection. Compensation consisted of a basic payment of 20 Euro per hour, with possible addition or subtraction depending on the results of the behavioural and fMRI task. Participants were always paid a minimum of 70 Euros for their average attendance of three and a half hours. The personality, DTI, and blood-related results will be reported in other publications.

After the initial introduction and training session (both the practice and the full fMRI task are deposited in the Supplementary Database, see Supplementary Information), participants were asked to lie in a Siemens Trio 3.0 T scanner (Siemens, Erlangen, Germany) and were accustomed to special response grips (Nordic NeuroLab, Bergen, Norway). The subjects viewed the experimental screen via video goggles (Nordic NeuroLab, Bergen, Norway) that were fixated on a head coil. A system update of the MRI scanner at the end of 2013 led to a mandatory adjustment of the T1 protocols, thus resulting in two ways of structural imaging data collection. Before the scanner update, participants underwent measurements with a standard 8-channel head coil. The scans commenced with a localizer scan that was followed by a structural scan containing T1-weighted images (TR = 1570 ms; TE = 3.42 ms; flip angle = 15). After the scanner update, a standard 12-channel head coil was used and the scans also started with a localizer scan, followed by a structural scan containing T1-weighted images (TR = 1660 ms; TE = 2.75 ms; flip angle = 9). During the T1 measurement, participants completed a behavioural paradigm investigating financial risk taking. This was a stock allocation task[66] (see Supplementary Fig. S4), which was implemented in Presentation v14 (the paradigm is deposited in the Supplementary Database, see Supplementary Information; Neurobehavioral Systems, Berkeley, California, USA). In the stock allocation task, each subject was asked to make ten independent investment decisions by splitting up a fixed maximum investment amount of 23 Euro to either a risky (stock) or a riskless (bond) asset. Each subject saw two equally likely stock return rates, the bond return rate, and a reminder of the maximum investment amount. These return rates varied in each trial, during which subjects were asked to enter the amount that they would like to invest in the stock, with the remaining funds automatically being invested in the bond. The average amount allocated to the stock was taken as an estimate of individual risk preference, thus meaning that a higher investment represented higher levels of financial risk taking. The return rate was only revealed at the end of the experiment, at which point one trial was randomly selected by the program and integrated in the total compensation.

The investing task (Fig. 1, the paradigm is deposited in the Supplementary Database, see Supplementary Information) was adapted from a previously established behavioural paradigm[25] to an fMRI setting to measure the blood-oxygenated-level dependent (BOLD) signal during financial investment decisions. It was implemented in Presentation v14 (Neurobehavioral Systems, Berkeley, California, USA). While subjects completed the paradigm, T2*-weighted echoplanar images (EPIs) were collected using a standard 8-channel (before the scanner update) or 12-channel (after the scanner update) head coil. The scanning parameters were similar both before and after the scanner update (TR = 2500 ms; TE = 30 ms; flip angle = 90; 37 3 mm slices in ascending order; field of view = 192 mm; approx. 840 volumes) except for a change in voxel size (before the scanner update: $3 \times 3 \times 3$ mm; after the scanner update = $2 \times 3 \times 3$ mm). Each participant started with an initial endowment of 25 Euros and had to choose between a risky (stock) and a non-risky (bond) financial option in 96 total trials. Before each set of six trials, which made up one of the 16 blocks, it was shown to the subject for 2 s whether he was in the loss or the gain condition. Each participant completed 16 blocks (eight gain and eight loss), shown in random order. An initial screen of a block was followed by a jittered interstimulus interval (ISI, 1 to 3 s). The participants then had maximally 3 s to decide between a stock and a bond. Two risk levels seen via possible stock outcomes were implemented and remained consistent throughout each block: high risk (0 vs. 12 Euro or −12 vs. 0 Euro) and low risk (2 vs. 10 or −2 vs. −10 Euro). Each subject completed each of the four conditions (gain − high risk; gain − low risk; loss - high risk; loss - low risk) in a pseudo-randomized fashion four times. The bond always remained the same (6 or −6 Euros) in each condition. The chosen option was highlighted with a green frame for 0.75 s. After another jittered ISI of 3.5 to 7 s and independent of the choice, the outcome of the stock was shown for 3 s. Each block was randomly assigned to contain either a good or a bad stock. Due to the thorough instructions and practice trials given before entering the MRI scanner, subjects knew that a good stock had a higher outcome probability of 70% and a lower outcome probability of 30%. A bad stock had the opposite probabilities. An objective Bayesian probability of the stock being either good or bad was estimated using the previous outcomes within the same block. This estimate was not presented to the participants. The subjects then had up to 3 s to enter a subjective probability estimate of the stock being good each time after having seen the stock outcome. Participants received an incentive of 10 Euro cents for each answer within 5% of the objective estimation. This amount was then added to the final balance. At the end of each trial, the subjects saw the updated balance for 3 s. A behavioural variable from the investing paradigm that was included in the analysis was the ratio of stock to bond choices, but only in the first trial of each block (used as a measure of behavioural risk taking). This was done to avoid any bias by the learned stocks' outcome probabilities. Two additional behavioural variables were obtained via the investing paradigm. The average absolute value of the difference between the objective and the subjective estimate of the stock being a good stock was taken as a measure of risk learning and was termed stock estimation error. Its non-absolute variant was taken as a behavioural measure of risk optimism.

After the scanning session, participants completed three subscales of the Intelligence-Structure-Test (IST) 2000R: verbal, numerical, and figural intelligence[34]. These subscales included questions concerning analogies (verbal intelligence), numerical series (numerical intelligence), and matrices (figural intelligence). The subscale scores were normalized to the respective age groups (26 to 30, 31 to 40, and 41 and older) and resulted in three variables of interest: verbal, numerical, and figural intelligence (Table 1).

After the intelligence test, participants were asked to fill in a questionnaire consisting of demographic, risk preference, as well as financial knowledge questions (Supplementary Document, see Supplementary Information). These questions were mainly taken from two sources: the German Socio-Economic Panel (SOEP) study developed by the German Institute for Economic Research (Deutsches Institut für Wirtschaftsforschung (DIW))[67], as well as from a questionnaire created by the Munich Center for the Economics of Aging (MEA). The MEA questions aimed at assessing financial knowledge and real-life financial decisions. These questions investigated debt literacy[68], financial literacy[69], and numeracy[70] and were previously used in other surveys such as the Survey of Health, Ageing and Retirement in Europe (SHARE). Additional demographic financial questions were specifically created for this study. An example of this was our binary dependent variable asking about active stock trading ("Do you trade stocks yourself?", question 21 in the Supplementary Document, see Supplementary Information). In total, 9 variables from the handout were chosen for our analysis (Table 1). Most of these variables were represented by one question, except for years of education, financial literacy, debt literacy, and numeracy. The years of education were the sum of the following fixed years in the German school system: main school/Hauptschule (9 years), secondary school/Mittlere Reife (10 years), ten-class general educational polytechnic secondary school/Polytechnische Oberschule (10 years), university of applied sciences entrance qualification/Fachhochschulreife (12 years), high-school diploma/Abitur (13 years); the higher education years were set as follows: none (0 years), university degree/Hochschulabschluss (5 years (average diploma time)), Apprenticeship/Lehre & Meisterschule (1.5 years), training for civil servants/Beamtenausbildung (2 Jahre), college/Fachhochschule (4 years (average diploma time)), others (1 year). Regarding financial literacy (questions 39, 40, and 41 in the Supplementary Document, see Supplementary Information), debt literacy (questions 42 and 43), and numeracy (questions 45, 46, and 47), the amount of correct answers was calculated to represent each variable. The numbers of the relevant questions taken from the handout (Supplementary Document, see Supplementary Information) are listed in Table 1. After completing the handout, participants completed two personality questionnaires (NEO-FFI[64] and rRST-Q[65]), blood was collected, and the participants got to know their final payout, which was delivered to the participants via money transfer.

Exclusions. Out of the invited 210 participants, twelve participants had to be fully excluded due to claustrophobia, neurological diseases or psychological disorders, and failing to return the consent form. Furthermore, 33 participants were excluded from the analysis that included fMRI data due to technical issues during data acquisition and excessive movements of participants during the fMRI task (>2.5°, >5 mm). The remaining 165 participants were on average 38.9 ± 6.7 SD years old. Of these 165 participants, 43 were measured before a mandatory scanner update and 122 afterwards.

Statistical Analysis. *Functional magnetic resonance imaging (fMRI) analysis.* Functional magnetic resonance imaging (fMRI) datasets from 165 participants were used for the fMRI second-level analysis. Preprocessing of the functional images was done using Statistical Parametric Mapping 12 (SPM12, Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB R2014 (MathWorks, Natick, Massachusetts, USA). Preprocessing included realignment, slice-time correction, spatial normalization to the Montreal Neurological Institute (MNI) space using the anatomical T1 image of each participant, and a final smoothing step using a Gaussian kernel with full-width at half-maximum (FWHM) of 8 mm.

One GLM was specifically designed to estimate brain activation during reward prediction error (RPE) processing (GLM described in Supplementary Table S1) and another GLM was used to estimate brain activation during the choice and feedback phase (see Supplementary Table S2, this script can be found in the Supplementary Database, see Supplementary Information). Both models included the canonical hemodynamic response function (HRF) implemented in SPM12. They also included a high-pass filter of 128 Hz as well as a correction for autocorrelations. The onset regressors of the first GLM were the onset of the choice screen, stock payoff feedback, stock estimation, and balance feedback, which were all further split into trials when the subject chose the stock and trials when the subject chose the bond (see Supplementary Table S1). Additionally, the stock payoff feedback onset had three parametric modulators, consisting of the RPE, the reward prediction (RP), and the trial payoff (see Supplementary Table S1). All parametric modulators were orthogonalised in ascending order. The RP was calculated as the objective probability of the stock being good. The RPE was calculated as the difference between the updated objective probability of the stock being good at the time of the newly presented payoff feedback and the objective probability of the stock being good at the time before the new payoff feedback was presented. The activation that correlated positively with the RPE at the onset of the payoff feedback after having chosen the stock was used to assess the reliability of the paradigm (Fig. 1) in relation to previous literature, which consistently found RPE-related activation in the VS and the vmPFC[2,9,10,15,26–30].

The onset regressors used in the second GLM were the onset of choice screen, stock payoff feedback, stock estimation, and balance feedback (see Supplementary Table S2). Each of these regressors were divided into the gain and loss domain, as well as having chosen the stock or the bond. The stock payoff feedback regressors were additionally split into a good or a bad outcome (see Supplementary Table S2). The onset of the choice screen was given the duration of the time until button press and the other regressors were modeled as stick functions. The only parametric modulator was the trial payoff, which was used during the payoff feedback. Following the estimation of this GLM, 14 contrasts of interest were defined and analyzed on the group level (a sample script of this GLM and all contrast results for the group-level analysis can be found in the Supplementary Database, see Supplementary Information).

Weighted beta value extraction and their association with active stock trading. Next, five regions of interest were used to extract weighted beta estimates from the choice and stock payoff feedback contrasts (Fig. 2b, all regions of interest masks are deposited in the Supplementary Database, see Supplementary Information). The first region of interest was the vmPFC (MNI coordinates at around 0, 46, −8), obtained from a meta-analysis concerning the valuation system (see vmPFC mask in Fig. 9 of[9]). The second and third regions of interest were 6 mm radius spheres in the bilateral VS (MNI coordinates: ±12, 8, −8) and the right anterior insula (AI, MNI coordinates: 36, 24, 2), obtained from the authors of a recent neuroeconomic study investigating reward and loss activation during a stock market experiment[1]. The fourth region of interest was made using the MARSeille Boîte À Région d'Intérêt (MarsBaR) toolbox implemented in Matlab and creating a 6 mm radius sphere at the location of the left AI (MNI coordinates: −32, 25, 3). This location was taken from Table S3 of a previous study assessing risk[6] and was the same "risk prediction signal" table that was previously used for the creation of the right AI in a study that investigated trading behaviour under risk in a stock market experiment[1]. Due to the fact that the coordinates were in Talairach space (−31, 22, 7.7), we contacted the authors of the previous neuroeconomic publication[1] in order to use the same MNI to Talairach converter[71]. As a control variable and fifth region of interest, we created a 6 mm radius sphere in the right fusiform face area (FFA, MNI coordinates: 40, −50, −18) as described in a meta-analysis of 105 functional MRI studies assessing emotional face processing[31]. Using these regions of interests, weighted beta estimates were extracted for all contrasts (see Supplementary Table S4), except for the FFA mask, which was only used to extract weighted beta estimates for the first contrast. Kernel density plots were then made for each weighted beta estimate (see Fig. 3 and Supplementary Figs S1 and S2).

The analysis was done using STATA version 13 (Stata-Corp LP, College Station, Texas, USA). The data set and script can be found in the Supplementary Database, see Supplementary Information. Before continuing with the analysis, it was established that 157 complete datasets could be used to study active stock trading. At first, two sample t-tests (uncorrected) were performed to see which weighted beta estimates were significantly associated with the self-reported measures of real-life stock trading (see Supplementary Table S4). Because only the left and right AI revealed significant activation for the contrast stock choice vs. bond choice in the gain domain, we focused on the bilateral AI for the subsequent analysis.

Investigation of the possible mechanisms behind the association between AI activation and real-life stock trading. We first selected variables that were previously related to stock market participation and that could influence the association between the AI activation and real-life stock trading (Tables 1 to 3; distribution plots are shown in Fig. 3). These included variables that assessed financial constraints[16,17], education[16,17,22], the understanding of financial matters[20,21], and cognitive abilities[18,19] (Table 1). Next, we tested their influence on the AI and real-life stock trading association using multiple regression analysis (Tables 2 and 3).

In line with previous financial risk taking literature that used the concept of beliefs and preferences[14], we then grouped all risk-related behavioural and self-assessment measures into categories of risk tolerance and optimism. The risk optimism category included variables that related to beliefs regarding the outcomes of risky choices and the risk tolerance category included variables relating to the willingness to bear risks (see Supplementary Table S5). Guided by economic theory, logistic regressions using active stock trading as the dependent variable (DV) were calculated for each of the variables individually (see Supplementary Tables S6 and S7). The significantly associated variables from the risk optimism and risk tolerance categories were then used for principal component analysis (PCA, see Supplementary Tables S8 and S9). This PCA approach was already successfully used in risk taking research before, specifically to determine whether a single principal component was able to determine risk taking in several contexts[36]. The primary components found in the two PCAs (see Supplementary Tables S8 and S9) were labeled risk optimism index (ROI) and risk tolerance index (RTI). These indices of preferences and beliefs about risk taking (their distribution is shown in Fig. 3) were then added to the previous regression models to test their influence on the association of the AI activation and real-life stock trading (Tables 2 and 3). We ex-ante expected that AI activation, ROI and RTI would have independent contributions to real-life stock trading. However, we found that the connection between AI and real-life stock trading became insignificant once ROI and RTI were included as possible explanatory variables of active stock trading (Tables 2 and 3). As a result, we conducted ex-post regression analyses with the left and right AI activation as the dependent variables and either ROI or RTI, or both indices, as the independent variables (Table 4). To then formally test the mechanism behind the association of AI activation and real-life stock trading, we performed a mediation analysis using the Sobel-Goodman (SG) mediation test with subsequent bootstrapping of the effect, in which we used the ROI and RTI as mediator variables (see Fig. 4 and Supplementary Table S10). A mediation was considered significant if the indirect effect (a*b), but not the direct effect (c) were significant (see Fig. 4 and Supplementary Table S10).

Data and code availability. The relevant data, code, and materials are deposited in the Harvard Dataverse. They can be accessed via this link, which contains a ".zip" file with the questionnaire (Supplementary Document, see Supplementary Information), as well as the Matlab scripts and regions of interests used in the study. Additionally, all the group-level SPM ".mat" files described in the fMRI contrast overview table (see Supplementary Tables S2 and S3) are included in the ".zip" file. Finally, both the behavioural experiments (stock allocation task and investing paradigm) are included, as well as the final data set and scripts used for the analysis (programmed in Stata v13.1).

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8. Appendix

8.1 Full List of Publications

Publications, further studies, and other articles are listed from newest to oldest. The ones not worked on during the time of my doctoral studies are italicized.

8.1.1 Publications in Peer-reviewed Journals

Häusler AN, Kuhnen CM, Rudorf S, Weber B (2018) Preferences and beliefs about financial risk taking mediate the association between anterior insula activation and self-reported real-life stock trading. Scientific Reports 8:1-13.

Häusler AN, Artigas SO, Trautner P, Weber B (2016) Gain- and loss-related brain activation are associated with information search differences in risky gambles: An fMRI and eye-tracking study. eNeuro 3:1–13.

Häusler AN, Becker B, Bartling M, Weber B (2015) Goal or gold: Overlapping reward processes in soccer players upon scoring and winning. PLOS ONE 10(4) e0122798:1–16.

Keeley RJ, Wartman BC, Häusler AN, Holahan MR (2010) Effect of juvenile pretraining on adolescent structural hippocampal attributes as a substrate for enhanced spatial performance. Learn Mem 17: 344-354.

8.1.2 Submitted Manuscripts

Häusler AN, Bec-Gerion A, Jeske K-J, Rudorf S, Weber B. Would you buy this insurance? The association between insurances and personality traits. Submitted to the *Journal of Consumer Psychology*.

8.1.3 Manuscripts in Preparation

Häusler AN, Madhyastha T, Rudorf S, Grabowski T, Weber B. Investigating the structural basis of real-life financial risk taking: A DTI approach.

Häusler AN, Oroz Artigas S, Mierau A. The neural underpinnings of superior pass performance in skilled soccer players.

Häusler AN, Iannilli F, Amunts K, Mohlberg H, Schleicher A, Zilles K. An evolutionary study of the red nucleus.

8.1.4 Other Published Articles

Häusler AN, Weber B. 2018. Why risk assessments should be included in job application processes, job placements, and career advice. Frankfurt Institute for Risk Management and Regulation. Yearbook 2018, pp. 128-129.

Häusler AN, Weber B. 2017. Approaches to study risk taking in neuroscience. Frankfurt Institute for Risk Management and Regulation. Yearbook 2017, pp. 210-212.

Häusler AN Weber B. 2016. Warum unser Hirn bei Aktien aussetzt (Why stocks are letting our brain fail). AnlegerPlus 10/2016, pp.70.

Häusler AN, Weber B. 2016. Cognitive biases in predicting, valuating, and handling risks. Frankfurt Institute for Risk Management and Regulation. Yearbook 2016, pp. 256-258.

Häusler AN, Weber B. 2015. Implications from neuroeconomics for the understanding of investment behavior. Frankfurt Institute for Risk Management and Regulation. Yearbook 2015, pp. 86-87.