Fachbereich Erziehungswissenschaft und Psychologie
der Freien Universität Berlin

The Influence of Incidental Emotions on Decision Making under Risk

Dissertation

zur Erlangung des akademischen Grades
Doktor der Naturwissenschaften (Dr. rer. nat)
im Fach Psychologie

Vorgelegt von:
Mag. rer. nat.
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Berlin, 2017

Vorblatt

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Datum der Disputation: 12.09.2017

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt,

- dass ich die vorliegende Arbeit selbstständig und ohne unerlaubte Hilfe verfasst habe,
- dass ich mich nicht bereits anderwärts um einen Doktorgrad beworben habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze und
- dass ich die zugrunde liegende Promotionsordnung vom 08.08.2016 kenne.

Berlin, 11.07.2017 Stefan Schulreich

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Acknowledgments

The present thesis would not have been possible without the support of numerous people. First of all, I would like to thank my supervisor Hauke Heekeren for providing me enough freedom to pursue my own academic interests and for his excellent support. I sincerely appreciate his trust, patience, encouragement and guidance through all phases of my dissertation project.

I am also most grateful to Holger Gerhardt for his mentoring and our collaboration in most of the phases of my dissertation project, but also for our numerous theoretical and methodological discussions, which clearly deepened my understanding and allowed me to answer my research questions more comprehensively.

I am very grateful to Yana Heussen and our collaboration in the first phase of my doctoral project, which was as fruitful as it was enjoyable. I would also like to thank Dar Meshi for his support in our neuroscientific study and his helpful comments, and in particular for introducing me to fMRI analysis. Special thanks also to my other co-authors Peter Mohr and Stefan Kölsch for their support in methodological and theoretical issues, and to Ferdinand Binkofski.

I am also thankful to the members of my dissertation committee for helping me to complete the final step of this dissertation.

Thanks to all (former) members of the Heekeren lab for our numerous scientific and non-scientific discussions and an enjoyable time together. Special thanks to Ramzi Fatfouta, for his contagious enthusiasm and the many laughs in our joint office, and to Hannah Brühl, Carmen Morawetz, Ulf Tölch, and Julia Rodríguez Buritica.

I also want to thank Evgeniya Kirilina, Christian Kainz, and Till Nierhaus for their support in the neuroimaging laboratory, and Michael Kuhlmann as well as Jana Lüdkte for their support in the behavioral laboratories. Special thanks also to Katja Mériau, Aleksandra Gulka, and Heike Netzer for their support and patience in administrative matters.

I am also grateful to the Cluster of Excellence "Languages of Emotion" for the stimulating environment and for funding the first phases of my dissertation project (and, again, thanks to Hauke for enabling funding for the remaining phases).

Importantly, I owe many thanks to my family, especially to my beloved parents Edeltraud and Adolf, who unconditionally supported me during the ups and downs of life as a PhD student. Without them I would not be where I am today. Thank you with all my heart.

Summary

Human choice is strongly guided by emotions, even when these emotions are incidental, i.e. unrelated to a decision at hand. Yet, most theoretical frameworks in the domain of value-based decision making are either completely devoid of emotion or lack a mechanistic understanding of the interaction of emotion and deliberative decision making. By applying both a behavioral and a neuroscientific approach, the present thesis investigated the influence of incidental emotions on decision making under risk as well as the neurocognitive processes than can give rise to such effects.

In Study 1, we found that incidental happiness was positively associated with optimistic probabilistic weighting of potential monetary outcomes in the gain domain, reflected in the elevation parameter of a prospect-theoretic probability-weighting function. In Study 2, we observed that incidental fear cues increased monetary loss aversion for mixed gambles. Moreover, affective-interpersonal features of psychopathic personality attenuated this emotion-induced effect on loss aversion. Going beyond behavioral models that are mute to the sources of loss aversion, we provide a neural mechanism for emotion-induced increases in loss aversion in Study 3. In this functional magnetic resonance imaging study, we observed emotion-induced shifts from positive to negative value coding in a distributed set of brain regions, including the amygdala. Therefore, our results suggest that loss aversion and emotion-induced changes in its magnitude are mediated by the context-dependent involvement of distinct valuation processes.

Taken together, these findings illustrate that future research should place a greater emphasis on linking emotion, choice, and neurocognitive processes to arrive at a full process-based understanding of emotional effects on decision making.

Zusammenfassung

Menschliche Entscheidungen werden oftmals von Emotionen gesteuert, sogar wenn diese Emotionen inzidentell sind, d.h., nicht mit der jeweiligen Entscheidung zusammenhängen. Dennoch befassen sich die meisten theoretischen Modelle zu wertbasierten Entscheidungen entweder gar nicht mit Emotionen oder sie liefern kein mechanistisches Verständnis der Interaktion von Emotion und reflektiertem Entscheiden. Durch eine kombinierte verhaltens- und neurowissenschaftliche Herangehensweise untersuchte die vorliegende Dissertation den Einfluss von inzidentellen Emotionen auf Entscheidungen unter Risiko sowie jene neurokognitiven Prozesse, die diesen Einfluss vermitteln.

In Studie 1 fanden wir einen positiven Zusammenhang zwischen inzidenteller Fröhlichkeit und optimistischer Wahrscheinlichkeitsgewichtung von potentiellen monetären Gewinnen, der sich im Elevations-Parameter einer auf der Prospect Theory basierenden Wahrscheinlichkeits-Gewichtungsfunktion widerspiegelte. In Studie 2 beobachteten wir dass inzidentelle Furchtreize die monetäre Verlustaversion in gemischten Lotterien steigerten. Außerdem fanden wir heraus dass affektiv-interpersonelle Facetten psychopathischer Persönlichkeit den emotionsinduzierten Effekt auf Verlustaversion verminderten. In Studie 3 entdeckten wir einen neuronalen Mechanismus für die emotionsinduzierte Steigerung der Verlustaversion und gingen damit über verhaltensorientierte Modelle hinaus, die keine Informationen zu den Ursachen von Verlustaversion liefern. In dieser funktionellen Magnetresonanztomographie-Studie beobachteten wir emotionsinduzierte Verlagerungen von positiver Wertkodierung hin zu negativer Wertkodierung in mehreren, verteilten Hirnregionen, inklusive der Amygdala. Unsere Ergebnisse deuten daher darauf hin, dass Verlustaversion und emotionsinduzierte Veränderungen in ihrer Ausprägung durch eine kontext-abhängige Beteiligung von distinkten Bewertungsprozessen vermittelt werden.

Zusammenfassend illustrieren diese Ergebnisse dass zukünftige Forschung ein größeres Augenmerk auf die Verbindungen von Emotionen, Entscheidungen und neurokognitiven Prozessen legen sollte um ein vollständigeres prozessbasiertes Verständnis von emotionalen Effekten auf das Entscheidungsverhalten zu erlangen.

List of Original Publications

This dissertation is based on the following original research articles
(published or submitted articles are enclosed in the appendix):

Study 1

Schulreich, S.*, Heussen, Y. G.*, Gerhardt, H.*, Mohr, P. N. C., Binkofski, F. C., Kölsch, S., & Heekeren, H. R. (2014). Music-evoked incidental happiness modulates probability weighting during risky lottery choices. *Frontiers in Psychology: Decision Neuroscience*, *4*, Article 981 (1-17).

The original article is online available at: https://doi.org/10.3389/fpsyg.2013.00981

Contribution of the doctoral candidate[1]:
general concept (substantially), literature research (substantially), development of methods (substantially), experimental programming (substantially), data acquisition (predominantly), data analysis (substantially), discussion of results (substantially), preparation of manuscript (substantially)

Study 2

Schulreich, S., Gerhardt, H., & Heekeren, H. R. (2016). Incidental fear cues increase monetary loss aversion. *Emotion*, *16*(3), 402-412.

The original article is online available at: https://doi.org/10.1037/emo0000124

Contribution of the doctoral candidate[1]:
general concept (predominantly), literature research (entirely), development of methods (entirely), experimental programming (entirely), data acquisition (entirely), data analysis (predominantly), discussion of results (predominantly), preparation of manuscript (predominantly)

Study 3

Schulreich, S., Gerhardt, H., Meshi, D., & Heekeren, H. R. (submitted to *Proceedings of the National Academy of Sciences of the United States of America*). Emotion-induced increases in loss aversion are associated with shifts towards negative neural value coding.

Contribution of the doctoral candidate[1]:
general concept (predominantly), literature research (entirely), development of methods (predominantly), experimental programming (entirely), data acquisition (entirely), data analysis (predominantly), discussion of results (predominantly), preparation of manuscript (predominantly)

* equally contributed

[1] Contribution of the candidate is rated using a 4-level scale: entirely – predominantly – substantially – partially

List of Abbreviations

ACC	Anterior cingulate cortex
BOLD	Blood oxygen level dependent
EEG	Electroencephalography
fMRI	Functional magnetic resonance imaging
FSL	FMRIB's Software Library
H	Hypothesis
ICA	Independent component analysis
ICA-AROMA	ICA-based strategy for automatic removal of motion artifacts
LPM	Linear probability model
PCL-R	Psychopathy Checklist-Revised
PET	Positron emission tomography
PPI-R	Psychopathic Personality Inventory-Revised
RLP	Random lottery pairs
RMG	Random mixed gambles
RQ	Research questions
SCR	Skin conductance response
SOA	Stimulus onset asynchrony
TriPM	Triarchic Psychopathy Measure

Let's not forget that the little emotions are the great captains of our lives
and we obey them without realizing it.

—Vincent Van Gogh (1853 - 1890)

1. Introduction

Human choice is often guided by emotions (Bechara, Damasio, & Damasio, 2000; Lerner, Li, Valdesolo, & Kassam, 2015; Seymour & Dolan, 2008), even when they are incidental, i.e., unrelated to the decision at hand (Angie, Connelly, Waples, & Kligyte, 2011; Lerner et al., 2015; Loewenstein & Lerner, 2003). This insight, however, has emerged only slowly and had been preceded by a long-standing ignorance of emotions within the major disciplines that investigate decision making such as economics. Even psychologists' contributions to decision making first focused predominantly on cognitive processes (e.g., Kahneman & Tversky, 1979; Tversky & Kahneman, 1974), reflecting an ongoing cognitive revolution in psychology at that time (Baars, 1986; G. A. Miller, 2003), before emotional processes have become (again) into focus. This development is paralleled by an increasing focus on emotions in behavioral economics (Loewenstein, Weber, Hsee, & Welch, 2001; Rick & Loewenstein, 2008) and in neuroeconomics (Phelps, Lempert, & Sokol-Hessner, 2014; Volz & Hertwig, 2016), which both have emerged as interdisciplinary endeavors to study decision making. The present work owes its origins to these developments and aims to contribute to our understanding of the role of emotions in decision making under risk.

For scholars and laymen alike, the effects of incidental emotions on risky choice are particularly puzzling. Moreover, the mechanisms that mediate such effects are currently not well understood given that traditional research on decision making under risk relied on observable choice behavior, neglecting the underlying processes. Recent conceptual and technological advances, however, allow for a more process-oriented approach. In particular, neuroscientific methods such as functional magnetic resonance imaging (fMRI) provide valuable insights into decision processes (Clithero, Tankersley, & Huettel, 2008). By combining a behavioral and a neuroscientific approach, the present thesis investigated incidental emotional effects on decision making under risk as well as their underlying mechanisms.

This dissertation is organized as follows: In Chapter 1, I will begin by giving a thorough theoretical and empirical background on decision making under risk. Here, I will introduce the concept of risk and risk attitudes, followed by an introduction to economic and behavioral models of decision making under risk, with a focus on Prospect Theory. I will then continue with describing the relationship between emotions and decision making. Here, I will present a framework for decision-related emotions and describe their links to Prospect Theory, with a focus on two of the theory's major constructs—probability weighting and loss aversion. In the last part of the introduction, I will give a summary of our current understanding of the neural basis of risky choice, with a particular focus on loss aversion and emotion-induced variations in its magnitude. In the course of this general introduction, I will identify open questions in the literature, which the present dissertation aimed to answer. In Chapter 2, I will give a summary on the explicit research questions and will formulate hypotheses. In Chapter 3, I will then describe the materials and methods used to test these hypotheses. In Chapter 4, I will give succinct summaries of the three empirical studies that form the core of this dissertation. Finally, in Chapter 5, I will discuss the empirical findings and put them into a broader theoretical context. By integrating the findings from behavioral modeling and neuroimaging, I will also develop a neurocognitive model of emotion-induced effects on loss aversion. Chapter 6 concludes by summing up the main findings of this dissertation.

1.1. Decision Making under Risk

Making decisions under risk is an integral part of our lives, whether we decide on a financial investment, on whether to leave home with an umbrella on a cloudy day or on whether to have unprotected sex. Two dimensions can describe lay peoples' conceptions of risk—unknown risk (hazards that are judged to be unknown, new, delayed) and dread risk (hazards associated with dread, fatal consquences; Slovic, 1987). Risk is also often associated with the possibility of loss or harm (Furby & Beyth-Marom, 1992; March & Shapira, 1987).

In economics, there has been a long-standing distinction between certainty, risk and ambiguity (Camerer & Weber, 1992; Ellsberg, 1961; Knight, 1921): *Certainty* refers to outcomes that are certain (i.e., 100% probability) and also known to be certain. *Risk* refers to probabilistic outcomes whose probabilities are known to the decision-maker (e.g., flipping a fair coin, buying a lottery ticket). *Ambiguity* refers to all cases with unknown probabilities, regardless of whether the outcomes are certain or probabilistic (e.g., deciding between potential romantic partners). All the experiments throughout this thesis used monetary gambles where potential outcomes and probabilities were made explicit to participants and therefore fall into the second category, i.e., decision making under risk.

While the previous economic concepts treat risk as a state (i.e., it is either present or not), risk can also be defined as a metric (Markowitz, 1952). From this perspective, risk is understood as increasing with variance in the probability distribution of possible outcomes, regardless of whether a potential loss is involved (although losses can have a particular influence on risk preferences, see below). For instance, one common definition is that an option can be considered riskier if it can be expressed as a mean-preserving spread of another option (Rothschild & Stiglitz, 1970), e.g., a lottery with a 50% chance of winning €10 and €0 otherwise (expected value = €5) is a mean-preserving spread of a sure outcome of €5 and thus riskier. From this example, it is also evident that risk encompasses not just potential negative or less positive outcomes (*downside risk*; here €0), but also potential positive outcomes (*upside risk*; here €10). The last point is often ignored in lay definitions of risk, although it is an important feature in many decisions, since, compared to a safe option (here €5), an option without a potential, relatively more positive outcome (here €10) would usually always be considered inferior. It is the combination of upside and downside risk that makes risky decisions often such an intricate matter. As mentioned before, the empirical studies of this thesis investigated decision making under risk, defined as a state, but also adopt the metric perspective of risk as variance.

1.1.1. Risk Preferences

People's attitudes toward risk differ substantially (see, e.g., Dohmen, Falk, Huffman, & Sunde, 2010) and can be characterized by their degree of risk aversion, which can be defined as the tendency to prefer a sure outcome over a gamble of equal expected value (Wakker, 2010). For instance, in the gamble example above, a risk-averse person prefers the safe option of €5 instead of the gamble with a 50% chance of winning €10 and €0 otherwise. In contrast, a preference for the gamble characterizes a risk-loving person. Risk preferences, however, not only differ between individuals, but also within individuals, e.g., depending on the framing of decision options (Tversky & Kahneman, 1981). In the following, we will see how risk preferences and decision making can be described by formal models.

1.1.2. Economic Models of Decision Making under Risk

Over the course of centuries, various theories and formal models of decision making have been developed. Certainly, they have several historical roots, but a particular epistolary exchange between the French mathematicians Pascal and Fermat (1654) is often regarded as the birth of the systematic study of decision making. In this exchange, Pascal and Fermat laid the ground for *Expected-Value Theory*, which assumes that decision makers choose the option with the highest expected value. Expected value is defined as

$$EV = \Sigma p_i x_i.$$

Here, p_i and x_i are the probability and magnitude of each outcome of a risky option, respectively. Returning to the example given above, a risky gamble that offers a 50% chance of winning €10 and €0 otherwise, the EV = 0.5 * 10 + 0.5 * 0 = €5. However, as mentioned before, many people would prefer a sure outcome of €5 over this gamble, despite identical expected values of those two options—a common phenomenon termed risk aversion (see, e.g., Wakker, 2010). In this case, Expected-Value Theory predicts indifference and fails to explain risk aversion.

Another major milestone was Bernoulli's seminal text on *Expected-Utility Theory* (Bernoulli, 1738/1954), which builds on Expected-Value Theory but replaces objective monetary amounts with subjective utilities with marginally diminishing returns, i.e., utility does not increase linearly, but the increase in utility per additional unit declines progressively. For instance, a change from €1 to €2 has a larger subjective weight than a change from €1,000 to €1,001. *Expected utility* is defined as

$$EU = \Sigma p_i u(x_i).$$

Here, $u(x_i)$ is a monotonically increasing function of objective monetary amounts x_i. Importantly, in contrast to Expected-Value Theory, Expected-Utility Theory can explain widespread risk aversion by a concave utility function, which was originally proposed to be logarithmic. To illustrate this, let us return to our gamble example from above: According to Expected-Value Theory, one should be indifferent between the gamble that offers a 50% chance of winning €10 and €0 otherwise and a sure option of €5. In contrast, due to decreasing marginal utility (i.e., a concave utility function), Expected-Utility Theory predicts that the utility for the sure €5 will be larger than half (50% probability) the utility of the gamble's gain of €10, explaining why most people would prefer the sure option (i.e., show risk aversion).

Not before the middle of the last century, Expected-Utility Theory received an axiomatization, i.e., the necessary and sufficient conditions under which the theory holds were mathematically proven (Von Neumann & Morgenstern, 1947). When, and only when, a decision maker satisfies the following four axioms, their decision behavior could be described by a utility function and maximization of utility, and thus as rational. These four axioms are:

1. *Completeness*: For any two alternatives A and B, the individual has well-defined preferences, i.e., either prefers A to B, is indifferent between A and B, or prefers B to A.
2. *Transitivity*: Given completeness, for any three alternatives, the individual's preferences are consistent, i.e., if A is preferred to B and B is preferred to C, then A is preferred to C.
3. *Continuity*: Given the ordering of the three alternatives above, there is a probabilistic compound of the best alternative A and worst alternative C that is equivalent to the intermediate alternative B, i.e., there is a probability p such that the individual is indifferent between B and the following lottery: pA + (1-p)C.
4. *Substitution* or *Independence*: An individual's preference for A to B is independent of the presence of a probabilistic mixture with a third alternative C, i.e., pA+(1-p)C is preferred to pB+(1-p)C (In the case of C = 0, the options thus reduce to pA preferred to pB).

However, several violations of these axioms were observed soon after their formulation – rendering Expected-Utility Theory a normative rather than a truly descriptive model. For instance, one of the first and influential violations was the *certainty effect*, also known as *Allais paradox* (Allais, 1953). An illustrative demonstration was given by Kahneman and Tversky (1979, p. 266). In their study, participants faced two hypothetical choices:

Choice Problem 1: Choice between an 80% chance of winning 4,000 ILP (Israeli Pounds) [A] or a sure outcome of 3,000 ILP [B].

Choice Problem 2: Choice between a 20% chance of winning 4,000 ILP [C] or a 25% chance of winning 3,000 ILP [D].

While the majority of subjects (i.e., 80%) chose B over A, implying that $u(3{,}000) > 0.8u(4{,}000)$, the majority of subjects (i.e., 65%) chose C over D, implying the opposite preference order, $0.2u(4{,}000) > 0.25u(3{,}000)$, equivalent to $0.8u(4{,}000) > u(3{,}000)$ (multiplied by 4). This pattern constitutes a violation of the substitution or independence axiom, since alternatives in Choice Problem 2 are probability mixtures of the alternatives in Choice Problem 1 (i.e., each alternative was weighted with a p of 0.25). Importantly, this violation indicates that a change from certainty to 25% chance loomed larger (hence *certainty effect*) than a change from 80% to 20% chance.

When investigating choices that involved potential losses, Kahneman and Tversky (1979, p. 268) observed another violation of Expected-Utility Theory. For instance, participants were given Choice Problem 1 from above and a mirrored Choice Problem 1_{loss} in the loss domain:

Choice Problem 1: Choice between an 80% chance of winning 4,000 ILP [A] or a sure gain of 3,000 ILP [B].

Choice Problem 1_{loss}: Choice between an 80% chance of losing 4,000 ILP [C] or a sure loss of 3,000 ILP [D].

Remember that the majority (i.e., 80%) of participants chose B over A, indicating risk aversion. However, in the loss domain, the majority (i.e., 92%) chose the gamble C over the sure loss D, indicating risk seeking. This reversal was termed the *reflection effect*, because the reflection of prospects around 0 reversed the preference order. Risk seeking in the loss domain cannot be explained by an extrapolation of the concave utility function to the loss domain, calling for a model that accounts for reference dependence. In an attempt to explain such violations and provide a more descriptive account of actual choice behavior, a new model has been developed: *Prospect Theory* (Kahneman & Tversky, 1979).

1.1.3. Prospect Theory As A Behavioral Model of Decision Making under Risk

Prospect Theory goes beyond Expected-Utility Theory by 1) replacing the utility function $u(x_i)$ over states of wealth with a value function $v(x_i)$ over gains and losses relative to a reference point (e.g., the status quo), and 2) by introducing nonlinear weighting of probabilities, i.e., the value of an outcome is weighted not by its objective probability but receives a decision weight $w(p_i)$ that is a nonlinear transformation of the outcome's probability p_i. Furthermore, in *Cumulative Prospect Theory* (Tversky & Kahneman, 1992), probability weighting is rank-dependent (following Quiggin, 1982), i.e., the decision weight attached to an outcome depends on the rank of that outcome with respect to other outcomes in the gamble. In (Cumulative) Prospect Theory, the value of a simple prospect is then given by

$$V(x,p) = w(p_i)v(x_i)$$

Reference dependence of the value function allows for different curvatures in the gain and loss domain—typically concave for gains and convex for losses. It is this reference-dependent reflection of the curvature of the value function that can explain the *reflection effect* mentioned before, i.e., risk aversion in the gain domain and risk seeking in the loss domain. It also explains a similar effect, the so-called *framing effect* (Tversky & Kahneman, 1981). In contrast to the reflection effect, the outcome domain is not changed objectively, but is framed to appear to involve the other domain. For instance, when people are given €50 as an initial endowment and in a second step they can decide between a sure payoff of €20 ("keep €20") and a gamble with some probability of keeping all or losing all, they will be more risk-averse than when they have to decide between a sure loss of €30 ("lose €30") and the same gamble. Please note that the final outcome for both sure payoffs would be €20, i.e., the objective outcome domains did not change, but their framing. Just as the reflection effect, the framing effect can be explained by a reference-dependent value function in Prospect Theory.

Moreover, Prospect Theory postulates a kinked value function with a steeper slope for losses than for gains, a feature termed *loss aversion*, with the effect that "losses loom larger than gains" (Kahneman & Tversky, 1979, p. 279), which results in risk aversion in mixed gambles. For instance, subjects typically reject mixed gambles that offer a 50% probability of gaining money and a 50% probability of losing money, unless the potential gain is at least about one and a half times or twice as large as the potential loss (e.g., Gächter, Johnson, & Herrmann, 2010; Kahneman & Tversky, 1979).

A popular parameterization of the value function expresses its reference dependence (Tversky & Kahneman, 1992):

$$vx_i = \begin{cases} x_i^{\alpha} \ if \ x_i \geq 0 \\ -\lambda(-x_i)^{\beta} \ if \ x_i < 0. \end{cases}$$

Here, α and β represent the curvature parameters in the gain and loss domains, respectively. Please note that the parameter position indicates a power function. Typically, the estimated parameter values are α<1, indicating a concave value function for gains that can explain commonly observed risk aversion in the gain domain, and β<1, indicating a convex value function for losses that can explain commonly observed risk seeking in the loss domain. The λ parameter models the degree of loss aversion, i.e., λ>1 indicates commonly observed loss aversion, λ=1 indicates loss (and thus risk) neutrality, and λ<1 indicates gain seeking. The value function is schematized in Figure 1, Panel A.

Not just the value function, but also the probability weighting function has been considered reference-dependent, but here with regard to its natural end points of impossibility (p = 0) and certainty (p = 1). Just as the expected utility (in Expected-Utility Theory) and value functions (in Prospect Theory) capture diminishing sensitivity to changes in the outcomes, the probability weighting function captures diminishing sensitivity to changes in probability with increasing distance from the reference points. This parallels insights from psychophysics on reference-dependence and diminishing marginal sensitivity in several perceptual domains (Fechner, 1948; Stevens, 1957).

The postulated shape of the probability weighting function is an inverse S (see Figure 1, Panel B), reflecting overweighting of low probabilities, underweighting of high probabilities, and lowest sensitivity to probability changes in the intermediate range. This property can explain the *Allais paradox* or *certainty effect* that we encountered above. Specifically, in Choice Problem 1, the alternative A associated with an 80% probability [4,000 ILP, 80%] receives a decision weight that is lower than its objective probability. This is not the case for the sure outcome B [3,000 ILP, 100%], which receives a decision weight identical to its objective probability of 100%. Together, this renders the sure, but smaller outcome B relatively more attractive. However, in Choice Problem 2, the probabilities associated with the two alternatives C and D, 20% [4,000 ILP, 20%] and 25% [3,000 ILP, 25%], respectively, receive similar decision weights (in fact, due to overweighting of smaller probabilities, the difference in decision weights is slightly reduced relative to the difference based on unweighted, objective probabilities). This renders the similarly weighted, but larger outcome C more attractive. Hence, the observed preference reversal in the Allais paradox can be explained by nonlinear probability weighting.

The nonlinear, inverse S-shaped weighting function generally fits aggregate experimental data well (Fehr-Duda & Epper, 2012; Stott, 2006), but there is considerable heterogeneity on an individual participant level with the most common curves being inverse S-shaped or convex (Fehr-Duda & Epper, 2012; Gonzalez & Wu, 1999; van de Kuilen & Wakker, 2011). Two-parameter models of probability weighting further distinguish between the curvature of the probability weighting function, which reflects sensitivity to changes in probability, and the elevation of the probability weighting function, which is thought to reflect "attractiveness" to gamble or "optimism/pessimism" across probability levels (e.g., Fehr-Duda & Epper, 2012; Gonzalez & Wu, 1999, see also Chapter 3.5.2.).

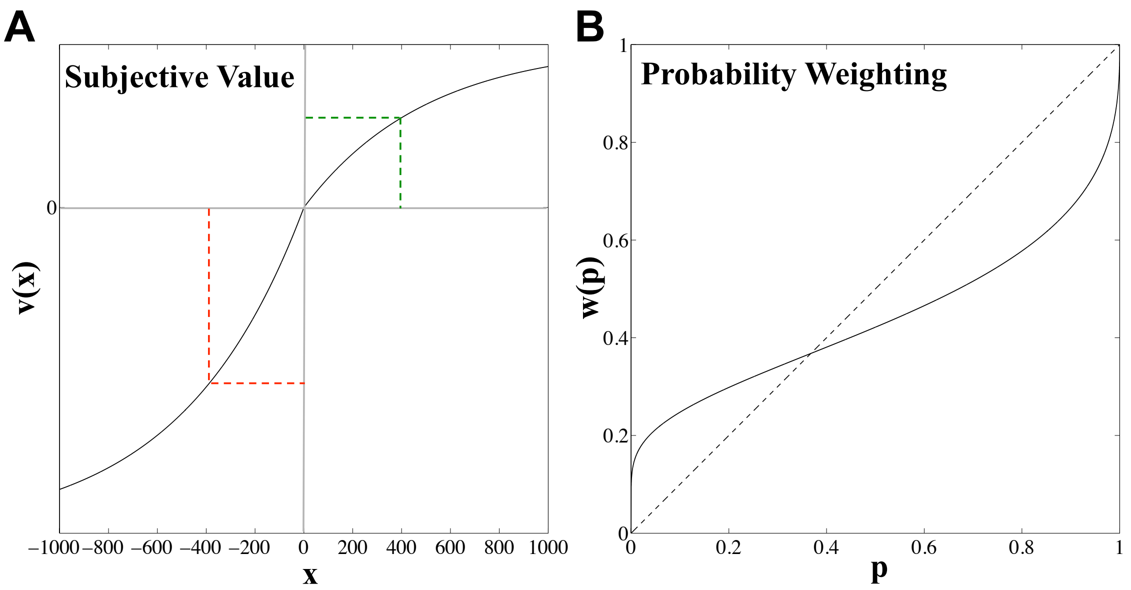

Figure 1. Value and probability weighting functions in Prospect Theory. *Panel A:* Value function that maps outcomes x (e.g., monetary gains and losses) to subjective values v(x), which have arbitrary units. The function is typically concave for gains and convex for losses and has a steeper slope for losses than for gains, i.e., loss aversion (also illustrated by the dashed colored lines reflecting different subjective values for a gain and a loss of equal magnitude). *Panel B:* Nonlinear probability weighting that maps probabilities p to decision weights w(p). The commonly observed inverse S-shaped function reflects overweighting of small probabilities, underweighting of moderate and high probabilities, and diminished sensitivity to probability changes in the intermediate range. The function thereby deviates from linear weighting (dashed 45° line).

Together with a reference-dependent value function, the probability weighting function can also explain the commonly observed four-fold pattern of risk attitudes (Tversky & Kahneman, 1992). More precisely, while both a concave value function and underweighting of high probabilities can explain risk aversion for high-probability gains (in favor of a smaller sure gain), risk seeking for low-probability gains (common, e.g., in real-world lotteries) can be explained by the overweighting of small probabilities. In a similar vein, while both a convex value function and underweighting of high probabilities can explain risk seeking for high-probability losses—with often devastating consequences—risk aversion for low-probability losses (reflected, e.g., in the popularity of insurances) can mainly be explained by overweighting of small probabilities. Such gains in explanatory power have raised the belief "… that probability nonlinearity will eventually be recognized as a more important determinant of risk attitudes than money nonlinearity" (Prelec, 2000, p. 89). However, as we have seen, both concepts jointly explain risky choice. Prospect Theory's concept of loss aversion adds further explanatory value. Specifically, in mixed prospects, risk aversion appears to be predominantly driven by loss aversion (Novemsky & Kahneman, 2005). This high explanatory power of Prospect Theory is reflected in its common designation as a descriptive model (i.e., explaining how people actually make decisions), in contrast to previous models like expected value theory and expected utility theory, which are now commonly regarded as normative models (i.e., explaining how rational agents would make decisions).

Since the development of Prospect Theory, subjective transformations of outcomes and probabilities, loss aversion, and phenomena like the framing effect have commonly been considered cognitive biases. However, there has been an increasing interest in whether they also reflect affective processes, as it soon became clear that decision making also depends on expected emotional outcomes (e.g., Bell, 1985; Gul, 1991; Loomes & Sugden, 1986) as well as emotions felt at the time of choice (e.g., Reimann & Bechara, 2010). Before we delve into the relationship between emotions and Prospect Theory, let me first give you a general introduction to decision-related emotions.

1.2. Emotions and Decision Making

Decision scientists have been indifferent to emotions for a long time. Recently, however, it is increasingly acknowledged that different kinds of emotions are involved in decision making (Lerner et al., 2015; Rick & Loewenstein, 2008). Before turning to decision-related emotions, let me first give a brief working definition of emotions.

1.2.1. Emotions—A Working Definition

Despite the widespread use of emotions in lay theories (Ong, Zaki, & Goodman, 2015; Tamir, John, Srivastava, & Gross, 2007) and language to describe and explain behavior, there is no consensual, unitary scientific definition of emotions, although there is some consensus regarding, e.g., common antecedents and functions of emotions (Izard, 2010; Scherer, 2005). A common conceptual and heuristic understanding of emotion is that they comprise multiple interrelated components—cognitive appraisals, psychophysiological activation, action tendencies, motor expressions (e.g., facial), and subjective feelings—as postulated by the *component process model* of emotions (Scherer, 2009). In this framework, an emotion is defined as an episode of interrelated, synchronized changes in all or most of these components in response to the evaluation of an external or internal stimulus event as relevant to major concerns of the organism (Scherer, 2005). A multi-componential perspective allows addressing decision-related emotions and their effects on behavior on several levels, e.g., in terms of appraisal and action tendencies (Lerner & Keltner, 2000; Lerner et al., 2015), which might provide unique as well as complementary insights. In the following chapter, I will continue by describing how decision-related emotions can be classified.

1.2.2. Decision-Related Emotions

Contemporary theoretical accounts distinguish between several types of decision-related emotions, for instance, by the associated stage in the decision process, their source, and their compliance with normative decision theory (Lerner et al., 2015; Rick & Loewenstein, 2008), which is consequentiatlistic and postulates that decision makers only assess utility based on future consequences (and not current affective states) and their likelihood. Figure 2 below gives an overview of these decision-related emotions.

For instance, so-called *expected emotions* are emotions that are anticipated to be experienced when the outcomes of a decision materialize. They are not experienced at the moment of choice, where they are only reflected in cognitions about the future emotions. In decision sciences, it is now widely accepted that people use expected emotions to form preferences (e.g., disappointment and elation; Bell, 1985; Gul, 1991; Loomes & Sugden, 1986). For instance, a decision maker can anticipate feeling disappointment when a recently bought stock declines in price afterwards and decides against the purchase to avoid potential disappointment. This type of emotion is consistent with a consequentialist perspective in that utility can also arise from experienced outcome-related emotions. Nevertheless, it took a while until their importance had been acknowledged.

In contrast to expected emotions, *immediate emotions* are actually experienced at the moment of choice and can be further subdivided in two kinds of emotions:

1) *Integral emotions*, like expected emotions, arise from anticipating the consequences of one's decision, but are experienced at the moment of choice. For instance, a decision maker might experience immediate fear when thinking about a potential huge loss after buying a stock. In principle, these emotions can also be incorporated into a consequentialist framework. Specifically, they might effectively signal decision makers their own tastes and values. Compelling evidence for this view comes from studies that investigated patients with injuries to the ventromedial prefrontal cortex (vmPFC) that cause emotional impairments (Bechara, Damasio, Tranel, & Damasio, 1997; Bechara, Tranel, Damasio, & Damasio, 1996). These patients repeatedly selected choice options with a high risk in decision-making tasks, resulting in a net loss, even when they cognitively understood the consequences. Physiological measures of skin conductance responses indicated that vmPFC-lesioned patients had deficient anticipatory arousal to risky options. Such anticipatory signals have been considered "*somatic markers*" that signal healthy individuals to avoid high risks (Reimann & Bechara, 2010). Interestingly, vmPFC-lesioned patients display physiological reactions when they experience losses or gains (Bechara, Damasio, Damasio, & Lee, 1999), which might enable

them to expect future emotional consequences (i.e., expected emotions) without experiencing anticipatory emotions (i.e., integral emotions) that directly guide choice.

2) *Incidental emotions* are also experienced at the moment of choice. In contrast to integral emotions, they arise from situational or dispositional sources that are objectively unrelated to the decision at hand, but can influence this very decision (Angie et al., 2011; Lerner et al., 2015; Loewenstein & Lerner, 2003). Thereby, they pose a fundamental and likely insurmountable challenge to normative decision theory, which postulates that utility is based on the integration of only future consequences and their likelihood, but not current affective states. However, incidental emotions are also a challenge to more recent theories and behavioral models of decision making such as Prospect Theory, which has not explicitly addressed emotions in the first place. However, as we will see in the next chapters, considerable progress has been made in linking emotions and Prospect Theory. The present thesis aims to advance the field by investigating the effects of incidental emotions on decision making under risk from a prospect-theoretic perspective.

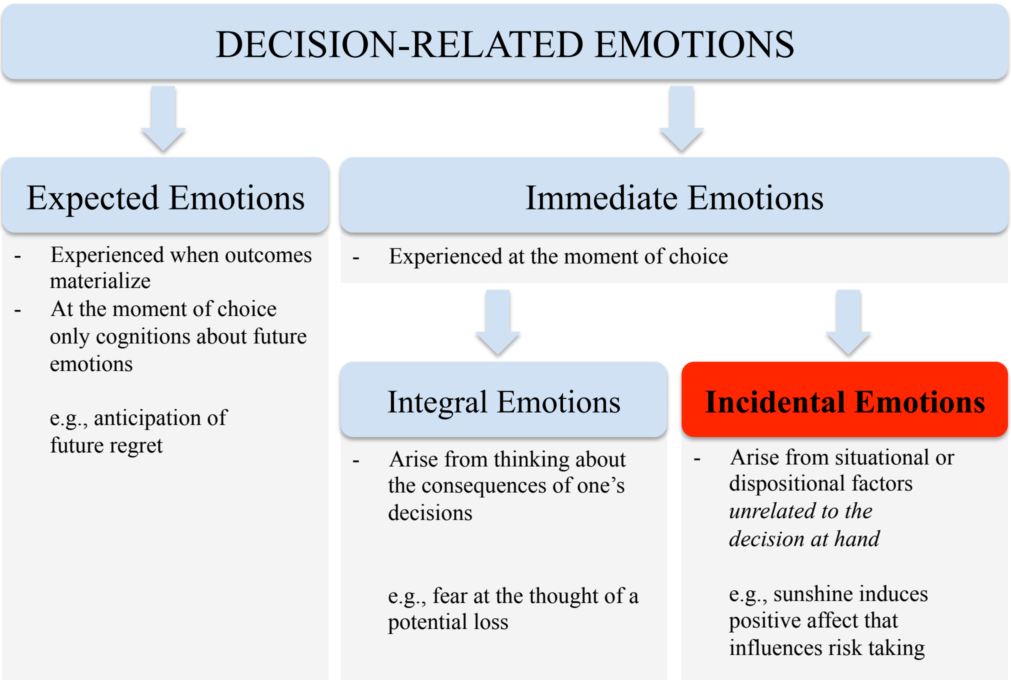

Figure 2. Different types of decision-related emotions.

1.2.3. Emotions and Prospect Theory

Prospect Theory's principles of reference-dependence and diminishing marginal sensitivity resonated well with those established in the psychophysics of perception (Fechner, 1948; Stevens, 1957), and, in general, cognitive conceptions have been implicitly or even explicitly prevailing. A widely held implicit assumption, however, is that subjective value at least partially reflects emotions, which in turn guide choice. In fact, this assumption has been made relatively explicit by Kahneman, stating that "… Humans described by Prospect Theory are guided by the immediate emotional impact of gains and losses …" (Kahneman, 2011, p. 286/287). This description roughly corresponds to the notion of integral emotions that arise from thinking about the consequences of one's decisions (e.g., the fear at the thought of a potential loss), although it could also refer to emotions experienced when outcomes materialize and which are cognitively anticipated in the present.

In the following chapters, I will show that both types of emotions have been associated with prospect-theoretic features, in particular with probability weighting and loss aversion. However, despite a growing body of evidence that also linked incidental emotions and decision making (see, e.g., Angie et al., 2011; Pham, 2007), the number of experimental studies that investigated the influence of *incidental emotions* on probability weighting and loss aversion is limited. Hence, I will also identify gaps in the literature on the links between incidental emotions and Prospect Theory that the present thesis aims to close.

1.2.4. Emotions and Probability Weighting

The consideration of expected and integral emotions, in particular with regard to probability weighting, has led to interesting insights in modeling of risky choice. For instance, according to one account, probability weighting can result from anticipated elation or disappointment (i.e., expected emotions) regarding the future realization of an uncertain payoff (Bell, 1985; Brandstätter, Kühberger, & Schneider, 2002; Gul, 1991; Walther, 2003). For instance, overweighting of small probabilities could result from anticipated elation after winning, given that winning was very unlikely, and underweighting of large probabilities can result from anticipated disappointment of not winning, given that winning was very likely (Brandstätter et al., 2002). The authors have shown that nonlinear power surprise functions for elation and disappointment allow the reconstruction of the typically observed inverse S-shaped probability-weighting function. Interestingly, it has also been found that disappointment looms larger than elation. Importantly, this offers a plausible psychological interpretation of over- and underweighting, whereas Prospect Theory's notion of diminishing sensitivity is not sufficient to imply such a pattern (e.g., permanent over- or underweighting would also be in line with this notion, as noted by Brandstätter et al., 2002). However, one major drawback of this account is that the introduced emotional terms were mainly defined as anticipated expectancy violations (see above), but have not been linked to actual affective experience (see, e.g., Brandstätter et al., 2002).

In a similar vein, but related to integral emotions, it has been hypothesized that the extent of probability weighting depends on the "affective richness" of potential outcomes and elicited hope or fear at the time of choice (Rottenstreich & Hsee, 2001). To be specific, overweighting of small probabilities is thought to result from the differentiation of situations in which some hope of winning exists (whenever $p > 0$) from situations in which there is no hope (in case of impossibility of winning). Likewise, underweighting of large probabilities is thought to result from the differentiation of situations in which some fear of not winning exists (whenever $p < 1$) from those in which there is no fear (in case of certainty of winning). Although changes from impossibility or certainty to possibility are emphasized by these emotions, changes in the intermediate range of probabilities may be de-emphasized (e.g., fear vs. not fear looms larger than slightly less vs. more fear). Furthermore, hope and fear should be stronger for affect-rich outcomes (e.g., a kiss, a vacation, or receiving an electric shock) compared to relatively affect-poor outcomes (e.g., a moderate cash prize). Consistent with these hypotheses, Rottenstreich and Hsee found a more strongly curved probability-weighting function for affect-rich compared to affect-poor outcomes, which reflects both the postulated over- and underweighting effects as well as diminished sensitivity to changes in the intermediate range of probabilities.

This phenomenon was also investigated in a recent fMRI study, which found that several brain areas were differentially activated in decisions on affect-poor and affect-rich outcomes (Suter, Pachur, Hertwig, Endestad, & Biele, 2015). For instance, affect-rich choice was associated with increased amygdala activity, consistent with emotional reactivity. Moreover, brain activity in regions that were more active during affect-poor choice (e.g., supramarginal gyrus) correlated with decision weights estimated via behavioral modeling, indicating that these regions display sensitivity to probability (changes). This finding is also consistent with the idea that sensitivity to probability (changes) is decreased in affect-rich decisions. Although these findings have been associated with integral emotions that are felt at the time of choice, evidence on their involvement is only indirect (e.g., increased amygdala activity during affect-rich choice in Suter, Pachur, Hertwig, Endestad, & Biele, 2015). Moreover, the reported effects could also be explained by the anticipation of emotions following future outcomes (i.e., expected emotions), which was the only emotional variable directly assessed (e.g., by self-reports, Suter, Pachur, Hertwig, et al., 2015). Taken together, although there remain open questions on the nature of the involved emotions, these findings provide evidence in favor of an emotional influence on probability weighting.

In contrast to expected and potential integral emotions, the influence of incidental emotions on probability weighting is far less understood. Incidental emotions are, like integral emotions, experienced at the moment of choice, but might influence decision making in a different manner. One early indication that incidental emotions might affect probability weighting is their influence on probability judgments. For instance, happy people make more optimistic probabilistic judgments and sad people make more pessimistic judgments (Johnson & Tversky, 1983; Wright & Bower, 1992), suggesting that similar effects might be observable in the subjective weighting of probabilities in risky choice.

Somewhat surprisingly, there has been almost only correlative and indirect evidence on the influence of incidental affect on probability weighting when this dissertation commenced. For instance, one study found seasonal and weather-dependent effects on probability weighting in US market price data, which were interpreted as mood effects though this assertion is speculative, as affective states have not been assessed. Data from fall (i.e., a season with decreasing daylight duration) and from days with high cloud coverage could be explained by a *more strongly inverse S-shaped* probability-weighting function compared to other seasons and lower sky coverage. In contrast, another study found a *more elevated* probability-weighting function (i.e., more optimistic weighting across probabilities) for both gains and losses in women (but not in men) that regarded the current day to be more promising than usual, which was also speculated to be an effect of mood (Fehr-Duda, Epper, Bruhin, & Schubert, 2011). However, to prove a causal effect of incidental emotions, it is indispensable to experimentally manipulate incidental emotions, optimally accompanied by a manipulation check (e.g., emotional self reports), and to investigate emotion-induced changes in probability weighting, which was the aim of Study 1 (for a summary, see Chapter 4.1.).

1.2.5. Emotions and Loss Aversion

There is a considerable body of evidence showing that loss aversion is intimately tied to emotions. For instance, participants that reported a high ability to identify and describe emotions (i.e., low alexithymia; Bibby & Ferguson, 2011) or objectively showed high interoceptive awareness (i.e., in a heart-beat detection task; Sokol-Hessner, Hartley, Hamilton, & Phelps, 2015) also displayed increased loss aversion compared to lower-scoring participants. Other studies focused on affective features of choice options. For instance, choice on hedonic goods (e.g., sweets) that induce pronounced affective reactions is associated with greater loss aversion than choice on affect-poor utilitarian goods (e.g., glue sticks; Dhar & Wertenbroch, 2000). Another example is that people are more willing to pay for insurance against potential loss of an object, the more affection they have for the object, even when holding monetary worth constant (Hsee & Kunreuther, 2000)—which could be explained by differences in loss aversion. Together, these studies suggest that loss aversion seems to be at least partly determined by expected or integral emotions, although the relative contribution of the two is not always clear.

In contrast to probability weighting, incidental emotional effects on loss aversion are better established, though evidence is still limited. Early studies found that incidental positive affect, induced by the receipt of a small bag of candy, was associated with more thoughts about losing in a thought-listing task (Isen & Geva, 1987), and with greater negative utilities of losses compared to control (Isen, Nygren, & Ashby, 1988). In contrast, a recent study found increased loss aversion for incidental negative affect (Stancak et al., 2015). Specifically, the presentation of unpleasant odor (methylmercaptan) was associated with greater loss aversion than pleasant odor (jasmine) or clean air, and the effects could be attributed to changes in odor pleasantness, but not intensity (i.e., arousal, but see Sokol-Hessner, Lackovic, et al., 2015). Emotional influence on loss aversion, however, is not always related to increased loss aversion. For instance, induced anger has been associated with reduced loss aversion (Campos-Vazquez & Cuilty, 2014). It is thus important to increase our understanding of the unique effects of specific emotions and affective dimensions on loss aversion.

One emotion that has received strong theoretical emphasis in loss aversion is fear. In fact, it has been even hypothesized that loss aversion is an expression of fear (Camerer, 2005). Neural systems mediating fear and anxiety overlap with those implicated in the computation of value and choice in decision making (Hartley & Phelps, 2012), and in particular with loss processing (described in more detail in Chapters 1.3.2. and 1.3.3.), which suggests a tight link between loss aversion and fear. Indirect evidence for such a link has also been provided by some behavioral studies. For instance, a serotonin transporter polymorphism (5-HTTLPR) has been associated with enhanced fear conditioning, trait anxiety, and increased risk taking when the alternative was framed as a sure loss—consistent with increased sensitivity to losses (Crişan et al., 2009). In addition, the effect of unpleasant odors on loss aversion mentioned above has also been interpreted in terms of signaled threat or danger (Stancak et al., 2015).

Despite these putative links between fear and loss processing, there has been no direct investigation of the influence of incidental fear cues on loss aversion so far. To close this gap, Study 2 aimed to establish this influence on a behavioral level (see Chapter 4.2.) and Study 3 investigated the underlying neural mechanisms (see Chapters 4.3. and 5.2.).

Personality constructs related to affective reactivity can also shed light on the relationship between incidental fear and loss aversion. One such personality construct is psychopathy—at its high end primarily characterized by deficits in affective processing and antisocial behavior (Cleckley, 1941; Hare & Neumann, 2008). Understanding psychopathy as a multidimensional and not unitary construct allows disentangling unique and differential effects related to dissociable psychopathic traits (Fowles & Dindo, 2009; Patrick & Bernat, 2009; Patrick, Fowles, & Krueger, 2009), which has also been demonstrated in my work on performance monitoring that is not subject of this dissertation (for a review, see Schulreich, 2016; and see Schulreich, Pfabigan, Derntl, & Sailer, 2013). In particular affective-interpersonal features of psychopathy, e.g., the higher-order factor fearless dominance in the Psychopathic Personality Inventory-Revised (PPI-R, Alpers & Eisenbarth, 2008), are plausible moderators of the influence of incidental fear cues on loss aversion, given that they reflect dispositional fear deficits (N. E. Anderson, Stanford, Wan, & Young, 2011; López, Poy, Patrick, & Moltó, 2013; Patrick et al., 2009). Such a moderation effect would corroborate an affective interpretation of potential effects of incidental fear cues on decision making. Therefore, Studies 2 and 3 also investigated whether such a moderation effect exists.

1.3. From Choice Data to Neural Data

So far, I identified some open questions in the behavioral literature about the influence of incidental emotions on decision making under risk and the moderating role of personality. These questions can be readily answered using choice data—the primary source of information and level of analysis in most economic and behavioral decision studies. Choice data alone, however, do not tell us how people exactly make decisions. For instance, while Prospect Theory implies that people behave as if they calculated weighted sums of subjective utilities and probabilities of all outcomes, answering the question on how people make decisions requires data that also tell us something about the underlying processes (see, e.g., Johnson, Schulte-Mecklenbeck, & Willemsen, 2008; Schulte-Mecklenbeck, Kühberger, & Ranyard, 2011). Furthermore, it is possible that different processes mediate similar or even identical choice behavior (i.e., equifinality), which poses a problem for models based on choice data alone. Problems of equifinality, however, might be solvable by employing a process-centered approach that is based on additional sources of information.

Two examples of process-centered data are eye-tracking data (e.g., Glöckner & Herbold, 2011) our mouse-tracking data (e.g., Schulte-Mecklenbeck et al., 2011), which could be used to infer sequential information processing steps in decision making. Another way of opening the "black box" is the acquisition of neural data, which tell us something about how neural circuits process specific kinds of information. Thereby, neurobiological knowledge can introduce constraints (e.g., biological plausibility) in the development of better models of decision making (Clithero et al., 2008).

Going beyond choice data, the present thesis also employed a neuroscientific approach to establish a link between choice behavior and its underlying mechanisms. Specifically, in Study 3 (see Chapter 4.3.), we complement our behavioral research of Study 2 on the effect of incidental fear cues on loss aversion by investigating the neural mechanisms that give rise to this effect. Thereby, we also build upon previous research on brain systems involved in value-based decision making and emotion. Hence, I will first give a general introduction to the neural basis of decision making under risk, before turning to the current understanding of the neural basis of loss aversion and emotion-induced changes in its magnitude.

1.3.1. Neural Basis of Decision Making under Risk

Decision making under risk is commonly seen as a type of value-based decision making, where the values of different options are first assessed, compared to each other, and the option with the highest value is chosen (see, e.g., Rangel, Camerer, & Montague, 2008). There is a rapidly increasing number of studies investigating value-based decision making in humans, most of them using fMRI due to its high flexibility in experimental control and in the analysis of specific events. Particular useful sources of information, however, are meta-analyses that integrate the findings of a multitude of fMRI studies, thereby detecting particularly reliable neural features (see, e.g., Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2013; Liu, Hairston, Schrier, & Fan, 2011). These meta-analyses have often included both decisions under risk (e.g., risky gambles, Tom, Fox, Trepel, & Poldrack, 2007) as well as decisions that did not include risk (e.g., on desirable or undesirable food items, Plassmann, O'Doherty, & Rangel, 2010). However, given that valuation and choice are integral features of both kinds of decisions, one can benefit from integration across these domains and the resulting high statistical power to detect reliable and common representations of valuation and choice.

One robust meta-analytic finding is that subjective value is positively associated with brain activity in the (ventral) striatum and the vmPFC/rostral anterior cingulate cortex (rACC) in the decision phase (Bartra et al., 2013; Clithero & Rangel, 2013; Levy & Glimcher, 2012). Moreover, it has been suggested that the vmPFC (and possibly other regions, e.g., the striatum) represents subjective value across different kinds of rewards (e.g., food, money) in a "single neural currency", i.e., when two disparate kinds of rewards are equally desirable for the subject, brain activity will be identical (Bartra et al., 2013; Levy & Glimcher, 2011, 2012). As already mentioned, the main strength of meta-analyses is that the integration of findings from a large array of studies allows for detection of reliable neural correlates of specific decision-related features. One major limitation, however, is that such an integration is only feasible for variables that a large number of studies have in common, e.g., some (binary or parametric) regressor that indicates variations in subjective value (see, e.g., Bartra et al., 2013). Furthermore, as already mentioned, these meta-analyses included studies on decisions that involved no risk. Hence, to better understand the neural basis of specific decision- and risk-related features (e.g., probabilities, variance) and behavioral phenomena (e.g., loss aversion) that have not been differentiated in the meta-analyses above, original studies are indispensable sources of information.

In this regard, fMRI studies on decision making have focused on a multitude of specific variables and phenomena. Many studies in the field targeted the neural representations of objective choice parameters. For instance, several studies found brain areas tracking gain magnitudes, e.g., the ventral striatum including the Nucleus accumbens (e.g., Canessa et al., 2013; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Tobler, O'Doherty, Dolan, & Schultz, 2007; Tom et al., 2007), whereas loss-related findings have been more inconsistent (as discussed in greater detail in Chapter 1.3.2.). Some studies also found brain regions that tracked reward probabilities, including also the striatum as well as the medial PFC (e.g., Berns & Bell, 2012; Knutson et al., 2005; Tobler et al., 2007). Given the partial overlap of the processing of gains and probabilities, some studies also reported neural representations of expected value, which integrates these two features into one single metric, e.g., in the striatum (e.g., Knutson et al., 2005; Preuschoff, Bossaerts, & Quartz, 2006; Tobler et al., 2007; Yacubian et al., 2006). Furthermore, there are studies that observed neural representations of risk (e.g., defined as variance), e.g., in the anterior insula (e.g., Mohr, Biele, Krugel, Li, & Heekeren, 2010; Preuschoff, Quartz, & Bossaerts, 200; and for a meta-analysis, see, Mohr, Biele, & Heekeren, 2010).

Neural activity tracking integrated (i.e., expected) value and its constituent elements (e.g., gains, probabilities) is consistent with economic Expected-Value Theory formulated long ago. However, these findings are also in line with expected utility theory or Prospect Theory, of which expected value theory can be seen as a special case (e.g., lacking subjective transformations of outcomes and probabilities, as postulated by Prospect Theory). Given that Prospect Theory describes actual decision behavior pretty well (see Chapter 1.1.3.), it comes as no surprise, that neuroeconomic research soon targeted the special assumptions of Prospect Theory and the behavioral phenomena it explains (e.g., context-dependent preference reversals).

For instance, one fMRI study investigated the neural correlates of the framing effect (De Martino, Kumaran, Seymour, & Dolan, 2006), which illustrates the prospect-theoretic principle of reference dependence impressively. Participants received an initial endowment (e.g., "You receive £50") and were asked to choose between a sure payoff and a gamble afterwards. The critical manipulation was that once the sure payoff was framed as a gain (e.g., "keep £20") and once framed as a loss (e.g., "lose £30"), whereas the gamble (i.e., "keep all" and "lose all" associated with particular probabilities) was not changed. Please note, that the final objective outcomes of the sure options are the same in both frames (here, £20). Despite this, the authors replicated the well-known framing effect (Tversky & Kahneman, 1981)—risk aversion in the gain frame and risk seeking in the loss frame. At the neural level, this study found increased amygdala activity when participants decided in accordance with the framing effect, whereas the ACC was more active when decisions ran counter to the framing effect. Hence, this study illustrates that Prospect Theory's principle of reference-dependence can be linked to specific structures and mechanisms in the brain.

In a similar vein, brain activity can also be directly associated with the preference parameters derived from prospect-theoretic models. For instance, there are some fMRI studies that investigated the neural correlates of probability weighting (Berns, Capra, Chappelow, Moore, & Noussair, 2008; Hsu, Krajbich, Zhao, & Camerer, 2009; Paulus & Frank, 2006; and for a positron emission tomography study, see Takahashi et al., 2010). A methodological prerequisite for detecting neural representations of a nonlinear (inverse S-shaped) probability weighting function was to explicitly include probabilities near to certainty and impossibility, because previous studies commonly focused on intermediate, roughly linear parts of the function (e.g., Knutson et al., 2005; Tobler et al., 2007). Aware of this prerequisite, one research group then modeled separate regressors for linear and nonlinear components of the probability weighting function for gains and found both related to activity in the dorsal striatum (Hsu et al., 2009). Furthermore, the authors also observed a positive correlation between behavioral nonlinearity in probability weighting and nonlinearity of striatal responses across subjects. Another study also found neural representations for nonlinear probability weighting of aversive outcomes, e.g., in the striatum and anterior insula (Berns, Capra, Chappelow, Moore, & Noussair, 2008).

Another central construct in Prospect Theory is loss aversion, which also received great attention in decision neuroscience. In the following, I will dedicate two chapters to an introduction to the neural basis of loss aversion and possible neural mechanisms underlying emotion-induced changes in its magnitude, given that Study 3 of the present thesis builds upon this body of knowledge.

1.3.2. Neural Correlates of Loss Aversion

In recent years, a number of studies accumulated evidence on the neural mechanisms of loss aversion. For instance, one influential fMRI study investigated whether neural responses to losses and gains would reflect behaviorally observed neural loss aversion (Tom et al., 2007). To this end, participants made repeated decisions whether to accept or reject a mixed gamble offering a 50% chance of gaining and a 50% chance of losing variable amounts of money. The authors hypothesized that loss aversion could be mediated either by the recruitment of brain structures that are thought to mediate negative emotions towards potential losses, e.g., the amygdala (Duvarci & Pare, 2014; Lang, Davis, & Öhman, 2000; LeDoux, 2003) or by an asymmetric response to losses versus gains within a single system that codes subjective value, e.g., the ventral striatum or vmPFC (Bartra et al., 2013; Clithero & Rangel, 2013; Levy & Glimcher, 2012). Their findings were in favor of the second hypothesis. Specifically, they found a distributed set of regions that displayed activations for gains and deactivations for losses, e.g., the striatum, vmPFC, and dorsal ACC, consistent with positive value coding. Crucially, they also observed that the deactivation slope for losses was steeper than the activation slope for gains in most of these areas, similar to the overweighting of losses relative to gains in behavioral loss aversion. Consequently, this asymmetric response pattern was termed "neural loss aversion". Importantly, neural loss aversion was positively correlated with behavioral loss aversion, e.g., in the bilateral ventral striatum. In contrast to loss-related deactivations, Tom et al. (2007) found no brain regions that responded to increasing losses with increasing brain activity, which would had indicated negative value coding and, possibly, negative emotions.

The last finding is surprising, given previously observed activations for potential losses, e.g., in the amygdala (e.g., Basten, Biele, Heekeren, & Fiebach, 2010; Hahn et al., 2010; Kahn et al., 2002), although these studies did not directly investigate loss aversion. One neuropsychological study, however, found sharply reduced monetary loss aversion in two patients with focused bilateral amygdala lesions compared to matched controls, suggesting that the amygdala causally contributes to loss aversion (De Martino, Camerer, & Adolphs, 2010). However, this study did not provide information on the underlying amygdalar mechanisms that could give rise to loss aversion.

A later study also found structural evidence for an amygdalar contribution to loss aversion (Canessa et al., 2013). By using multivariate source-based morphometry (SBM) and univariate voxel-based morphometry (VBM) to process anatomical MRI data, a structural amygdala-thalamus-striatum network has been detected, whose gray matter volume positively predicted behavioral loss aversion. The same study also included an fMRI experiment, in which a neural loss aversion response—characterized by a steeper slope for loss-related deactivations relative to gain-related activations—was observed in some of the same areas as in the Tom et al. study (e.g., in the striatum). However, Canessa et al. also found a few regions, including the amygdala and the posterior insula, which displayed loss-related activations that also positively predicted behavioral loss aversion. Similarly, another fMRI study observed greater amygdala activations for loss relative to gain outcomes, which also predicted monetary loss aversion (Sokol-Hessner, Camerer, & Phelps, 2013). Another electroencephalography (EEG) study used source modeling to investigate outcome-related processes (Kokmotou et al., 2017) and found that loss aversion was associated with increased brain activity to loss outcomes in the vmPFC/orbitofrontal cortex. However, one needs to be cautious when comparing neural correlates observed during the decision stage and during the outcome stage, given that the underlying structures and mechanisms might differ (Bartra et al., 2013; Clithero & Rangel, 2013; Liu et al., 2011). In contrast to the Tom et al. study, these studies indicate that loss-related activations, e.g., in the amygdala, at least partially contribute to loss aversion.

However, two recent studies observed instead loss-related deactivations in amygdala activity, that were also stronger than gain-related activations (i.e., neural loss aversion) in the more recent study (Pammi et al., 2015; Pammi, Ruiz, Lee, Noussair, & Sitaram, 2017). Taken together, while there is considerable evidence in favor of a causal contribution of the amygdala to loss aversion, its functional role in loss aversion is currently only incompletely understood.

Overall, the observations of different forms of value coding—deactivations for losses in some studies, activations for losses in others—may at first glance seem inconsistent. However, they add to a growing body of evidence of two opponent—excitatory and inhibitory—loss (and gain) signals within disparate, but overlapping motivational systems (Brooks & Berns, 2013; Seymour, Maruyama, & De Martino, 2015). The first, reward-oriented system is thought to display enhanced neural activity for gains and inhibited neural activity for losses, i.e., positive value coding. Neural loss aversion, i.e., stronger deactivations for increasing losses relative to gain-related activations (e.g., Canessa et al., 2013; Tom et al., 2007) is consistent with such a mechanism, although the asymmetry of these bidirectional responses represents an additional, behaviorally relevant, feature. However, there is also evidence of a second, punishment-oriented system that displays enhanced neural activity to losses and inhibited neural activity to gains. These signals are partially generated in direct adjacency to reward-oriented signals, e.g., in the striatum (Brooks & Berns, 2013; Seymour, Daw, Dayan, Singer, & Dolan, 2007; Seymour et al., 2015). Similarly, electrophysiological studies in rodents (Gore et al., 2015; Shabel & Janak, 2009) recently combined with optogenetic methods (Beyeler et al., 2016), also indicate the existence of different neuronal populations that display excitatory or inhibitory responses to losses (and gains) within the amygdala. Some neurons displayed opposite responses to positive and negative outcomes (i.e., increased activity for aversive and decreased activity for appetitive outcomes; increased activity for appetitive and decreased activity for aversive outcomes), others to appetitive or aversive outcomes only. All of these patterns can give rise to the different value responses detected in human fMRI studies. Since these neuronal subpopulations are spatially intermingled (see, e.g., Beyeler et al., 2016), it might be impossible or at least difficult to disentangle excitatory and inhibitory responses to the same stimulus with fMRI, unless one signal clearly dominates the other, since fMRI does not provide a single-cell spatial resolution. In other words, within a small neuronal population, fMRI may only detect the response type that is stronger or spatially more extended relative to others, while oppositely signed signals of similar strength and extension would (partially) cancel each other out.

Interestingly, there are also amygdala neurons that respond to both appetitive and aversive stimuli in a similar manner (e.g., excitatory responses to both, Shabel & Janak, 2009), which might be a neural mechanism for salience-like responses, i.e., enhanced value-unspecific brain activity to both positive and negative outcomes, which has also been associated with loss aversion (Gelskov, Henningsson, Madsen, Siebner, & Ramsøy, 2015; Gelskov, Madsen, Ramsøy, & Siebner, 2016). However, given that behavioral loss aversion reflects a value asymmetry, neural mechanisms that causally generate loss aversion should also reflect value-specific activity.

Taken together, there is evidence that loss aversion might be mediated by two distinct valuation mechanisms that are tuned to rewards and punishments, respectively. However, it is an open question to what degree each mechanism contributes to loss aversion and whether these distinct valuation processes are differentially involved in different contexts. As we will see in the next chapter, incidental emotions may represent one contextual factor that alters valuation—a possibility explored in Study 3 of the present thesis (see Chapter 4.3.).

1.3.3. Neural Correlates of Emotion-Induced Changes in Loss Aversion

There is an increasing interest in the neural mechanisms underlying the influence of incidental emotions on decision making in diverse domains such as intertemporal decisions (e.g., Luo, Ainslie, & Monterosso, 2014; Sohn et al., 2015) and social decisions (e.g., Harlé, Chang, van 't Wout, & Sanfey, 2012). However, only a few neuroscientific studies investigated the link between emotions and prospect-theoretic phenomena such as loss aversion. For instance, one study (Sokol-Hessner et al., 2013) that we encountered above did not just observe that greater amygdala activity to loss relative to gain outcomes was associated with greater loss aversion, but also found that cognitive reappraisal—an emotion-regulation strategy—reduced amygdala activity to loss outcomes (and psychophysiological arousal in a previous study, Sokol-Hessner et al., 2009) and thereby loss aversion. This suggests that negative value coding in the amygdala might be linked to negative emotion, at least when loss outcomes materialize. However, only two recent studies experimentally manipulated incidental emotions at the time of choice and investigated their effect on loss aversion at the neural level (Charpentier, De Martino, Sim, Sharot, & Roiser, 2015; Engelmann, Meyer, Fehr, & Ruff, 2015).

One of these studies found that enhanced amygdalar-striatal connectivity predicted increases in monetary loss aversion in a mixed-gambles task following the presentation of fearful or happy faces, relative to neutral faces and objects (Charpentier et al., 2015). This indicates that the amygdala is centrally involved in mediating emotional effects on decision making, consistent with its previously demonstrated role in the generation of loss aversion (De Martino et al., 2010) and in affective processing, in particular of fear and threat (Lang et al., 2000; LeDoux, 2003; Tovote, Fadok, & Lüthi, 2015) or arousal (A. K. Anderson et al., 2003; P. A. Lewis, Critchley, Rotshtein, & Dolan, 2007, but see Anders, Eippert, Weiskopf, & Veit, 2008). Amygdalar-striatal connections are critically involved in the generation of avoidance behaviors (Amorapanth, LeDoux, & Nader, 2000; LeDoux & Gorman, 2001), consistent with the observed emotion-induced increases in loss aversion. However, the study by Charpentier et al. did not report value-related amygdala activity that predicted emotion-induced changes in loss aversion. Hence, the exact functional role of the amygdala in the generation of emotion-induced changes in loss aversion (and of loss aversion in general) remains unclear.

The second study compared decisions on mixed gambles under threat of electrical shock and in a safe context (Engelmann et al., 2015). Surprisingly, while the authors observed loss aversion across contexts, they did not observe emotion-induced changes in its magnitude. However, gamble acceptance (and thus, possibly, loss aversion) was predicted by context-dependent valuation. Specifically, increasing striatum and vmPFC activity for increasing subjective expected value, i.e., positive value coding, positively predicted gamble acceptance in the neutral context. In contrast, increasing insula activity for decreasing subjective expected value, i.e., negative value coding, negatively predicted gamble acceptance in the threat-of-shock context. By contrast, the authors did not report any value-related amygdala activity that predicted choice. Interestingly, apart from possible gain-related changes, in particular greater loss-related activations are one plausible source of the observed shifts towards negative coding, but this possibility has not been explored so far.

In Study 3 of the present thesis (see Chapter 4.3.), we aimed to further elucidate the neural mechanisms underlying the influence of incidental affect—incidental fear cues in particular—on monetary loss aversion. On the basis of the literature described so far, there are two plausible hypotheses on the mediating mechanisms, which are also illustrated in Figure 3 and described in the following.

The first one is based on the idea that in particular excitatory loss signals in the amygdala (e.g., Basten et al., 2010; Canessa et al., 2013; Sokol-Hessner et al., 2013) may account for fear-cue induced increases in loss aversion—given the prominent role the amygdala plays in fear processing (Lang et al., 2000; LeDoux, 2003; Tovote et al., 2015) and given preferential processing of threat-related relative to appetitive stimuli under fear-related affective states (e.g., Cavanagh, Urry, & Shin, 2011). Moreover, amygdala responses to fearful movies have been found to enhance subsequent activation to unrelated threat-related stimuli (Pichon, Miendlarzewska, Eryilmaz, & Vuilleumier, 2015). Similarly, we expected a general increase in amygdala activity after the presentation of fear cues in combination with increased activation in response to increasing monetary losses, reflecting negative value coding. In fact, the amygdala might be part of a broader, distributed network that displays an emotion-induced shift from positive to negative value coding that also includes, e.g., the striatum, vmPFC, and insula (Engelmann et al., 2015). Crucially, Study 3 tested whether such effects mediate emotion-induced increases in monetary loss aversion.

The second, alternative hypothesis is that emotion-induced changes in loss aversion might be mediated by a positive-value–coding mechanism via enhanced deactivations for losses relative to activations for gains (i.e., neural loss aversion), e.g., in the striatum (Canessa et al., 2013; Tom et al., 2007).

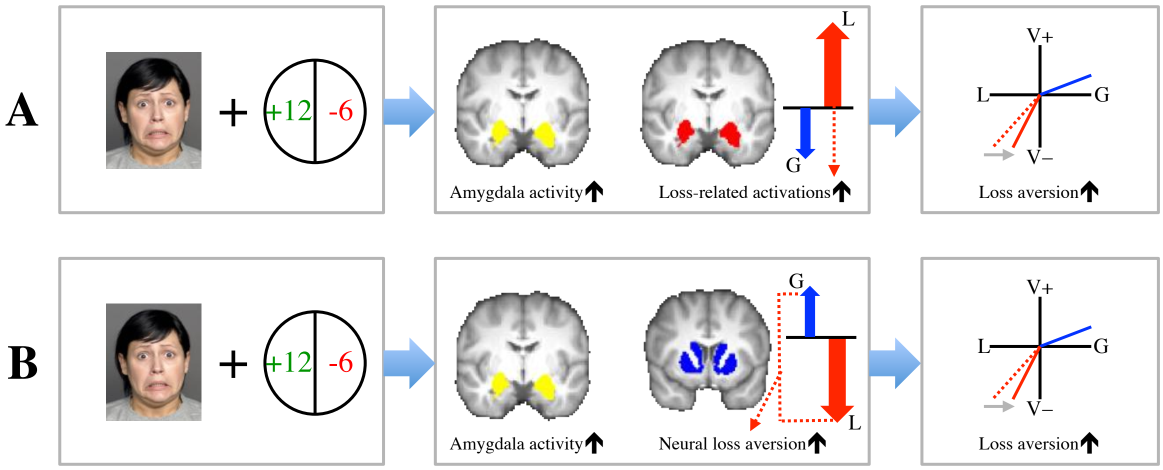

Figure 3. Hypotheses on the neural mechanisms that mediate the influence of incidental fear cues (i.e., fearful faces in Study 3) on monetary loss aversion in a mixed-gambles task. *Panel A:* The first hypothesis (H5 in Chapter 2) states that incidental fear cues enhance amygdala activity which primes the processing of monetary payoffs via *loss-related activations* in particular, e.g., in the amygdala and, possibly, a distributed set of regions. This effect, in turn, mediates emotion-induced increases in behavioral loss aversion. *Panel B:* The second, alternative hypothesis states that emotion-induced increases in amygdala activity enhance *loss-related deactivations* relative to gain-related activations (i.e., neural loss aversion) in regions that typically display such a pattern in a neutral context, e.g., the striatum. Increases in neural loss aversion mediate emotion-induced changes in behavioral loss aversion. *Note:* G = Gain, L = Loss, V+ = positive subjective value, V– = negative subjective value.

2. Summary of Research Questions (RQ) and Hypotheses (H)

In this chapter, I will give a succinct summary of the research questions identified above and formulate hypotheses that the empirical studies of the present thesis aimed to test.

RQ1: Is there an influence of incidental emotions (e.g., incidental happiness) on probability weighting?

Study 1 aimed to address this question by experimentally manipulating incidental emotions via music as well as modeling risk preferences (for more details, see Chapters 3.2. and 3.5.2.). Based on previous evidence of incidental emotional effects on probability judgments (Johnson & Tversky, 1983; Wright & Bower, 1992) and indirect evidence of incidental emotional effects on probability weighting (e.g., Fehr-Duda et al., 2011), hypothesis H1 was formulated:

H1: *Music-evoked incidental emotions are associated with changes in risk taking and probability weighting. Specifically, incidental happiness is positively related to the elevation of the probability-weighting function.*

Based on the observation that emotional effects are typically fleeting (Andrade & Ariely, 2009; Isen & Gorgoglione, 1983), hypothesis H2 was formulated:

H2: *The effect of music-evoked incidental emotions on decision making declines over time.*

RQ2a: Is there an influence of incidental fear cues on loss aversion?

Study 2 aimed to address this question by experimentally manipulating the affective context by presenting fearful vs. neutral faces prior or during decisions on mixed gambles as well as by estimating the degree of loss aversion via behavioral modeling (for more details, see Chapters 3.2. and 3.5.2.). Based on the neural overlap of fear processing and decision making (Hartley & Phelps, 2012) and behavioral evidence consistent with increased loss-sensitivity in fear/anxiety-prone individuals (e.g., Crişan et al., 2009), hypothesis H3 was formulated:

H3: *Incidental fear cues increase monetary loss aversion compared to neutral cues.*

RQ2b: Is the influence of incidental fear cues on loss aversion moderated by psychopathic personality, in particular affective-interpersonal features?

Study 2 aimed to address this question by administering the PPI-R (Alpers & Eisenbarth, 2008, see Chapter 3.4.)—a self-report questionnaire to measure psychopathic personality—and by including personality scores in the behavioral modeling. Based on evidence that psychopathic personality, in particular the affective-interpersonal traits (e.g., PPI-R fearless dominance), is associated with deficient fear-reactivity (e.g., López et al., 2013; Patrick et al., 2009), hypothesis H4 was formulated.

H4: *Psychopathic personality, in particular PPI-R fearless dominance (but not PPI-R self-centered impulsivity) moderates the effect of incidental fear cues on loss aversion. Specifically, higher fearless dominance is associated with an attenuated effect of incidental fear cues on loss aversion.*

RQ3a: What are the neural mechanisms that mediate emotion-induced changes in loss aversion?

Study 3 aimed to address this question by adapting the experimental design of Study 2 for fMRI (for more details on fMRI, see Chapter 3.6.). Based on evidence of fear-related (e.g., Lang et al., 2000; LeDoux, 2003; Tovote et al., 2015) and loss-related processing in the amygdala (e.g., Basten et al., 2010; Canessa et al., 2013; Sokol-Hessner et al., 2013) as well as emotion-induced shifts from positive to negative value coding in the striatum, vmPFC, and insula (Engelmann et al., 2015), hypothesis H5 was formulated.

H5: *Incidental fear cues enhance amygdala activity relative to neutral cues. This general increase is accompanied by altered value processing, i.e., emotion-induced increases in activations for losses in the amygdala and, possibly, shifts towards negative value coding in other regions as well (e.g., striatum, insula, vmPFC). These emotion-induced shifts in valuation mediate increases in behavioral loss aversion (for an illustration of this hypothesis and an alternative hypothesis, please see again Figure 3, Panel B above).*

RQ3b: How is the influence of psychopathic personality on emotion-induced changes in loss aversion mediated at the neural level?

Study 3 aimed to address another research question that follows from evidence in Study 2 in favor of H4, i.e., affective-interpersonal features of psychopathy attenuated emotion-induced increases in loss aversion. Study 3 aimed to replicate this effect using the Triarchic Measure of Psychopathy (TriPM, Patrick, 2010, see Chapter 3.4.), for which the affective-interpersonal traits TriPM boldness and meanness are thought to display the same behavioral effect. At the neural level, the moderation effect on emotion-induced changes in loss aversion might be mediated by altered value responses in the amygdala, given that affective-interpersonal features of psychopathy have been related to amygdala hypoactivation during emotion processing (e.g., Gordon, Baird, & End, 2004). Hypothesis 6 states:

H6: *The attenuating effect of affective-interpersonal psychopathic traits (e.g., TriPM boldness and meanness) on emotion-induced increases in loss aversion is mediated by attenuated emotion-induced increases in amygdala activations for losses.*

3. General and Specific Methodology

In this chapter, I will give a summary of the experimental and statistical methods used for the elicitation of risk preferences (via lottery choice procedures), affective manipulation and measurement, personality assessment, analysis of choice behavior (e.g., via estimation of prospect-theoretic parameters), and for the investigation of neural processes (via fMRI).

3.1. Lottery Choice Procedures

There are various simple and transparent methods to elicit risk attitudes that are believed to provide reliable results (for an overview, see Harrison & Rutström, 2008). Here, I will focus on the *random lottery pairs* (RLP) procedure (Hey & Orme, 1994) that has been used in Study 1 (gains-only), and a *random mixed gambles* (RMG) procedure (gains and losses) that has been used in Studies 2 and 3 to elicit monetary loss aversion.

3.1.1. Random Lottery Pairs (RLP) Procedure

In the RLP procedure, subjects are presented multiple pairs of lotteries with varying outcomes and probabilities and thus levels of risk and are asked to pick one of the lotteries in each pair. In Study 1, each lottery consisted of two possible, strictly positive payoffs and associated probabilities. The restriction to the gain domain allowed us to abstract from loss aversion, which facilitated behavioral modeling (described in Chapter 3.5.2.) and increased detectability of emotional effects on probability weighting. The use of only risky prospects could also have had benefits in this regard, since certain payoffs might provide a striking reference point and could potentially induce sign-dependency and loss aversion, as argued by Harrison & Rutström (2008). The payoffs and probabilities were visualized on screen by a pie chart (see Figure 4). The lotteries differed form each other in their riskiness. To be specific, a lottery was considered riskier than another lottery if it can be expressed as a mean-preserving spread of the other lottery (Rothschild & Stiglitz, 1970), but we obtained qualitatively identical results if we considered variance as the risk measure, which is also common in the literature. For instance, in Figure 4, the bottom lottery is the riskier lottery for both risk definitions. The set of lottery pairs was designed to allow for a precise estimation of preference parameters in the range that has been observed in previous studies (e.g., Harrison & Rutström, 2008; Stott, 2006). Probabilities ranged from 10% to 90% to allow for a reliable estimation of the probability weighting function.

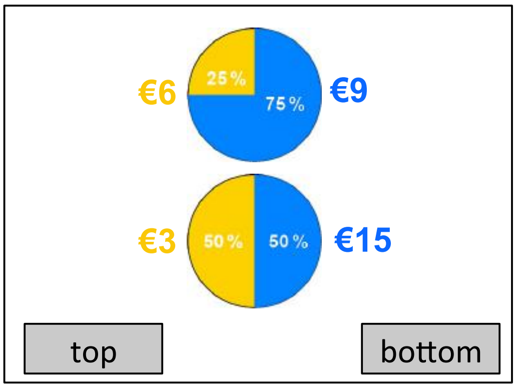

Figure 4. Example of a lottery pair with the two choice options in Study 1.

3.1.2. Random Mixed Gambles (RMG) Procedure

Since we were interested in loss aversion in Studies 2 and 3, we had to include gains and losses simultaneously as gain-only and loss-only prospects do not elicit loss aversion, which is defined as increased weighting of losses relative to gains (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). To this end, participants had to decide on a pseudo-randomized series of mixed gambles with equal (i.e., 50%) probability of winning or losing variable amounts of money (e.g., ranging from ±€6 to ±€20 in steps of €2 in Study 3). Participants could accept or reject each gamble (rejection equals the acceptance of a sure outcome of €0). The mixed gambles were presented in a simple visual form (e.g., as pie charts in Study 3, also see Figure 6 in Chapter 3.2. below).

3.1.3. Random Incentive Mechanism

Lottery procedures often come with a random incentive mechanism (see, e.g., Harrison & Rutström, 2008; Starmer & Sugden, 1991) under which subjects respond in multiple decision trials but only one trial is randomly selected for payoff at the end of the experiment. The subject's preferred (RLP procedure) or accepted (RMG procedure) lottery is then played out for real. For mixed gambles, this could result in a gain or in a loss. Rejected mixed gambles and unchosen lotteries in the RLP procedure are not played out.

This mechanism has four main advantages: 1) It provides an incentive for truthful responding of ones preferences, 2) It excludes wealth effects arising from paying more than one choice sequentially during the experiment (i.e., changes in wealth might affect decision making), 3) it excludes portfolio effects arising from paying more than one choice at the end of the experiment (i.e., one might prefer a combination of options, whereas one option is clearly preferred over another when the pair is evaluated independently), and 4) it reduces expenditures (i.e., reduced subject payments compared to payoffs from multiple trials). Due to theses appealing features, it has been used in many experimental studies (e.g., De Martino et al., 2010; Hey & Orme, 1994) and in our experiments as well.

In Studies 2 and 3, subjects were endowed with an initial amount of money (in cash) to compensate for eventual losses—a frequent procedure in decision tasks involving the possibility of real losses (e.g., De Martino et al., 2010; Sokol-Hessner et al., 2009). Subjects were told that the money was theirs to risk during the study and to place it into their wallets or purses. This procedure allows for non-hypothetical decision making (i.e., with real monetary stakes), meets ethical requirements (i.e., no net financial losses but only relative losses for research participants) and facilitates subject recruitment (compared to the possibility of a net loss).

3.2. Emotion Manipulation

Although emotions elicited under natural conditions are often stronger and inherently have higher ecological validity, laboratory-based experimental manipulations are considered the via regia to ensure internal validity, enabling causal inferences. A diversity of emotion induction methods have been applied in emotion research (for reviews and systematic comparisons, see, e.g, Gerrards-Hesse, Spies, & Hesse, 1994; Jallais & Gilet, 2010; Westermann, Spies, Stahl, & Hesse, 1996).

For instance, musical stimuli have been found useful for eliciting emotional states (Juslin, Liljeström, Västfjäll, Barradas, & Silva, 2008; Juslin & Västfjäll, 2008; Koelsch et al., 2013; Zentner, Grandjean, & Scherer, 2008) and were also used in Study 1. To be specific, we used instrumental excerpts—happy and sad pieces—and random tone sequences that have also been used in previous studies (Koelsch et al., 2013; Pehrs et al., 2013), together with a no-music control condition (for a complete list of the musical pieces, see the original research paper in the appendix). To note, musical stimuli are not just a handy means of emotional manipulation, but also interesting from an ecological perspective, because of their ubiquity in everyday life, e.g., background music while making purchasing decisions in a store (Garlin & Owen, 2006).

Subjects participated in four separate sessions that comprised four experimental conditions, i.e., "happy" music, "sad" music, random tones, and no music (i.e., a within-subject design), which were about one week apart. In each session (except the no-music condition), multiple musical pieces were presented in a 6-min block via headphones, followed by a block of pairwise lottery choices lasting approximately 10 min. This procedure was repeated twice, so that there were 2 music blocks and two choice blocks per session. The music blocks and choice blocks were immediately followed by an emotion-rating task (described in Chapter 3.3). In the no-music condition, only the emotion-rating tasks and choice blocks were presented. The sequence of experimental events is illustrated in Figure 5.

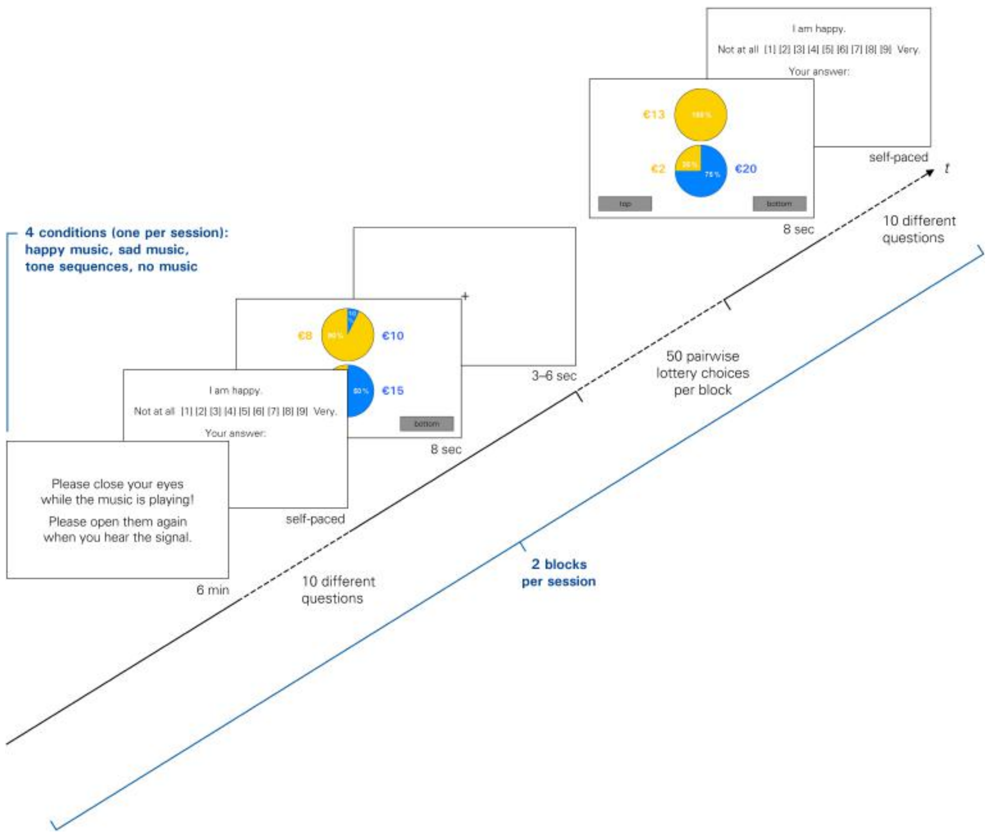

Figure 5. Sequence of events forming an experimental block in Study 1.

In Studies 2 and 3, we used facial stimuli—fearful and neutral faces—from a well-validated research data base (FACES; Ebner, Riediger, & Lindenberger, 2010) to induce affective processing (fearful faces) or as a control condition (neutral faces). Facial affective primes have been repeatedly used in the literature, among others in decision-making studies (e.g., Luo et al., 2014; Winkielman, Berridge, & Wilbarger, 2005). Faces have evolutionarily acquired signaling value. For instance, fearful faces warn conspecifics of potential threats (Adolphs, 2002). They also prepare the organism to encounter a potential threat by increasing attention to subsequent stimuli (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Taylor & Whalen, 2014) and preferentially activate the amygdala (Fusar-Poli et al., 2009) with accompanying peripheral physiological arousal, e.g., enhanced skin-conductance responses (Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002). Together, although the presentation of fearful faces might not automatically result in a full-blown experience of fear or anxiety, facial fear cues can be considered adequate affective signals.

Facial cues were presented simultaneous (Study 2, Experiment A) or briefly prior (Study 2, Experiment B, and Study 3, see Figure 6) to each decision trial in a pseudo-randomized order. The latter priming procedure used stimulus onset asynchronies (SOAs) of 250 ms, which is in the range of SOAs (0 ms – 100 ms) that have been found to elicit robust priming effects in previous priming studies (Hermans, De Houwer, & Eelen, 2001; Hermans, Spruyt, & Eelen, 2003). Furthermore, the priming procedure with preceding primes was embedded in a gender-discrimination task in which participants were instructed to silently evaluate the gender of the face unless they were asked to explicitly respond with a button press in randomly interspersed gender-discrimination trials ("Gender?" question instead of a gamble). This procedure was used for two reasons: 1) Emotional faces embedded in a gender-discrimination task (i.e., relatively implicit emotion recognition) elicit stronger amygdala activity compared to faces in an explicit emotion-recognition task (Critchley et al., 2000), and 2) implicit emotion processing resembles everyday implicit psychological processes (see, e.g., Bargh & Chartrand, 1999; Kliemann, Rosenblau, Bölte, Heekeren, & Dziobek, 2013).

In contrast to the design of Study 1, which was well-suited to detect the hypothesized behavioral effects on probability weighting, the experimental paradigm used in Study 2 was also perfectly adaptable for event-related fMRI (Study 3), given that its within-subjects manipulation was implemented in a single experimental session (in contrast to four separate sessions in Study 1).

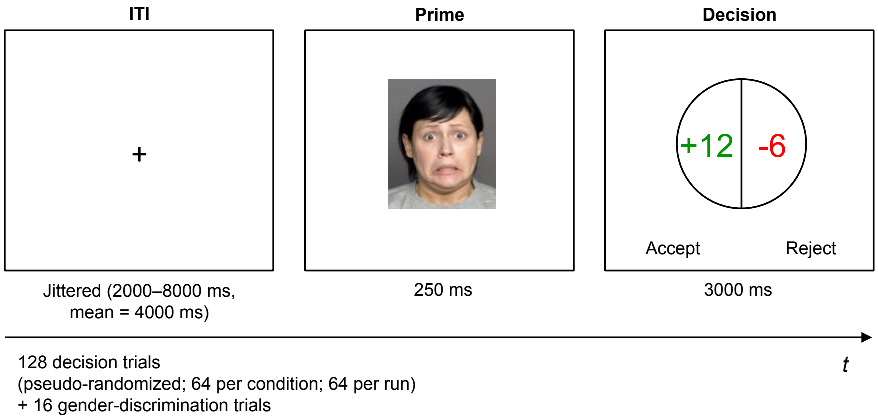

Figure 6. Sequence of events in a trial in Study 3.

3.3. Emotion Measurement

Success of affective manipulation can be secured in two complementary ways: 1) By using potent emotional stimuli, and 2) by measuring the emotional response post-manipulation. As mentioned above, we used well-validated affective material from previous research (Ebner et al., 2010; Koelsch et al., 2013; Pehrs et al., 2013) to address point 1. To address point 2, one can measure different emotional components, e.g., subjective feelings, cognitive appraisals or peripheral- and neurophysiological responses (Scherer, 2009).

In Study 1, we decided to focus on subjective feelings, in particular basic emotions (e.g., happiness)—a more promising approach than using a two-dimensional emotion model of valence and arousal (see, e.g., Russell, 1980), because basic emotions can not only be described in terms of valence and arousal but also other appraisal dimensions that have been found relevant for risky decision making (e.g., certainty and control; Lerner & Keltner, 2000). To this end, we used 9-point rating scales to measure a set of current affective states (see Figure 5), i.e., happiness and sadness (e.g., “I am happy”), an inverse proxy for arousal (i.e., calmness), and items unrelated to a basic emotion (e.g., “I slept well last night”) to reduce potential experimenter demand effects (Orne, 1962) and obscure the objective of emotion ratings (“non-deceptive obfuscation”; Zizzo, 2010). The emotion-rating task was administered immediately after musical stimulation and after the decision blocks again, which also allowed us to investigate time trends in emotional effects.

In Studies 2 and 3, we deliberately decided not to measure subjective feeling states after emotional manipulation for two reasons: 1) to not interfere with affective priming through briefly presented stimuli with an optimal SOA (described above), and 2) to keep the experiment to a reasonable length (i.e., emotion ratings after each prime presentation would have an enormous cost of time). Post-experimental measurements or after multiple trials would not be useful, because they do not capture transient emotional states over single trials of alternating conditions. To corroborate an affective interpretation of any observed behavioral effect in Study 2, we investigated the moderating influence of a personality construct associated with reduced fear reactivity, i.e., psychopathy (e.g., López et al., 2013; Patrick et al., 2009).

In Study 3, we acquired skin conductance responses (SCRs) and neuroimaging data (see Chapter 3.6.). Unfortunately, SCR measurements suffered from a severe loss of data due to technical reasons, which made it impossible to perform a reliable analysis (consequently, SCR data is not reported here). At the brain level, after the presentation of fearful faces, one expects activity in brain areas that have been related to affective processes, in particular fear and anxiety (e.g., Duvarci & Pare, 2014; Lang et al., 2000; LeDoux, 2003; Tovote et al., 2015), such as the amygdala. Hence, brain activation following affective stimuli represent an important measure of emotional processes, although from this data alone it is unclear whether this reactivity is also associated with (conscious) subjective emotional experience.

3.4. Personality Assessment

In Studies 2 and 3, we were also interested whether psychopathic personality moderates the influence of incidental fear cues on loss aversion. As mentioned before, we prefer a multidimensional over a unitary construct perspective of psychopathy, because the latter might obscure differential contributions of dissociable psychopathic traits (see, e.g., Patrick & Bernat, 2009; Schulreich, 2016; Schulreich et al., 2013). To this end, we used psychometric instruments that provide a multidimensional operationalization of psychopathy, the Psychopathic Personality Inventory-Revised (PPI-R; Alpers & Eisenbarth, 2008; Lilienfeld & Andrews, 1996) in Study 2, and the Triarchic Psychopathy Measure (TriPM Patrick, 2010, German translation by H. Eisenbarth) in Study 3, both self-report questionnaires.

The PPI-R consists of eight subscales. The majority of the contained scales form two higher-order factors—fearless dominance and self-centered impulsivity (see, e.g., Benning, Patrick, Hicks, Blonigen, & Krueger, 2003). The German version of the PPI-R has a satisfactory internal consistency with a Cronbach's alpha of .85 in a student sample (.72–.88 for the subscales; Alpers & Eisenbarth, 2008). The TriPM consists of three scales that attempt to measure the 3 phenotypic domains postulated by the triarchic model of psychopathy (Patrick & Drislane, 2014; Patrick et al., 2009): boldness, meanness, and disinhibition. The TriPM also has satisfactory internal consistency with Cronbach's Alphas of .77 for boldness, .88 for meanness, and .84 for disinhibition in an US-American forensic sample (Stanley, Wygant, &

Sellbom, 2013). In the non-forensic, German-speaking sample of Study 3, Cronbach's alphas were .78 for boldness, .72 for meanness, .81 for disinhibition, and .75 for the total score.

An interesting feature of both measures is their focus on core personality traits compared to the Psychopathy Checklist-Revised (PCL-R; Hare, 2003) that is commonly used in forensic contexts and which focuses somewhat less on personality but more on (criminal) behavior. Since the PCL-R is based on interview data and criminal records, it is not applicable in community samples (where there are usually no criminal records), whereas the PPI-R and TriPM are.

As mentioned before, affective-interpersonal features of psychopathy (e.g., the PPI-R higher-order factor fearless dominance and its subscales or TriPM boldness and meanness) were of particular interest for the study, because these traits have been associated with reduced fear reactivity (N. E. Anderson et al., 2011; Blair et al., 2004; López et al., 2013; Patrick et al., 2009) and are thus plausible moderators of the effect of incidental fear cues on loss aversion.

3.5. Analysis of Choice Behavior

We analyzed decision data in two ways—using a model-free approach (choice frequency analysis) and a model-based approach (structural regressions).

3.5.1. Choice Frequencies

Our first model-free approach was to analyze choice frequencies without assuming any latent component. This is the most basic measure of the influence of incidental emotions on risk attitudes. In fact, risk aversion has been solely defined by observable choices (e.g., as the tendency to prefer a sure outcome over a gamble of equal expected value; Wakker, 2010), although it coincides with the concavity of the utility function under Expected-Utility Theory, which is why this concavity itself is often termed risk aversion (see, e.g., Sokol-Hessner et al., 2009; Stancak et al., 2015)—in my view a misnomer if one considers that under non-expected-utility theories like (Cumulative) Prospect Theory, risk aversion can also be explained by other constructs. A simple choice frequency analysis, however, provides limited information on latent components that are thought to drive risk preferences such as probability weighting.

3.5.2. Behavioral Modeling: Structural Regression Models

Our second model-based approach was estimating structural models of latent choice processes (see, e.g., Harrison & Rutström, 2008). This approach is particularly attractive for prospect-theoretic specifications, where several core parameters jointly characterize risk attitudes. In these structural regressions, expected utility (under Expected-Utility Theory) or expected subjective value (under Cumulative Prospect Theory) of lotteries is determined by the payoffs, probabilities, and preference parameters linked to them (e.g., curvature of the utility function, probability weighting parameters). A latent index that governs the difference in expected utility or expected subjective value of two lotteries in the RLP procedure (or between a lottery and the sure alternative €0 in the RMG procedure) is then mapped to the observed choices.

In Study 1, we assumed a power utility function with constant relative risk aversion (CRRA), which is often used in economic modeling and also used in Cumulative Prospect Theory models (e.g., Tversky & Kahneman, 1992). Here, utility was defined as

$$u(x; \rho) = x^{1-\rho},$$

where ρ determines the curvature of the utility function, i.e., a larger ρ goes along with increased curvature of the utility function and—all other things equal—increased risk aversion. We also tried other specifications of the utility function, but power utility performed best, consistent with a previous extensive model comparison (Stott, 2006). Notably, power specifications have also received early empirical support in psychophysical functions that link (changes in) objective stimulus intensities and subjective perceptions across several perceptual continua (Stevens, 1957). As mentioned above, changes in money could also be regarded in a psychophysical manner, which adds theoretical appeal to power functions.

For the probability-weighting function, we used a popular two-parameter version (Prelec, 1998),

$$w(\rho; \alpha, \beta) = exp\{-\beta(-log\ p)^{\alpha}\}.$$

Here, $w(p;\alpha,\beta)$ is the decision weight, p is the objective probability, and α and β are the probability-weighting parameters. Two-parameter versions have received broad empirical support, in particular for explaining between-subjects heterogeneity, and are thought to reflect different psychological phenomena (see, e.g., Fehr-Duda & Epper, 2012; Gonzalez & Wu, 1999). The parameter α primarily influences the curvature of the probability-weighting function (e.g., inverse S-shape) and reflects sensitivity to probability changes (with typical overweighting of small probabilities, underweighting of large probabilities, and decreased sensitivity to changes in the intermediate probability range). The parameter β primarily influences the elevation of the probability-weighting function and reflects the "attractiveness" of gambling (Gonzalez & Wu, 1999) or "optimism/pessimism" (Fehr-Duda & Epper, 2012; Fehr-Duda et al., 2011) in form of over- or underweighting across the probability range. For an illustration, see Figure 7. Since we investigated only risky decision making in the gain domain in Study 1, there was no need to include separate value-function and probability-weighting parameters for losses or a loss aversion parameter, which facilitated the estimation process and interpretation.

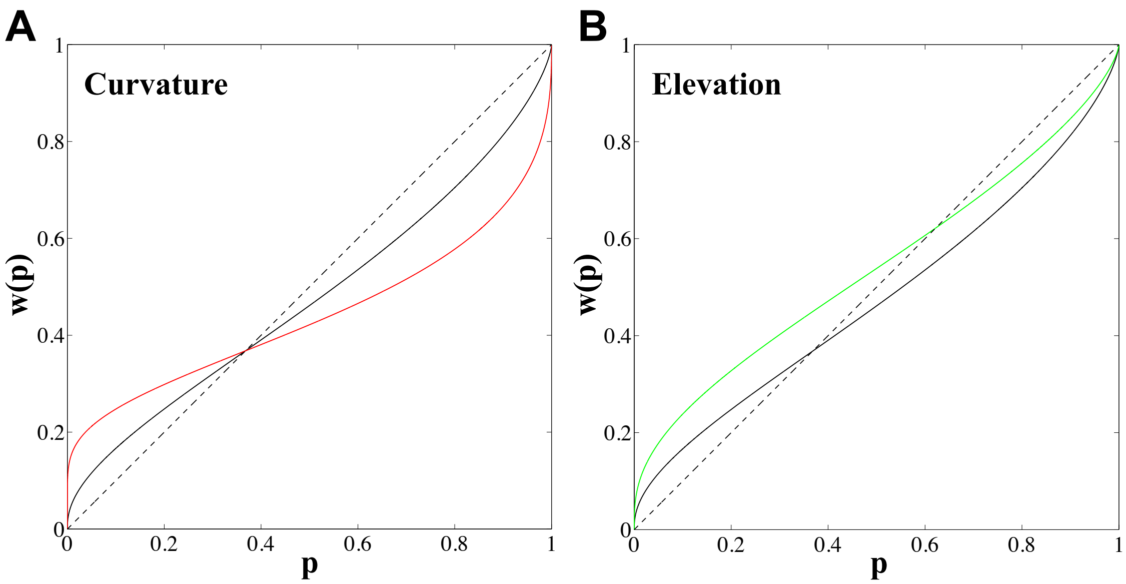

Figure 7. Two-parameter probability weighting. *Panel A*: Two nonlinear weighting functions that differ primarily in curvature. Relative to the black solid line, the red line reflects stronger overweighting of small probabilities, stronger underweighting of medium to large probabilities, and more strongly diminishing sensitivity to probability changes in the intermediate range. *Panel B:* Two nonlinear weighting functions that differ primarily in elevation. Relative to the black solid line, the green line reflects greater decision weights (i.e., "optimism") across probability levels. All depicted functions deviate from linear weighting (dashed lines).

In Studies 2 and 3, we were specifically interested in monetary loss aversion. Our design featured mixed gambles with equal probabilities (i.e., 50%) of potential gains and losses of small (to moderate) magnitude. Under an expected-utility framework, commonly observed degrees of risk aversion over small stakes would imply unrealistic degrees of risk aversion over large stakes and it has been argued that loss aversion (rather than the curvature of the utility function) is a more plausible account for risk aversion in small-stake mixed gambles (Rabin, 2000). There is also empirical evidence that loss aversion provides a complete account for risky gambles with equal probabilities of gains and losses (Novemsky & Kahneman, 2005). Assuming a piecewise-linear utility function is therefore a common simplification in the literature, next to assuming identical probabilistic decision weights for gains and losses (see, e.g., De Martino et al., 2010; Tom et al., 2007).

To estimate loss aversion, we fitted a logistic regression to all participants' binary choice data (mixed-effects model in Study 2) or on the individual-participant level (Study 3). In this regression, the loss regressor l is associated with the coefficient λ, which allows estimating the weight of losses relative to gains (regressor g), i.e., the degree of loss aversion. In line with Prospect Theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992), λ captures differences in the slopes of a kinked value function (e.g., a steeper slope for losses than for gains).

Decision making is not deterministic, but a stochastic process, as a decision maker usually does not make choices that are perfectly consistent with the assumed model. This is accounted for by a link function that maps the latent indices to observed choices, e.g., a logit or a probit link function, to name two commonly used specifications (see, e.g., Harrison & Rutström, 2008; Stott, 2006). In all three studies, we have used the logit link specification. This allowed us to estimate the stochastic component of decision making. To this end, we used the Fechner error specification that reflects the dispersion (flatness) of this link function and thus ranges from zero noise to random choice. Including a stochastic component can be of substantial theoretical importance, because inferences on risk preferences can also depend on the assumed error model. For instance, although there is evidence that lower cognitive ability is associated with greater risk aversion (Dohmen et al., 2010), this relationship might be spurious. Allowing for heterogeneity of decision noise in structural estimations, one study found that reduced cognitive ability was related to random decision making rather than to altered risk preferences (Andersson, Holm, Tyran, & Wengström, 2013).

Emotional effects on preference and noise parameters were modeled via dummy regressors that coded for music conditions (Study 1) or face conditions (Study 2) or by estimating parameters for each condition separately (Study 3). For instance, in Study 3 this can be formally expressed as

$$y_{c,s,t} = f\left[\left(\frac{g_{c,s,t} + \lambda_{c,s} l_{c,s,t}}{\sigma_{c,s}}\right) + \varepsilon_{c,s,t}\right],$$

where y is the binary choice (accept vs. reject mixed gamble), f is the logistic link function, g is the gain regressor, l is the loss regressor, λ is the loss aversion parameter, c indexes the experimental condition (i.e., neutral or fearful), s indexes subjects, and t indexes trials, and ϵ is the error term.

Structural regression models were set up in MATLAB (The Mathworks, Inc.). (Non-linear) maximum likelihood estimation was used to estimate the parameters of interest. Maximum likelihood estimation delivers parametric values for which the observed choices are the most probable given the model (see, e.g., Harrison & Rutström, 2008; Myung, 2003).

3.6. Functional Magnetic Resonance Imaging (fMRI)

In Study 3, we used fRMI to identify neural mechanisms of the influence of incidental fear cues on monetary loss aversion. This method allows for the indirect investigation of neural activity via changes of magnetic properties of hemoglobin due to oxygenation, i.e., changes in the so-called blood oxygen level dependent (BOLD) signal (for a review, see Logothetis, 2008). BOLD signals are more strongly related to local field potentials than multi-unit spiking activity and thereby seem to reflect input and local processing rather than spiking output (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Functional MRI has some advantages over other neuroscientific methods (see, e.g., Huettel, Song, & McCarthy, 2009) such as a superior spatial resolution than EEG, which only allows for estimating neuronal sources via source modeling (e.g., Pascual-Marqui, 2002). Furthermore, fMRI is noninvasive in contrast to positron emission tomography (PET), which also offers high spatial resolution but necessitates the use of radioactive tracers. On the other hand, temporal resolution is inferior (seconds-resolution) compared to EEG (milliseconds-resolution) due to the lagged hemodynamic response, but superior than with PET. The improved temporal resolution relative to PET led to a methodological evolution from blocked designs that blended multiple events and processes towards event-related designs that allowed for flexible controlling of experimental manipulations and analysis of specific events (see, e.g., Dale & Buckner, 1997). This flexibility was also increasingly exploited in decision neuroscience in order to disentangle different processes associated with valuation and choice.

When fMRI is combined with an experimental manipulation of psychological processes by presenting certain kinds of stimuli (e.g., emotional primes) and/or engaging the subjects in a certain task (e.g., decision making), one can infer that the associated psychological processes caused observed stimulus- or task-dependent brain activity (Poldrack & Farah, 2015). Two mechanistic levels can be effectively addressed by fMRI—neuronal-population and network mechanics (Poldrack & Farah, 2015). For instance, task-activation studies aim to identify neuronal populations based on the psychological processes that cause them to be activated (or less activated). Population brain activity was assessed via a univariate fMRI analysis in Study 3.

Participants were scanned at the Center for Cognitive Neuroscience Berlin (CCNB) at the Freie Universität Berlin, Germany, using a 3-Tesla Magnetom Trio scanner (Siemens Healthcare Diagnostics GmbH, Erlangen, Germany) and 12-channel head coil. Stimuli were presented on LCD goggles (Resonance Technology Inc., Northridge, California) and responses were recorded using the software package Presentation (Neurobehavioral Systems, Inc.). Anatomical images were acquired using a T1-weighted MP-RAGE protocol (256 × 256 matrix, 176 sagittal slices of 1 mm thickness). Functional images were acquired as T2*-weighted gradient-echo-planar images (repetition time = 2 s, echo time = 30 ms, matrix = 64 × 64, flip angle = 70°, field of view = 192 mm, interslice gap = 0.6 mm). A total of 37 oblique-axial slices (3 × 3 × 3 mm voxels) parallel to the anterior commissure–posterior commissure line were collected per volume. A total of 270 volumes were collected per functional run, with 2 runs per participant (each of approximately 9 min duration).

Data were preprocessed and analyzed using FMRIB's Software Library (FSL, v. 5.0.7, Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012) on the High-Performance Computing system at Freie Universität Berlin (http://www.zedat.fu-berlin.de/Compute). The first preprocessing steps included: within-run motion correction to the middle volume (MCFLIRT, Jenkinson, Bannister, Brady, & Smith, 2002), slice-timing correction, brain extraction (BET, S. M. Smith, 2002), and spatial smoothing with a Gaussian kernel of 5 mm full-width at half-maximum (FWHM).

Subsequently, we used an ICA-based strategy for automatic removal of motion artifacts (ICA-AROMA, Pruim, Mennes, van Rooij, et al., 2015). ICA-AROMA is a well-validated procedure to correct for secondary effects of head motion. This toolbox performs data denoising in three steps: First, it runs an independent-component analysis (ICA), i.e., a multivariate exploratory decomposition into independent components (MELODIC, Beckmann & Smith, 2004); second, it classifies independent components into signals of interest or motion-related noise based on multiple criteria (i.e., high-frequency content, correlation with motion parameters, edge fraction, and cerebrospinal fraction); at last, it removes noise components from the data via FSL's regfilt function. ICA-AROMA outperformed several other motion correction procedures, including a relatively sophisticated Volterra expansion with 24 motion parameters, in a recent validation study (Pruim, Mennes, Buitelaar, & Beckmann, 2015).

After ICA-based denoising, we performed high-pass temporal filtering with a cutoff of 100 s. Functional images were registered to each participant's structural image using boundary-based registration (BBR, Greve & Fischl, 2009) (Greve & Fischl, 2009)and then normalized to the Montreal Neurological Institute (MNI) space (resolution 2 × 2 × 2 mm^3) via nonlinear registration with a warp resolution of 10 mm.

To investigate task-related activations, we set up a general linear model (GLM) of the BOLD signal using 9 task-related regressors and their temporal derivatives, convolved with a double-gamma hemodynamic response function (HRF), and with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). The task-related regressors modeled prime-gamble trials per condition, gains and losses as parametric modulators per condition, prime-gender (discrimination) trials per condition, and missed trials.

Individual contrast images were calculated and then submitted to a higher-level mixed-effects analysis using FMRIB's Local Analysis of Mixed Effects tool in FSL (FLAME 1 & 2). In our neuroimaging analysis, we first investigated neural responses to gain and losses as well as the previously observed asymmetry in loss and gain responses (Canessa et al., 2013; Tom et al., 2007) in the neutral condition, i.e., in the absence of emotional cues that enhance loss aversion. Then, we investigated condition-dependent changes in these responses. On the group level, our model also included participants' loss aversion parameters in the neutral condition (baseline loss aversion, $\lambda_{neutral}$) and emotion-dependent changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$)—both derived from quantitative behavioral modeling—as behavioral covariates of interest.

Based on previous research on the neural basis of loss aversion, emotion and context-dependent valuation (e.g., Canessa et al., 2013; Engelmann et al., 2015; Tom et al., 2007; Tovote et al., 2015), we focused on specific regions of interest (ROI), i.e., the amygdala, the striatum, the insula, and the vmPFC (6321 voxels in total), in our neuroimaging analysis. Here, a false-discovery rate (FDR) correction with $p < .05$ and a minimum cluster extent of 15 voxels ($k \geq 15$) was applied. In an exploratory whole-brain analysis, we used a cluster-defining threshold of uncorrected $p < .001$ (i.e., $z > 3.1$) and a family-wise error (FWE) cluster correction with $p < .05$.

4. Summary of Empirical Studies and Specific Discussion

4.1. Study 1: Music-Evoked Incidental Happiness Modulates Probability Weighting during Risky Lottery Choices

(Schulreich et al., 2014, *Frontiers in Decision Neuroscience*).

Background and Objective: As outlined in the introduction, previous research has shown that incidental emotional states can influence probability judgments (Johnson & Tversky, 1983; Wright & Bower, 1992) and there is also correlative and indirect evidence on such incidental emotional effects on probability weighting (Fehr-Duda et al., 2011; Kliger & Levy, 2008). To provide more direct evidence, we experimentally manipulated incidental affect and investigated its influence on risk taking and probability weighting in the gain domain.

Method: Our final sample included 41 subjects (28 women; mean age, 27.37 years; SD = 7.83 years). The experiment featured a within-subject design consisting of four conditions in separate sessions (see Figure 5 above). In each condition, participants first listened to different kinds of auditory stimuli—"happy" music, "sad" music, or sequences of random tones—or experienced no auditory stimulation and completed a repeated pairwise lottery choice task over real monetary stakes (gains only) afterwards. We checked for the success of emotional manipulation via simple rating scales measuring basic emotional states (e.g., happiness) after musical stimulation and after decision blocks.

We analyzed choice data in a twofold way: First, we analyzed choice frequencies as model-free measures of risk attitudes; Second, we modeled choice data with structural regressions based on Cumulative Prospect Theory (Tversky & Kahneman, 1992) and a two-parameter model of probability weighting (Prelec, 1998). In addition, we also modeled time trends to analyze the time course of emotional effects with increasing temporal distance between musical stimulation and choice.

Results: Affective manipulation checks revealed that the different manipulation conditions evoked different degrees of happiness, i.e., listening to "sad" music and random tones significantly reduced happiness compared to "happy" music, with no music in-between (see Figure 8 below).

These differences in affective state were accompanied by changes in decision behavior. We found that participants chose the riskier lotteries significantly more often in the "happy" music and no music condition than in the "sad" music and random tones conditions; see **Table 1**). In addition, we observed time trends indicating a decreasing emotional influence on decision making as the distance between musical stimulation and risky choice increased (see Table 1 and Figure 9—not included in the original research article), consistent with a fleeting emotional effect that was also indicated by affective ratings post-choices (see Figure 8).

Behavioral modeling via structural regressions indicated that the observed changes in risk taking could be attributed to changes in the elevation parameter of the probability-weighting function, i.e., higher decision weights of the larger outcomes in the "happy" condition compared to the "sad" music and random tones conditions (see Figure 10). Importantly, the elevation parameter also correlated positively with self-reported music-evoked happiness between-subjects.

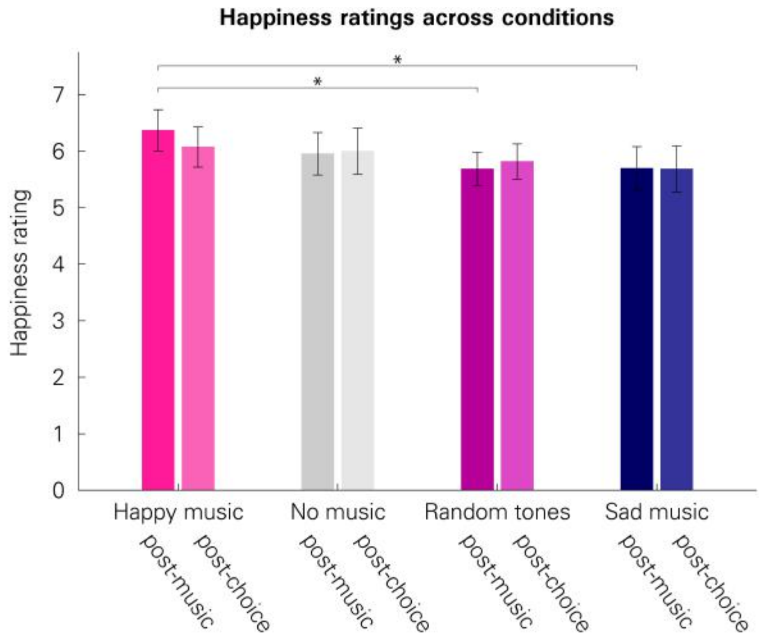

Figure 8. Subjective happiness ratings across the four conditions. Darker bars illustrate the values immediately after musical stimulation ("post-music"); brighter bars illustrate the values after the lottery choice blocks ("post-choice"). Error bars represent 95% confidence intervals. The scale ranged from 1 (not happy at all) to 9 (very happy). An asterisk indicates significant difference at the 5% level. Reprinted from "Music-evoked incidental happiness modulates probability weighting during risky lottery choices " by S. Schulreich, Y. G. Heussen, H. Gerhardt, P. N. C. Mohr, F. C. Binkofski, S. Kölsch, & H. R. Heekeren, 2014, *Frontiers in Psychology: Decision Neuroscience*, 4, 981. Copyright [2014] by the authors.

Table 1. Random-effects linear probability models (LPMs) for the choice of the riskier lottery across the four conditions. Reprinted from "Music-evoked incidental happiness modulates probability weighting during risky lottery choices" by S. Schulreich, Y. G. Heussen, H. Gerhardt, P. N. C. Mohr, F. C. Binkofski, S. Kölsch, & H. R. Heekeren, 2014, *Frontiers in Psychology: Decision Neuroscience*, 4, 981. Copyright [2014] by the authors.

	LPM 1	LPM 2		
Condition	**Average frequency (%)**	**Average frequency (%)**	**Initial frequency (%)**	**Time trend (%)**
Happy music	47.40%$^{\text{tones, sad}}$	47.48%$^{\text{tones, sad}}$	50.50%$^{\text{tones, sad}}$	−0.12%$^{\text{0, tones, sad}}$
No music	46.48%$^{\text{tones, sad}}$	46.43%$^{\text{sad}}$	49.11%$^{\text{tones, sad}}$	−0.11%$^{\text{sad}}$
Random tones	44.20%$^{\text{happy, no}}$	44.20%$^{\text{happy}}$	43.12%$^{\text{happy, no}}$	+0.04%$^{\text{happy}}$
Sad music	43.72%$^{\text{happy, no}}$	43.75%$^{\text{happy, no}}$	40.27%$^{\text{happy, no}}$	+0.14%$^{\text{0, happy, no}}$

LPM 1 included only dummy regressors to detect differences between the conditions. In addition to that, LPM 2 also modeled the temporal distance from the last musical stimulation (as the number of trials completed since the last musical stimulation). The "time trends" column thus indicates by how much (in percentage points) the relative frequency at which the riskier lottery was chosen changed on average with each additional completed trial. t-tests were used to assess whether the parameter estimates are different from 0.

Significance at $p < 0.05$ *indicated via superscripts:*

$^{\text{happy}}$ *significantly different from the "happy music" condition;* $^{\text{no}}$ *significantly different from the "no music" condition;* $^{\text{tones}}$ *significantly different from the "random tone sequences" condition;* $^{\text{sad}}$ *significantly different from the "sad music" condition;* ^{0} *significantly different from 0 (for the time trends).*

To account for individual differences in participants' risk taking, individual random effects were included for the respective reference condition.

Figure 9. Choice frequencies across trials and regression lines reflecting time trends. The effect of musical stimulation on choice declined over time.

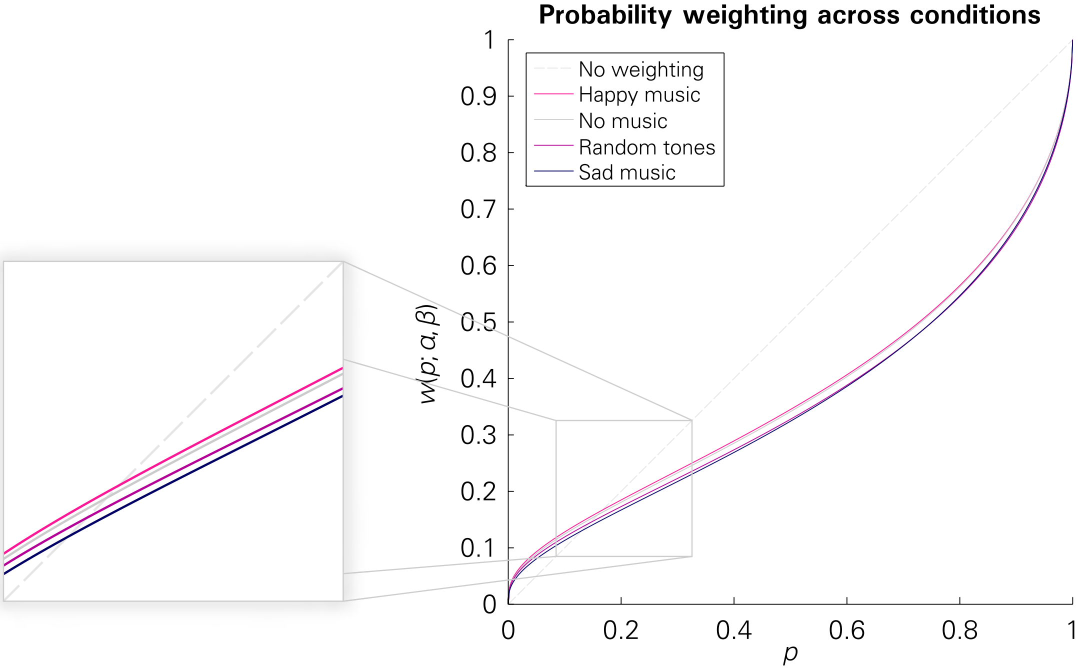

Figure 10. Probability weighting functions in the four conditions. Greater elevation of the probability weighting function in the "happy" music condition compared to the random tones condition and "sad" music condition. Reprinted from "Music-evoked incidental happiness modulates probability weighting during risky lottery choices " by S. Schulreich, Y. G. Heussen, H. Gerhardt, P. N. C. Mohr, F. C. Binkofski, S. Kölsch, & H. R. Heekeren, 2014, *Frontiers in Psychology: Decision Neuroscience*, 4, 981. Copyright [2014] by the authors.

Discussion: Our findings complement previous studies on the effect of incidental emotions on probability judgments (Johnson & Tversky, 1983; Wright & Bower, 1992) and go beyond indirect and correlational data on the link between incidental emotions and probability weighting in risky choice (Fehr-Duda et al., 2011; Kliger & Levy, 2008). Our findings also address RQ1 and support H1 and H2:

RQ1: Is there an influence of incidental emotions (e.g., incidental happiness) on probability weighting?

H1: *Music-evoked incidental emotions are associated with changes in risk taking and probability weighting. Specifically, incidental happiness is positively related to the elevation of the probability-weighting function.*

H1 is supported by our data. By experimentally manipulating emotional states, we provide evidence in favor of a causal effect of incidental happiness on risk attitudes in the gain domain that can be explained by changes in probability weighting. Increased (decreased) incidental happiness was associated with a higher (lower) elevation of the probability weighting function, which could be framed as a form of optimism (pessimism) in risky decision making.

To note, while listening to "sad" music and random tones decreased self-reported happiness, "happy" music did not significantly increase happiness compared to no music. Difficulties in increasing positive affect have been repeatedly reported in the literature. For instance, Gasper (2004) let her participants write about happy, sad, and neutral events to induce different affective states, but the positive emotion induction did not increase positive affect. She argued that positive emotion induction could have been inefficient because individuals are usually by default mildly happy (Diener & Diener, 1996), thus making it difficult to amplify their positive feelings. A mildly happy default state was also observable in our data (i.e., a score about 6 on a scale from 1-9 [lowest to highest happiness] also in the no-music condition) and further increases in happiness might necessitate stronger induction techniques. Nevertheless, the observed positive relationship between the degree of self-reported happiness and probability weighting indicates that not just decreases in happiness (e.g., caused by "sad" music), but also increases in happiness can have an influence on decision making.

H2: *The effect of music-evoked incidental emotions on decision making declines over time.*

H2 is supported by our data. The observed fleeting influence of musical stimulation on choice behavior over time (i.e., a decline within minutes) is consistent with previous observations of fleeting emotional effects (e.g., Andrade & Ariely, 2009; Isen & Gorgoglione, 1983) and corroborates an affective interpretation of the observed effects.

4.2. Study 2: Incidental Fear Cues Increase Monetary Loss Aversion
(Schulreich, Gerhardt, & Heekeren, 2016, *Emotion*)

Background and Objective: As outlined in the introduction, previous evidence suggests a link between loss and fear processing (e.g., Crişan et al., 2009; Hartley & Phelps, 2012), but the influence of incidental fear cues on loss aversion it thus far unclear. To close this gap, we designed two experiments to manipulate the affective context and investigate its influence on monetary loss aversion. Furthermore, we investigated whether such an influence is moderated by psychopathic personality, in particular fearless dominance, which has been associated with reduced fear reactivity (e.g., N. E. Anderson et al., 2011; Patrick et al., 2009).

Method: In two experiments, we presented fearful and neutral faces during (Experiment 1) or prior (Experiment 2) choices to accept or reject mixed gambles with equal probability (i.e., 50%) of winning or losing variable amounts of money. Potential gains and losses ranged from ±€5 to ±€14 in steps of €1 (10 x 10 = 100 gambles per face condition). 29 participants (20 female; mean age, 26.79 years [SD = 5.23 years]) were included for analysis in Experiment 1, 24 participants (13 female; mean age, 24.29 years [SD = 5.31 years]) in Experiment 2. Decision data was analyzed in two ways: First, participant's choices were analyzed as model-free measures of risk attitudes; Second, quantitative behavioral modeling via mixed-effects models allowed investigating emotional effects on loss aversion and decision noise (Fechner error specification), similar to previous studies (see, e.g., Tom et al., 2007). Psychopathic personality was assessed via the PPI-R (Alpers & Eisenbarth, 2008, see Chapter 3.4.) and the higher-order factors fearless dominance and self-centered impulsivity were derived. This allowed us to include psychopathic personality traits as covariates and potential moderators in our models.

Results: In both experiments, we found that the presentation of fearful faces, relative to neutral faces, increased risk aversion—an effect that could be attributed to increased loss aversion (see Figure 11, Panel a, for Experiment 1), whereas there was no significant emotion-induced change in choice consistency. Replication of the effect demonstrated its robustness. Moreover, we found that the influence of incidental fear cues on loss aversion was moderated by psychopathic personality such that the effect was practically absent in participants scoring high in fearless dominance (in particular social influence/potency) and highest in low-scoring participants (see Figure 11, Panel b, for Experiment 1). In contrast, self-centered impulsivity was not a significant moderator. Both psychopathic traits were not significantly associated with baseline loss aversion.

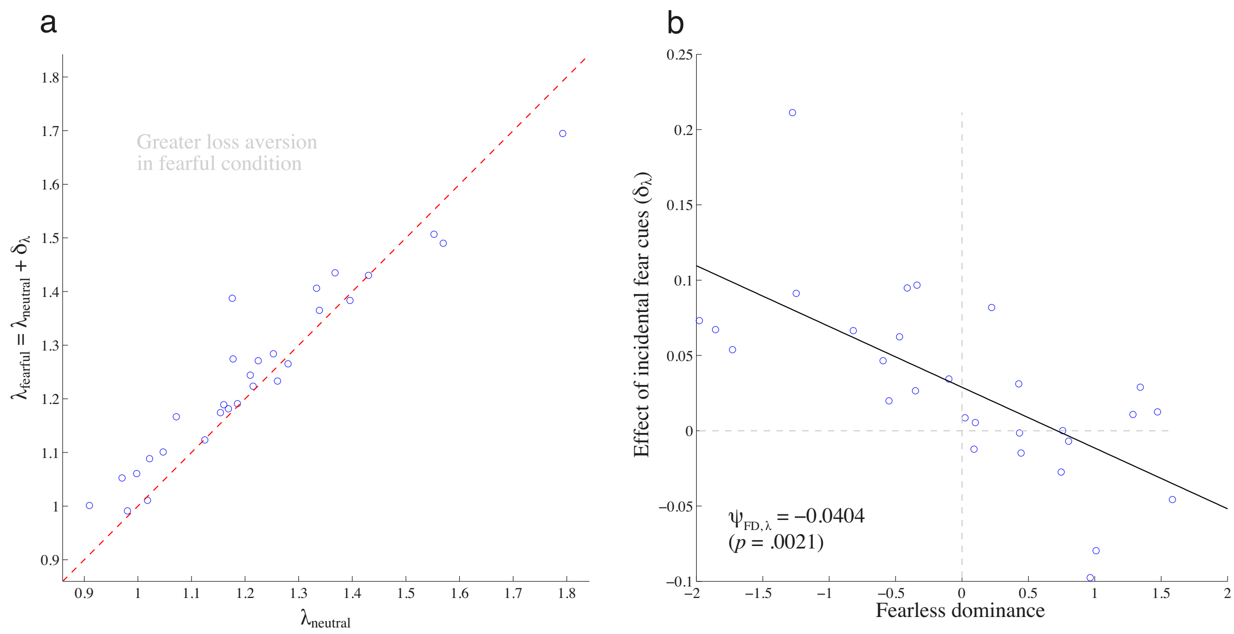

Figure 11. Experiment 1: Greater loss aversion in the fearful condition compared to the neutral condition. Fearless dominance attenuated emotion-induced effects on loss aversion. *Panel a* depicts individual estimates, based on the individual random effects included in the regression analysis, of the degree of loss aversion (λ) in the neutral-face and fearful-face condition; data points above the 45° line are associated with greater loss aversion in the fearful-face condition. *Panel b* depicts a scatterplot and a linear regression line that illustrates the inverse relationship between fearless dominance and the size of the effect of incidental fear cues on loss aversion (δ_{λ}). The graph also contains two dashed lines that intersect at 0 on both axes (i.e., average fearless dominance score [horizontal axis]; no change in loss aversion [vertical axis]) and that delineate four sectors into which the data points fall. For the lower half of fearless dominance scores, all the data points lie within the upper-left sector, indicating that those participants all showed higher loss aversion in the fearful-face condition. Reprinted with permission from "Incidental fear cues increase monetary loss aversion" by S. Schulreich, H. Gerhardt, & H. R. Heekeren, 2016, *Emotion*, 16(3), 402-412. Copyright [2015] by APA.

Discussion: Our results highlight the sensitivity of loss aversion to the affective context and provide further and direct evidence for a link between fear and loss processing, as suggested before (e.g., Camerer, 2005; Hartley & Phelps, 2012). Our findings also address RQ2a and RQ2b and provide support for H3 and H4:

RQ2a: Is there an influence of incidental fear cues on loss aversion?

H3: *Incidental fear cues increase monetary loss aversion compared to neutral cues.*

H3 was supported by our data. In both experiments of Study 2, we observed significantly reduced risk taking when participants were primed with fearful faces compared to neutral faces. Importantly, this effect could be attributed to decreased loss aversion in the fearful-face condition, but not to differences in choice consistency (i.e., Fechner noise).

RQ2b: Is the influence of incidental fear cues on loss aversion moderated by psychopathic personality, in particular fearless dominance?

H4: *Psychopathic personality, in particular PPI-R fearless dominance (but not PPI-R self-centered impulsivity) moderates the effect of incidental fear cues on loss aversion. Specifically, higher fearless dominance is associated with an attenuated effect of incidental fear cues on loss aversion.*

H4 is largely supported by our data. In both studies, we observed that the influence of incidental fear cues on loss aversion was moderated by psychopathic personality. To be specific, high fearless dominance (Experiment 1) and high social influence/potency (Experiment 2)—a facet of fearless dominance—attenuated emotion-induced increases in loss aversion, consistent with deficient fear processing (e.g., N. E. Anderson et al., 2011; López et al., 2013; Patrick et al., 2009). The missing effect for the higher-order factor fearless dominance in Experiment 2 might be due to insufficient statistical power or genuine context-related differences. In any case, high social influence/potency emerged as the most robust facet that showed a moderation effect, consistent with a study that found a specific association between an interpersonal facet of psychopathy (i.e., an analogue of PPI-R social influence) and reduced amygdala activity when processing fearful faces (Carré, Hyde, Neumann, Viding, & Hariri, 2013). Importantly, the observed moderation effect corroborates an affective interpretation of the influence of incidental fear cues on loss aversion.

4.3. Study 3: Emotion-Induced Increases in Loss Aversion Are Associated With Shifts towards Negative Neural Value Coding

(Schulreich, Gerhardt, Meshi, & Heekeren, *submitted to Proc. Natl. Acad. Sci. USA*)

Background and Objective: In this neuroscientific study, we extend our previous behavioral study (Study 2) by investigating the neural mechanisms that give rise to emotion-induced increases in loss aversion. Thereby, we also build upon previous studies on the neural basis of loss aversion in general (e.g., Canessa et al., 2013; Sokol-Hessner et al., 2013; Tom et al., 2007) as well as on emotional effects on loss aversion (Charpentier et al., 2015; Engelmann et al., 2015). Specifically, we investigated whether context-dependent changes in neural value processes mediate the influence of incidental fear cues on monetary loss aversion.

Method: We analyzed data from 27 participants (15 female; mean age, 21.81 years [*SD* = 3.55 years]). All subjects participated in a decision-making task that we previously used in Study 2 and that we adapted for fMRI. In this task, participants decided to accept or reject mixed gambles while in the MRI scanner. Potential gains and losses ranged from ±€6 to ±€20 in steps of €2 (8 x 8 = 64 gambles per condition) and were associated with identical probabilities, i.e., 50%. To manipulate affect, we briefly presented images of fearful (or neutral) faces before each lottery choice (also see Figure 6 above), as in Experiment 2 of Study 2.

We analyzed gamble acceptance rates and used quantitative behavioral modeling to estimate loss aversion and emotion-induced changes in its magnitude. Neuroimaging data was preprocessed (including, e.g., ICA-based removal of motion-related noise, see Chapter 3.6.) and analyzed in FSL (Jenkinson et al., 2012). Here, we set up a general linear model that included regressors for face-gamble trials as well as parametric modulators denoting gains and losses (per condition), among others, which were used to calculate contrasts of interest (e.g., contrasting loss-related brain activations in the fearful vs. neutral condition). Furthermore, behaviorally determined monetary loss aversion in the neutral condition as well as emotion-induced changes in loss aversion were included as covariates of interest in our group-level model. This allowed for investigating whether (changes in) neural value processing mediated (changes in) behavioral loss aversion. Furthermore, we investigated the relationships between loss aversion and value processing with respect to psychopathic personality, measured with the TriPM (Patrick, 2010, see Chapter 3.4.), given the observed moderation effect of psychopathic personality on emotional influences on loss aversion in Study 2.

Results: At the behavioral level, we replicated the emotion-induced increase in monetary loss aversion observed in Study 2. At the neural level, we observed an emotion-induced shift from positive to negative value coding in a distributed set of brain regions, including the amygdala. More precisely, we found that loss aversion following the presentation of neutral faces was mainly predicted by greater *deactivations* for losses relative to *activations* for gains (i.e., neural loss aversion), e.g., in the striatum and the amygdala (Figure 12). In contrast, emotion-induced increases in loss aversion were mainly predicted by greater *activations* for losses in the fearful condition, e.g., in the amygdala (Figure 13) and the vmPFC, which accompanied a general emotion-induced increase in bilateral amygdala activity following the presentation of fearful relative to neutral faces. In addition, we observed emotion-induced reductions of deactivations for losses (and neural loss aversion) in regions that displayed these responses in the neutral condition, e.g., the striatum (Figure 14).

Furthermore, similar to Study 2, we observed a moderation effect of psychopathic personality on emotion-induced changes in loss aversion. However, instead of TriPM boldness, which is strongly overlapping with PPI-R fearless dominance (Patrick et al., 2009; Stanley et al., 2013) that displayed this effect in Study 2, we observed that a different affective-interpersonal facet, TriPM meanness, attenuated emotion-induced increases in loss aversion. Crucially, this effect was partially mediated by attenuated emotion-induced increases in amygdala activations for losses (Figure 15).

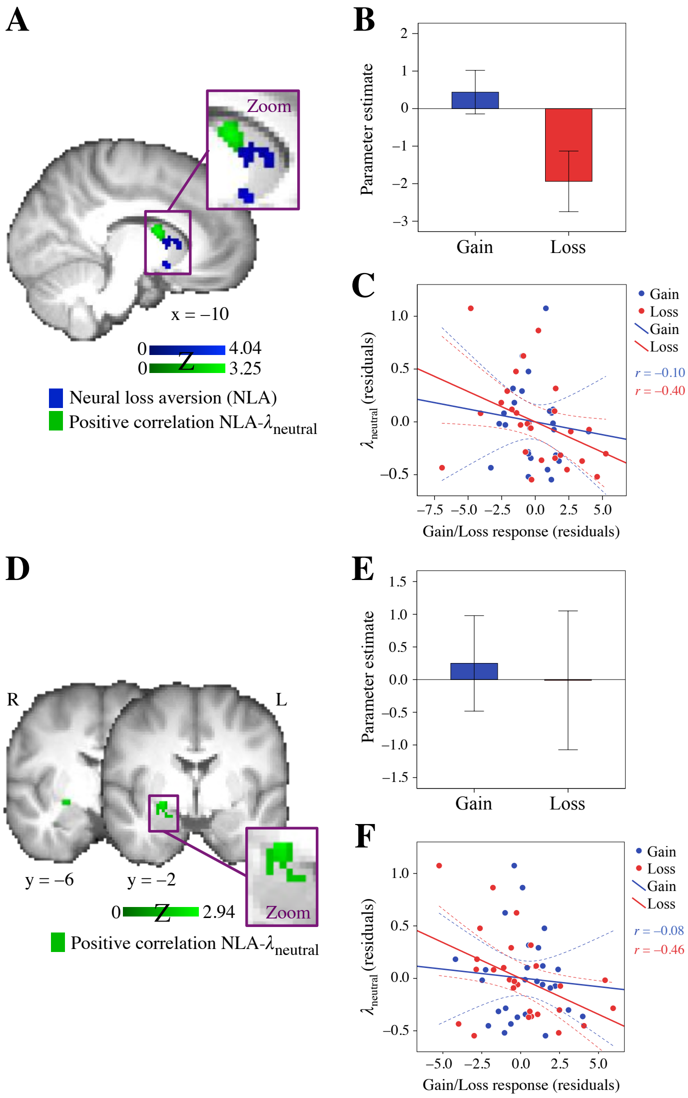

Figure 12. Neural loss aversion in the neutral condition. *Panel A:* Neural loss aversion, i.e., greater deactivations for losses relative to activations for gains ($-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}} > 0$) in the striatum (blue). Neural loss aversion was also positively correlated with behavioral loss aversion, e.g., in the left caudate (green). *Panel B:* Parameter estimates for the gain and loss regressors for the left caudate cluster that displayed neural loss aversion. *Panel C:* Relationships between neural gain and loss responses and behavioral loss aversion in the left caudate (green cluster in Panel A). Greater deactivations for losses significantly predicted greater loss aversion, λ_{neutral} (partial regression plot, i.e., controlling for emotion-induced changes in loss aversion, $\lambda_{\text{fearful}} - \lambda_{\text{neutral}}$). *Panel D:* Neural loss aversion was positively correlated with behavioral loss aversion in the right superficial and centromedial amygdala (green). *Panel E:* Parameter estimates for the gain and loss regressors for the amygdala cluster. *Panel F:* Relationships between neural gain and loss responses and behavioral loss aversion in the amygdala cluster. Greater deactivations for losses significantly predicted greater loss aversion (partial regression plot). *Note:* All statistical tests were small-volume FDR-corrected with $p < .05$ and $k \geq 15$. Error bars/lines represent 95% CIs (including between-subject variance).

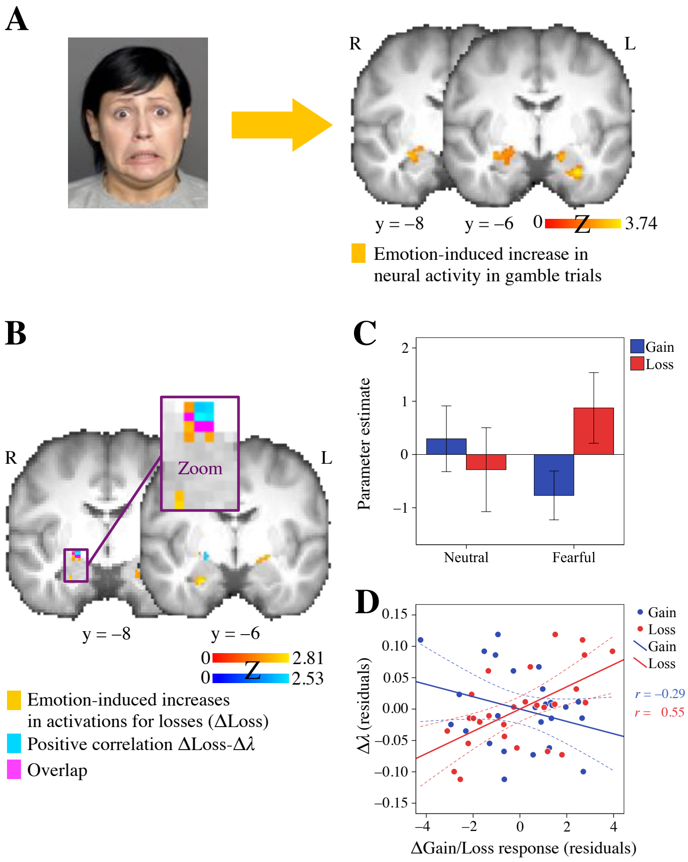

Figure 13. Emotion-induced changes in amygdala activity and value coding. *Panel A:* Increased bilateral amygdala activity during gamble trials (onset: face presentation) in the fearful condition compared to the neutral condition (red-yellow). *Panel B:* Increased bilateral amygdala activations for losses in the fearful condition (red-yellow), which were also associated with emotion-induced increases in loss aversion in the right superficial and centromedial amygdala (light-blue). *Panel C:* Parameter estimates for the gain and loss regressors per condition for the right superficial and centromedial amygdala (red-yellow cluster in Panel B). *Panel D:* Relationships between emotion-induced changes in gain and loss responses and changes in behavioral loss aversion in the right superficial and centromedial amygdala (light-blue cluster in Panel B). Greater emotion-induced activations for losses significantly predicted emotion-induced increases in loss aversion (partial regression plot, i.e., controlling for $\lambda_{neutral}$). *Note:* All statistical tests were small-volume FDR-corrected with $p < .05$ and $k \geq 15$. Error bars/lines represent 95% CIs (including between-subject variance).

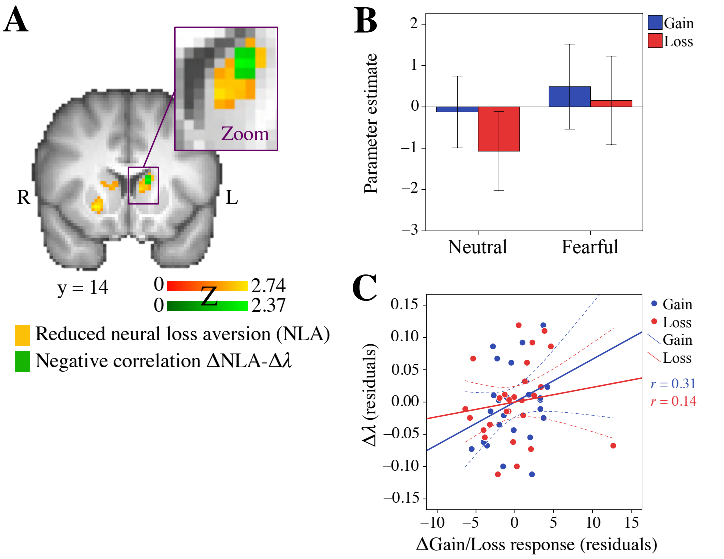

Figure 14. Emotion-induced changes in neural loss aversion. *Panel A:* Reduced neural loss aversion (i.e., $-\beta_{Loss} - \beta_{Gain}$) in the bilateral striatum in the fearful condition compared to the neutral condition (red-yellow). Decreases in neural loss aversion were associated with emotion-induced increases in behavioral loss aversion in the left caudate (green). *Panel B:* Parameter estimates for the gain and loss regressors per condition for the left caudate (red-yellow cluster in Panel A). *Panel C:* Relationships between emotion-induced changes in gain and loss responses and changes in behavioral loss aversion in the left caudate (green cluster in Panel A). Descriptively, increasing activations for gains and losses were associated with increasing loss aversion, but neither correlation was statistically significant (partial regression plot). Their combined effect, however, led to significant reductions in neural loss aversion, which is based on stronger deactivations (and not activations) for losses relative to activations for gains. *Note:* All statistical tests were small-volume FDR-corrected with $p < .05$ ($k \geq 15$). Error bars/lines represent 95% CIs (including between-subject variance).

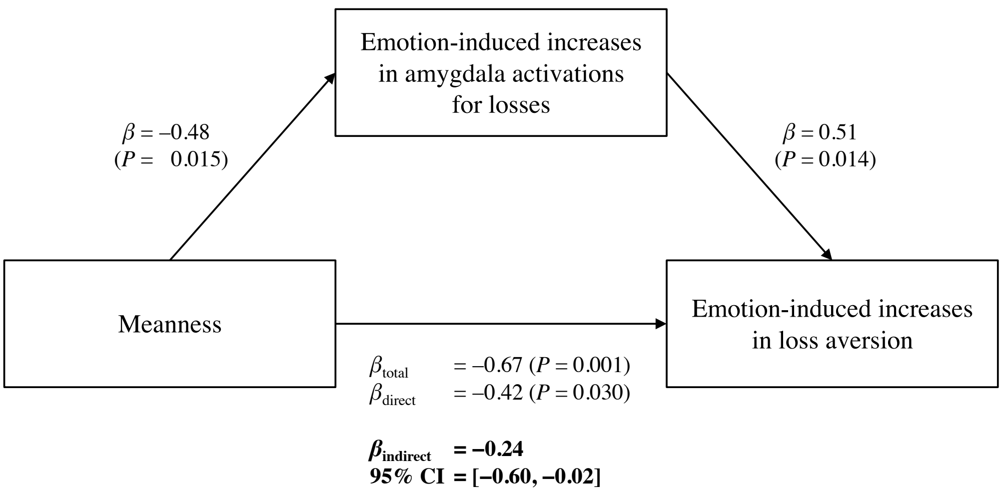

Figure 15. TriPM meanness attenuated emotion-induced increases in loss aversion, and this effect was partially mediated by attenuated emotion-induced increases in amygdala activations for losses. The mediation model illustrates total, direct, and indirect effects of TriPM meanness on emotion-induced changes in monetary loss aversion. β coefficients represent standardized regression coefficients while controlling for boldness, disinhibition and loss aversion in the neutral condition (not illustrated). β_{total} is the total effect of meanness on emotion-induced changes in loss aversion, β_{direct} is the direct effect after the mediator (i.e., emotion-induced changes in amygdala activations for losses) had been taken into account, and $\beta_{indirect}$ is the indirect effect, i.e., the effect of meanness on emotion-induced changes in loss aversion that was mediated by a change in amygdala activations for losses. For the indirect effect, bias-corrected bootstrapping (50,000 bootstrap samples) provided a 95% confidence interval that did not span 0, indicating a significant partial mediation.

Discussion: Our neuroscientific study extends previous behavioral reports (including Study 2) on emotion-induced changes in loss aversion by providing a neural mechanism that gives rise to such effects. Furthermore, our study also complements previous fMRI studies that provided mixed results on the neural basis of loss aversion in general (e.g., Canessa et al., 2013; Gelskov et al., 2015; Pammi et al., 2017; Sokol-Hessner et al., 2013; Tom et al., 2007) or did not report value-related amygdala activity mediating emotion-induced changes in loss aversion (Charpentier et al., 2015; Engelmann et al., 2015). Our findings also address RQ3a and RQ3b and provide support for H5 and H6:

RQ3a: What are the neural mechanisms that mediate emotion-induced changes in loss aversion?

H5: *Incidental fear cues enhance amygdala activity relative to neutral cues. This general increase is accompanied by altered value processing, i.e., emotion-induced increases in activations for losses in the amygdala and, possibly, shifts towards negative value coding in other regions as well (e.g., striatum, insula, vmPFC). These emotion-induced shifts in valuation mediate increases in behavioral loss aversion.*

H5 was supported by our data. Specifically, we observed a general emotion-induced increase in bilateral amygdala activity following fearful relative to neutral faces. This was accompanied by a shift from positive to negative value coding in a distributed set of brain regions, including the amygdala, the striatum, insula and the vmPFC. While loss aversion was mainly predicted by stronger deactivations for losses relative to activations for gains (i.e., neural loss aversion) in the neutral condition, emotion-induced changes in loss aversion were mainly predicted by stronger activations for losses, i.e., negative neural value coding.

RQ3b: How is the influence of psychopathic personality on emotion-induced changes in loss aversion mediated at the neural level?

H6: *The attenuating effect of affective-interpersonal psychopathic traits (e.g., TriPM boldness and meanness) on emotion-induced increases in loss aversion is mediated by attenuated emotion-induced increases in amygdala activations for losses.*

H6 was also largely supported by our data. Specifically, we observed that TriPM meanness (but not boldness and disinhibition) attenuated emotion-induced increases in loss aversion and that this effect was partially mediated by attenuated emotion-induced amygdala activations for losses at the neural level.

5. General Discussion

5.1. Incidental Emotions and Prospect Theory

Prospect theory has long been devoid of emotion, but it is increasingly acknowledged that the processes captured by this behavioral model are in fact intimately tied to emotion (e.g., Rottenstreich & Hsee, 2001; Suter, Pachur, Hertwig, et al., 2015). The present work extends previous research on the long-ignored link between emotions and Prospect Theory by providing causal evidence of incidental emotional effects on probability weighting and loss aversion. Specific links between prospect-theoretic components and emotions could contribute to our mechanistic understanding of emotional influences on decision making. In the following two chapters, I will discuss the links revealed in Studies 1 and 2 regarding probability weighting and loss aversion, respectively, and put these results in a broader theoretical context. In doing so, I will adopt both an emotional and a decision-related perspective.

5.1.1. Incidental Happiness and Probability Weighting

Going beyond previous indirect and correlational evidence on incidental emotional effects (Fehr-Duda et al., 2011; Kliger & Levy, 2008), Study 1 provides causal evidence that incidental emotions affect probability weighting. To be specific, varying degrees of incidental happiness were associated with an increased elevation (i.e., optimism for higher incidental happiness) or decreased elevation (i.e., pessimism for reduced incidental happiness) of the probability-weighting function, but not with the curvature parameter. These findings provide information regarding two important and interrelated issues in emotion and decision research: First, what are the critical functional components of emotions that interact with decision making? Second, what psychological processes are reflected by emotion-induced changes in probability weighting?

With regard to emotional components, happiness-induced increases in risk taking are consistent with the appraisal-tendency framework proposed by Lerner and colleagues (see, e.g., Lerner & Keltner, 2000, 2001), which states that appraisal tendencies evoked by certain emotions can carryover to judgments or decisions when their central appraisal dimensions overlap. As far as risk evaluations are concerned, certainty and control are crucial dimensions. Hence, emotions that are strongly characterized by high or low certainty and control are expected to have a large influence on risk evaluations and risky decisions. Lerner and colleagues demonstrated, for instance, that fear and anger—although of the same valence—have opposite effects on risk perceptions and risky decisions, i.e., fear (high uncertainty, high situational control) increased risk perceptions and reduced risk taking; anger (high certainty, high personal control) reduced risk perceptions and increased risk taking. Happiness is characterized by high certainty and a moderate sense of personal control (C. A. Smith & Ellsworth, 1985), and a carryover of appraisal tendencies to decision making could therefore explain increased risk taking.

Emotions and underlying appraisals are also associated with specific motivational and action tendencies (Frijda, 2009; Lowe & Ziemke, 2011). For instance, happiness has been associated with an approach-tendency (Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Frijda, 1987; Seidel, Habel, Kirschner, Gur, & Derntl, 2010), among others, which can explain the observed positive relationship with risk taking. Another motivational tendency that has received specific attention in early studies on affective influence on decision making is mood maintenance. Isen and colleagues (1988) have argued that positive affect is associated with a desire to maintain this positive state, which is consistent with their finding of increased negative subjective value of losses in elated subjects, as losses would interfere with positive affect. Another possible interpretation of their findings, however, is that the receipt of a small bag of candy (i.e., the experimental manipulation in their study) might not just evoke emotions but also appraisals of possession, which might have increased sensitivity to losses. In any case, our findings appear inconsistent with the mood-maintenance hypothesis, because increased happiness was associated with increased risk taking. However, Isen et al. (1988) noted that while mood maintenance could explain the observed effects in the loss domain, positive affect might be related with increased risk taking in the gain domain due to changes in probability weighting. Study 1 provided direct evidence for this conjecture.

Importantly, our behavioral modeling results also provide indications of involved decision-related processes. Given that the probability-weighting parameters were dissociable in our study, our findings suggest that two-parameter versions of the probability-weighting function (e.g., Prelec, 1998) might capture different underlying processes and are therefore recommended over one-parameter versions, consistent with prior work that found two-parameter versions particularly suitable to explain heterogeneity in probability weighting (Fehr-Duda & Epper, 2012; Gonzalez & Wu, 1999).

However, the underlying mechanisms are only poorly understood. In this regard, the mechanisms underlying emotion-evoked changes in the curvature of the probability-weighting function are incompletely, but better understood than those underlying changes in the elevation parameter. Several theoretical accounts postulate that the probability weighting function, in particular its curvature, at least partly reflects emotions. As already outlined in the introduction, the inverse S-shape of the probability weighting function can result from expected emotions such as elation and disappointment (Brandstätter et al., 2002) or integral emotions such as hope and fear. For instance, integral emotions are hypothesized to be stronger for affect-rich (e.g., a kiss) relative to affect-poor outcomes (e.g., money), leading to a more strongly S-shaped curvature for affect-rich outcomes (Rottenstreich & Hsee, 2001; Suter, Pachur, Hertwig, et al., 2015). In other words, affect-rich outcomes appear to be associated with increased sensitivity to changes from impossibility to possibility and from certainty to possibility, but decreased sensitivities to changes in probability in-between (Figure 16, Panel A).

In fact, the evaluation of affect-rich outcomes might be even better described by probability neglect, i.e., the tendency to completely disregard probability when making risky decisions (Sunstein & Zeckhauser, 2010). For instance, there is evidence for a switch from an expectation-based calculus (i.e., an integration of outcome and probability, as modeled in Cumulative Prospect Theory) for affect-poor outcomes to heuristic decision modes characterized by ignorance of probabilities (e.g., minimax or maximax decision rules) for affect-rich outcomes (Pachur, Hertwig, & Wolkewitz, 2013; Suter, Pachur, & Hertwig, 2015; see Figure 16, Panel A). This does not imply that Cumulative Prospect Theory was unable to explain changes in decision behavior. Choice over affect-rich outcomes could still be described in the framework of Cumulative Prospect Theory (Suter, Pachur, & Hertwig, 2015; Suter, Pachur, Hertwig, et al., 2015), but parametric changes would imply different psychological mechanisms, i.e., changes in sensitivity to probabilities, rather than complete probability neglect implied by the better fitting heuristic models (Suter, Pachur, & Hertwig, 2015).

Importantly, there is also data going beyond choice on this matter. Differential processing of probabilities for affect-poor and affect-rich outcomes has also been observed at the neural level (Suter, Pachur, Hertwig, et al., 2015). For instance, brain activation in regions that correlated with decision weights was larger during affect-poor choices, indicating that processing of probabilities was more pronounced during affect-poor compared to affect-rich choices. In addition, process-tracing data on information acquisition showed that people pay less attention to probability information in affect-rich compared to affect-poor choices (Pachur et al., 2013), consistent with different modes of decision making.

In contrast, the observed effects of incidental happiness in Study 1 are inconsistent with a decision mode characterized by insensitivity to probabilities, since changes in the elevation parameter imply changes in decision weights across the whole range of probabilities rather than altered sensitivity to changes of these probabilities (Figure 16, Panel B). This demonstrates that, although being a descriptive rather than a process model (Berg & Gigerenzer, 2010), Prospect Theory is able to narrow down potential mechanisms through their dissociable parameters.

The exact nature of the putative probability-sensitive mechanisms underlying our observation, however, awaits further process-oriented investigation. On the one hand, happiness-evoked changes in decision weights might reflect a direct effect on the processing of probabilities, which could be assessed by obtaining measures of brain activity in probability-processing areas (e.g., supramarginal gyrus; Suter, Pachur, Hertwig, et al., 2015). For instance, larger decision weights might be the result of biased probability processing within these areas, reflecting optimistic probabilistic processing (e.g., due to appraisals of certainty). A neural overlap between brain areas that have been associated with probability weighting and with the experience of happiness, e.g., in the anterior cingulate cortex and striatum (see, e.g., Vytal & Hamann, 2010), might allow for such an integration of emotion and probability processing. On the other hand, changes in the elevation of the probability-weighting function might not be related to changes in the processing of probabilities per se, but might instead reflect changes in outcome processing, e.g., changes in attention to outcome values as discussed by Wu (1999). In line with that, happy participants have been found to display an increased attentional focus on rewards (Tamir & Robinson, 2007). Neuroimaging and process-tracing techniques like eye tracking or (computer) mouse tracking (see, e.g., Schulte-Mecklenbeck et al., 2011) are promising methods to further investigate the processes that mediate (emotional effects on) probability and outcome processing.

Another interesting question is whether incidental emotions operate through changing integral or expected emotions, which, in turn, influence probability weighting. For instance, Rottenstreich and Hsee (2001) noted that the elevation parameter might be subject to integral emotions such as savoring and dread (Loewenstein, 1987; Lovallo & Kahneman, 2000). Alternatively, Brandstätter and colleagues (2002) noted that increased sensitivity to disappointment, but not elation, would be associated with more pronounced underweighting than overweighting (and vice versa), reflected in the elevation of the probability-weighting function and its inflection point. Given that we used moderate and only positive monetary outcomes in Study 1 that are unlikely to create strong positive or negative integral or expected emotions (compared to, e.g., kisses and electric shocks in the studies of Rottenstreich & Hsee, 2001), a direct effect of incidental emotions is plausible, but we cannot rule out an indirect channel via altered integral or expected emotions.

In sum, Study 1 has shown that incidental happiness is positively associated with the elevation parameter of the probability-weighting function. This finding extends previous research on the effect of expected and integral emotions on the curvature parameter and indicates that—instead of changes in sensitivity to probability or a switch to heuristic decision making characterized by probability neglect—the influence of incidental happiness on choice is likely mediated by a different, probability-sensitive mechanism. Neuroscientific and process-tracing techniques represent promising methods to explore this mechanism in future research.

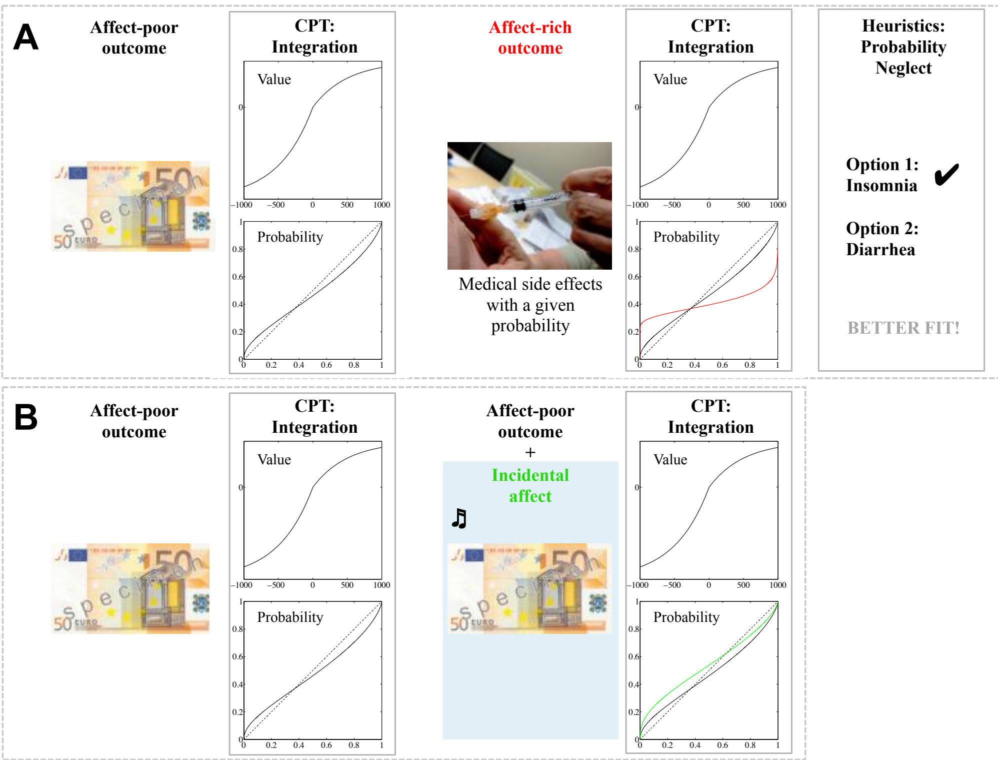

Figure 16. Different decision-related mechanisms involved in choices over affect-rich outcomes and in choices under incidental emotional influence. *Panel A* illustrates choices over affect-poor outcomes (e.g., money) on the left and over affect-rich outcomes (e.g., medical side effects) on the right. Choices over affect-poor outcomes can be adequately modeled with Cumulative Prospect Theory, consistent with an integration of subjective values and probabilities. While Cumulative Prospect Theory can also model choices over affect-rich outcomes in terms of an integrative mechanism with diminished sensitivity to probability changes (indicated via the red line in the probability-weighting function), heuristic models that ignore probabilities at all (e.g., minimax and maximax) often show a better model fit (Suter, Pachur, & Hertwig, 2015). To note, medical side effects were matched to monetary amounts to allow for behavioral modeling in that study. For simplicity, only a change in the curvature parameter (red line) is shown in the right probability-weighting function, because it illustrates changes in sensitivity to probability changes. (Suter et al., however, also observed changes in the elevation parameter, consistent with a focus on the most attractive among bad outcomes in heuristic processing). *Panel B* illustrates choices over affect-poor outcomes (i.e., money) on the left and choices over the same outcomes under incidental emotional influence (i.e., induced by music in Study 1) on the right. In contrast to choices over affect-poor outcomes, our model-based findings (based on Cumulative Prospect Theory) indicated preserved sensitivity to probability (changes), but changes in the elevation of the probability weighting function (green line in the right probability-weighting function). *Note:* Euro image © European Central Bank. Vaccination image by Daniel Paquet, licensed under the Creative Commons Attribution 2.0. Generic license (https://creativecommons.org/licenses/by/2.0/deed.en)

5.1.2. Incidental Fear and Loss Aversion

Despite a postulated link between fear and loss aversion (Camerer, 2005; Hartley & Phelps, 2012), the influence of incidental fear on loss aversion had been unclear. In Studies 2 and 3, we found that the presentation of fearful relative to neutral faces—stimuli that signal potential threats—increased risk aversion and that this effect could be attributed to increased loss aversion. We also found that psychopathic personality traits related to diminished fear reactivity moderated this effect. Higher PPI-R fearless dominance (in particular social influence/potency) attenuated the influence of incidental fear cues on loss aversion—corroborating an affective interpretation of the effect of facial cues on loss aversion (for a discussion of the contributions of our findings to the personality literature, see Chapter 5.3.).

Our findings complement previous studies on incidental emotional effects on loss aversion. For instance, one early study found that elated participants displayed greater negative utilities of losses compared to controls (Isen et al., 1988). Another study found unpleasant odor to increase loss aversion compared to pleasant odor or clean air—an effect that could be attributed to odor pleasantness, but not intensity (Stancak et al., 2015), whereas incidental anger has been associated with reduced loss aversion (Campos-Vazquez & Cuilty, 2014). Together with our findings, this body of literature provides important information on which functional components of emotions might interact with decision making and on potential psychological processes reflected by changes in loss aversion.

Notably, a two-dimensional perspective of emotion with valence and arousal as central dimensions (as postulated, e.g., by the circumplex model of affect; Russell, 1980), cannot fully explain the effects of incidental emotions on loss aversion reported above. First, because same-valenced contexts showed opposite directional effects on loss aversion (i.e., unpleasant odor and fearful faces increased loss aversion; induced anger decreased loss aversion), and opposite-valenced contexts showed the same directional effect on loss aversion (i.e., unpleasant odor and elation both increased loss aversion). Second, the observations that odor pleasantness, but not intensity (i.e., a proxy for arousal), was associated with odor effects on loss aversion, and that incidental anger (high arousal) was associated with reduced loss aversion, appear inconsistent with the idea that loss aversion is mediated by arousal. This conjecture was recently put forward, based on observations that emotion regulation reduced peripheral-physiological arousal as well as loss aversion (Sokol-Hessner et al., 2009), and that pharmacological attenuation of arousal by the beta-blocker propranolol reduced loss aversion (Sokol-Hessner, Lackovic, et al., 2015). However, it is possible that loss aversion is at least partly determined by arousal in a neutral context, whereas the observed emotional effects on loss aversion might be due to other mechanisms. For instance, fear-related effects have been related to certainty appraisals (high uncertainty) and control appraisals (situational control), which are crucially involved in mediating fear effects on risk taking (see, e.g., Lerner & Keltner, 2000, 2001). More generally, multiple mechanisms with similar or opposite directional effects might interactively determine loss aversion. In any case, it appears important to distinguish specific emotions and investigate the specific mechanisms underlying emotion-induced changes of loss aversion.

As mentioned before, emotions and underlying appraisals are also associated with specific action tendencies. Some theories postulate that action tendencies associated with fear depend on the imminence of threat (e.g., Bracha, 2004; Bracha, Ralston, Matsukawa, Williams, & Bracha, 2004; Gray, 1988). Fearful faces signal a potential threat (and are therefore less threat-imminent compared to, e.g., an imminent attack of a conspecific or a predator). When the potential threat—in our case a monetary loss—is avoidable, people commonly do so ("flight" response). From this perspective, the observed emotion-induced increase in loss aversion reflects a facilitated avoidance response. Interestingly, the above mentioned effect of unpleasant odors on loss aversion has also been interpreted in terms of signaled threat or danger and defensive responses (Stancak et al., 2015), consistent with previous observations of augmented startle responses after the presentation of unpleasant odors (Ehrlichman, Brown, Zhu, & Warrenburg, 1995; Miltner, Matjak, Braun, Diekmann, & Brody, 1994). Fearful faces, however, are a more suitable experimental choice in order to draw such conclusions, because they represent more direct signals of potential threat.

These fear models, however, also postulate other possible action tendencies such as defensive aggression ("fight" response) in case of imminent and unavoidable threats. Defensive aggression tendencies, in turn, might have different effects on loss aversion than avoidance tendencies. Specifically, the phenomenon of defensive aggression illustrates the intrinsic link between the fear and the anger/rage system (Panksepp, 1998). Thus, fear-induced defensive aggression might have effects more closely resembling those of evoked anger, such as increased risk-taking (Lerner & Keltner, 2001) and reduced loss aversion (Campos-Vazquez & Cuilty, 2014), which represents an interesting subject for future research. Another open question is whether fear-related effects on decision making also depend on the specific source of threat, given that fear elicited by painful stimuli or conditioned cues, predators, and aggressive conspecifics are processed in partly dissociable neural circuits (C. T. Gross & Canteras, 2012).

Behavioral modeling of loss aversion provides further indications of underlying decision-related processes. Since loss aversion reflects the weight of losses relative to gains in risky choice, emotion-induced changes in loss aversion point towards either loss-specific effects or different weighting by integrative mechanisms. However, the exact processes underlying prospect-theoretic parameters are only poorly understood. To draw mechanistic conclusions, it will be indispensable to go beyond mere choice data. One possibility is to use behavioral process-tracing techniques to further investigate underlying processes (e.g., Schulte-Mecklenbeck et al., 2011). For instance, just as probability weighting might reflect attention to probabilities, the loss aversion parameter might be associated with the relative attention paid to losses compared to gains (alternatively, losses might themselves induce attention, see, e.g., Yechiam & Hochman, 2013). Another possibility is to investigate neurobiological processes, which, in turn, can inform models of emotion-dependent changes in decision making. This was the aim of Study 3 of the present thesis. Hence, in the following, I will put the neuroscientific findings of that study in a broader context.

5.2. A Neurocognitive Model of Emotion-Induced Changes in Loss Aversion

Previous research on the neural basis of loss aversion in general and emotion-induced changes in loss aversion in particular have provided mixed results on the specific underlying value-related mechanisms. In the following, however, I propose a neurocognitive model of emotion-induced changes in loss aversion that aims to integrate previous observations and our own findings from Study 3. The model is illustrated in Figure 17 below.

At the top, the model depicts the stimulus input level. Most neuroscientific studies in the field focused on decision-related processes following the presentation of mixed gambles (e.g., Canessa et al., 2013; Charpentier et al., 2015; Tom et al., 2007), i.e., gambles including both a potential gain and a potential loss (see upper block in Figure 17), while others focused on neural processes following singular gain- or loss outcomes (not depicted, see, e.g., Kokmotou et al., 2017; Sokol-Hessner et al., 2013). Most studies did not experimentally manipulate emotions (but see Charpentier et al., 2015; Engelmann et al., 2015). In contrast, we briefly presented fearful or neutral faces prior to the gambles to affectively prime decision making (right and left side of the upper block in Figure 17, respectively).

In the central block, the model depicts putative neurocognitive processes that follow the stimulus input and which are critically involved in the generation of loss aversion. The key proposals are 1) that decision making rests on distinct valuation processes and 2) that these valuation processes are modulated by emotional context and personality.

The first proposal is based on previous research and our own findings. For instance, several studies observed that monetary loss aversion in a neutral context was associated with stronger neural *deactivations* for losses relative to activations for gains (neural loss aversion), e.g., in the striatum (Canessa et al., 2013; Charpentier et al., 2015; Pammi et al., 2017; Tom et al., 2007). In contrast to the other cited studies, Canessa et al. also observed the opposite pattern, i.e., *activations* for losses that predicted monetary loss aversion, e.g., in the amygdala. In Study 3, we also observed regions that displayed different types of value processing in the neutral condition. Specifically, we also found several regions that displayed stronger deactivations for losses relative to gains (neural loss aversion), which positively predicted monetary loss aversion. In contrast to Canessa et al., but in line with a recent study (Pammi et al., 2017), we also observed neural loss aversion in the right amygdala, which also predicted behavioral loss aversion (but not in Pammi et al., 2017). Furthermore, we also observed negative value coding in the neutral condition (e.g., activations for losses, deactivations for gains) in the vmPFC, left amygdala and insula. Taken together, these findings indicate that decisions on mixed gambles can evoke two distinct valuation systems—one displaying positive value coding via *deactivations* for losses (and activations for gains), and the other displaying negative value coding via *activations* for losses (and deactivations for gains). These systems are depicted on the left and right side of the central block in Figure 17, respectively.

The second key proposal of the model is that these distinct valuation processes are employed in a context-dependent fashion and are subject to interindividual differences. Study 3 provided evidence for both. For instance, we observed a general increase in amygdala activity following the presentation of fearful relative to neutral faces, accompanied by an emotion-induced shift from positive towards neural value coding (compare the left and right side of the central block in Figure 17). More precisely, while loss aversion following the presentation of neutral faces was mainly predicted by greater *deactivations* for losses relative to activations for gains (neural loss aversion), emotion-induced increases in loss aversion were mainly predicted by greater *activations* for losses. Interestingly, these context-dependent shifts were partly observed in overlapping regions, e.g., in the right amygdala. Notably, we also observed emotion-induced reductions in deactivations for losses (and, thus, neural loss aversion), e.g., in the striatum (not depicted). Our findings are line with a recent study that investigated decision making under threat of shock and in a neutral context (Engelmann et al., 2015). Although this study did neither find emotion-induced changes in the degree of loss aversion nor in amygdala-related activity, the authors report a similar context-dependent shift in valuation: increasing striatum and vmPFC activity to increasing subjective expected value (i.e., positive value coding) positively predicted gamble acceptance (thus, possibly, loss aversion) in the neutral context; increasing insula activity to decreasing subjective expected value (i.e., negative value coding) negatively predicted gamble acceptance in the threat-of-shock context, while positive value coding in the striatum and vmPFC was diminished. Although the authors did not investigate loss and gain responses separately, the observed shifts in value coding could have been mediated by a shift from deactivations for losses (and neural loss aversion) to activations for losses, as we have found in Study 3. In both studies, diminished positive value coding (e.g., in the striatum) may have resulted either from a compromised coding of losses in form of deactivations or from concurrent activations for losses (i.e., negative value coding) that would partially or fully cancel out deactivations in a summed fMRI signal. Taken together, both the findings of Engelmann et al. and our findings suggest that the emotional context is an important factor determining the employment of distinct valuation processes.

The model also proposes interindividual differences as another factor that contributes to the differential involvement of valuation processes. Specifically, in Study 3, we observed that the psychopathic trait meanness attenuated emotion-induced increases in loss aversion and that this effect is partially mediated by attenuated emotion-induced increases in amygdala activations for losses. Hence, psychopathic personality moderated the emotion-induced employment of negative value processing (see the attenuation effect depicted in Figure 17).

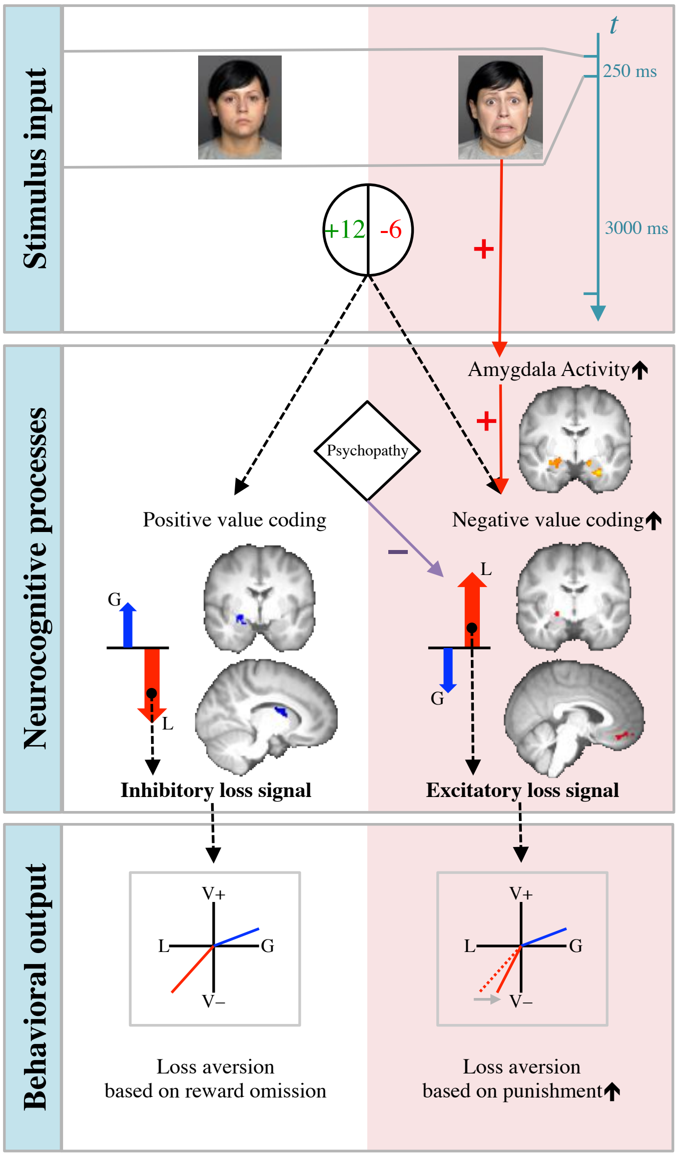

Figure 17. Neurocognitive model of emotion-induced changes in loss aversion. The model proposes two different neural valuation mechanisms that are involved in the generation of behavioral loss aversion through inhibitory loss signals and excitatory loss signals, respectively. Crucially, incidental fear cues increase general amygdala activity as well as excitatory loss signals, and thereby loss aversion. Furthermore, psychopathic personality attenuates the effect of incidental fear cues on loss aversion via attenuated excitatory loss signals.

On a more general level, the proposed neurocognitive processes are consistent with a growing body of evidence for two opposing neural loss (and gain) signals—inhibitory and excitatory—that have been related to distinct, but overlapping motivational systems (Brooks & Berns, 2013; Seymour et al., 2015). For instance, consistent with electrophysiological and optogenetic evidence in rodents (e.g., Beyeler et al., 2016; Gore et al., 2015; Shabel & Janak, 2009), we found intermingled excitatory *and* inhibitory signals for losses in the human amygdala. As an extension to these previous accounts, the model introduces two specific variables that modulate the relative contributions of excitatory and inhibitory loss (but also gain) signals—the incidental affective context and psychopathic personality.

The bottom block of the model depicts the behavioral output level. Both excitatory and inhibitory loss signals determine behavioral loss aversion, though in different degrees in the neutral vs. affective context. Given that loss aversion in a neutral context was associated with positive value coding, characterized by neural loss aversion, it might be conceptualized as loss aversion based on (expected) reward omission (i.e., reductions or absence of positive value). By contrast, emotion-induced increases in loss aversion were associated with shifts towards negative value coding, and might be conceptualized as loss aversion based on (expected) punishment (i.e., presence of negative value). Hence, going beyond behavioral models of decision making that are mute to the sources of loss aversion, the neurocognitive model suggests that loss aversion is based on context-dependent involvement of distinct valuation processes.

The aim of the proposed model is to provide a framework for future research on the role of the documented valuation processes and on their context-dependent employment. It includes two specific factors—incidental fear cues and psychopathic personality—that were found to modulate the proposed valuation mechanisms. However, it is likely that there are multiple factors that have such modulatory effects (e.g., the incentive structure of the decision making task, as hypothesized by Seymour et al., 2015). Notably, also conceptually related stimuli and contexts could induce different processes. For instance, pain-related processes might explain the greater shift towards negative value coding in the insula during threat of shock (Engelmann et al., 2015) than after fearful faces (Study 3), which more reliably enhance amygdala activity (Fusar-Poli et al., 2009). Hence, it will be important to systematically compare valuation processes across multiple contexts to gain further insights into their neural underpinnings as well as functional significance. In this regard, the model raises further important questions. For instance, it is possible that positive and negative value coding are mediated or modulated by different neurotransmitter systems. While reward-related responses are typically associated with a dopaminergic mesotelencephalic circuit (e.g., Brooks & Berns, 2013; Schultz, Dayan, & Montague, 1997; Seymour et al., 2015), there is an ongoing debate on whether aversive signals are mediated by different neurotransmitters (see, e.g., Boureau & Dayan, 2011). Another important issue will be to understand the interactions of multiple brain regions that display similar or distinct value coding, and the behavioral significance of such interactions. For instance, a recent study found that emotion-induced changes in loss aversion were associated with increased amygdala-striatal functional connectivity (Charpentier et al., 2015), consistent with previous evidence showing that amygdala signals to the striatum are crucial for generating avoidance behavior (e.g., Amorapanth et al., 2000; LeDoux & Gorman, 2001). Hence, future research would benefit from a greater emphasis on the functional interrelationships of the nodes that comprise distinct neural valuation networks.

5.3. Psychopathic Personality

Studies 2 and 3 also contribute to the literature on psychopathic personality by extending previous research on decision making in psychopathy, but also by favoring a certain class of structural models of psychopathy over others.

Previous studies on decision making in psychopathy have repeatedly reported negative economic consequences. For instance, psychopathic male criminals failed to learn to avoid disadvantageous, risky options, which can result in a net monetary loss (Mitchell, Colledge, Leonard, & Blair, 2002) and undergraduates that score high in psychopathic traits displayed a larger preference for smaller immediate monetary rewards over larger delayed rewards in a hypothetical time discounting task (J. D. Miller & Lynam, 2003).

However, psychopathic personality can also promote positive or mixed economic outcomes. In the social domain, male criminal psychopaths, in particular those high in certain facets of PPI-R self-centered impulsivity, showed a higher proclivity for competitive, non-cooperative behavior in a prisoner's dilemma game compared to non-criminal controls, resulting in higher monetary gains (Mokros et al., 2008). College students with affective-interpersonal psychopathic traits accepted more unfair offers of proposers in an Ultimatum Game compared to lower-scoring participants, which can increase monetary outcomes (Osumi & Ohira, 2010; but see Koenigs, Kruepke, & Newman, 2010). Readily accepting unfair offers, however, can also have negative consequences, since altruistic punishment (i.e., rejecting unfair offers at a personal cost) is an important factor in establishing—often fruitful— cooperation (see, e.g., Fehr & Gächter, 2002). In a similar vain, competitive and uncooperative behavior can undermine fruitful cooperation.

Studies 2 and 3 extend this research by demonstrating another domain in which psychopathic personality can lead to positive economic outcomes by attenuating incidental emotion-induced increases in loss aversion, which, on average, results in higher monetary outcomes. Taken together, these findings favor a context-dependent perspective (e.g., regarding the incentive or social structure of the task).

Importantly, our findings also contribute to a more general debate on the structure of psychopathy and its underlying etiological dimensions. As already mentioned, we found that PPI-R fearless dominance—in particular, social influence—diminished the effect of incidental fear cues on loss aversion in Study 2, whereas PPI-R self-centered impulsivity did not moderate this effect. Although we did not observe a moderation effect of TriPM boldness (strongly overlapping with PPI-R fearless dominance) in Study 3, we observed the same moderation effect for TriPM meanness, which also captures affective-interpersonal features of psychopathy (Patrick et al., 2009). The differential effects of affective-interpersonal and impulsive-antisocial traits speaks against a unitary construct perspective, but favors instead multidimensional models of psychopathy (e.g., Fowles & Dindo, 2009; Patrick & Bernat, 2009; Patrick et al., 2009). These models have already received considerable support from domains as diverse as emotion processing (e.g., Gordon et al., 2004), romantic attachment (Savard, Brassard, Lussier, & Sabourin, 2015), and neural performance monitoring (for a review, see Schulreich, 2016; and see Schulreich et al., 2013), among others.

The observed moderator effect of affective-interpersonal psychopathic traits is consistent with deficient fear processing as a core feature of psychopathy (Lykken, 1995; Patrick et al., 2009), but could also be explained by other affective-interpersonal mechanisms (e.g., reduced empathy, Stanley et al., 2013). The observed effects, however, could also be explained by an entirely different framework, which postulates that psychopathy is characterized by an impaired integration of contextual information due to an attention-related deficit (Baskin-Sommers & Newman, 2013; Newman & Lorenz, 2003). However, this framework does not offer explanations for differential effects of subcomponents of psychopathy. Together, while behavioral findings illustrate that affective-interpersonal psychopathic traits decrease the susceptibility to incidental fear cues in decision making, future research is needed to shed more light on the specific mechanisms that mediate this effect. One first endeavor in this regard was Study 3, which found that the moderation effect of TriPM meanness on emotion-induced changes in loss aversion was mediated by altered value processing in the amygdala, consistent with previous evidence of altered amygdala functioning in psychopathy (e.g., Gordon et al., 2004).

5.4. Methodological Limitations

Both benefits and shortcomings lie in the experimental methods used in the empirical studies of this thesis, which I will discuss in this chapter. For instance, despite the use of well-validated affective material (Koelsch et al., 2013; Pehrs et al., 2013), the strength of emotional manipulation was moderate at best in Study 1 (and was not [Study 2] or only indirectly assessed via brain activity [Study 3], as discussed below). In Study 1, the musical stimuli successfully altered incidental happiness, although significant increases in happiness beyond the mildly positive default state (i.e., in the no-music condition) could not be achieved (as discussed above and also observed before; see, e.g., Gasper, 2004), and sadness was not significantly changed at all. Nevertheless, we could observe small to moderate emotion-dependent changes in risk attitudes. Future research might benefit from more potent emotion induction techniques, e.g., well-validated video material (see, e.g., J. J. Gross & Levenson, 1995; Rottenberg, Ray, & Gross, 2007). However, intense feelings, especially when being fully recognized, can result in attenuated emotional effects on decision making due to an enhanced ability to control emotional bias (Seo & Barrett, 2007). Hence, investigating the consequences of subtle, potentially cognitively less controllable, emotions is a highly relevant research subject. Their importance is further emphasized by the fact that many, if not most, emotional stimuli in everyday life are of small to moderate intensity (e.g., listening to background music or receiving a casual smile).

Emotion measurements allow directly linking changes in emotions to changes in decision making. While some studies used emotion measurements to distinguish post-hoc between responders and non-responders to the emotion-elicitation procedure (e.g., Wacker, Heldmann, & Stemmler, 2003), we performed a regression analysis that predicted changes in probability weighting by each individual's self-reported emotional state in Study 1.

In Studies 2 and 3, this approach was not possible. As mentioned before, we deliberately refrained from acquiring emotional ratings during the task in these studies in order not to interfere with affective priming. In Study 2, we accounted for individual differences by including a personality construct that has been related to emotional reactivity (i.e., fearless dominance) as a moderator variable, corroborating an affective interpretation of the observed effects. In Study 3, substantial loss of skin conductance data precluded an assessment of the success of emotional manipulation via peripheral-physiological measures. However, central-physiological data were consistent with a successful emotional manipulation, as we found significantly increased amygdala activity after the presentation of fearful relative to neutral faces. An induced emotional state is plausible given the affective material used (Ebner et al., 2010), but other interpretations cannot be ruled out as the amygdala plays a central role in fear processing, but not exclusively so (see, e.g., Cunningham & Brosch, 2012). Optimally one would prefer a measure with high specificity (i.e., only related to a specific state or process such as a specific emotion, but not with others), but this desideratum is, at best, also only partially fulfilled by other emotion measures (e.g., peripheral-physiological data; for a review, see, e.g., Kreibig, 2010).

Of course, specificity is not just a matter of measurement, but already of emotion elicitation, since manipulations might induce a blend of affective states rather than a single specific state (an observation already made early, see, e.g, Polivy, 1981). Constructive replications with different kinds of emotion elicitation and measurement procedures can therefore corroborate affective interpretations of the observed effects and might also offer additional insights into crucial emotional dimensions (e.g., appraisal dimensions).

The decision-making tasks used also had some shortcomings. For instance, it is impossible to disentangle changes in the value function from changes in probability weighting from choice data on two-outcomes lotteries only (Wakker, 2010), unless one restricts both functions to specific parametric forms (in Study 1: power utility and Prelec two-parameter probability weighting). Specifically, reduced elevation of the probability weighting function is observationally equivalent to an increased curvature of the value function, i.e., both lead to increased risk aversion. Hence, our findings are consistent with changes in probability weighting, but we cannot rule out that the value function also captures the observed changes in risk taking. The use of a more complex option set that better discriminates prospect-theoretic parameters as well as the use of process-tracing or neuroscientific methods could help to disentangle these possible effects.

Regarding Studies 2 and 3, changes in risk aversion in the mixed-gambles tasks used were well reflected by changes in loss aversion (but not decision noise). However, future studies would benefit from including gain-only trials (see, e.g., De Martino et al., 2010; Sokol-Hessner et al., 2013) as well as loss-only trials to better disentangle unique effects on loss aversion from other risk-related effects (e.g., changes in the curvature of the utility function). Including only mixed-gamble trials also had one major advantage, i.e., keeping the experiments shorter. This helped to increase subjects' attention to the task and to reduce potential habituation effects that are typically observed for emotional material (see, e.g., Breiter et al., 1996). Habituation effects would undermine behavioral modeling and statistical power to detect effects in general, because only a part of the decisions would then be affected by emotions. However, future studies might pilot/use different experiment lengths and compare habituation effects, thereby exploring the possibility to increase the length of the experiment by including additional informative trials (e.g., gain-only and loss-only trials).

5.5. Future Directions

Before closing, I would like to give a personal view on possible future directions in the field. I already outlined some specific open questions in the chapters above, but I would like to discuss possible general developments in two particular domains: behavioral modeling of decision making and neuroscientific analysis.

Paradoxically, behavioral models like Prospect Theory have been developed to enrich economic models with insights from cognitive psychology, but should be better regarded as paramorphic or as-if models rather than process-oriented models (for a discussion, see, e.g., Berg & Gigerenzer, 2010). Instead of a true cognitive revolution, they resemble more the behaviorists' paradigm by refraining from opening the "black box", i.e., cognitive (and affective; Volz & Hertwig, 2016) processes that mediate the relationship between stimulus and response. Nevertheless, Prospect Theory can constrain possible mechanistic explanations. For instance, the constant curvature parameter of the probability-weighting function across emotional conditions in Study 1 is inconsistent with decision modes that are characterized by probability neglect, and changes in the elevation parameter point to different mechanisms, as discussed above. However, without explicitly modeling underlying processes, our understanding of the observed behavioral effects will remain limited.

As an alternative to traditional economic or behavioral economics models, process models have recently received increased attention (see, e.g., Johnson & Ratcliffe, 2014; Johnson et al., 2008). Process models attempt to describe and predict how people actually make decisions, e.g., by modeling steps that people take and what kind of information is processed in what way in each of these steps. In other words, the interest of process models does not just lie in the prediction of choice, but also in the qualitative nature of the decision algorithm. These specific process assumptions are testable with process-tracing data such as provided by eye tracking or computer-mouse tracking (for an overview, see, e.g., Schulte-Mecklenbeck et al., 2011). In other words, process models require process data. These data allow for rejection of inadequate models and development of better models.

This is exactly where neuroscience comes in, as neuroscientific data also provides information on underlying processes. Study 3 of the present thesis gives an illustrative example. Going beyond previous behavioral models that are mute to the sources of loss aversion (such as Prospect Theory), we provide evidence that loss aversion and context-dependent changes in its magnitude are based on the context-dependent involvement of distinct neural valuation processes. Future research will benefit from placing a greater emphasis on acquiring process data to develop true process models of decision making. In the course of this, the development of such models will also benefit from a direct integration of emotional components (see, e.g., Charpentier, De Neve, Li, Roiser, & Sharot, 2016), and such models will likely better explain choice behavior as well as underlying processes than traditional models that are devoid of emotion (Volz & Hertwig, 2016).

6. Conclusion

The present thesis provides causal evidence that incidental emotions have an influence on risky choice that can be attributed to prospect-theoretic components. Specifically, incidental happiness was associated with more optimistic probabilistic weighting in the gain domain, and incidental fear cues increased monetary loss aversion in mixed gambles. Although prospect-theoretic parameters give some indications on potential underlying processes, process data are required to develop true process models of decision making. Going beyond behavioral models that are mute to the sources of loss aversion, we found that emotion-induced increases in loss aversion were mediated by a context-dependent shift in neural value processing. This illustrates that future research should place a greater emphasis on linking emotion, choice, and neurocognitive processes to arrive at a full mechanistic understanding of emotional effects on decision making.

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8. Appendix

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The official citation that should be used in referencing this material is: Schulreich, S., Heussen, Y. G., Gerhardt, H., Mohr, P. N. C., Binkofski, F. C., Kölsch, S., & Heekeren, H. R. (2014). Music-evoked incidental happiness modulates probability weighting during risky lottery choices. *Frontiers in Psychology: Decision Neuroscience*, *4*, Article 981 (1-17). https://doi.org/10.3389/fpsyg.2013.00981

Journal homepage: https://www.frontiersin.org/journals/psychology

Original article: https://www.frontiersin.org/articles/10.3389/fpsyg.2013.00981/full

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 07 January 2014
doi: 10.3389/fpsyg.2013.00981

Music-evoked incidental happiness modulates probability weighting during risky lottery choices

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We often make decisions with uncertain consequences. The outcomes of the choices we make are usually not perfectly predictable but probabilistic, and the probabilities can be known or unknown. Probability judgments, i.e., the assessment of unknown probabilities, can be influenced by evoked emotional states. This suggests that also the weighting of known probabilities in decision making under risk might be influenced by incidental emotions, i.e., emotions unrelated to the judgments and decisions at issue. Probability weighting describes the transformation of probabilities into subjective decision weights for outcomes and is one of the central components of cumulative prospect theory (CPT) that determine risk attitudes. We hypothesized that music-evoked emotions would modulate risk attitudes in the gain domain and in particular probability weighting. Our experiment featured a within-subject design consisting of four conditions in separate sessions. In each condition, the 41 participants listened to a different kind of music—happy, sad, or no music, or sequences of random tones—and performed a repeated pairwise lottery choice task. We found that participants chose the riskier lotteries significantly more often in the "happy" than in the "sad" and "random tones" conditions. Via structural regressions based on CPT, we found that the observed changes in participants' choices can be attributed to changes in the elevation parameter of the probability weighting function: in the "happy" condition, participants showed significantly higher decision weights associated with the larger payoffs than in the "sad" and "random tones" conditions. Moreover, elevation correlated positively with self-reported music-evoked happiness. Thus, our experimental results provide evidence in favor of a causal effect of incidental happiness on risk attitudes that can be explained by changes in probability weighting.

Keywords: decision making, happiness, incidental emotions, music, probability weighting, prospect theory, risk, risk aversion

INTRODUCTION

Making decisions under risk is an integral part of our lives: we order meals that we have not tried yet, buy products that we have never used before, and we decide how to invest money for ourselves, for friends, or for customers. In both economics and psychology, risk is often understood as a function of the variability of outcomes. People's attitudes toward this variability differ substantially (see, e.g., Dohmen et al., 2011) and can be characterized by their degree of risk aversion (or risk proclivity, respectively). A risk-averse person prefers a sure outcome over any gamble that has the same expected value; for a risk-loving person, the opposite holds (Wakker, 2010, p. 52). For instance, a risk averter prefers €5 for sure over the gamble that pays €10 with a probability of 75% and −€10 with 25% probability.

In (cumulative) prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), risk attitudes expressed in people's decisions are attributed to several constructs that describe how the available options are subjectively evaluated. The three constructs are (1) comparison of the objective outcomes with a reference point, (2) transformation of the resulting gains and losses into subjective values, and (3) transformation of the objective probabilities associated with the possible outcomes into subjective decision weights for those outcomes. The two subjective transformations are formalized by the value function and the probability weighting function, respectively. Both functions are thought to reflect the often observed psychophysical characteristic of diminishing marginal sensitivity, i.e., less sensitivity to changes in outcomes and probabilities, the farther they are away from the respective reference points. This results in a convex value function for losses and a concave value function for gains. For gains and losses, the reference point can be, for instance, the status quo (i.e., the current wealth level). For probability weighting, the extreme cases of impossibility ($p = 0$) and certainty ($p = 1$) are the two natural points of reference (Fox and Poldrack, 2013). This results in an inverse S-shaped form of the probability weighting function, reflecting the common empirical finding that small probabilities are overweighted and large probabilities are underweighted.

Studies that used semiparametric (Abdellaoui et al., 2011) or parametric (Fehr-Duda et al., 2010) specifications of the value and the probability weighting function suggest that probability weighting is more susceptible to situational influences than outcome valuation. As a consequence, there is increasing interest in the factors that determine the shape of the probability weighting function—especially its two main characteristics, curvature and elevation (see the discussion in Gonzalez and Wu, 1999).

One important factor that influences probability weighting seems to be affect, as several theoretical accounts of the determinants of probability weighting suggest. According to one account, the commonly observed inverse S-shape of the probability weighting function results from anticipated elation or disappointment regarding the future realization of an uncertain payoff (Gul, 1991; Brandstätter et al., 2002; Walther, 2003). For instance, one might anticipate disappointment from a failure to achieve a highly probable gain. This in turn is thought to translate into decision weights for high probabilities that are lower than the actual probabilities.

In a similar vein, Rottenstreich and Hsee (2001) hypothesized that the extent of probability weighting depends on the "affective richness" of potential outcomes. Confirming their hypothesis, the authors found that "affect-rich" outcomes—i.e., outcomes which participants anticipate to elicit strong emotional reactions (such as receiving an electric shock or a kiss)—were associated with more pronounced probability weighting than less "affect-rich" outcomes (such as receiving money). The authors speculated that hope and fear generated by affect-rich outcomes give rise to the shape of the probability weighting function. Although these studies focused on the curvature of the probability weighting function, it has been pointed out that also the elevation parameter might capture an emotional influence (Rottenstreich and Hsee, 2001).

Importantly, not only emotions related to the decision outcomes might be reflected in probability weighting. Even incidental emotions, which are characterized by being unrelated to the judgments and decisions at issue (Loewenstein and Lerner, 2003; Weber and Johnson, 2009), were found to have an influence on probability judgments, i.e., the assessment of unknown probabilities. For instance, happy people made more optimistic probabilistic judgments and sad people more pessimistic judgments (Johnson and Tversky, 1983; Wright and Bower, 1992). It is thus plausible that similar effects are observable in the subjective weighting of known probabilities in decision making under risk. The elevation of the probability weighting function is thus a promising target of affect, with greater elevation representing more optimistic attitudes and reduced elevation more pessimistic attitudes toward risky situations.

While there is a considerable body of evidence on the influence of incidental emotions on decision making under risk, only a few studies linked incidental emotions specifically to the constructs postulated by cumulative prospect theory (CPT). For instance, Isen et al. (1988) found that positive affect made participants value losses more negatively, while it had no significant effect on the valuation of gains. Thus, positive affect made participants more loss-averse. The authors, however, restricted their design to two-outcome lotteries with 50%/50% probabilities and did not investigate the role of probability weighting. In a recent study, Fehr-Duda et al. (2011) provided correlational evidence that they interpreted as an effect of mood on the elevation of the probability weighting function for both gains and losses in women, but not in men. Women that regarded the current day to be more promising than usual made decisions that are consistent with more optimistic probability weighting. A similar link was also suggested in another study that revealed a correlation between seasonal and weather conditions and probability weighting, which the authors also interpreted as mood effects (Kliger and Levy, 2008).

Studies without direct manipulation and measurement of affective states leave open the question whether incidental emotions are indeed the mediator of the effects mentioned above. To answer this question, it is necessary to establish a causal effect of incidental emotions on risk attitudes that is consistent with probability weighting in particular. One way to prove a causal effect is to experimentally manipulate incidental emotions, record participants' self-reported emotions, and investigate the emotion-induced changes in probability weighting.

To this end, we employed a variant of the Random Lottery Pairs procedure (Hey and Orme, 1994) and manipulated emotions within-subject by playing different types of music to our participants. They listened to happy and sad music as well as to sequences of random tones or to no music at all.

To determine whether the emotion manipulation had an effect on participants' decision making, we compared the frequencies with which they chose the riskier lotteries between conditions. Furthermore, we estimated preference parameters via structural regressions based on CPT and tested whether probability weighting changed between conditions.

Based on the studies that established a link between incidental emotions and optimistic or pessimistic probability judgments (Johnson and Tversky, 1983; Wright and Bower, 1992), we hypothesized that probability weighting in decision making under risk would be affected in a similar way. Specifically, we hypothesized that participants in the "happy" condition exhibit increased probabilistic optimism in the sense that they attach higher decision weights to the larger outcomes. In contrast, listening to sad music should lead to more pessimistic probability weighting, i.e., lower decision weights associated with the larger outcomes. We expected this effect to manifest itself also in a relationship between the self-reported emotional state and the extent of probability weighting.

Because an increased elevation of the probability weighting function implies a reduction in risk aversion (see Wakker, 2010, chapter 5), it follows from these hypotheses that participants should choose the riskier lottery more frequently after listening to happy music than after listening to sad music.

Research has repeatedly demonstrated that the intensity of evoked emotions gradually decreases over time (Isen et al., 1972; Isen and Gorgoglione, 1983; Gard and Kring, 2007; Andrade and Ariely, 2009). Thus, we hypothesized that music-evoked emotional effects on risk attitudes would be strongest at the beginning and then diminish. This would corroborate an affective interpretation of the effects on decision making.

MATERIALS AND METHODS

PARTICIPANTS

We recruited 46 participants through bulletin-board appeals at Freie Universität Berlin and an e-mail mailing list to which previous and prospective participants had subscribed. Four participants had to be excluded from the analysis because they did not participate in all sessions. One participant was dropped from the analysis because she stated in the post-experimental questionnaire that she had chosen arbitrarily between the lotteries presented. The remaining 41 participants (28 women; 13 men) had a mean age of 27.37 years ($SD = 7.832$ years). All participants gave written informed consent prior to the experiment.

PROCEDURE

Experimental design

In a within-subject design, participants were exposed to auditory stimulation: (1) happy or (2) sad music or (3) sequences of random tones, while (4) no music was played in the fourth condition. Each of the four experimental conditions was tested in a separate session. The order of the conditions was randomized, and all sessions were one week apart. In three of the conditions, up to four participants were present in the lab simultaneously. Each participant sat in front of a computer equipped with headphones and enclosed in cubicles to prevent eye contact with the other participants during the experiment. All tasks were presented on a computer screen (except the post-experimental questionnaires, which were handed out on paper), and all data were recorded using the software Presentation (Neurobehavioral Systems, Inc.). Responses were made via a standard keyboard.

The experimenter handed out instructions and read them aloud. Subsequently, participants answered a quiz on the instructions to make sure that they had understood the lottery choice task. At the beginning of the music conditions, participants shortly listened to the musical pieces for familiarization. In the "no music" condition, participants filled in the demographic questionnaires.

The main experiment started with the emotion evocation and the emotional rating task (see below). In the "no music" condition, it started with the emotion rating task right away, while in all other conditions, participants first listened to music for exactly 6 min via headphones. The subsequent block of pairwise lottery choices lasted approximately 10 min, comprised 50 trials (plus five initial learning trials), and was followed by the second emotion rating task (see **Figure 1**). In each trial, participants were asked to choose one of two lotteries within a time frame of 8 s. Participants did not receive any feedback on earnings in-between trials. The trials were separated by a variable interval (3–6 s), which served as a short period of rest and as a means to minimize potential anticipation effects and repetitive behavioral patterns. The entire sequence was repeated—except for the familiarization phase and the learning trials—so that each condition included two music blocks, four emotion ratings tasks (two post-music, two post-choice), and 100 lottery choices in total. The same set of 100 different lottery pairs (see **Table A1** in the Appendix) was used in each condition.

At the end of each session, participants filled in a questionnaire concerning their choice strategies and thoughts on the experiment's purpose. None of the participants mentioned any hypothesis concerning an emotion-specific connection between the type of music played and their level of risk aversion. After the final session, participants learned their individual earnings and received them in cash. These consisted of a randomly determined payoff according to the gamble they had chosen in one randomly selected trial plus the total attendance fee of €24 for all four sessions.

Musical stimuli

The musical stimuli were chosen to evoke (a) happiness, (b) sadness, and (c) neither happiness nor sadness. The latter stimuli we refer to as "random tones" (for the complete list of stimuli see **Table A2**). The happy pieces and random tone sequences had been used in a recent study (Koelsch et al., 2013). Half of the sad pieces were used by Pehrs et al. (2013), overlaid with an acoustically identical electronic beat.

The happy pieces consisted of 12 instrumental excerpts of 30 s duration each from various epochs and styles (classical music, Irish jigs, jazz, reggae, South American, and Balkan music). Sad pieces were classical and indie-pop pieces with a duration of 60 s each, selected on the basis of features that have been shown to evoke sad feelings, i.e., minor key, slow tempo, and low pitch variation (Juslin and Laukka, 2004; Lundqvist et al., 2009). The 12 random tone sequences featured acoustically changing stimuli of 30 s duration. These isochronous tones for which the pitch classes were randomly selected from a pentatonic scale (see Koelsch et al., 2013) were created with the help of the MIDI toolbox for MATLAB (Eerola and Toiviainen, 2004).

The manipulation check revealed that the random tones were not affectively neutral (see Results). Consequently, the "no music" condition remains as the one condition in which the affective state was not manipulated.

All stimuli were non-vocal pieces, edited with Praat (version 5.0.29, Boersma, 2002) to feature a 1.5-s fade-in and fade-out and the same intensity (70 dB). The total duration of the sad music pieces matched the total duration of the auditory stimulation in the other conditions (i.e., 6 min).

Emotion rating

In the computerized, self-paced emotion rating task, participants reported their current emotional state by indicating the degree to which they agreed with three statements concerning happiness ("I am happy"), sadness ("I am sad"), and calmness ("I am calm"). The latter served as a reverse proxy for arousal. The scale ranged from 1 ("I completely disagree") to 9 ("I completely agree"). These items correspond to those typically used to infer basic emotions (e.g., in the Differential Emotions Scale, see Izard et al., 1993). Basic emotions have proven to be more informative than the concept of valence alone to study the effect of emotions on risky choices (Lerner and Keltner, 2000, 2001).

To reduce potential experimenter demand effects (Orne, 1962) and to obscure the objective of the emotion ratings from the participants in the sense of "non-deceptive obfuscation" (Zizzo, 2010), seven additional ratings were acquired that were not directly related to basic emotional states (e.g., "I slept well last night"; for the complete list, see **Table A3** in the Appendix).

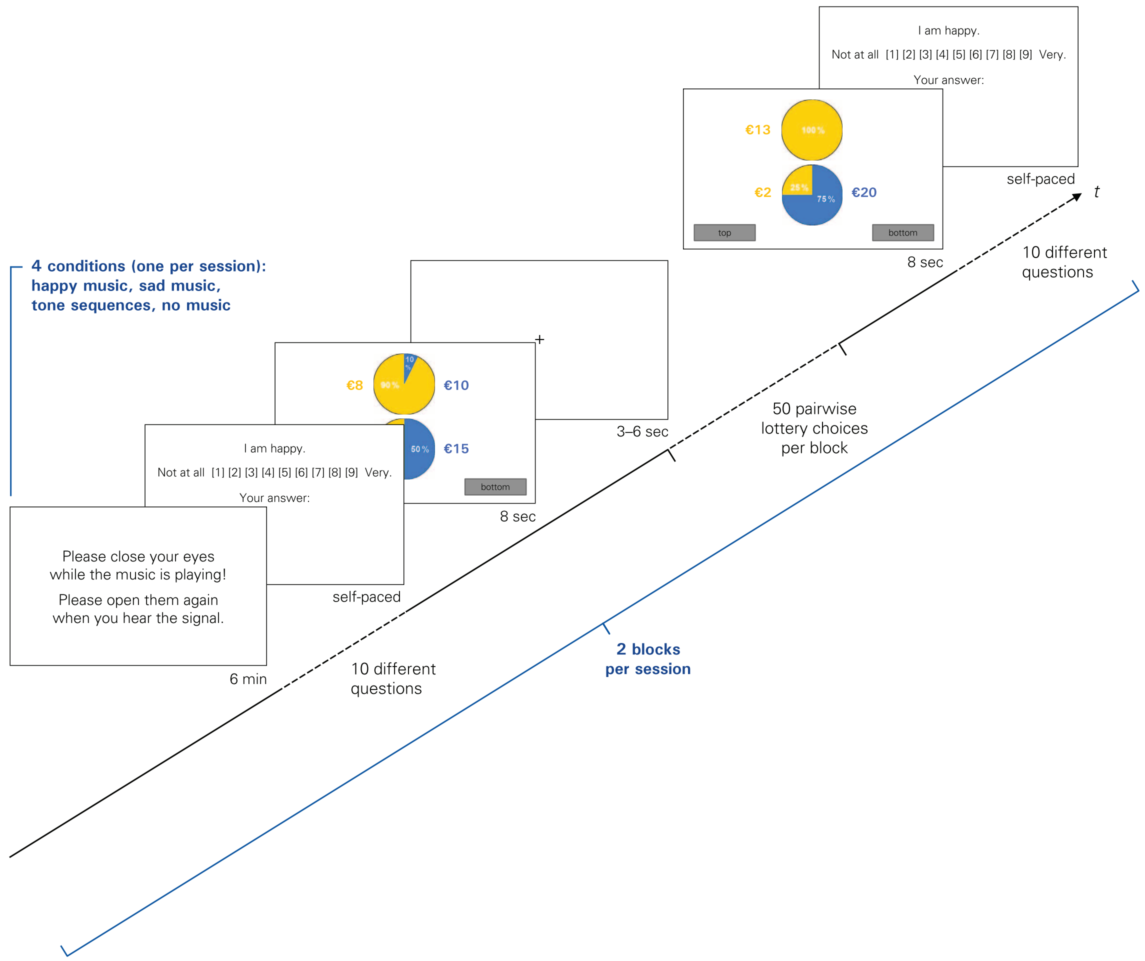

FIGURE 1 | The sequence of events forming one block in the experiment. Each condition consisted of two such blocks, separated by a short break.

Lottery choice task

For the lottery choice task, we used a variant of the Random Lottery Pairs procedure (Hey and Orme, 1994). In each trial t, participants were shown a lottery pair $\{\boldsymbol{A}_t, \boldsymbol{B}_t\}$ out of a set of 100 lottery pairs (for the complete list, see **Table A1** in the Appendix) in pseudo-random order. The pseudo-random order differed per session/condition and per subject.

Each lottery $\boldsymbol{L}$ consisted of two possible, strictly positive payoffs $(x_{L,1}, x_{L,2})$, denoted in euro, and the associated probabilities $(p_{L,1}, p_{L,2}) = (p_{L,1}, 1 - p_{L,1})$. We limited our study to the gain domain for the following reasons: first, neuroimaging and lesion studies suggest that losses and gains are processed differently in the human brain (Tom et al., 2007; De Martino et al., 2010). Second, to increase the power for the detection of an effect, a sufficient number of decision trials is needed. Third, mixed gambles would have required the estimation of additional parameters, making even more observations necessary. We therefore chose to dedicate all our experimental trials to only one domain.

The payoffs and probabilities were visualized on screen by a pie chart (see **Figure 1**), which is a common graphical representation of lotteries in this type of experiments (Harrison and Rutström, 2008). Apart from some "catch trials," we ensured that within each pair, no lottery first-order stochastically dominated the other lottery.

The lotteries differed from each other in their riskiness. A lottery can be considered riskier than another lottery if it can be expressed as a mean-preserving spread (MPS) of the other lottery (Rothschild and Stiglitz, 1970). Since risk averters dislike the wider spread, making them choose the riskier lottery requires adding some compensation for the wider spread—a "risk premium"—to the riskier lottery. We denote this risk premium by m. Within a lottery pair $\{\boldsymbol{A}_t, \boldsymbol{B}_t\}$, we thus call the lottery $\boldsymbol{A}_t$ the riskier lottery if it has a wider spread than $\boldsymbol{B}_t$, such that $\boldsymbol{A}_t = \text{MPS}(\boldsymbol{B}_t) + m_t$ (m_t being a sure payoff)[1].

[1]We obtain qualitatively identical results if we consider variance as the risk measure—i.e., if we take the presence of a mean–variance trade-off as the criterion for one lottery (the one with the higher variance, but also the higher average payoff) to be riskier than the other. A wider spread implies increased variance, but not vice versa, so that the two measures coincide in many but not all of our trials.

The set of lottery pairs was designed to allow estimating preference parameters with relatively high precision in the range that has been found in previous studies (see, e.g., the examples given in Harrison and Rutström, 2008; Table 5 in Stott, 2006). That is, for degrees of risk aversion usually observed in lab experiments, we expected participants to sometimes choose the riskier and sometimes the less risky lottery. In addition, the payoffs of our lotteries were associated with probabilities spanning 10 to 90% to cover a broad enough range to reliably estimate the parameters of the probability weighting function.

Positioning of the lotteries on screen was counterbalanced within-subject: in some trials, the riskier lottery was presented in the upper half of the screen, and sometimes in the lower one. Moreover, we counterbalanced the position of the larger payoff on screen between-subjects: for half of the participants, the larger payoff was illustrated by the left side, and for the other half, by the right side of the pie chart.

STATISTICAL ANALYSES

Emotion ratings

To check whether the experimental manipulation had the desired emotional effects, we calculated repeated-measures ANOVAs using the four conditions as the within-subject factor. As dependent variables in these ANOVAs we used the ratings in three affective dimensions (happiness, sadness, and calmness). For each dimension, we analyzed the ratings obtained immediately after the musical stimulation ("post-music ratings"). In these analyses, we used the average of the two post-music ratings per condition and per participant. We also calculated an ANOVA for the average post-choice ratings to investigate if emotional effects persisted over time.

Lottery choices

Relative frequency with which the riskier lottery was chosen. We analyzed how often the riskier of the lotteries included in a pair was chosen in those trials in which one lottery is riskier than the other according to the measure explained above. This is the most basic measure of the influence of music-evoked emotions on risk attitudes.

These choice frequencies were compared across the four conditions. To establish whether there are significant differences between the four conditions, we estimated linear probability models (LPMs)[2]. That is, we regressed choice of the riskier lottery on condition dummies. Let us denote participant *i*'s choice in trial *t* by $r_{i,t}$, and set $r_{i,t} = 1$ if the riskier lottery was chosen by *i* in trial *t*, and $r_{i,t} = 0$ otherwise. The regression equation then is

$$r_{i,t} = \beta_{\text{hap},i} + \delta_{\beta,\text{nom}} D_{\text{nom},i,t} + \delta_{\beta,\text{ton}} D_{\text{ton},i,t} + \delta_{\beta,\text{sad}} D_{\text{sad},i,t} + \varepsilon_{i,t}.$$

β_{hap} is the relative frequency at which the riskier lottery was chosen in the "happy" condition (which here serves as the reference condition). $\delta_{\beta,\text{nom}}$ captures the difference in the choice of the riskier lottery in the "no music" condition vis-à-vis the "happy" condition, while $\delta_{\beta,\text{ton}}$ does the same for the "random tone sequences" condition, and $\delta_{\beta,\text{sad}}$ for the "sad" condition. D is the respective condition dummy regressor, and $\varepsilon_{i,t}$ is an error term with mean zero. Our regression allowed for heterogeneity in risk aversion in the reference category between subjects *i* via individual random effects in the regression's constant term, here $\beta_{\text{hap},i}$.

A more versatile regression also included regressors $d_{i,t}$ measuring how many trials had passed since the last musical stimulation. This was done to investigate whether the effect of the evoked emotions on risk attitudes diminished over time. We denote the associated coefficients by $\tau_{\beta,\text{cond}}$:

$$\begin{aligned} r_{i,t} = {} & \beta_{\text{hap},i} + \tau_{\beta,\text{hap}} d_{i,t} D_{\text{hap},i,t} + \left(\delta_{\beta,\text{nom}} + \tau_{\beta,\text{nom}} d_{i,t}\right) D_{\text{nom},i,t} \\ & + \left(\delta_{\beta,\text{ton}} + \tau_{\beta,\text{ton}} d_{i,t}\right) D_{\text{ton},i,t} \\ & + \left(\delta_{\beta,\text{sad}} + \tau_{\beta,\text{sad}} d_{i,t}\right) D_{\text{sad},i,t} + \varepsilon_{i,t}. \end{aligned}$$

To simplify comparison of the more extensive model with the reduced model, the regressor $d_{i,t}$ was centered.

Participants failed to respond in only 72 out of $41 \times 4 \times 100 = 16{,}400$ trials (0.439%), such that we had to omit these trials in the analysis. In the LPMs, the number of observations is lower, since not all trials featured a "risky–less risky" trade-off as defined above via mean-preserving spreads; 70 out of the 100 lottery pairs we used involved a trade-off of this kind (while others involved, e.g., mean–variance trade-offs).

We compared several models, which differed in the number of random effects—i.e., individual random effects were included either only in the baseline risk aversion or also in the between-condition changes and/or in the time trends. The two models described in detail above yielded the lowest Bayesian Information Criteria (BICs).

Structural regressions. To find out whether changes in participants' choices between conditions can indeed be attributed to changes in probability weighting, we estimated structural regression models (see, e.g., Harrison and Rutström, 2008, section 2.2; Wilcox, 2011). These are based on cumulative prospect theory (CPT). In CPT, monetary payoffs and the probability of receiving these payoffs are transformed into subjective values via a value (utility) function u and a probability weighting function w, respectively.

If participants assign a subjective value V to a lottery in line with CPT, probability weighting is applied to the probability of the larger payoff (see Tversky and Kahneman, 1992). That is, if we denote the larger payoff in lottery $\boldsymbol{L} = (x_{\boldsymbol{L},1}, p_{\boldsymbol{L},1}; x_{\boldsymbol{L},2}, p_{\boldsymbol{L},2})$ by $x_{\boldsymbol{L},1}$, the subjective value V is given by

$$V(\boldsymbol{L}; \boldsymbol{\theta}) \equiv w\left(p_{\boldsymbol{L},1}; \boldsymbol{\theta}_w\right) u\left(x_{\boldsymbol{L},1}; \boldsymbol{\theta}_u\right) + \left[1 - w\left(p_{\boldsymbol{L},1}; \boldsymbol{\theta}_w\right)\right] u\left(x_{\boldsymbol{L},2}; \boldsymbol{\theta}_u\right).$$

$\boldsymbol{\theta}$ is a vector combining the parameter vectors $\boldsymbol{\theta}_w$ and $\boldsymbol{\theta}_u$ that determine the shape of the probability weighting function and the shape of the utility function, respectively. It is these parameters

[2]Using a probit or logit model instead of the linear probability model yields qualitatively identical results. However, the estimates obtained via an LPM are easier to interpret.

and their potential modulation by the emotional state that we are interested in.

Regarding the transformation of the payoffs, we assume—in line with many previous studies (e.g., Tversky and Kahneman, 1992)—a power utility function[3], i.e.,

$$u\,(x;\,\boldsymbol{\theta}_u) = u(x;\,\rho) = x^{1-\rho},$$

such that a larger ρ goes along with increased curvature of the utility function—i.e., all other things equal, increased risk aversion[4]. For the probability-weighting function, we use a popular two-parameter version (Prelec, 1998),

$$w\left(p;\,\boldsymbol{\theta}_w\right) = w\left(p;\,\alpha,\beta\right) = \exp\{-\beta(-\log p)^{\alpha}\}.$$

Here, $w(p; \alpha, \beta)$ is the decision weight, p is the objective probability, and α and β are parameters. Two-parameter versions of probability weighting have found broad empirical support due to their ability to explain individual differences or differences between choice domains (Gonzalez and Wu, 1999; Abdellaoui, 2000; Bleichrodt and Pinto, 2000; Abdellaoui et al., 2010; Capra et al., 2012). Importantly, the two parameters are moreover thought to reflect different psychological phenomena (see, e.g., Gonzalez and Wu, 1999). The parameter α primarily influences the slope of the probability weighting function: for $\beta = 1$, $\alpha < 1$ results in overweighting of small and underweighting of large probabilities, with the consequence of relative insensitivity $[\partial w(p; \alpha, 1)/\partial p < 1]$ in the intermediate range. The parameter β primarily reflects the elevation of the weighting function and can be interpreted as reflecting the "attractiveness" of gambling: for $\alpha = 1$, $\beta > 1$ results in an underweighting of all probabilities $[w(p; 1, \beta) < p]$. That is, in CPT, a less elevated weighting function assigns a lower decision weight to the higher outcome—see the formula for $V(\boldsymbol{L}; \rho, \alpha, \beta)$. This has also been interpreted as a form of "pessimism" (in Fehr-Duda et al., 2011). Through the reduced decision weight on the higher lottery outcome, reduced elevation of the probability weighting function translates to greater risk aversion.

Based on this, for each lottery pair $\{\boldsymbol{A}, \boldsymbol{B}\}$, the difference in the subjective values, $\Delta V(\boldsymbol{A}, \boldsymbol{B}; \boldsymbol{\theta}) \equiv V(\boldsymbol{A}; \boldsymbol{\theta}) - V(\boldsymbol{B}; \boldsymbol{\theta})$, is determined. A decision maker whose preferences can be represented by the subjective value function V chooses $\boldsymbol{A}$ over $\boldsymbol{B}$ whenever the subjective value of $\boldsymbol{A}$ is larger than that of $\boldsymbol{B}$, i.e., $\Delta V(\boldsymbol{A}, \boldsymbol{B}; \boldsymbol{\theta}) > 0$, and vice versa. Of course, participants do not make choices that are perfectly consistent with the assumed model. The most frequently used binary-choice regressions—the logit and the probit specification—account for this by mapping the difference in subjective valuation, $\Delta V(\boldsymbol{A}, \boldsymbol{B}; \boldsymbol{\theta})$, to choice probabilities via a strictly increasing, symmetric ("sigmoid") link function F. Formally,

$$\Pr[\boldsymbol{A}|\{\boldsymbol{A},\boldsymbol{B}\};\,\boldsymbol{\theta},\sigma] = F[\Delta V(\boldsymbol{A},\boldsymbol{B};\,\boldsymbol{\theta})/\sigma] \quad \text{and}$$
$$\Pr[\boldsymbol{B}|\{\boldsymbol{A},\boldsymbol{B}\};\,\boldsymbol{\theta},\sigma] = 1 - F[\Delta V(\boldsymbol{A},\boldsymbol{B};\,\boldsymbol{\theta})/\sigma].$$

We use the logit specification, such that the link function F is the logistic distribution function, $F[\Delta V] = 1/[1 + e^{-\Delta V}]$[5].

The parameter σ governs the dispersion (flatness) of the link function. It is often called the Fechner noise parameter (see Harrison and Rutström, 2008). The larger σ (i.e., the more noise), the smaller the fraction gets, with the effect that $\sigma \rightarrow \infty$ is equivalent to random choice (i.e., $F \rightarrow$ ½). Conversely, $\sigma \rightarrow 0$ means that no noise is present in participants' choices from the perspective of the model, and the choice probabilities converge to a step function.

Based on both theoretical and econometric considerations, it has been suggested to modify this common approach (Wakker, 2010, p. 85; Wilcox, 2011), because it suffers from the fact that the utility assigned to a certain payoff in expected utility theory or CPT is only unique up to an affine transformation (Wilcox, 2011, p. 90). However, the common approach effectively takes the ordinal quantity subjective utility to be a cardinal quantity. Wilcox (2011) shows that this has the consequence that being "more risk-averse" in the theoretical sense (Pratt, 1964) and being "stochastically more risk-averse" do not coincide: it is easy to find pairs, e.g., of a lottery $\boldsymbol{B}$ and a sure payoff $A = \mathrm{E}[\boldsymbol{B}]$ for which the difference in subjective valuation, ΔV, approaches zero if one increases the degree of risk aversion (ρ ↑). Consequently, the predicted probability of choosing either alternative approaches ½—which is non-sensical, since greater risk aversion (ρ ↑) should imply a predicted probability of choosing the sure payoff that increases and approaches one.

A remedy to this problem is to replace the difference in subjective valuation, ΔV, by the difference between the certainty equivalents of these valuations (Wakker, 2010, p. 85; Von Gaudecker et al., 2011, p. 676)—i.e., sure amounts of money that carry the same subjective value as the lotteries. Under power utility, the certainty equivalent of a subjective value V is given by

$$CE(\boldsymbol{L};\,\boldsymbol{\theta}) \equiv u^{-1}\,[V(\boldsymbol{L};\,\boldsymbol{\theta});\,\rho]\,.$$
$$= \begin{cases} [(1-\rho)V(\boldsymbol{L};\,\boldsymbol{\theta}) + 1]^{1/(1-\rho)} & \text{if } \rho \neq 1 \\ \exp[V(\boldsymbol{L};\,\boldsymbol{\theta})] & \text{if } \rho = 1. \end{cases}$$

We can then define, for each lottery pair $\{\boldsymbol{A}, \boldsymbol{B}\}$, the difference in the certainty equivalents, $\Delta CE(\boldsymbol{A}, \boldsymbol{B}; \boldsymbol{\theta}) = CE(\boldsymbol{A}, \boldsymbol{\theta}) - CE(\boldsymbol{B}, \boldsymbol{\theta})$. With this, the specification of the CPT-based latent-variable model becomes:

$$\Pr[\boldsymbol{A}|\{\boldsymbol{A},\boldsymbol{B}\};\,\boldsymbol{\theta},\sigma] = F[\Delta CE(\boldsymbol{A},\boldsymbol{B};\,\boldsymbol{\theta})/\sigma].$$

Let $\boldsymbol{C}_t$ denote the lottery that was actually chosen in trial t, and let $\mathbf{1}_{\boldsymbol{A}_t}$ be the indicator function such that $\mathbf{1}_{\boldsymbol{A}_t}(\boldsymbol{C}_t) = 1$ if $\boldsymbol{A}_t$ was

[3]We tried different specifications of the utility function. All yielded comparable fits, but power utility performed best (in line with the findings by Stott, 2006).

[4]To be precise, we used power utility of the form $u(x; \rho) = (x^{1-\rho} - 1)/(1 - \rho)$. This is completely equivalent to the often used $u(x; r) = x^r$, with $r = 1 - \rho$. The main advantage of using $1 - \rho$ as the exponent is the intuitive meaning of ρ: an increase in ρ indicates an increase in risk aversion—whereas for x^r, a decrease in r indicates an increase in risk aversion.

[5]Using a probit instead of a logit specification leads to negligible changes. Like Stott (2006), we found the logit model to provide the best fit.

chosen and 0 if $\boldsymbol{B}_t$ was chosen in t. The few trials in which participants failed to respond (72 out of 16,400) are omitted from the analysis. Let $D_{\text{cond},t}$ be a dummy regressor that equals 1 only in trials t belonging to the respective condition cond and 0 otherwise; for instance, when choosing the "happy" condition as the reference condition, the dummy regressors would cover cond ∈{"no music," "random tones," "sad music"}. T is the total number of trials in the experiment.

Non-linear maximum likelihood estimation maximizes the log-likelihood

$$\ell(\boldsymbol{\theta}, \boldsymbol{\Delta_\theta}, \sigma, \boldsymbol{\delta}_\sigma) \equiv$$

$$\sum_{t=1}^{T} \left\{ \mathbf{1}_{A_t}(\mathbf{C}_t) \log F \left[\frac{\Delta CE(\boldsymbol{A}_t, \boldsymbol{B}_t; \boldsymbol{\theta} + \sum_{\text{cond}} \boldsymbol{\delta}_{\boldsymbol{\theta},\text{cond}} D_{\text{cond},t})}{\sigma + \sum_{\text{cond}} \delta_{\sigma,\text{cond}} D_{\text{cond},t}} \right] + \right.$$

$$\left. \{\mathbf{1} - 1_{A_t}(C_t)\} \log \left\{ 1 - F \left[\frac{\Delta CE(\boldsymbol{A}_t, \boldsymbol{B}_t; \boldsymbol{\theta} + \sum_{\text{cond}} \boldsymbol{\delta}_{\boldsymbol{\theta},\text{cond}} D_{\text{cond},t})}{\sigma + \sum_{\text{cond}} \delta_{\sigma,\text{cond}} D_{\text{cond},t}} \right] \right\} \right\}.$$

That is, $(\hat{\boldsymbol{\theta}}, \widehat{\boldsymbol{\Delta}}_{\boldsymbol{\theta}}, \hat{\sigma}, \hat{\boldsymbol{\delta}}_\sigma) \equiv \arg\max \ell(\boldsymbol{\theta}, \boldsymbol{\Delta_\theta}, \sigma, \boldsymbol{\delta}_\sigma)$. $\boldsymbol{\theta}$ and σ are the preference and noise parameters that describe behavior in the reference condition. The matrix $\boldsymbol{\Delta_\theta}$ and the vector $\boldsymbol{\delta}_\sigma$ capture the changes in $\boldsymbol{\theta}$ and the changes in the Fechner noise parameter σ, respectively, between the reference condition and the three remaining conditions.

We compared a full model that permitted condition-wise changes in both the value function parameter (ρ) and the probability weighting function parameters (α, β) with a more parsimonious model that only allowed for changes in probability weighting. To account for between-subject heterogeneity in the valuation of outcomes and in probability weighting, these regressions allowed for individual random effects in ρ, α, and β. Allowing for changes in the curvature of the value function did not significantly improve the model's fit to the data, as assessed by a likelihood-ratio test. Therefore, we report the parameter estimates of the more parsimonious model in detail. F-statistics were calculated, and individual coefficients were tested for significance.

Complementary structural regressions. We investigated the link between incidental emotions and probability weighting in a complementary way by using participants' self-reported happiness ratings as explanatory variables. Specifically, we calculated for each participant the average of the four happiness ratings in the "no music" condition and used this individual average as a between-subject regressor. The average score of the "no music" condition represents baseline happiness, as there was no experimental manipulation of affect in this condition. We then calculated, for each participant, the deviation of the condition-specific happiness ratings (i.e., one value per condition, calculated as the average of the four ratings obtained per condition) from his/her individual baseline happiness; this deviation served as a within-subject regressor.

In other words, this regression allowed us to investigate (a) whether participants who are happier in general exhibit more/less pronounced probability weighting, and (b) whether the music-evoked within-subject variation in reported happiness also predicts the extent of probability weighting for the respective trials. Both the curvature and the elevation of the probability weighting function were modeled as depending on the condition-specific happiness ratings, whereas the curvature of the value function was assumed to be invariant across conditions. Our hypothesis was that both the between-subject and the within-subject effect would point in the same direction: the greater self-reported happiness, the lower the degree of probabilistic pessimism. The same procedure was used for the individual sadness and calmness ratings.

RESULTS

MUSIC-EVOKED INCIDENTAL EMOTIONS

To test whether participants' emotional states were altered by our experimental manipulation, we compared the self-reported emotions between the conditions. As expected, participants' self-reported happiness was affected by the music that they had listened to (see **Figure 2**). Immediately after musical stimulation ("post-music"), participants' self-reported happiness varied significantly between conditions [$F_{(3,\ 120)} = 2.745, p = 0.046$]. This effect vanished until the second emotion rating at the end of a block, approximately 10 min later ["post-choice"; $F_{(3,\ 120)} = 0.816, p = 0.487$]. This is consistent with a diminishing intensity of evoked incidental emotions over time.

As expected, pairwise comparisons revealed that immediately after the musical stimulation, participants reported to be happier when they had listened to happy music than to sad music [$t_{(40)} = 2.219$, $p = 0.032$]. This also holds for the comparison between happy music and random tone sequences [$t_{(40)} = 2.877$, $p = 0.006$]. Reported happiness for random tone sequences was not significantly different from reported happiness for sad music [$t_{(40)} = -0.047$, $p = 0.962$]. Taken together, this indicates that the "random tone sequences" condition was affectively more

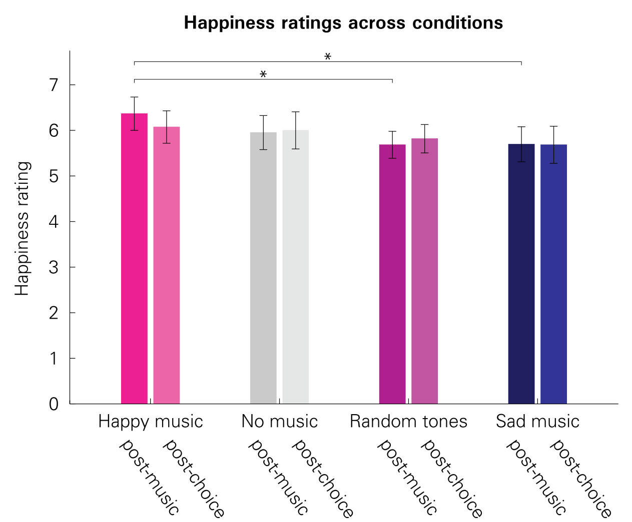

FIGURE 2 | Subjective happiness ratings across the four conditions. Darker bars illustrate the values immediately after musical stimulation ("post-music"); brighter bars illustrate the values after the lottery choice blocks ("post-choice"). Error bars represent 95% confidence intervals. The scale ranged from 1 (not happy at all) to 9 (very happy). An asterisk indicates significant difference at the 5% level.

similar to the “sad” condition rather than being affectively neutral. No other differences were significant (all $p > 0.149$).

Mirroring the lowest happiness ratings, sadness ratings were highest in the “sad” condition. The within-subject effect for condition was only marginally significant, however, for the ratings taken directly after the musical stimulation [$F_{(3,\ 120)} = 2.190$, $p = 0.093$]. This trend toward significance might be due to a difference between the “sad” and “no music” condition [$t_{(40)} = 2.41$, $p = 0.021$], indicating that sad music was associated with greater sadness than no experimental manipulation (no music). The remaining comparisons were, however, not significant (all $p > 0.152$). Differences in the post-choice ratings were also not significant [$F_{(3,\ 120)} = 1.759, p = 0.159$].

Calmness ratings, which we consider an inverse indicator of arousal, did not show any significant post-music differences [$F_{(3,\ 120)} = 1.435$, $p = 0.236$] or post-choice differences [$F_{(3,\ 120)} = 1.251, p = 0.294$].

In summary, ratings reveal that music differentially altered the emotional state of happiness and that this effect diminished over time. Happy music was associated with greater happiness, whereas sad music and random tone sequences were associated with lower happiness compared to the “happy” condition.

LOTTERY CHOICES

Choice of the riskier lottery

Participants chose the riskier lottery most often in the “happy” condition and least often in the “sad” condition. The relative frequencies of the riskier lottery being chosen in the four conditions are visualized in **Figure 3**.

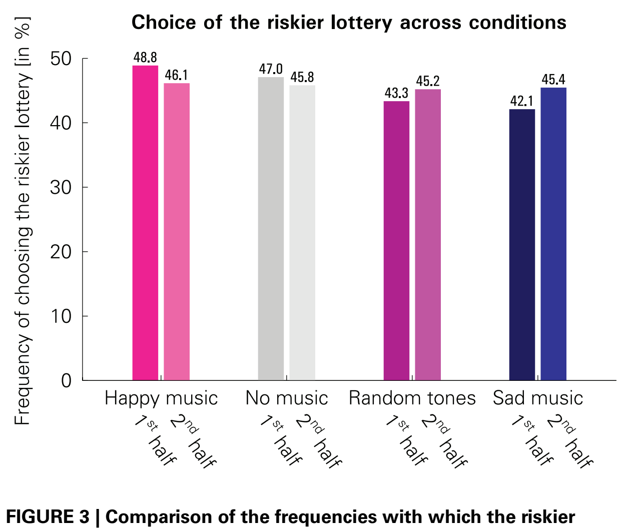

FIGURE 3 | Comparison of the frequencies with which the riskier lottery was chosen across the four conditions in the first 25 trials of a block following musical stimulation (1st half) and in the remaining 25 trials of a block (2nd half). (Please note that this chart is shown only for illustrative purposes and is not used for statistical inference, because the statistical analysis needs to account for both between-subject and within-subject variation; see the description of LPM 1 and LPM 2 in the “Materials and methods” section.)

Linear probability models (LPMs) were used to test whether these differences are statistically significant. In contrast to LPM 1, LPM 2 not only allows for analyzing the average effect of the conditions on choices, but it also permits analysis of the initial effects—i.e., the estimated frequency at which participants chose the riskier lottery immediately following musical stimulation—and time trends.

F-tests for overall condition effects were significant for both models [LPM 1: $F_{(3,\ 11444)} = 4.7725$, $p = 0.0025$; LPM 2: $F_{(3,\ 11440)} = 4.8329$, $p = 0.0023$], indicating differences in risk attitudes between the conditions. The results are presented in **Table 1**. As hypothesized, the “happy” and the “sad” condition were the two extreme conditions, with the riskier lottery being chosen most often in the “happy” condition.

These two conditions differed from each other significantly ($p = 0.0013$) in LPM 1. The “happy” condition also differed significantly from “random tones” ($p = 0.0053$). In addition, the “sad” ($p = 0.0192$) and the “random tones” condition ($p = 0.0464$) were associated with higher risk aversion than “no music.”

These results carry over to LPM 2, except that for the difference between “random tones” and “no music” there was only a trend toward significance ($p = 0.0509$). In LPM 2, the estimated initial effects—i.e., choice of the riskier lottery immediately after having listened to the music—are even more pronounced than the average effects in both LPMs.

The estimated time trends in LPM 2 show that participants became more risk-averse over time when they started out with relatively low risk aversion (i.e., in the “happy” and “no music”

Table 1 | Random-effects linear probability models for the choice of the riskier lottery across the four conditions.

Condition	LPM 1	LPM 2		
	Average frequency (%)	Average frequency (%)	Initial frequency (%)	Time trend (%)
Happy music	$47.40^{tones,sad}$	$47.48^{tones,sad}$	$50.50^{tones,sad}$	$-0.12^{0,tones,sad}$
No music	$46.48^{tones,sad}$	46.43^{sad}	$49.11^{tones,sad}$	-0.11^{sad}
Random tones	$44.20^{happy,no}$	44.20^{happy}	$43.12^{happy,no}$	$+0.04^{happy}$
Sad music	$43.72^{happy,no}$	$43.75^{happy,no}$	$40.27^{happy,no}$	$+0.14^{0,happy,no}$

LPM 1 included only dummy regressors to detect differences between the conditions. In addition to that, LPM 2 also modeled the temporal distance from the last musical stimulation (as the number of trials completed since the last musical stimulation). The “time trends” column thus indicates by how much (in percentage points) the relative frequency at which the riskier lottery was chosen changed on average with each additional completed trial. t-tests were used to assess whether the parameter estimates are different from 0.

Significance at $p < 0.05$ indicated via superscripts:

^{happy}significantly different from the “happy music” condition; ^{no}significantly different from the “no music” condition; ^{tones}significantly different from the “random tone sequences” condition; ^{sad}significantly different from the “sad music” condition; ^{0}significantly different from zero (for the time trends).

To account for individual differences in participants’ risk taking, individual random effects were included for the respective reference condition.

conditions), and they became less risk-averse over time when starting out with relatively high risk aversion (i.e., in the "random tone sequences" and "sad music" conditions). The time trends are significantly different from zero for the two most extreme conditions, i.e., the "happy" ($p = 0.0256$) and the "sad" condition ($p = 0.0130$), and there was a trend toward significance for no music ($p = 0.0509$). At the end of each block, there were no significant differences in the choice frequencies between conditions anymore (all pairwise $p > 0.21$). This is what one would expect for a diminishing emotional influence over time. An F-test rejects the hypothesis that time had no influence on choices [$F_{(4,\ 11440)} = 3.8951, p = 0.0037$]. The estimates for several conditions differed significantly from each other (see **Table 1**).

In summary, analysis of the relative frequency with which participants chose the riskier lottery provides evidence in favor of an influence of music-evoked incidental emotions on risk attitudes.

Structural regressions

To test our hypothesis that the influence of incidental emotions on risk attitudes can be explained through changes in probability weighting, we estimated preference parameters via structural regression models. First, we estimated a full model that simultaneously allowed for between-condition changes in the curvature of the value function (ρ) and in the probability weighting parameters (α, β). The full model revealed an overall (jointly) significant effect of music-evoked emotions on the estimated preference parameters [$F_{(9,\ 16304)} = 3.1268, p = 0.0009$].

Allowing for between-condition changes in the value function parameter (ρ) did, however, not significantly improve the model fit compared to a reduced model that only allowed for changes in the probability weighting parameters (log-likelihood ratio = 1.0159, $p = 0.7974$). This indicates that—as to be expected based on theoretical considerations—changes in the curvature of the value function do not explain additional variation in participants' decisions beyond what is explained by changes in probability weighting. As a consequence, we focused on the more parsimonious model[6].

According to this reduced model, there was a significant effect of music-evoked emotions on the estimated preference parameters [$F_{(6,\ 16307)} = 4.5233,\ p = 0.0001$]. Changes in the elevation parameter β were significant between the "happy" and the "sad" and the "happy" and the "random tones" condition, respectively (see **Table 2**), as well as between "sad" and "no music" (−0.0614; $p = 0.001$) and "random tones" to "no music" (−0.417, $p = 0.0243$)[7]. No between-condition changes in the sensitivity parameter α reached significance (all p-values > 0.49). That is, listening to happy music was associated with a significant increase in the elevation of the probability weighting function—i.e., higher (more optimistic) decision weights of the larger outcomes—compared to listening to random tone sequences and to sad music. Listening to sad music and random tones was also associated with lower (more pessimistic) decision weights than not listening to any music. The respective probability weighting functions are illustrated in **Figure 4**. A regression in which we interacted the between-condition regressors with a gender dummy revealed no significant difference in the effect of emotions on the probability weighting of men and women.

To assess the magnitude of the observed effects, it is useful to translate the changes in preference parameters into changes in monetary units. Based on the estimated preference parameters—including the individual random effects—and the estimated between-condition changes in these parameters, it is possible to calculate the (subjective) certainty equivalents of all the lotteries presented to the participants across trials. One can then calculate the risk premium for each lottery, which is defined as the difference between the expected value of a lottery and its certainty equivalent. When averaging across lotteries and across participants, we find that the mean risk premium implied by the estimated parameters is €1.34 (14.05% of the mean expected value) in the "sad" condition, while it is €1.24 (12.93%) in the "happy" condition. This means that the average risk premium is 8.17% (1.12 percentage points) higher after listening to the sad music compared to the happy music used in our experiment.

We further investigated the link between incidental emotions and risk attitudes in a complementary fashion by estimating

Table 2 | Structural regression model: estimates of preference parameters—sensitivity and elevation of the probability weighting function in the "happy music" condition as well as changes of the parameters in the remaining conditions.

Condition	Coefficient	*p*-value
ρ: CURVATURE OF VALUE FUNCTION		
Average over all conditions	0.2467	0.006
α: SENSITIVITY OF PROBABILITY WEIGHTING FUNCTION		
Happy music (reference condition)	0.5476	<0.001 (H_0: α = 1)
Δ No music	+0.0035	0.864
Δ Random tones	−0.0105	0.603
Δ Sad music	+0.0017	0.934
β: ELEVATION OF PROBABILITY WEIGHTING FUNCTION		
Happy music (reference condition)	1.3003	0.002 (H_0: β = 1)
Δ No music	+0.0154	0.392
Δ Random tones	+0.0576	0.002
Δ Sad music	+0.0769	<0.001
σ: FECHNER NOISE		
Average over all conditions	0.6945	<0.001

Wald tests were used to assess whether the parameter estimates are different from 0. While the benchmark for the curvature of the value function is 0 (ρ = 0 in the case of a linear value function), it is 1 for the other two parameters (α = 1 and β = 1 in the absence of probability weighting). Thus, except for α and β, each statistical test reported here was calculated under the null hypothesis (H_0) that the coefficient equals 0. A decrease in α indicates a decrease in the sensitivity to variation in probability; an increase in β indicates a decrease in the elevation of the probability weighting function. Individual random effects were included in α, β, ρ, and σ, but not in the between-condition changes. A logit regression model was used. Please note that our results can be compared to studies that used $u(x; r) = x^r$ by calculating $r = 1 - \rho$.

[6]We did not include time trends in this model, because this would have doubled the already large number of probability-weighting–related parameters to be estimated from 8 to 16.

[7]The between-condition changes in the elevation parameter β remain significant also when not allowing α to vary between the conditions.

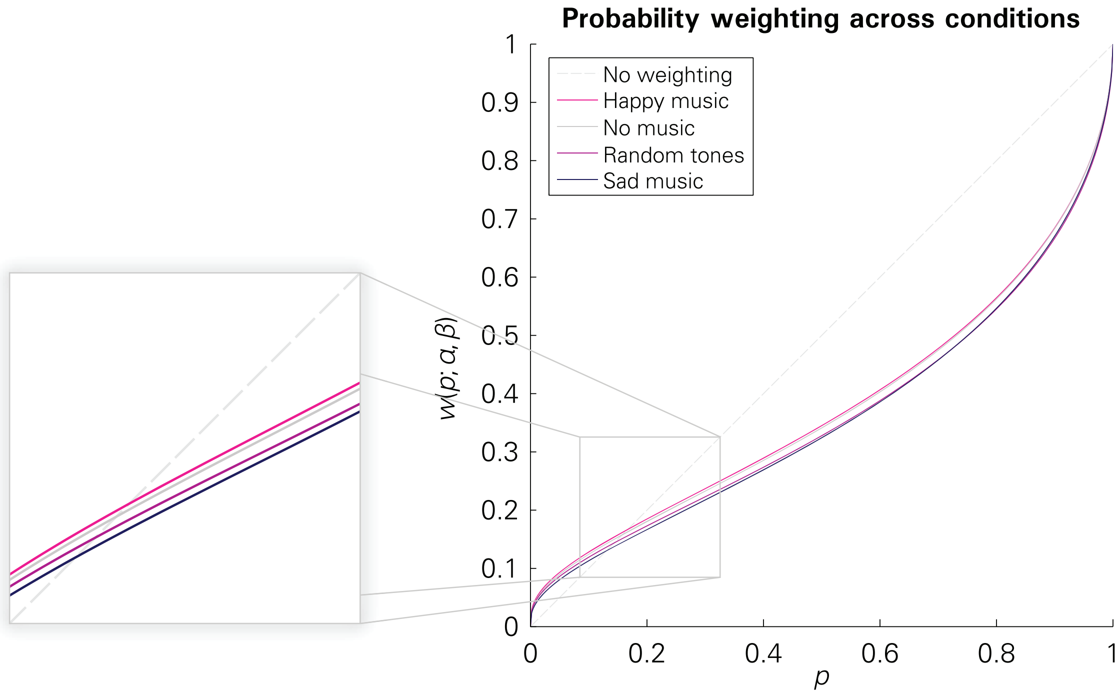

FIGURE 4 | Probability weighting functions in the four conditions based on the parameter estimates for the structural regression model reported in Table 2.

participants' probability weighting parameters as functions of their individual happiness ratings (for the results, see **Table 3**). Put differently, the regression included two explanatory variables—between-subject differences in average happiness in the "no music" condition and within-subject deviation from this average resulting from the musical stimulation.

We found a significant relationship between the within-subject regressor—i.e., the music-evoked variation in happiness—and the elevation of the probability weighting function ($p = 0.003$). Specifically, the happier participants were, the more elevated their probability weighting function was, resulting in decreased risk aversion with increasing happiness.

As expected, this pattern was also found for the between-subject variation observed in the "no music" condition (although here the associated coefficient did not reach significance, $p = 0.143$): participants who were happier in the "no music" condition tended to be less risk-averse, indicated by a more elevated probability weighting function.

While the latter—between-subject—finding is correlational, the former—within-subject—finding again supports the interpretation that evoked emotions *causally* influence risk attitudes.

As far as calmness is concerned, we only found a trend toward significance for participants who were overall less calm/more aroused to have a more elevated probability weighting function ($p = 0.068$). Importantly, we did not observe an analogous effect for the music-evoked (within-subject) changes in arousal ($p = 0.276$). We also did not find any significant effect of self-reported sadness on the elevation parameter of the probability weighting function—neither for the between-subject regressor ($p = 0.666$) nor for the within-subject regressor ($p = 0.185$). Hence, we found happiness to be the only emotional experience that was related to the elevation parameter of the probability weighting function at the individual level.

In summary, the results of our structural regressions confirmed the observed differences in how often the riskier lottery was chosen in the "happy" condition on the one hand and the "sad" and "random tone sequences" conditions on the other hand. Importantly, however, the structural regressions go beyond that by showing that the changes in participants' choices can be explained through changes in how they convert objective probabilities into subjective decision weights—in particular through changes in the elevation parameter of the assumed probability weighting function. The hypothesized affective nature of this link is corroborated by our finding that both self-reported happiness in the "no music" condition and music-evoked changes in happiness were positively related to the elevation of the probability weighting function and thus negatively related to risk aversion.

DISCUSSION

Cumulative prospect theory (CPT; Tversky and Kahneman, 1992) is a theory of decision making under risk that is very prominent in both psychology and economics. In this framework, risk attitudes are understood as arising from an interplay between subjective valuation of (monetary) outcomes and probability weighting. Previous studies have demonstrated an affect-congruent influence of incidental emotions on the assessment of unknown probabilities of potential events, for example, more optimistic judgments in happy participants and more pessimistic probabilistic

Table 3 | Structural regression model: estimates of preference parameters—sensitivity and elevation of the probability weighting function as functions of the between-subject and within-subject variation in self-reported happiness.

Self-reported happiness	Coefficient	*p*-value
ρ: CURVATURE OF VALUE FUNCTION		
Average over all conditions and participants	0.3418	<0.001
α: SENSITIVITY OF PROBABILITY WEIGHTING FUNCTION		
Average in "no music" condition over all participants	0.5900	<0.001 (H_0: $\alpha = 1$)
Deviation of participants' average in "no music" condition from cross-subject mean (between-subject regressor)	+0.0093	0.683
Deviation of participants' block-specific rating from "no music" condition (within-subject regressor)	−0.0221	0.180
β: ELEVATION OF PROBABILITY WEIGHTING FUNCTION		
Average in "no music" condition over all participants	1.1393	0.198 (H_0: $\beta = 1$)
Deviation of participants' average in "no music" condition from cross-subject mean (between-subject regressor)	−0.0437	0.143
Deviation of participants' block-specific rating from "no music" condition (within-subject regressor)	−0.0853	0.003
σ: FECHNER NOISE		
Average over all conditions and participants	1.0471	<0.001

Wald tests were used to assess whether the parameter estimates are different from 0. While the benchmark for the curvature of the value function is 0 ($\rho = 0$ in the case of a linear value function), it is 1 for the other two parameters ($\alpha = 1$ and $\beta = 1$ in the absence of probability weighting). Thus, except for α and β, each statistical test reported here was calculated under the null hypothesis (H_0) that the coefficient equals 0. A decrease in α indicates a decrease in the sensitivity to variation in probability; an increase in β indicates a decrease in the elevation of the probability weighting function. The standard errors—and thus the associated p-values—were adjusted for 41 clusters on the subject level. A logit regression model was used. Please note that our results can be compared to studies that used $u(x; r) = x^r$ by calculating $r = 1 - \rho$.

judgments in sad participants (Johnson and Tversky, 1983; Wright and Bower, 1992). We hypothesized that such an effect would also exist on probability weighting in decision making under risk.

We found experimental evidence in favor of a *causal* effect of incidental emotions on risk attitudes that is consistent with changes in probability weighting. To measure risk attitudes and probability weighting, we employed a variant of the Random Lottery Pairs procedure (Hey and Orme, 1994) and varied both outcomes and probabilities of real monetary gambles in the gain domain. Participants' incidental emotions were manipulated within-subject by listening to happy and sad music as well as random tone sequences or no music at all, and evaluated by self-reported emotional ratings.

Our two-step statistical analysis yielded that participants' decisions differed between conditions and that these differences can be explained by changes in probability weighting. First, we compared the choice frequencies between conditions. Risk aversion decreased from the "happy" to the "random tones" and "sad" conditions. Second, we allowed for emotion-dependent changes in the probability weighting function in a structural regression rooted in CPT. We found a significantly higher elevation in the "happy" than in the "sad" and the "random tones" condition. That is, participants made decisions as if the probabilities of the larger payoffs received a higher decision weight in the "happy" condition and lower weights in the other two. This could be regarded as a form of optimism or pessimism, respectively. Listening to sad music and random tones was also associated with more pessimism than not listening to any music. The sensitivity parameter was not affected. Thus, affectively mediated changes in risky choices do not seem to result from altered sensitivity to probability changes but from a change in decision weights across probabilities.

Several arguments support the claim that these effects can be attributed to incidental emotions. First, the effects correspond closely to differences in self-reported happiness between these conditions. Happy music was associated with greater happiness, whereas sad music and random tones were associated with decreased happiness. Second, we found that the effect on decisions diminished over time—just as the effect on self-reported happiness. Third, music-evoked happiness correlated positively with the estimated elevation of the probability weighting function: when happiness was greater, the larger payoffs received a higher decision weight; when happiness was reduced, the larger payoffs received a lower decision weight. Taken together, this evidence is compatible with an effect of incidental emotions on the elevation of the probability weighting function during decision making under risk.

Our results are consistent with well-established effects of incidental emotions on probability judgments reported in the psychological literature. For instance, happy people make more optimistic probabilistic judgments, while sad people make more pessimistic judgments (Johnson and Tversky, 1983; Wright and Bower, 1992). Extending this body of evidence, our results suggest that not only judgments of unknown probabilities are altered, but that also the weighting of known probabilities in decision making under risk is affected by incidental emotions.

This is in line with indirect evidence that suggests an effect of incidental emotions on probability weighting. In a correlational study, Fehr-Duda et al. (2011) found that women that regarded the current day to be more promising than usual made decisions as if they weighted the larger payoffs more optimistically. This has been interpreted as an effect of mood on the elevation of the probability weighting function in women. In a similar vein, weather and seasonal effects on decision making were attributed to the effect of bad mood on probability weighting (Kliger and Levy, 2008)—importantly, however, without distinguishing between sensitivity and elevation of the probability weighting function.

We complement this research in important ways by going beyond correlational data and providing evidence in favor of a causal effect of incidental emotions on risk attitudes that is consistent with changes in probability weighting in particular. Critically, we experimentally manipulated participants' incidental emotions. Moreover, we recorded participants' self-reported emotions to make sure that the experimental manipulation worked as intended. Taken together, this is evidence in favor of a causal effect of incidental emotions. Unlike Fehr-Duda et al. (2011), we found significant effects for our whole mixed-gender sample and no significant difference between men and women. Thus, gender does not seem to be the major determining factor in the effect of emotions on risk attitudes. Similar to the correlational evidence reported in Fehr-Duda et al. (2011), increased baseline happiness was associated with a more elevated probability weighting function, although not significantly so. This between-subject effect is also in line with the finding that people with high life satisfaction are more willing to take risks (German Socio-Economic Panel; Dohmen et al., 2011).

At first glance, our results may seem inconsistent with the findings of Isen et al. (1988). Isen et al. did not report a significant effect of evoked positive affect on risk attitudes in the gain domain. Their Figure 1 displays estimated utility functions whose curvature is less pronounced in the gain domain for the positive-affect than for the control participants. This would be consistent with reduced risk aversion over gains resulting from positive affect. However, no statistical test was performed to determine whether this difference was significant. Nevertheless, Isen et al. speculated that in the gain domain there might be a tendency for reduced risk aversion based on more optimistic probability weighting in happy participants. Importantly, our study provides empirical evidence for this very conjecture.

Previous research has already provided some theoretical accounts on the affect sensitivity of the probability weighting function. The inverse S-shape of the probability weighting function can result from the presence and integration of anticipatory emotions—e.g., elation and disappointment—in the decision process (Gul, 1991; Brandstätter et al., 2002; Walther, 2003). For instance, Brandstätter et al. (2002) demonstrated that an inverse S-shaped probability weighting function can be reconstructed from a so-called surprise function that reflects participants' measured anticipated happiness with regard to the outcome. In this framework, the anticipated disappointment that might result from a failure to achieve a highly probable gain is thought to translate into lower decision weights for high probabilities. In line with this, probability weighting was found to be more pronounced for outcomes believed to elicit stronger emotional responses (Rottenstreich and Hsee, 2001). However, it has been pointed out that anticipatory emotions could theoretically also alter the elevation of the function at each probability (Rottenstreich and Hsee, 2001). Our results indicate that not just anticipatory, but also incidental emotions contribute to probability weighting and that this is reflected in the elevation of the function. Incidental emotions might have a direct effect on the processing of probabilities, leading to optimism/pessimism in terms of decision weights. Alternatively, they might (also) operate through changing anticipatory emotions that affect the elevation of the probability weighting function indirectly. Given that we used very moderate and only positive monetary outcomes that are unlikely to create strong positive or negative anticipatory emotions—compared to stimuli used in other experiments, like receiving a kiss or a painful electric shock (Rottenstreich and Hsee, 2001)—we favor the former interpretation, but we cannot rule out the latter, indirect, channel.

Our research has several implications for future research. We have demonstrated that incidental emotions influence choices between monetary gambles in a way that is compatible with emotion-induced changes in the subjective weighting of known probabilities. An important next step would be to explore the underlying mechanism in greater detail. Process-tracing methods like eye tracking or (computer) mouse tracking might offer deeper insights into the psychological processes that underlie decision making (e.g., Schulte-Mecklenbeck et al., 2011) and affective influences. For instance, it has been shown that happy participants have a stronger attentional focus on rewards (Tamir and Robinson, 2007). It is possible that probability weighting ultimately reflects changes in attention to outcome values, as has also been pointed out by Wu (1999).

Neural data are another promising source of information. Different brain areas have been related to the processing of the basic components of gambles, i.e., of reward magnitude and probabilities (Tobler et al., 2007). Concerning probability weighting, previous research has associated non-linear probability weighting with non-linear neural responses in the striatum and anterior cingulate cortex (Paulus and Frank, 2006; Tobler et al., 2008; Hsu et al., 2009). Hence, if it is indeed probability weighting that is affected by incidental emotions, we should see emotion dependence of these neural responses. For instance, the striatum and anterior cingulate cortex are also associated with experiencing happiness, as a meta-analysis of studies on emotional processing revealed (Vytal and Hamann, 2010). A link between rewards and emotions is also plausible, given the association between activity in the striatum and anticipation of rewards as well as self-reported happiness generated by these rewards (Knutson et al., 2001). It is also possible that emotions not related to the decision at hand—i.e., incidental emotions—have an influence on reward processing in the striatum. It has been suggested that conditioned and unconditioned stimuli—and this would include a wide range of emotional stimuli evoking incidental emotions—influence instrumental, reward-based behavior via the ventral striatum (Cardinal et al., 2002). Recently, pleasurable music has been shown to facilitate reward-based learning, and the observed effect seems to be linked to striatal activation (Gold et al., 2013). Thus, we would expect that incidental emotions influence decision making, and probability weighting in particular, by altering activity in these brain areas that show such a functional overlap in reward and emotion processing. This might reflect the direct integration of incidental emotions into the decision process.

Obtaining neurobiological measures of emotion-induced changes in probability weighting are highly promising for future research, given that from the observation of choices alone, it is impossible to disentangle changes in the value function from changes in probability weighting when using two-outcome lotteries only (Wakker, 2010, chapter 5)—unless one restricts the involved functions to specific parametric forms (in our case, power utility in combination with Prelec-style two-parameter probability weighting). Specifically, reduced elevation of the probability weighting function is observationally equivalent to an increase in the curvature of the value function: both lead to increased risk aversion. As a consequence, our findings (and those of Fehr-Duda et al., 2011) are *consistent* with changes in probability weighting and thus our hypotheses, but *not exclusively so*, since the between-condition differences in our participants' choices can also be captured by the value function. The analysis of process or neural data might help disentangling the two possible effects.

Apart from those implications for future research, there are other methodological considerations and potential limitations more directly related to our research approach. In contrast to several previous studies on the influence of incidental affect on decision making that used between-subject designs (see, however, e.g., Knutson et al., 2008; Guitart-Masip et al., 2010), we employed a within-subject design because it has several advantageous features. First, our within-subject design is an ecologically more valid abstraction of the everyday decision environment of a person that is confronted with the same decision or similar decisions repeatedly while being in different affective states. In contrast, a between-subject design looks at different persons who make fewer decisions in only one affective state each. Second, a within-subject design increases statistical power because it prevents between-condition variance from being contaminated by between-subject variance.

Although within-subject designs potentially introduce confounds (e.g., via learning/time trends across sessions), there are reasons to believe that internal validity with respect to the effects of interest to our study is ensured, given that learning would rather diminish than exacerbate between-condition differences [8]. Taken together, we think that the experimental design that we used creates a balance between ecological and internal validity.

Regarding the set of lottery pairs, we focused, as already mentioned, on the gain domain for the following reasons: first, neuroimaging and lesion studies suggest that losses and gains are processed differently in the human brain (De Martino et al., 2010; but see Tom et al., 2007). Second, to increase the power for the detection of an effect, a sufficient number of decision trials is needed. Third, mixed gambles would have required the estimation of additional parameters, making even more observations necessary. We therefore deliberately chose to dedicate all our experimental trials to only one domain. However, the neuroimaging results just mentioned as well as evidence that probability weighting might be different in losses (Abdellaoui, 2000) should motivate future research to investigate the effects of incidental emotions on decision making in the loss domain.

A final remark on our emotional manipulation procedure is in order. While the music we used was able to evoke different levels of happiness, at a small to medium-sized effect, sadness was not reliably altered (which means that the sad music that we used was associated with decreased levels of happiness rather than greater sadness). Other emotion induction techniques might be more potent and also promising for future research (Gross and Levenson, 1995; Rottenberg et al., 2007). Alternatively, letting participants bring their own personal music that they know to evoke the desired emotional state might be a more potent form of induction, although the use of non-standardized, highly variable stimuli and inadvertently providing information about the study design to participants in advance might introduce various confounds.

Apart from this, different measures of emotional change—for instance, visually supported assessment scales like the Self-Assessment Manikin (Bradley and Lang, 1994) or psychophysiological measures (e.g., skin conductance response or facial electromyography)—could be used, because participants might find it difficult to report their affective states on a numbered scale. In addition, one could focus on the underlying appraisal dimensions of emotions (see, e.g., Lerner and Keltner, 2000, 2001). In this regard, we have found preliminary evidence that arousal is not the causal emotional dimension, since we did not find a significant within-subject association between the calmness ratings (our inverse proxy for arousal) and risk attitudes.

The type and strength of emotional manipulation in our study is especially interesting given that everyday life is characterized by the exposition to many emotional stimuli that are not extreme in most cases (e.g., listening to music, being smiled at, or meeting more or less liked colleagues; compared to, say, winning a world championship, witnessing a terrorist attack, or losing a loved one). Hence, our design has ecological validity with respect to decision making occurring under standard affective contexts, i.e., small to moderate emotional changes.

We consider this just as interesting as investigating the effects of rather big, but uncommon, emotional changes. Intense feelings, especially when being fully recognized, can result in reduced emotional effects on decision making via an enhanced ability to control emotional bias (Seo and Barrett, 2007). Even more intense changes in emotion might result in avoiding making a decision altogether and postponing it to less turbulent times. In contrast, people may be relatively unaware of the influence of subtle emotional changes on their decisions and hence may be unable to regulate it. We therefore consider investigating the consequences of subtle, but common changes in incidental emotions highly relevant.

CONCLUSION

Our study investigated within-subject the effects of incidental emotions on probability weighting by means of experimental manipulation and through measurement of changes in the affective state. We thereby complement previous studies on the

[8] When checking for time trends across experimental sessions, we found that subjects became significantly more consistent over time (i.e., the Fechner error, σ, exhibited a significantly negative time trend), but the estimated probability weighting parameters showed no significant time trends. Moreover, the results did not differ qualitatively from those reported in **Table 2**. To address potential order effects, we checked whether the initial condition had a lasting influence on risk attitudes—which was not the case: when averaging the individual random effects depending on the condition that subjects first participated in, the resulting order of the average random effects in the elevation parameter for the four conditions corresponded in no way to the order of the respective estimated condition differences.

effect of incidental emotions on probability judgments as well as previous—correlational—studies on the link between emotional states and probability weighting in decision making under risk. We found experimental evidence in favor of a causal influence of incidental happiness on risk attitudes. Via structural regressions based on CPT, we showed that these changes in risk attitudes can be attributed to affectively mediated changes in the elevation of the probability weighting function.

ACKNOWLEDGMENTS

We wish to thank Stavros Skouras and Corinna Pehrs for assistance with creating the musical stimuli. We would also like to thank our reviewers whose comments helped to improve the manuscript.

FUNDING

The study was financially supported by the Cluster of Excellence "Languages of Emotion" at Freie Universität Berlin and the Collaborative Research Center SFB 649 "Economic Risk," both funded by the DFG (German Research Foundation). Yana G. Heussen was supported through a Talent Grant of the Faculty of Mathematics and Natural Sciences, Rijskuniversiteit Groningen, The Netherlands. Holger Gerhardt received financial support from the Graduate School "Berlin School of Mind and Brain," funded by the DFG.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 12 October 2013; accepted: 09 December 2013; published online: 07 January 2014.

Citation: Schulreich S, Heussen YG, Gerhardt H, Mohr PNC, Binkofski FC, Koelsch S and Heekeren HR (2014) Music-evoked incidental happiness modulates probability weighting during risky lottery choices. Front. Psychol. ***4****:981. doi: 10.3389/fpsyg.2013.00981*

This article was submitted to Decision Neuroscience, a section of the journal Frontiers in Psychology.

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APPENDIX

Table A1 | Set of lottery pairs.

No.	Lottery *A*			Lottery *B*		
	$x_{A,1}$	$x_{A,2}$	$p_{A,1}$	$x_{B,1}$	$x_{B,2}$	$p_{B,1}$
1	5	10	0.25	6	9	0.10
2	5	10	0.25	6	9	0.25
3	3	15	0.50	6	9	0.25
4	4	15	0.50	6	9	0.50
5	3	15	0.50	5	10	0.90
6	3	15	0.50	6	10	0.75
7	2	20	0.50	4	12	0.75
8	3	15	0.50	7	9	0.50
9	4	15	0.50	7	9	0.75
10	2	20	0.75	5	10	0.90
11	2	20	0.75	3	15	0.25
12	2	20	0.75	4	15	0.75
13	7	12	0.75	8	10	0.50
14	3	15	0.50	7	12	0.50
15	3	15	0.50	6	12	1.00
16	6	15	0.75	7	9	0.50
17	7	15	0.75	7	9	0.10
18	6	15	0.75	8	8	0.50
19	6	15	0.75	9	9	0.50
20	3	15	0.50	8	10	0.25
21	3	14	0.50	8	10	0.10
22	3	15	0.50	6	9	0.50
23	3	15	0.75	5	10	0.10
24	2	20	0.50	5	10	0.50
25	3	20	0.50	5	10	0.25
26	6	15	0.75	6	10	0.50
27	6	14	0.75	6	10	0.50
28	3	15	0.50	8	8	0.10
29	3	15	0.50	7	7	0.25
30	3	15	0.50	6	15	0.25
31	3	14	0.50	6	15	0.10
32	6	12	0.50	7	9	0.50
33	6	12	0.50	7	9	0.25
34	8	15	0.75	6	10	0.10
35	8	15	0.90	6	10	0.90
36	3	15	0.50	7	9	0.50
37	4	12	0.50	7	9	0.10
38	3	15	0.25	11	11	0.25
39	3	15	0.10	11	11	0.50
40	6	9	0.25	8	10	0.50
41	6	9	0.25	8	10	0.90
42	3	15	0.25	4	12	0.90
43	3	15	0.25	5	12	0.10
44	4	12	0.50	6	9	0.50
45	5	12	0.50	6	9	0.25
46	4	12	0.10	11	11	0.50
47	4	12	0.25	11	11	0.75
48	4	12	0.50	7	12	0.50
49	4	12	0.25	6	10	0.90

(Continued)

Table A1 | Continued

No.	Lottery *A*			Lottery *B*		
	$x_{A,1}$	$x_{A,2}$	$p_{A,1}$	$x_{B,1}$	$x_{B,2}$	$p_{B,1}$
50	4	12	0.25	6	11	0.10
51	3	15	0.50	6	9	0.25
52	4	15	0.50	6	9	0.25
53	3	15	0.50	7	9	0.50
54	6	12	0.50	6	9	0.90
55	6	12	0.50	6	9	0.75
56	6	12	0.75	6	9	0.75
57	2	20	0.25	13	13	0.50
58	4	20	0.25	13	13	0.75
59	3	15	0.50	7	12	0.90
60	3	15	0.50	7	13	0.25
61	4	12	0.25	8	15	0.75
62	4	12	0.25	8	16	0.50
63	2	20	0.10	17	17	0.50
64	2	20	0.10	16	16	1.00
65	2	20	0.50	7	9	0.50
66	2	20	0.50	7	9	0.10
67	4	12	0.25	9	13	0.50
68	4	12	0.25	9	13	0.50
69	4	12	0.25	5	10	0.25
70	4	12	0.25	5	10	0.10
71	2	20	0.50	7	12	0.50
72	2	19	0.50	6	9	0.10
73	2	20	0.50	6	9	0.50
74	3	15	0.10	13	13	0.25
75	3	15	0.10	13	13	0.50
76	5	10	0.25	7	9	0.50
77	5	10	0.25	7	9	0.10
78	2	20	0.50	3	15	0.25
79	2	20	0.50	3	14	0.25
80	3	15	0.50	4	12	0.10
81	3	15	0.50	5	12	0.50
82	2	20	0.50	4	12	0.25
83	2	20	0.50	4	11	0.10
84	3	15	0.75	4	15	0.90
85	3	15	0.75	5	15	0.50
86	5	10	0.10	9	13	0.10
87	5	10	0.10	9	13	0.25
88	6	10	0.10	9	13	0.50
89	6	11	0.25	4	7	0.50
90	6	12	0.75	4	7	0.90
91	6	11	0.50	3	8	0.90
92	6	11	0.75	3	8	0.10
93	6	8	0.50	3	5	0.50
94	6	9	0.75	4	9	0.25
95	5	9	0.50	4	8	0.50
96	5	5	1.00	3	5	0.75
97	5	7	0.50	4	6	0.50
98	4	6	0.25	3	5	0.90
99	5	8	0.10	5	8	0.75
100	5	7	0.50	4	6	0.75

Table A2 | Musical stimuli.

Category	Composer (Artist)	Title
Happy	Joel Francisco Perri	El Canto de Mi Antara
	Craobh Rua	The Lucky Penny
	Scotch Mist	Shetland Tune
	Alfredo de Angelis	Pregonera
	Romanian Folk Dance	Batuta de la Adancata
	Louis Armstrong	St. Louis Blues
	Niccoló Paganini	Violin Concerto No. 1, 3rd movement
	Jonathan Richman	Egyptian Reggae
	Johann Joachim Quantz	Concerto for Flute and Orchestra, No. 256 in A Major – allegro Di Molto
	Franz Anton Hoffmeister	Concerto for viola and orchestra in D major: I. Allegro
	Georg Friedrich Händel	Arrival of the Queen of Sheba (Sinfonia from the opera Solomon)
	Michael Praetorius	Dances from Terpsichore: 6. Volte
Sad	Samuel Barber	Adagio for Strings
	Goran Bregovic and Athens Symphony Orchestra	Elo Hi (Canto Nero)
	Himlar Örn Hilmarsson	The Black Dog and the Scottish Play
	Frédéric Chopin (1837)—Alfred Eschwé and Razumovsky Sinfonia	Marche funebre from Piano Sonata No. 2 in B Flat Minor, Op. 35
	The Cure	Trust
	The Cure	Apart

Table A3 | Statements used in the emotion ratings.

German original	English translation
Ich bin ruhig.	I am calm.
Ich bin sehr neugierig.	I am very curious.
Ich habe alles unter Kontrolle.	I have everything under control.
Ich bin fröhlich.	I am happy.
Ich bin traurig.	I am sad.
Ich führe ein stressiges Leben.	I lead a stressful life.
Ich fühle mich wohl.	I am comfortable.
Ich bin entspannt.	I am relaxed.
Ich fühle mich sicher.	I feel safe.
Letzte Nacht habe ich gut geschlafen.	I slept well last night.

THEORETICAL NOTE

We pointed out that for two-outcome lotteries, it is impossible in the framework of CPT to dissociate the shape of the value (utility) function from the shape of the probability weighting function (see Wakker, 2010, chapter 5), unless one restricts the functions to specific parametric forms.

To be precise, Wakker (2010) shows that the observational equivalence—or "data equivalence," as he calls it—between expected utility with a non-linear utility function and rank-dependent utility (CPT in the gain domain) with a non-linear probability weighting function holds for two-outcome lotteries for which the lower outcomes are zero. This can be easily extended, however, as follows:

Let e be the certainty equivalent of a two-outcome lottery that pays a high payoff x_h with probability p_h and a low payoff x_l, where $x_h > x_l \geq 0$, with probability $1 - p_h$. Then, for expected utility, we have $u(e) = p_h u(x_h) + (1 - p_h)u(x_l)$. Normalizing $u(x_h) = 1$ and $u(x_l) = 0$, this reduces to $u(e) = p_h$. Under the assumption that $u(x)$ is strictly increasing in x, this can be rewritten as $e = u^{-1}(p_h)$, where u^{-1} denotes the inverse function of u.

Now consider the same certainty equivalent e to be instead generated by cumulative probability weighting with weighting function $w(p)$ in combination with linear utility. This generates the equality $e = w(p_h)x_h + [1 - w(p_h)]x_l$. Rearranging yields $w(p_h) = [e - x_l]/[x_h - x_l] = [u^{-1}(p_h) - x_l]/[x_h - x_l]$. Since $u^{-1}(0) = x_l$ and $u^{-1}(1) = x_h$, the $w(p_h)$ found in this way ranges from 0 to 1 and is thus a perfectly valid probability weighting function. It takes on the shape of the inverse function of the utility function $u(x)$, normalized in a suitable way.

Thus, the observational equivalence between expected utility with a non-linear utility function and rank-dependent utility with a non-linear probability weighting function holds for arbitrary two-outcome lotteries—and not only for those whose lower outcome is zero.

Disentangling the shape of the value (utility) function and the probability weighting function based on observed choices alone becomes possible when using lotteries that consist of at least three outcomes. However, doing so will still be hard statistically, since the parameters to be estimated continue to be interdependent, albeit to a lesser degree. For this reason, we suggest (see Discussion) to obtain additional non-choice data such as process-tracing data or neural data that might help to disentangle the underlying processes.

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Journal homepage: http://www.apa.org/pubs/journals/emo/

Final document: http://psycnet.apa.org/journals/emo/16/3/402

Incidental Fear Cues Increase Monetary Loss Aversion

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This work is part of S.S.'s doctoral dissertation. This work was supported by the Excellence Initiative of the German Federal Ministry of Education and Research through the German Research Foundation (DFG Grant EXC 302).

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Abstract

In many everyday decisions, people exhibit loss aversion—a greater sensitivity to losses relative to gains of equal size. Loss aversion is thought to be (at least partly) mediated by emotional—in particular, fear-related—processes. Decision research has shown that even incidental emotions, which are unrelated to the decision at hand, can influence decision making. The effect of incidental fear on loss aversion, however, is thus far unclear. In two studies, we experimentally investigated how incidental fear cues, presented during (Study 1) or before (Study 2) choices to accept or reject mixed gambles over real monetary stakes, influence monetary loss aversion. We find that the presentation of fearful faces, relative to the presentation of neutral faces, increased risk aversion—an effect that could be attributed to increased loss aversion. The size of this effect was moderated by psychopathic personality: Fearless dominance, in particular its interpersonal facet, but not self-centered impulsivity, attenuated the effect of incidental fear cues on loss aversion, consistent with reduced fear reactivity. Together, these results highlight the sensitivity of loss aversion to the affective context.

Keywords: decision making, loss aversion, incidental emotions, fear, psychopathy

Incidental Fear Cues Increase Monetary Loss Aversion

Many everyday economic decisions do not only involve potential gains, but also potential losses. In such decisions, the majority of people exhibit so-called loss aversion. That is, they show a greater sensitivity to potential losses relative to potential gains of equal size (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). For instance, people typically reject mixed gambles that offer a 50% chance of gaining money and a 50% risk of losing money, unless the potential gain is at least about one and a half times or twice as large as the potential loss (e.g., Gächter, Johnson, & Herrmann, 2010; Kahneman & Tversky, 1979). Loss aversion helps to explain widespread risk aversion (Kahneman & Lovallo, 1993) and is therefore an important concept both in judgment-and-decision-making research and in behavioral economics.

Camerer (2005) hypothesized that loss aversion is an expression of fear. Indeed, two lines of evidence suggest that fear-related processes are crucially involved in loss aversion. First, neural systems mediating fear and anxiety are intertwined with those associated with the computation of value and choice in economic decision making (Hartley & Phelps, 2012). For instance, amygdala activity and physiological arousal (e.g., skin conductance responses) have been related to fear processing (LeDoux, 2003; Phelps, Connor, Gatenby, Gore, & Davis, 2001) as well as to the anticipation of financial losses (e.g., Hahn et al., 2010; Kahn et al., 2002) and loss aversion (Canessa et al., 2013; De Martino, Camerer, & Adolphs, 2010; Sokol-Hessner et al., 2009; Sokol-Hessner, Camerer, & Phelps, 2013).

Second, there is behavioral evidence pointing toward fear-dependent changes in loss processing. For instance, carriers of the short version of a serotonin transporter polymorphism (5-HTTLPR), who also exhibited enhanced fear conditioning and trait anxiety, were more susceptible to the so-called framing effect (Crişan et al., 2009). To be specific, they were more risk-seeking (i.e., chose a risky option over a sure option) when the alternative option was framed as a sure loss, consistent with changes in the processing of losses. Together, this evidence supports the hypothesis that fear-related processes play a role in loss processing and loss aversion.

Importantly, not only emotions related to the evaluation of the decision options (i.e., potential outcomes and their probabilities) but even incidental emotions—which are unrelated to the decision at hand—can influence decision making (e.g., Isen, Nygren, & Ashby, 1988; Loewenstein & Lerner, 2003; Schulreich et al., 2014). Despite the postulated link between fear and loss processing, the influence of incidental fear on loss aversion is thus far unclear. Investigating this effect is important on the background of the oft-postulated hypothesis that real-world economic behavior (e.g., investors' decisions in financial markets) is partly due to the influence of the affective context on loss aversion.

We designed two studies to experimentally manipulate the affective context and investigate its influence on loss aversion. Participants decided whether to accept or reject mixed gambles with potential gains and losses while they were simultaneously presented (Study 1) or primed beforehand (Study 2) with fearful or neutral face stimuli.

We chose face stimuli to manipulate the affective context because faces have signaling value. Fearful faces warn conspecifics of nearby potential threat (Adolphs, 2002). They also prepare the organism for encountering a potential threat by, for example, increasing attention to a subsequent stimulus (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Taylor & Whalen, 2014). Neurophysiologically, fearful faces preferentially activate the amygdala compared to, for instance, emotional scenes (Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002) and other facial emotional expressions (Williams et al., 2005). Both studies also found that these effects extend to peripheral physiological arousal indicated by skin conductance responses. Thus, fearful faces can be considered adequate signals to the defensive fear system—likely activating an emotion concept—which possibly facilitates defensive action such as avoidance. When it is possible to avoid a subsequent actual threat, e.g., by rejecting a potential loss, the organism will commonly do so (Bracha, Ralston, Matsukawa, Williams, & Bracha, 2004; Gray, 1988). Therefore, we predict higher loss aversion in the fearful-face than in the neutral-face condition.

While we expect incidental fear cues to increase loss aversion on average, we also hypothesize that the magnitude of this effect will vary across subjects, depending on personality traits related to fear processing and reactivity. One such personality trait is psychopathy. At its high end, psychopathy is primarily characterized by deficits in affective processing (e.g., lack of empathy) and antisocial behavior (Cleckley, 1941; Hare & Neumann, 2008), but it is conceptualized as a dimensional trait (Marcus, John, & Edens, 2004), i.e., even a non-clinical and non-forensic sample will typically consist of people with different degrees of psychopathic traits.

The psychopathic trait fearless dominance is a particularly plausible moderator of the influence of incidental fear cues on loss aversion. Fearless dominance has been conceptualized as a phenotypic expression of a dispositional fear deficit (e.g., Patrick, Fowles, & Krueger, 2009). It is expressed in psychophysiological indicators of deficient fear conditioning (López, Poy, Patrick, & Moltó, 2013) or inhibition of the fear-potentiated startle response (e.g., Anderson, Stanford, Wan, & Young, 2011) and deficits in the recognition of fearful faces (e.g., Blair et al., 2004), among others.

We predict that—due to their reduced fear reactivity—participants who score higher in fearless dominance will be (a) less loss-averse in general and (b) less susceptible to incidental fear cues compared to lower-scoring participants. The latter moderation might be particularly pronounced and robust for social influence (i.e., low social anxiety and high social potency)—the most interpersonal component of fearless dominance—because this facet has been associated with reduced amygdala activity when processing fearful faces (Carré, Hyde, Neumann, Viding, & Hariri, 2013). The presence of a moderation effect would be further support for the hypothesis that the affective context influences humans' degree of loss aversion.

Study 1

Methods

Participants. We recruited 29 participants (20 female, 9 male; mean age 26.79 years [*SD* = 5.233 years]) through bulletin-board appeals at Freie Universität Berlin and mailing lists. All participants gave written informed consent prior to the experiment, and the ethics committee at Freie Universität Berlin approved all procedures.

Experimental procedure. Prior to the experiment, participants received an initial endowment of €20 in cash, similar to previous experiments (e.g., De Martino et al., 2010). Participants were instructed to put the money into their wallets and were informed that it was already theirs. In the subsequent detailed instructions, participants were told that they would make decisions in multiple trials, that one trial would be randomly selected at the end of the session, and that the final payment would depend on their decision and the realized outcome in this particular trial (random incentive mechanism). This is a standard procedure in behavioral economics to encourage participants to evaluate each decision situation independently (Harrison & Rutström, 2008). It also ensures incentive compatibility through non-hypothetical decision making. The decision-making task (see below) was presented on a computer screen, using the software package Presentation (Neurobehavioral Systems, Inc.). After the decision-making task, participants completed the German version of the Psychopathic Personality Inventory—Revised (PPI-R, Alpers & Eisenbarth, 2008, see below). At the end of the session, one decision trial was randomly selected. Any net amount from subjects' endowment that remained after returning an eventual loss to the experimenter was theirs to keep, and any eventual gain was paid on top of the initial endowment.

Decision-making task and affective priming. Before the main experiment, participants were given five practice trials to familiarize themselves with the task. The main experiment consisted of a pseudo-randomized sequence of 200 trials. In each trial, we asked the participants to accept or reject a series of mixed gambles with equal (i.e., 50%) probability of winning or losing a variable amount of money. Potential gains and losses were presented numerically together with a reminder of the associated 50% probabilities on each side of the screen (see Figure 1). The positioning of the gains and losses on the left and right sides of the screen was counterbalanced between subjects. Each trial was uniquely and pseudo-randomly drawn from a symmetric gains/losses matrix, with potential gains ranging from +€5 to +€14 and potential losses from −€14 to −€5 in increments of €1 (100 gambles in total). Consequently, gains and losses as well as expected value and variance were orthogonal across trials.

To encourage participants to reflect on the subjective attractiveness of each gamble rather than to rely on a fixed decision rule, we used four response categories rather than two, ranging from "accept" to "rather accept" to "rather reject" to "reject," similar to Tom et al. (2007). Participants were informed that the first two response categories would be counted as an acceptance of the gamble, whereas the latter two would be regarded as a rejection. The four response categories were presented at the bottom of the screen with the labels "accept" and "reject" at their extremes.

Each gamble in the main experiment (but not in the training trials) was presented together with the image of a face located at the center of the screen. The face images served as emotional primes. In affective-priming experiments that used evaluative decision tasks with words as primes and targets, only short stimulus onset asynchronies (SOAs) in the range of 0 to 300 ms generated robust affective priming effects (Hermans, De Houwer, & Eelen, 2001; Hermans, Spruyt, & Eelen, 2003). Based on this, we used simultaneous priming (SOA = 0 ms) as a starting point. We expected this to result in a sufficiently strong overlap between the emotional activation that follows prime onset and decision-related processes so that effects of the incidental fear cues become observable. Each of the 100 gambles was presented twice (within-subject design): once paired with a neutral facial expression (neutral-face condition) and once paired with a fearful facial expression (fearful-face condition), so that the experiment consisted of 200 trials in total.

The priming conditions were pseudo-randomized across trials per participant, so that any condition effects observed are likely due to transient emotional influences rather than to changes in longer-lasting states that could underlie observed effects in blocked or between-subject designs. The combinations of gamble and facial identity were also pseudo-randomized per participant, but identical in both conditions. We used faces of 25 young males and 25 young females from a standardized and well-validated face database (Ebner, Riediger, & Lindenberger, 2010). Consequently, each face was presented twice per priming condition, and face identity was repeated four times in total. Face gender was counterbalanced across conditions.

Each decision trial was presented for 3500 ms, and participants were required to respond within this time window via a key press. The last response in each trial was logged for analysis. Participants were informed that if no key was pressed within this time window, they would pay a penalty of €1 if this trial was randomly selected for the final payment. This was supposed to incentivize subjects to always make a decision and to perform the task with sufficient concentration. The intertrial interval (ITI) was jittered and ranged from 1000 to 8000 ms (mean 4000 ms). The sequence of events per trial is depicted in Figure 1.

Psychopathic Personality Inventory—Revised (PPI-R). The PPI-R (Alpers & Eisenbarth, 2008) is a self-report questionnaire for assessing psychopathic traits. The PPI-R consists of eight subscales, the majority of which form two higher-order factors, fearless dominance and self-centered impulsivity (Benning, Patrick, Hicks, Blonigen, & Krueger, 2003). Its internal consistency is satisfactory, with an overall reported Cronbach's alpha of .85 and values ranging from .72 to .88 for the subscales (Alpers & Eisenbarth, 2008).

We calculated the scores for fearless dominance and self-centered impulsivity similarly to previous studies (e.g, Benning et al., 2003; Carlson & Thái, 2010; Schulreich, Pfabigan, Derntl, & Sailer, 2013). The only difference to previous calculations is our treatment of the fearlessness subscale. In the original version of the questionnaire, the subscales social influence and stress immunity loaded most strongly on the fearless dominance factor. In contrast, although termed "fearlessness" subscale, it loaded less strongly on fearless dominance and also cross-loaded substantially on self-centered impulsivity (Benning, Patrick, Blonigen, Hicks, & Iacono, 2005). Moreover, only part of the respective items in the German translation load on a "fearlessness" subscale—which, however, seems to be better captured by sensation seeking (Alpers & Eisenbarth, 2008). For these reasons, we deliberately refrain from using the fearlessness subscale when calculating the fearless dominance score. It seems that social influence and stress immunity are more reliable phenotypic expressions of underlying dispositional fearlessness and that they also represent a social dimension that might be of relevance for the processing of facial stimuli. Thus, the mean of the z-transformed social influence and stress immunity scores comprised the fearless dominance score, while the mean of the *z*-transformed blame externalization, rebellious nonconformity, Machiavellian egocentricity, and carefree nonplanfulness scores comprised the self-centered impulsivity score. The resulting higher-order scores were also *z*-transformed for statistical analysis.

Results

Participants failed to respond in only 1.069 trials (0.535%) on average (modal value: 0). The maximum number of missed trials was 8 (4%). Hence, participants completed the large majority, if not all, of the trials. Missed trials were omitted from further analyses. On average, it took subjects 1.56 seconds to reach a decision (1.56 seconds in the neutral-face condition and 1.55 seconds in the fearful-face condition).

There were no significant gender effects when we included gender in the following statistical models. We therefore only report the more parsimonious models without gender.

Choice frequencies. Participants' choices were our objective measure of risk aversion (i.e., the tendency to prefer a sure outcome over a gamble of equal expected value; Wakker, 2010). Although positive and negative expected values were symmetrical across all gambles, participants accepted less than 50% of the gambles. Across both conditions, the mean acceptance rate was 35.75%, which is significantly different from 50%, $t(28) = -7.173$, $p < 0.001$, $d = 1.332$, and consistent with risk-averse behavior.

To measure the effect of incidental fear cues and psychopathic personality on risk aversion, we first analyzed participants' mean acceptance rates in SPSS (Version 22, IBM Corporation). To compare acceptance rates between conditions, we used a Wilcoxon signed-rank test, which is nonparametric and thus makes fewer and weaker assumptions than its parametric counterparts. In the next step, we used the "general linear model" function in SPSS to estimate a linear regression that comprised Prime (fearful-face vs. neutral-face condition) as a within-subject factor and Fearless dominance and Self-centered impulsivity as between-subject factors.

We observed effects of both incidental fear cues and psychopathic personality. First, we found a significant effect of incidental fear cues on decision behavior. As hypothesized, participants accepted fewer gambles in the fearful-face condition (34.78%) than in the neutral-face condition (36.73%), with $Z = -2.833$, $p = .003$, $d = -1.237$ in the Wilcoxon signed-rank test and $\beta = 0.02$, $SE = 0.0054$, $F(1, 26) = 11.553$, $p = .002$, partial $\eta^2 = .308$ in the linear regression. This is consistent with increased risk aversion when being primed with incidental fear cues.

Second, we found that personality moderates this effect. Although fearless dominance was not generally associated with the choice frequencies (between-subject effect), $\beta = -0.012$, $SE = 0.0203$, $F(1, 26) = 0.941$, $p = .341$, partial $\eta^2 = .035$, there was a significant Prime × Fearless dominance interaction, $\beta = -0.017$, $SE = 0.0059$, $F(1, 26) = 8.09$, $p = .009$, partial $\eta^2 = .237$. This indicates that a higher fearless dominance score was associated with reduced susceptibility to incidental fear cues. In fact, the 7 participants scoring in the top 25% of fearless dominance accepted almost exactly the same percentage of gambles in the fearful-face (33.07%) as in the neutral-face condition (33%), $Z = -0.271$, $p = .786$, $d = -0.206$ in a Wilcoxon signed-rank test. That is, in these high-scoring participants, the effect of incidental fear cues on participants' choices was not significantly different from 0. This also means that we find no indication for a potential reversal of the priming effect (i.e., increased instead of decreased risk taking) in subjects who scored high in fearless dominance. In the bottom 25%, there was, as expected, a significant difference between choices in the fearful-face (34.82%) and in the neutral-face condition (39.68%), $Z = -2.366$, $p = .018$, $d = -3.996$. In contrast to Fearless dominance, there was neither a significant between-subject effect of Self-centered impulsivity nor a significant interaction of this variable with Prime (all *p*s > .395) in the linear regression.

In a subsequent analysis, we correlated the between-condition difference in the choice frequencies with the two subscales that comprise fearless dominance. Consistent with a previous finding of reduced amygdala activity in the interpersonal facet when processing fearful faces (Carré et al., 2013), we find that higher social influence scores were associated with a decreased influence of the incidental fear cues on the choice frequencies ($r = -.41$, $p = .027$). This relationship was also observed for stress immunity ($r = -.438$, $p = .018$).

Loss aversion. Going beyond the analysis of choice frequencies and risk aversion expressed in this measure, we used quantitative behavioral modeling as a complementary and more specific method to investigate the influence of incidental fear cues on decision making. Specifically, we assessed behavioral sensitivity to gains and losses by fitting a logistic regression to all participants' binary choice data (accept vs. reject). This regression delivers an estimate of the degree of loss aversion, λ. λ represents the relative impact of losses on decisions compared to gains. $\lambda > 1$ indicates that the participant is loss-averse, $\lambda = 1$ indicates that the participant weighs gains and losses equally, and $\lambda < 1$ indicates that the subject weighs gains more strongly than losses. In line with prospect theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992), this parameter captures differences in the slopes of a kinked value function (e.g., a steeper slope for losses than for gains) and these differences in subjective valuation can explain risk aversion in mixed gambles. For simplification, we assumed linear instead of curvilinear utility due to the relatively small monetary stakes involved; we also assumed identical decision weights of .5 for gains and losses. Both simplifications are common in the literature (e.g., De Martino et al., 2010; Tom et al., 2007). The face conditions were included as a dummy-coded variable and fearless dominance and self-centered impulsivity as covariates, so that we could estimate the change in loss aversion due to affective priming, psychopathic personality, and the moderation of the priming effect by psychopathic personality. Our regression model also included a Fechner noise parameter σ to account for the stochastic nature of decision making—a standard procedure in both experimental economics (see, e.g., Harrison & Rutström, 2008) and experimental psychology (see, e.g., Sokol-Hessner et al., 2009, 2013). Here, $\sigma \rightarrow \infty$ is equivalent to random choice (i.e., the logistic link function $f \rightarrow .5$), and $\sigma \rightarrow 0$ means that no noise is present in participants' choices from the perspective of the model. For details of the regression equation see footnote 1.

The nonlinear mixed-effects model was set up in MATLAB (version R2015a), and nonlinear maximum likelihood estimation was used to estimate the preference and noise parameters.

Parameter estimates of the nonlinear mixed-effects model are reported in Table 1. Baseline loss aversion in the neutral-face condition, $\lambda_{neutral}$, was significantly greater than 1, indicating that participants weighed losses more than gains of identical size ($\lambda_{neutral} = 1.2203$, $SE = 0.0352$, $p < .0001$). Hence, on average, participants exhibited loss-averse behavior.

Importantly, this analysis confirms our main findings from the analysis of the choice frequencies and suggests that the observed risk aversion could be explained by loss aversion. First, as hypothesized, we found that incidental fear cues increased loss aversion ($\delta_\lambda = +0.0289$, $SE = 0.0128$, $p = .0238$). To demonstrate that this result is not based on only few subjects exhibiting a large effect, we depict the individual estimates of the degree of loss aversion (λ) for both conditions in Figure 2 (Panel a). A solid majority of the participants (21 out of 29) showed greater loss aversion in the fearful-face than in the neutral-face condition.

Second, as in the analysis of the choice frequencies, psychopathic personality moderated the effect of incidental fear cues. Participants with higher fearless-dominance scores were less influenced by incidental fear cues than lower-scoring individuals ($\psi_{FD,\lambda} = -0.0404$, $SE = 0.0131$, $p = .0021$). This is also illustrated by a scatter plot and a regression line that visualize the inverse relationship between fearless dominance and the effect of incidental fear cues (δ_λ) in Figure 2, Panel b.

In contrast to this interaction effect, there were no other significant personality effects (all *p*s > .1112, see Table 1). Participants also showed no significant change between conditions in the Fechner error term σ ($\delta_\sigma = -0.0315$, $SE = 0.0602$, $p = .6012$).

Study 2

In the second study, we aimed for a conceptual replication using forward priming (instead of simultaneous priming) and an independent sample of subjects.

Method

Participants. We recruited 28 participants through bulletin-board appeals at Freie Universität Berlin and mailing lists. All participants gave written informed consent prior to the experiment, and the ethics committee at Freie Universität Berlin approved all procedures. Three participants had to be excluded from the analyses because they rejected all lotteries in one priming condition (two participants in the fearful-face condition, one participant in the neutral-face condition; with nearly full rejection in the other condition). Because binary regression models, like the logit model we used, require variability in responses, loss aversion parameters could not be estimated for these participants. Another participant had to be excluded because she did not perform the gender identification task at all, raising doubts on whether she processed the primes. This left 24 participants for the analyses (13 female, 11 male; mean age, 24.29 years [*SD* = 5.312 years]).

Experimental procedure. The experimental procedure was identical to Study 1 with the following exceptions: Instead of priming participants with fearful and neutral faces during the decision phase, we displayed the primes immediately beforehand with a duration of 250 ms, resulting in an SOA of 250 ms. This is within the range of SOAs (0–300 ms) that have been found to elicit robust affective priming effects in classical priming studies (Hermans et al., 2001, 2003).

We wanted to ensure that participants processed the primes attentively without being explicitly asked to evaluate the emotional category. Therefore, we framed the priming procedure as a gender recognition task, similar to a previous study that investigated priming effects on consumption behavior and value judgments (Winkielman, Berridge, & Wilbarger, 2005). Importantly, it has been shown that emotional faces embedded in a gender recognition task (i.e., implicit processing of facial expressions) activate the amygdala more strongly than faces presented in an explicit emotion identification task (Critchley et al., 2000), rendering this implicit task a particularly useful priming technique. Moreover, implicit emotion processing resembles everyday psychological processes, which are thought to be predominantly automatic or implicit (Bargh & Chartrand, 1999; Kliemann, Rosenblau, Bölte, Heekeren, & Dziobek, 2013). Participants were instructed to silently evaluate the gender of the displayed faces unless they were explicitly asked to respond. There were 20 randomly interspersed explicit gender recognition questions—“Gender?” with two response options, “male” and “female”—that were displayed after facial primes and instead of mixed gambles in these trials. In total, there were 220 trials: 200 prime–gamble trials and 20 prime–gender question trials. Requiring responses to a few randomly interspersed explicit gender questions ensures that the task is performed continuously while at the same time avoiding explicit responses in the majority of trials that could interfere with the subsequent decisions. All participants included in the analyses showed a minimal accuracy of 80% (modal value: 100%) in the gender recognition task, indicating that the primes were processed adequately.

The 25 male and 25 female face stimuli were again pseudo-randomly paired with the decision trials as in Study 1. Ten of the male faces (5 neutral, 5 fearful) and ten of the female faces (5 neutral, 5 fearful) were used an additional time in the gender recognition trials. The lotteries in the decision trials were presented for 3250 ms during which the participants had to respond. The ITI was jittered and ranged from 2000 to 3000 ms (mean: 2500 ms). The sequence of events in a trial is depicted in Figure 3.

Results

Participants failed to respond in only 1.667 trials (0.833%) on average (modal value: 0). The maximum number of missed trials was 13 (6.5%). Hence, all participants completed the large majority, if not all, of the trials. Missed trials were omitted from further analyses. On average, it took subjects 1.38 seconds to reach a decision (1.39 seconds in the neutral-face condition and 1.36 seconds in the fearful-face condition).

As in Study 1, there were no significant gender effects when we included gender in the statistical models. We therefore only report the more parsimonious models without gender.

Choice frequencies. As in Study 1, participants accepted less than 50% of the gambles across both conditions. The mean acceptance rate was 33.37%, which is significantly different from 50%, $t(23) = -5.930$, $p < 0.001$, $d = 1.22$, and consistent with risk-averse behavior.

Performing the same analyses as in Study 1, we found an effect of incidental fear cues on decision behavior. Participants accepted fewer gambles in the fearful-face condition (32.77%) than in the neutral-face condition (33.96%), with $Z = -2.187$, $p = .027$, $d = -0.998$ in the Wilcoxon signed-rank test and $\beta = 0.012$, $SE = 0.0053$, $F(1, 21) = 4.118$, $p = .047$, partial $\eta^2 = .174$ in the linear regression. This suggests increased risk aversion in the fearful-face condition. Concerning personality, however, there were no significant between-subject effects or between–within interaction effects (all ps > .349).

Loss aversion. We estimated a nonlinear mixed-effects model like in Study 1, including fearless dominance and self-centered impulsivity as covariates of interest. As in Study 1, participants were on average loss-averse in the neutral-face condition, $\lambda_{neutral} = 1.2930$, $SE = 0.0528$, $p < .0001$.

Again, we observed an effect of incidental fear cues on loss aversion. Consistent with Study 1 and the analysis of the choice frequencies, there was a marginally significant increase in loss aversion when participants were primed with fearful faces, $\delta_\lambda = +0.0209$, $SE = 0.0107$, $p = .0502$. We found an increase in loss aversion in the majority of the participants (20 out of 24). As far as personality is concerned, there was no significant effect of fearless dominance (although the point estimate had the expected direction), $\psi_{FD,\lambda} = -0.0171$, $SE = 0.0103$, $p = .1246$. There were also no other significant personality effects (all ps > .3942). There was a trend toward significance for the effect of the priming condition on the Fechner error term σ ($\delta_\sigma = -0.1567$, $SE = 0.0855$, $p = .0670$), indicating that the consistency in participants' decisions may have been increased in the fearful-face condition.

Although both subscales of fearless dominance—social influence and stress immunity—were found to significantly moderate the effect of incidental fear cues on loss aversion in

Study 1, we initially hypothesized that in particular the interpersonal facet of fearless dominance, i.e., social influence which reflects low social anxiety and high social potency, might show the most robust effect. This is because social influence had been found to be associated with reduced reactivity to fearful faces in a previous study (Carré et al., 2013). Therefore, we estimated a different nonlinear mixed-effects model to analyze the specific influence of the subscales of fearless dominance— social influence and stress immunity. As can be seen in Table 2, estimated baseline loss aversion, the effect of incidental fear cues, and the estimated Fechner noise parameter were very similar to the model reported in the previous paragraph. The effect of incidental fear cues on loss aversion is also depicted in Figure 4, Panel a.

We found that social influence significantly moderated the influence of incidental fear cues on loss aversion, $\psi_{\mathrm{SocInf},\lambda} = -0.0210$, $SE = 0.0107$, $p = .0484$. Hence, participants higher in social influence showed smaller increments in loss aversion when primed with fearful faces, i.e., they were less susceptible to the incidental fear cues. This is consistent with reduced reactivity to fearful faces (Carré et al., 2013). In contrast, stress immunity did not emerge as a significant moderator in this study ($p = .7155$). This could also explain why the broader concept of fearless dominance was not a significant moderator in the analysis that included the higher-order factors, because the effect of social influence is statistically harder to detect when aggregated with another subscale that has no significant effect. The scatterplot and regression line in Figure 4, Panel b, illustrate the inverse relationship between social influence and the effect of incidental fear cues on loss aversion. The higher the social influence score, the more the effect vanishes.

General Discussion

A link between fear and loss processing has been postulated by various researchers (e.g., Camerer, 2005; Hartley & Phelps, 2012), but few empirical studies have tested this hypothesis.

In particular, the influence of incidental fear cues on loss aversion has not been demonstrated so far. We, therefore, designed two studies to experimentally manipulate the affective context and investigate its influence on loss aversion. As expected, we found that, on average, the presentation of fearful faces—stimuli that signal potential threats—increased risk aversion compared to the presentation of neutral faces, an effect that could be explained by increased loss aversion. We conceptually replicated this effect in an independent sample with a different priming sequence.

Moreover, the effect on loss aversion was moderated by psychopathic personality. Participants higher in fearless dominance—in particular social influence (i.e., low social anxiety, high social potency)—were less influenced by incidental fear cues than participants lower in this psychopathic personality trait. This moderation effect of a fear-related personality construct corroborates the notion that loss aversion is influenced by the incidental affective context.

Decision Making and Incidental Emotions

A number of theories postulate that emotions are used to inform judgments and decisions (e.g., Bechara, Damasio, & Damasio, 2000; Loewenstein, Weber, Hsee, & Welch, 2001; Schwarz, 2012). These emotions can arise from the evaluation of the decision options in the form of integral or anticipatory emotions (e.g., fear at the thought of a stock's potential loss), but they can also stem from dispositional as well as situational sources that are objectively unrelated to the decision itself (incidental emotions, e.g., elicited by emotional expressions of others or background music; Loewenstein & Lerner, 2003; Rick & Loewenstein, 2008).

Our findings are consistent with reports that incidental affect influences decision making (e.g, Isen et al., 1988; Lerner & Keltner, 2001; Raghunathan & Pham, 1999; Schulreich et al., 2014). For instance, experimentally evoked variations in incidental happiness have been shown to cause changes in probability weighting in a recent study on risk attitudes (Schulreich et al., 2014). Our study adds to this literature by providing evidence in favor of the hypothesis that another common and consequential decision phenomenon, loss aversion, is influenced by incidental fear cues. By experimentally manipulating the affective context, we also go beyond the majority of studies which provide only correlational data linking fear and anxiety to risky decision making (but see, e.g., Raghunathan & Pham, 1999).

It is important to note that although changes in risk aversion in our mixed-gambles task were captured well by changes in loss aversion, future studies would benefit from including gain-only trials (see, e.g., De Martino et al., 2010; Sokol-Hessner et al., 2013) as well as loss-only trials to better disentangle the specific effect on loss aversion from other, more general, risk-related effects.

Concerning the neural mechanisms, recent fMRI studies indicated that the amygdala (Canessa et al., 2013; Sokol-Hessner et al., 2013) and the insula (Canessa et al., 2013) are involved in loss aversion. Both structures are thought to be central for affective processing, in particular, the processing of aversive emotional states such as fear and anxiety (Kim et al., 2011; LeDoux, 2003; Paulus & Stein, 2006; Phelps et al., 2001). Moreover, reduced amygdala activity during the processing of fearful faces was found to be related to the interpersonal facet of psychopathy (Carré et al., 2013). Therefore, the effects observed in the present study could well be mediated by these neural structures, possibly in interaction with other brain areas. For instance, the striatum is thought to integrate motivation with action values. In particular, input from the amygdala to the striatum that signals threat—as it is likely generated by fearful faces—seems to be critical for avoidance actions (LeDoux & Gorman, 2001). Moreover, striatal activation and deactivation were related to loss aversion (Tom et al., 2007). Thus, a neural circuit including the amygdala, the insula, and the striatum is a plausible candidate for mediating the observed behavioral effects—consistent with a multiple-systems perspective on decision making (Phelps et al., 2014).

Functions of Fear and Associated Action Tendencies

Our finding that incidental fear cues increase loss aversion also resonates well with psychological theories about the functions of fear and anxiety. Fear is associated with an evolved defense system whose function is to protect the individual from threats to survival—be it in the form of predators, aggressive conspecifics, dangerous features of the terrain, or natural disasters (Öhman & Mineka, 2001; Panksepp, 1998). In modern societies, however, threats and risks are not restricted to explicit life-threatening events. They also occur in evolutionarily rather new, but still consequential domains such as economic decision making.

To fulfill its protective function in these domains, activation of the fear system is related to certain dispositions to actions (Bracha et al., 2004; Gray, 1988). The sequence of actions depends on the imminence of the threat. For instance, initial, less threat-imminent cues that signal a potential threat prime the organism to respond to subsequent immediate threats. When it is possible to avoid an actual threat, the organism will commonly do so ("flight" response). This is exactly the context given in our experiment. Participants were exposed to facial cues signaling a potential threat and were then asked whether they wanted to accept or reject (i.e., avoid) a combination of potential gains and losses (i.e., risks/threats). Our finding of increased loss aversion when being primed with incidental fear cues is consistent with an avoidance response as postulated by functional models of fear.

These models, however, also postulate other possible action tendencies (e.g., "fight") which depend on the perceived imminence of the threat and the possibility of avoidance (Bracha et al., 2004; Gray, 1988). In future research, one could investigate more closely whether fear cues affect decision making in ways that depend on the specific action tendencies evoked by specific contexts, perceptions, and appraisals. For instance, in a previous study, incidental fear had differential effects on risk taking, depending on whether the uncertainty was generated by a random mechanism (risk aversion increased) or by the behavior of another person (risk aversion decreased; Kugler, Connolly, & Ordóñez, 2012).

Psychopathic Personality and Its Relation to Loss Aversion

Apart from the factors mentioned so far, personality traits also play an important role in determining behavior. Participants higher in fearless dominance—in particular, social influence (i.e., low social anxiety, high social potency)—were less susceptible to incidental fear cues than those lower in fearless dominance. In contrast, self-centered impulsivity was not a significant moderator of the influence of incidental fear cues on loss aversion. This is consistent with the notion that reduced fear reactivity is a core feature of psychopathy, in particular, of fearless dominance, and with models postulating dissociable psychopathic traits (e.g., Patrick et al., 2009; Schulreich et al., 2013). An open question for future research is whether fearless dominance, social influence in particular, moderates only the influence of facial (and possibly other social) signals of fear or generalizes to a variety of incidental cues of fear. Future studies might benefit from larger sample sizes to also clarify whether the differential effects of the fearless dominance facets we observed in Study 1 and Study 2 are indeed context-dependent effects, or if stress immunity did not emerge as a moderator in Study 2 due to insufficient statistical power.

Although fearless dominance, in particular social influence, reduced susceptibility to incidental fear cues, it was not associated with loss aversion in general. This may, at first glance, appear inconsistent with the low-fear hypothesis of psychopathy because loss aversion has been related to fear processing. However, potential losses might be more salient than the face stimuli because of their central task relevance. A less responsive fear system might still be capable of task-relevant loss-related processing but impaired at processing task-irrelevant fear cues. A different possibility is that, due to an attention-related deficit in psychopathy, it is only the processing of peripheral/contextual cues that is impaired (Baskin-Sommers & Newman, 2013), influencing all down-stream (e.g., fear-related) processes such as those related to loss aversion. To sum up, while our research demonstrates that fearless dominance, in particular, its social influence facet, decreases the susceptibility to incidental fear cues in decision making, future research is needed to shed more light on the specific mechanisms that mediate this effect.

Conclusion

In summary, our findings indicate that when individuals are presented with incidental fear cues that signal potential threat, loss aversion increases. Knowledge of such incidental effects and the moderating role of personality could enable us to make more specific and accurate predictions of economic behavior. Ultimately, making ourselves aware of the influence of the affective context on our financial decisions might help us overcome potentially disadvantageous decision biases.

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Footnotes

[1] Formally, the regression equation can be expressed as

$$A_{s,t} = f\left[\frac{g_{s,t} + l_{s,t}\,(\lambda_{\text{neutral},s} + \delta_{\lambda,s} F_{s,t} + \gamma_{\text{FD},\lambda}\,\text{FD}_s + \psi_{\text{FD},\lambda} F_{s,t}\,\text{FD}_s + \gamma_{\text{SCI},\lambda}\,\text{SCI}_s + \psi_{\text{SCI},\lambda} F_{s,t}\,\text{SCI}_s)}{\sigma_{\text{neutral}} + \delta_\sigma F_{s,t}} + \varepsilon_{s,t}\right].$$

The variables' meanings are as follows: (a) Indices: *s* is the subject ID, and *t* is the trial number. (b) Dependent variable: $A_{s,t}$ is 1 if subject *s* accepted the gamble in trial *t* and 0 otherwise. (c) Link function: *f* is the logistic function (logit regression model), $f[x] = 1 / [1 + \exp(-x)]$. (d) Regressors: $g_{s,t}$ is the gain that subject *s* could earn (with 50% probability) in trial *t*, and $l_{s,t}$ is the potential loss that subject *s* faced (with 50% probability) in trial *t*. $F_{s,t}$ is the condition dummy that equaled 1 in the fearful-face condition and 0 in the neutral-face condition. FD_s is the fearless-dominance score and SCI_s the self-centered impulsivity score of subject *s*. (e) Regression coefficients: $\lambda_{\text{neutral},\,s}$ is the degree of loss aversion in the neutral-face condition, and the coefficient $\delta_{\lambda,\,s}$ captures the change between the fearful-face and the neutral-face condition. Both λ_{neutral} and δ_λ are indexed by *s*, since we included individual random effects in baseline loss aversion and the between-condition change in loss aversion. $\gamma_{\text{FD},\,\lambda}$ and $\gamma_{\text{SCI},\,\lambda}$ are the coefficients that capture the influence of fearless dominance and self-centered impulsivity on loss aversion (average loss aversion across the two conditions), respectively. $\psi_{\text{FD},\,\lambda}$ is the coefficient on the interaction of the condition effect with the fearless-dominance score, and $\psi_{\text{SCI},\,\lambda}$ is the coefficient on the interaction of the condition effect with the self-centered impulsivity score. σ_{neutral} is the Fechner error in the neutral-face condition, and δ_σ is the change of the Fechner error term between the fearful-face and the neutral-face condition. (f) Error term: $\varepsilon_{s,t}$ is an error term with $E[\varepsilon_{s,t}] = 0$ and $\text{Var}[\varepsilon_{s,t}] = 1$.

Table 1

Nonlinear mixed-effects model, Study 1: Estimates of the degree of loss aversion (λ) as a function of priming condition and psychopathic personality as well as estimates of the Fechner noise parameter (σ).

	Coefficient	*SE*	*p*
Degree of loss aversion (λ)			
$\lambda_{neutral}$: baseline loss aversion (in neutral-face condition)	+1.2203	0.0352	< .0001
δ_{λ}: change in loss aversion due to fearful-face condition	+0.0289	0.0128	= .0238
$\gamma_{FD,\lambda}$: change in loss aversion due to fearless dominance	+0.0572	0.0359	= .1112
$\psi_{FD,\lambda}$: interaction of condition effect and fearless dominance	−0.0404	0.0131	= .0021
$\gamma_{SCI,\lambda}$: change in loss aversion due to self-centered impulsivity	+0.0358	0.0359	= .3193
$\psi_{SCI,\lambda}$: interaction of condition and self-centered impulsivity	−0.0001	0.0131	= .9967
Fechner noise parameter (σ)			
$\sigma_{neutral}$: baseline Fechner noise (in neutral-face condition)	+0.9896	0.0427	< .0001
δ_{σ}: change in Fechner noise due to fearful-face condition	−0.0315	0.0602	= .6012

Note. Wald tests were used to assess whether the loss aversion parameter in the neutral-face condition significantly differed from 1 (i.e., no loss aversion and risk neutrality) and whether the other parameters differed from 0. Error degrees of freedom = 5757. Log-likelihood = −864.6636. RMSE = 0.2767. BIC = 1769.70.

Table 2

Nonlinear mixed-effects model, Study 2: Estimates of the degree of loss aversion (λ) as a function of priming condition and psychopathic personality as well as estimates of the Fechner noise parameter (σ).

	Coefficient	*SE*	*p*
Degree of loss aversion (λ)			
$\lambda_{neutral}$: baseline loss aversion (in neutral-face condition)	+1.2930	0.0523	< .0001
δ_{λ}: change in loss aversion due to fearful-face condition	+0.0208	0.0108	= .0538
$\gamma_{SocInf,\lambda}$: change in loss aversion due to social influence	+0.0408	0.0580	= .4820
$\psi_{SocInf,\lambda}$: interaction of condition effect and social influence	−0.0210	0.0107	= .0484
$\gamma_{StrIm,\lambda}$: change in loss aversion due to stress immunity	−0.0577	0.0580	= .3199
$\psi_{StrIm,\lambda}$: interaction of condition effect and stress immunity	+0.0042	0.0114	= .7155
Fechner noise parameter (σ)			
$\sigma_{neutral}$: baseline Fechner noise (in neutral-face condition)	+1.3484	0.0625	< .0001
δ_{σ}: change in Fechner noise due to fearful-face condition	−0.1490	0.0854	= .0811

Note. Wald tests were used to assess whether the loss aversion parameter in the neutral-face condition significantly differed from 1 (i.e., no loss aversion and risk neutrality) and whether the other parameters differed from 0. Error degrees of freedom = 4748. Log-likelihood = −981.9752. RMSE = 0.2937. BIC = 2002.10.

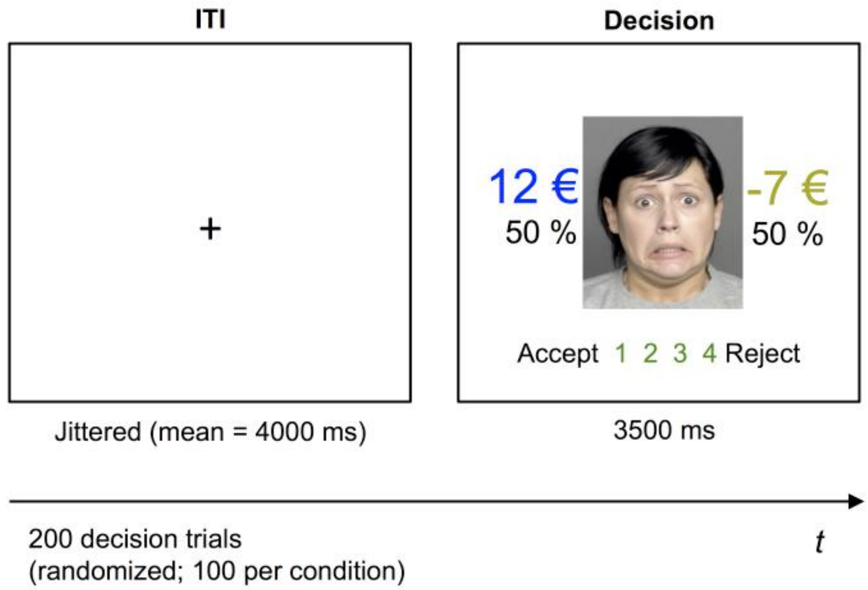

Figure 1. Sequence of events in a trial of Study 1.

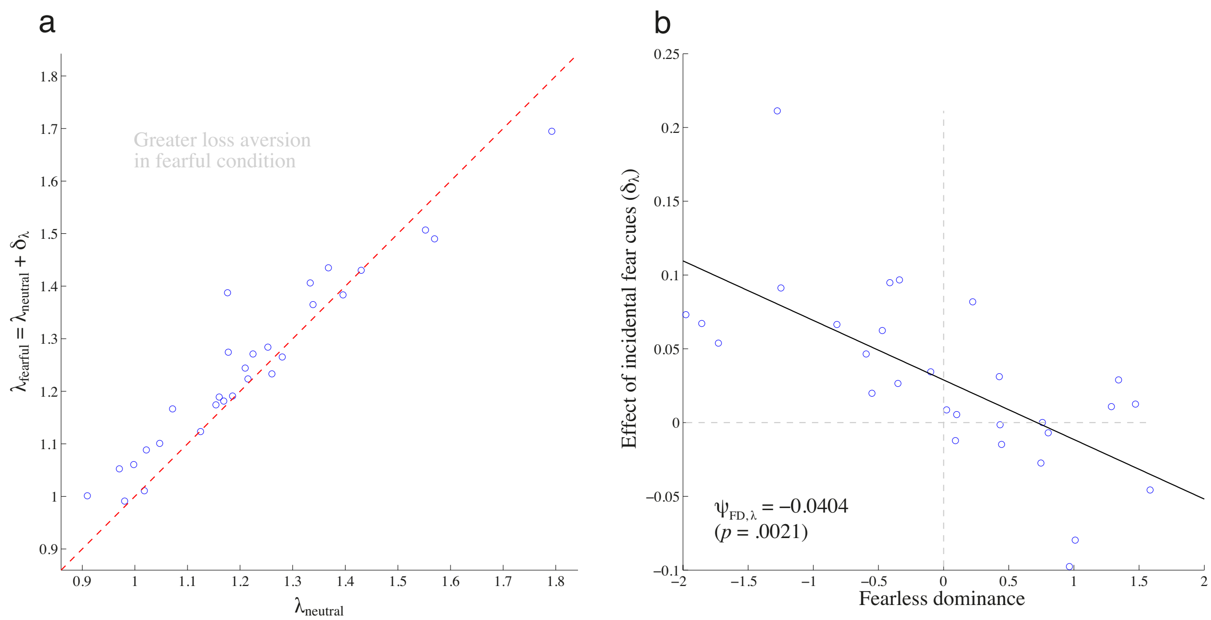

Figure 2. Study 1: Panel a depicts individual estimates, based on the individual random effects included in the regression analysis, of the degree of loss aversion (λ) in the neutral-face and fearful-face condition; data points above the 45° line are associated with greater loss aversion in the fearful-face condition. Panel b depicts a scatterplot and a linear regression line that illustrates the inverse relationship between fearless dominance and the size of the effect of incidental fear cues on loss aversion *(δ_λ)*. The graph also contains two dashed lines that intersect at 0 on both axes (i.e., average fearless dominance score [horizontal axis]; no change in loss aversion [vertical axis]) and that delineate four sectors into which the data points fall. For the lower half of fearless dominance scores, all the data points lie within the upper-left sector, indicating that those participants all showed higher loss aversion in the fearful-face condition.

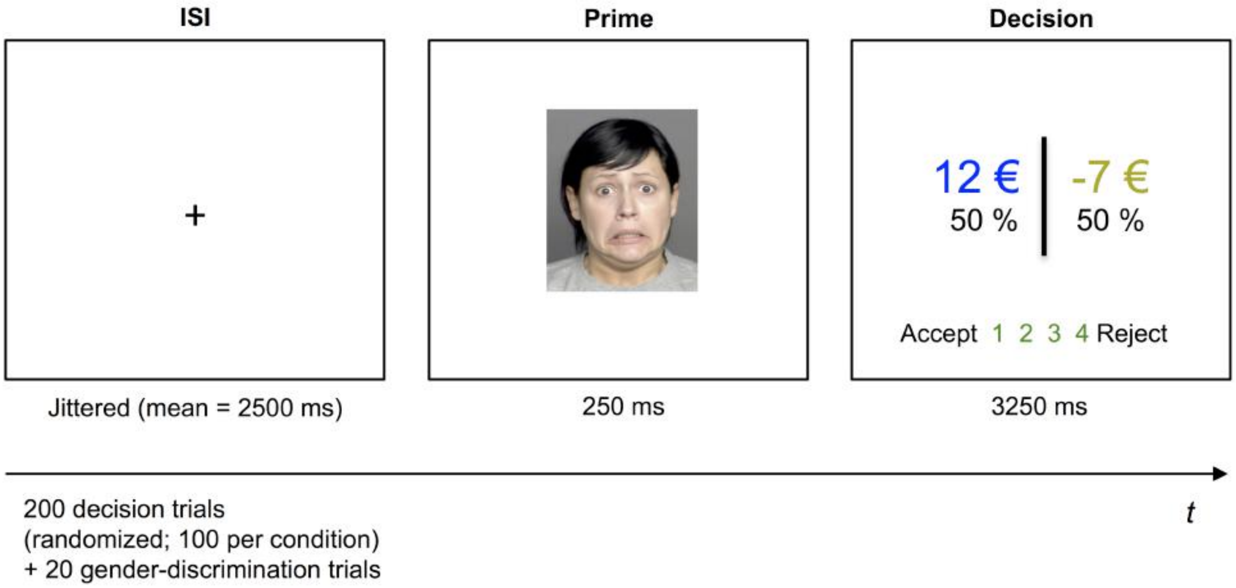

Figure 3. Sequence of events in a trial of Study 2.

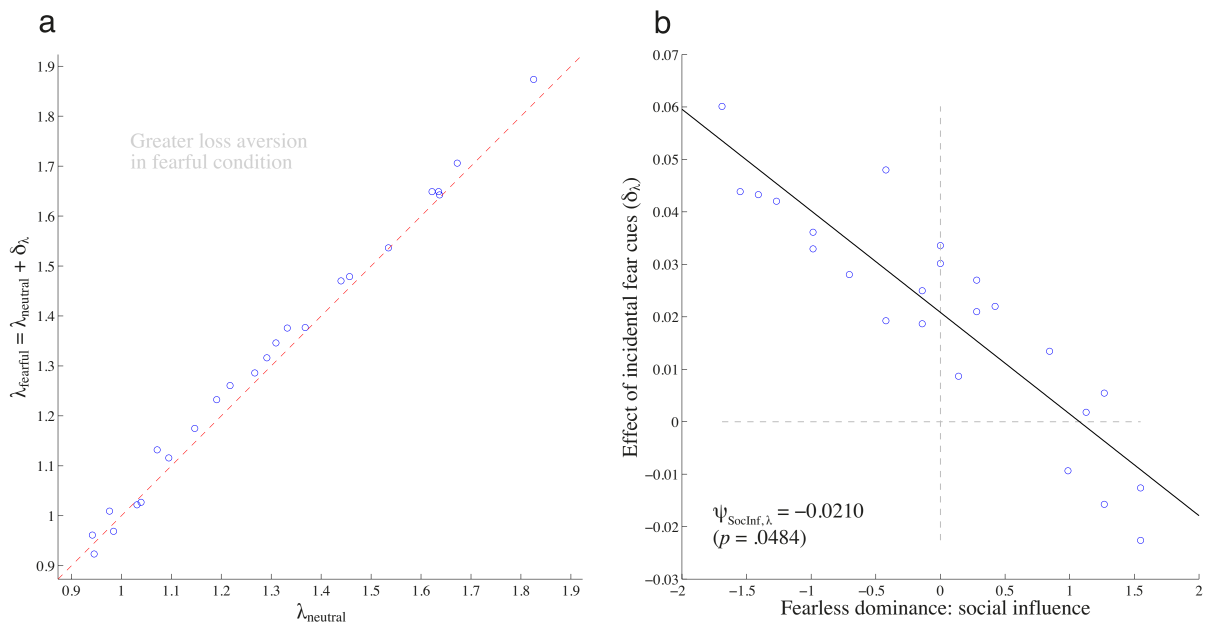

Figure 4. Study 2: Panel a depicts individual estimates, based on the individual random effects included in the regression analysis, of the degree of loss aversion (λ) in the neutral-face and fearful-face condition; data points above the 45° line are associated with greater loss aversion in the fearful-face condition. Panel b depicts a scatterplot and a linear regression line that illustrates the inverse relationship between social influence, one of the two subscales of fearless dominance, and the size of the effect of incidental fear cues on loss aversion *(δ_λ)*. The graph also contains two dashed lines that intersect at 0 on both axes (i.e., average social influence score [horizontal axis]; no change in loss aversion [vertical axis]) and that delineate four sectors into which the data points fall. For the lower half of social influence scores, all the data points lie within the upper-left sector, indicating that those participants all showed higher loss aversion in the fearful-face condition.

Emotion-induced increases in loss aversion are associated with shifts towards negative neural value coding

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Submitted to Proceedings of the National Academy of Sciences of the United States of America

Human choice is often guided by emotions, even when these emotions are incidental, i.e., unrelated to a particular decision. For instance, incidental fear cues presented before or during a lottery choice have been found to increase monetary loss aversion. Here we investigate the neural mechanisms that mediate this effect. Due to its role in fear processing and in the generation of loss aversion, the amygdala is a candidate region to find such mechanisms. However, its exact functional role in loss aversion and in its context-dependent variability is not well understood. We hypothesized that emotion-induced increases in amygdala activity in response to monetary losses mediate emotion-induced increases in loss aversion. While measuring brain activation via functional magnetic resonance imaging, we presented 27 participants with fearful or neutral faces before they made decisions about monetary gambles involving both gains and losses. We replicated a previously observed emotion-induced increase in loss aversion. At the neural level, we observed an emotion-induced shift from positive to negative value coding in a distributed set of brain regions, including the amygdala. More precisely, we found that loss aversion following the presentation of neutral faces was mainly predicted by greater *deactivations* for losses (relative to *activations* for gains). In contrast, emotion-induced increases in loss aversion were mainly predicted by greater *activations* for losses. Therefore, our results provide a neural mechanism for emotion-induced changes in loss aversion via context-dependent involvement of different valuation processes.

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amygdala | value | emotion | loss aversion | decision making

Human choice is often guided by emotions (1, 2). For example, financial investors may be gripped with fear during a stock market crash and choose to sell large parts of their portfolios. In this scenario, the emotion is related to the decision—fear is evoked by the potential loss of stock value. However, emotions that are unrelated to the decision at hand, called incidental emotions, can also influence decision making (2–4).

A component of decision making that may be particularly prone to emotional influences is loss aversion, characterized by a greater sensitivity to potential losses compared to potential gains of equal size (5). In a previous behavioral study, we found that incidental fear cues (images of fearful faces) presented before or during a lottery choice increased monetary loss aversion (4). It remains unclear, however, how this emotional effect on choice is mediated at the neural level. In particular, where and how do emotions and deliberative decision making interact?

One key biological structure that is involved in both affective processing and loss aversion is the amygdala. For instance, it is well established that the amygdala is critical for threat processing (6). At the same time, amygdala-lesioned patients exhibit substantially reduced loss aversion compared to matched controls (7), suggesting that the amygdala plays a causal role in the generation of loss aversion. Given this functional overlap, the amygdala is a plausible candidate for mediating the effects of incidental emotions on loss aversion.

However, what are the specific mechanisms that give rise to monetary loss aversion and emotion-induced changes in its strength? According to recent accounts, two types of loss signals are associated with distinguishable, but partially overlapping, motivational systems (8, 9). The first type of system codes positive value. This system generates *inhibitory* loss signals (i.e., reductions in neuronal activity). It consists of a mesocorticolimbic circuit that includes, e.g., the striatum (8–10). Within this circuit, greater loss-related *deactivations* compared to gain-related *activations*—a feature termed "neural loss aversion"—predict behavioral loss aversion (11, 12). The second type of system codes negative value. This system generates *excitatory* loss signals (i.e., increasing activity to increasing losses) and also includes, e.g., the striatum (8, 9). Notably, two studies found loss-related *activations* in the amygdala, which also predicted behavioral loss aversion (12, 13). However, other studies observed stronger amygdala *deactivations* for losses relative to gain-related activations [i.e., neural loss aversion (14)] or failed to find any loss-related amygdala activity (11, 15). Taken together, the amygdalar mechanisms that generate loss aversion are still far from clear.

Only two recent studies have investigated the influence of incidental emotions on loss aversion at the neural level. Neither reported value-related amygdala activity that predicted emotion-induced changes in loss aversion. However, one of these studies

Significance

For scholars and laymen alike, the influence of incidental emotions on decisions is puzzling. Moreover, the mechanisms giving rise to these effects are currently not well understood. Here, we show that emotion-induced changes in loss aversion can be explained by shifts from positive towards negative value coding—in particular from deactivations to activations for losses—in a distributed set of brain regions, including the amygdala. Therefore, our work goes beyond existing research based on behavioral models that are mute to the sources of loss aversion. Our results suggest that loss aversion is based on a context-dependent involvement of distinct valuation processes that represent losses in markedly different ways.

Reserved for Publication Footnotes

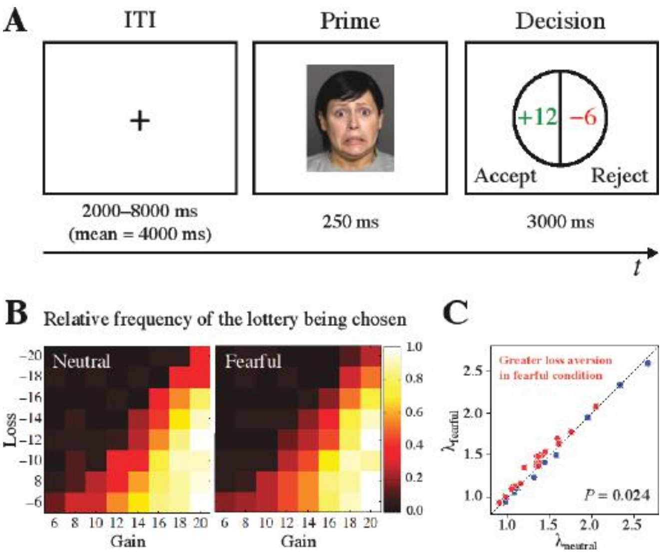

Fig. 1. Trial sequence and behavioral results. (*A*) Images of faces (fearful vs. neutral) were presented prior to mixed gambles (within-subject design with 2 × 64 face-gamble trials). The priming procedure was embedded in a gender discrimination task (for more details see *SI Methods*). Mixed gambles included potential gains and losses ranging from ±€6 to ±€20 in steps of €2 (8 × 8 = 64 gambles per condition, also see Panel *B*), and in all gambles, the two potential payoffs had identical probability (i.e., 50%). (*B*) Relative frequencies of the lottery being chosen in the two conditions across gain-loss combinations. (*C*) Estimates of the degree of loss aversion, λ, per condition. Red data points above the 45° line indicate greater loss aversion in the fearful condition (18 out of 28 participants, i.e., 66.67%); blue data points indicate no change or decreased loss aversion.

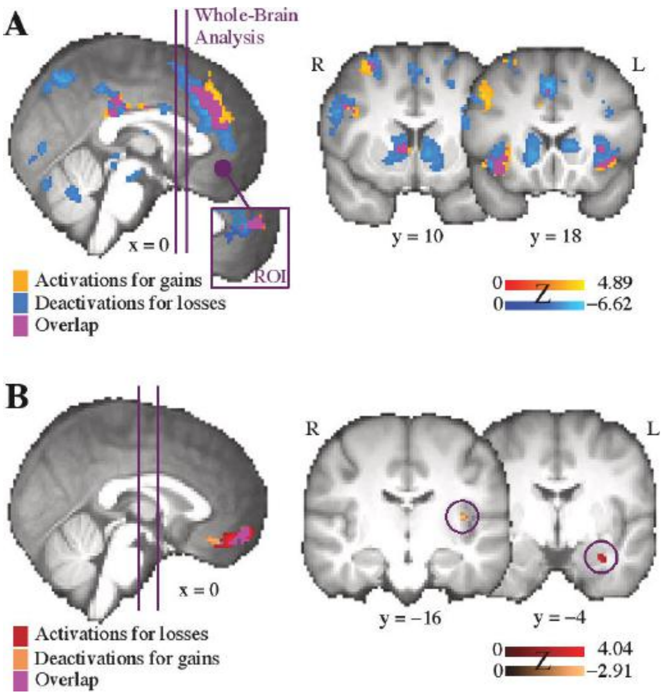

Fig. 2. Neural responses to gains and losses in the neutral condition. (*A*) Activations for gains ($\beta_{\text{Gain, Neutral}} > 0$) and deactivations for losses ($\beta_{\text{Loss, Neutral}} < 0$) (whole-brain analysis; cluster-corrected with $Z > 3.1$ and $P < 0.05$). Here, we depict whole-brain results because they overlap with ROI-based results, except that these responses were also present in the vmPFC ROI (rACC and paracingulate gyrus) and covered more voxels in the other ROIs. (*B*) Activations for losses ($\beta_{\text{Loss, Neutral}} > 0$) and deactivations for gains ($\beta_{\text{Gain, Neutral}} < 0$) in the vmPFC/mOFC; deactivations for gains in the posterior insula, and activations for losses in the left amygdala (ROI analysis; small-volume FDR-corrected with $P < 0.05$ and spatial extent threshold of $k \geq 15$ voxels).

found that enhanced amygdalar–striatal connectivity predicted increases in loss aversion following the presentation of emotional faces (16). The second study compared decisions under threat-of-shock and in a neutral context (17). Surprisingly, while the authors observed loss aversion across contexts, they did not observe emotion-induced changes in its magnitude. However, choice behavior was predicted by brain activity in a context-dependent manner. Specifically, increasing activity for increasing subjective expected value (i.e., positive value coding) in the striatum and the ventromedial prefrontal cortex (vmPFC) positively predicted gamble acceptance in the neutral context, whereas increasing insula activity for decreasing subjective expected value (i.e., negative value coding) negatively predicted gamble acceptance in the threat-of-shock context. Greater loss-related activations are one possible source of the observed shift towards negative value coding. This possibility, however, has not been explored so far.

In line with most previous studies (11, 12, 16), we separately analyzed loss and gain responses to identify more exactly the mechanisms underlying potential emotion-induced changes in valuation. Given the prominent role the amygdala plays in fear processing (6) and given preferential processing of threat-related relative to appetitive stimuli under fear-related affective states (18), we hypothesized that excitatory loss signals in the amygdala (12, 13, 19) can account for increases in loss aversion that are induced by fear cues. Moreover, amygdala responses to fearful movies have been found to enhance subsequent activation to unrelated threat-signaling stimuli (20). Similarly, we expected a general increase in amygdala activity after the presentation of fear cues in combination with increased activation in response to increasing monetary losses. The latter component would reflect negative value coding. In fact, the amygdala might be part of a broader, distributed network that displays an emotion-induced shift from positive to negative value coding, which also includes the striatum, vmPFC, and insula (17). Importantly, we tested whether such effects mediate emotion-induced increases in monetary loss aversion. Alternatively, changes in loss aversion might be mediated by a positive-value–coding mechanism via enhanced deactivations for losses relative to activations for gains, e.g., in the striatum (11, 12).

We collected and analyzed data from 27 participants (15 female; mean age, 21.81 years [*SD* = 3.55 years]; for more details, see *SI Methods*). All subjects participated in a decision-making task that we previously used in a behavioral study (4) and that we adapted for functional magnetic resonance imaging (fMRI). In this task, participants decided to accept or reject gambles consisting of both a potential gain and a potential loss, while in the MRI scanner. To manipulate affect, we briefly presented images of fearful (or neutral) faces before each lottery choice (for more information on the task, see Fig. 1 *A* and *SI Methods*). We chose fearful faces as emotional primes, because they signal potential threats and reliably enhance amygdala activity (21). After the experiment, participants also completed a self-report questionnaire on psychopathic personality (see *SI Methods* and *SI Results*).

Results

Behavioral Loss Aversion Is Increased in the Fearful Condition. Participants' choices served as an objective measure of risk aversion, i.e., the tendency to prefer a sure outcome over a gamble of equal expected value (22). Given that potential gains and losses were sampled from a symmetrical payoff matrix (see Fig. 1 *B*) and had identical probability (50%), the average expected value of all gambles was €0. Hence, a choice frequency of 50% would indicate risk neutrality. Alternatively, a choice frequency of 50% could indicate completely random choice; however, Fig. 1 *B* illustrates

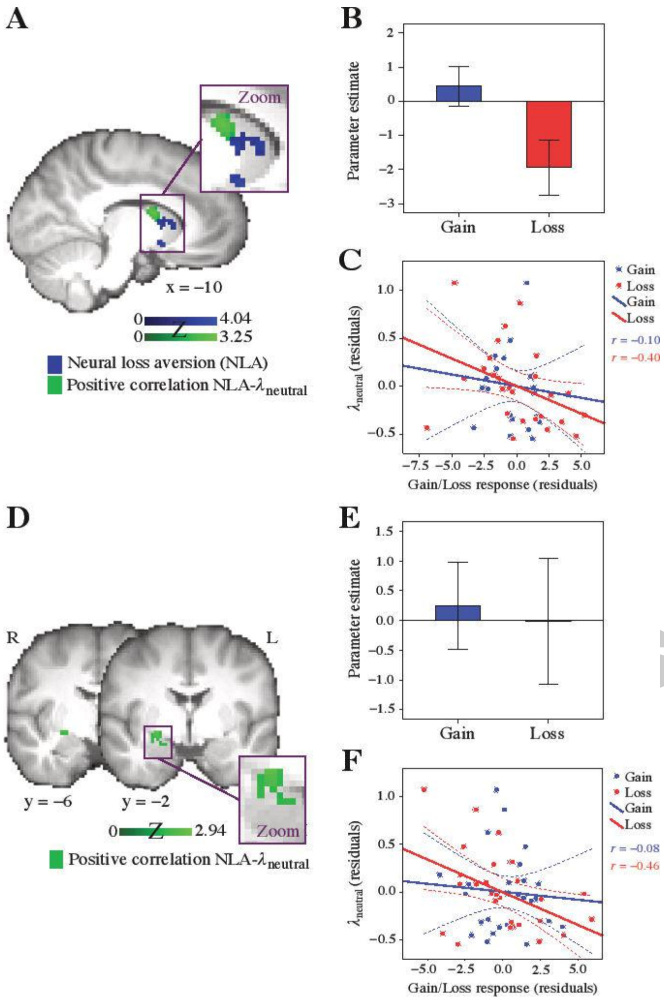

Fig. 3. Neural loss aversion in the neutral condition.(*A*) Neural loss aversion, i.e., greater deactivations for losses relative to activations for gains ($-\beta_{Loss,\ Neutral} - \beta_{Gain,\ Neutral} > 0$) in the striatum (blue). Neural loss aversion was also positively correlated with behavioral loss aversion, e.g., in the left caudate (green). (*B*) Parameter estimates for the gain and loss regressors for the left caudate cluster that displayed neural loss aversion. (*C*) Relationships between neural gain and loss responses and behavioral loss aversion in the left caudate (green cluster in Panel A). Greater deactivations for losses significantly predicted greater loss aversion, $\lambda_{neutral}$ (partial regression plot, i.e., controlling for emotion-induced changes in loss aversion, $\lambda_{fearful} - \lambda_{neutral}$). (*D*) Neural loss aversion was positively correlated with behavioral loss aversion in the right superficial and centromedial amygdala (green). (*E*) Parameter estimates for the gain and loss regressors for the amygdala cluster. (*F*) Relationships between neural gain and loss responses and behavioral loss aversion in the amygdala cluster. Greater deactivations for losses significantly predicted greater loss aversion (partial regression plot). *Note:* All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 15$. Error bars/lines represent 95% CIs (including between-subject variance).

that subjects' choices varied systematically with the offered gains and losses. In the neutral condition, the mean gamble acceptance rate was 31.81% (SD = 13.92%). This is significantly lower than 50%, $t(26) = -6.792$, $P < 0.001$, and indicates risk aversion. In the fearful condition, the mean acceptance rate was significantly reduced to 30.79% (SD = 13.66%), $t(26) = -1.880$, $P = 0.036$ (one-tailed), indicating that incidental fear cues increased risk aversion (Fig. 1 B).

Within the framework of Prospect Theory, loss aversion is a major source of risk aversion for mixed gambles (22). Hence, going beyond the analysis of choice frequencies, we used quantitative behavioral modeling as a more specific method to investigate emotion-induced changes in loss aversion (see *Methods*). In particular, we estimated each subject's degree of loss aversion, λ. Importantly, unlike simply calculating choice frequencies, this method also assesses how noisy subjects' choices are (via a Fechner noise parameter, σ, see *SI Results*). A parameter value $\lambda = 1$ indicates loss neutrality, while $\lambda > 1$ indicates loss aversion. In the neutral condition, participants were on average loss-averse, $\lambda_{neutral} = 1.43$ (SD = 0.42), since the estimate was significantly greater than 1, $t(26) = 5.225$, $P < 0.001$. Critically, incidental fear cues significantly increased loss aversion when compared to the neutral condition, $\lambda_{fearful} = 1.46$ (SD = 0.41), $t(26) = 2.401$, $P = 0.024$ (Fig. 1 *C*). Baseline loss aversion ($\lambda_{neutral}$) and emotion-induced changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$) were not significantly correlated between-subjects, $r = -0.24$, $P = 0.238$. For an analysis of response times, see *SI Results*.

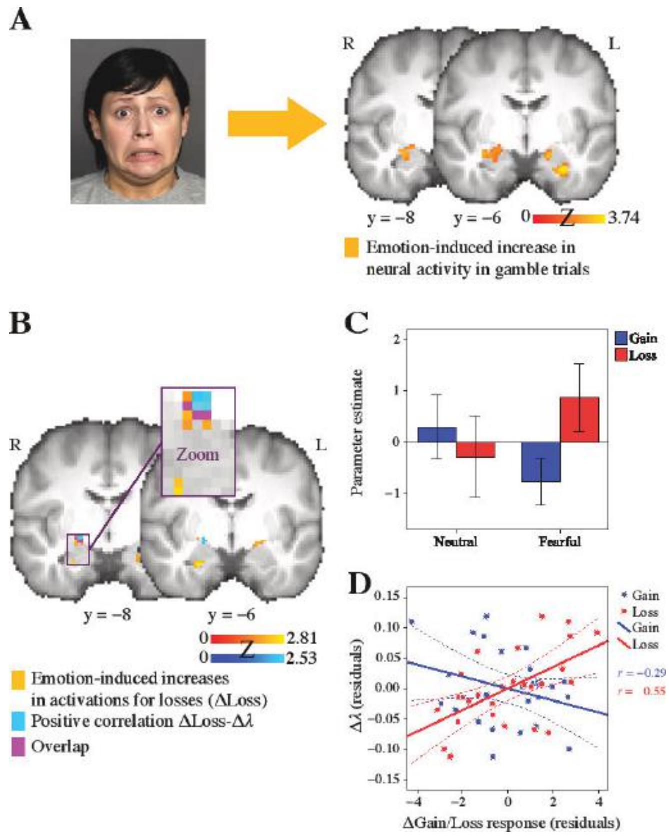

Fig. 4. Emotion-induced changes in amygdala activity and value coding. (*A*) Increased bilateral amygdala activity during gamble trials (onset: face presentation) in the fearful condition compared to the neutral condition (red-yellow). (*B*) Increased bilateral amygdala activations for losses in the fearful condition (red-yellow), which were also associated with emotion-induced increases in loss aversion in the right superficial and centromedial amygdala (light-blue). (*C*) Parameter estimates for the gain and loss regressors per condition for the right superficial and centromedial amygdala (red-yellow cluster in Panel *B*). (*D*) Relationships between emotion-induced changes in gain and loss responses and changes in behavioral loss aversion in the right superficial and centromedial amygdala (light-blue cluster in Panel *B*). Greater emotion-induced activations for losses significantly predicted emotion-induced increases in loss aversion (partial regression plot, i.e., controlling for $\lambda_{neutral}$). *Note:* All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 15$. Error bars/lines represent 95% CIs (including between-subject variance).

Behavioral Loss Aversion Is Related to Greater Neural Deactivations for Losses in the Neutral Condition. In our neuroimaging analysis, we first investigated neural activity in the neutral condition, i.e., in the absence of incidental fear cues that enhance loss aversion. We focused on the amygdala as an a priori region of

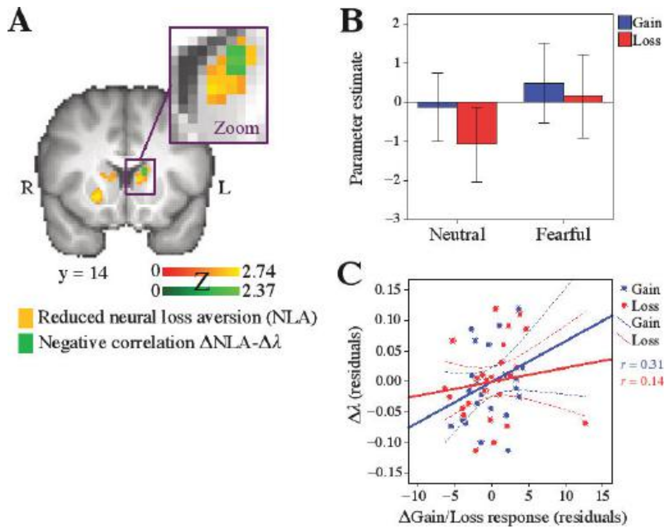

Fig. 5. Emotion-induced changes in neural loss aversion. (*A*) Reduced neural loss aversion (i.e., $-\beta_{Loss} - \beta_{Gain}$) in the bilateral striatum in the fearful condition compared to the neutral condition (red-yellow). Decreases in neural loss aversion were associated with emotion-induced increases in behavioral loss aversion in the left caudate (green). (*B*) Parameter estimates for the gain and loss regressors per condition for the left caudate (red-yellow cluster in Panel *A*). (*C*) Relationships between emotion-induced changes in gain and loss responses and changes in behavioral loss aversion in the left caudate (green cluster in Panel *A*). Descriptively, increasing activations for gains and losses were associated with increasing loss aversion, but neither correlation was statistically significant (partial regression plot). Their combined effect, however, led to significant reductions in neural loss aversion, which is based on stronger deactivations (and not activations) for losses relative to activations for gains. *Note:* All statistical tests were small-volume FDR-corrected with $P < 0.05$ ($k \geq 15$). Error bars/lines represent 95% CIs (including between-subject variance).

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interest (ROI), given its role in emotion processing (6) and loss aversion (7, 12, 16). Further ROIs were the striatum, vmPFC, and insula, given their role in (context-dependent) valuation (10, 17). Our ROI analysis was complemented by an exploratory whole-brain analysis.

First, we investigated parametric modulations of brain activation by potential gains and losses. Consistent with previous research (11, 12, 14, 16), we observed partially overlapping sets of positive-value coding regions that showed activations for gains ($\beta_{Gain,\,Neutral} > 0$) and deactivations for losses ($\beta_{Loss,\,Neutral} < 0$), including the bilateral striatum, ventral tegmental area, dorsal anterior cingulate cortex (dACC), paracingulate gyrus, and rostral ACC/vmPFC, among others (Fig. 2 *A* and Tables S1 for ROI-based results and S2 for whole-brain results). Moreover, we replicated a pattern previously termed "neural loss aversion" (11), i.e., greater deactivations for losses relative to activations for gains ($-\beta_{Loss,\,Neutral} - \beta_{Gain,\,Neutral} > 0$), e.g., in the striatum and paracingulate gyrus (Fig. 3 *A* and *B* and Tables S1 and S2).

We also observed opposite negative-value coding responses, i.e., activations for losses ($\beta_{Loss,\,Neutral} > 0$) and deactivations for gains ($\beta_{Gain,\,Neutral} < 0$) in the medial orbitofrontal cortex (mOFC)/vmPFC, as well as activations for losses in the left basolateral amygdala and deactivations for gains in the left posterior insula (Fig. 2 *B* and Table S1).

We also investigated whether neural value responses predicted behavioral loss aversion by including $\lambda_{neutral}$ as a covariate in our fMRI group-level analysis, and controlling for emotion-induced changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$). Here, we observed that more loss-averse participants displayed greater neural loss aversion (Table S1), e.g., in the bilateral caudate (Fig. 3 *A*), which was mainly due to increasing deactivations for losses with increasing behavioral loss aversion (Fig. 3 *C* and Tables S1 and 2).

On average, we did not find significant value responses in the right superficial and centromedial amygdala (Fig. 3 *E*). Crucially, however, we found that monetary loss aversion was positively associated with the contrast estimate for neural loss aversion (Fig. 3 *D*) and negatively associated with the contrast estimate for losses (Fig. 3 *F*) in this region. The latter correlation indicates that, in contrast to the nonsignificant mean effect, more loss-averse participants might have displayed deactivations to losses. Checking this for the top quartile of $\lambda_{neutral}$ values, we observed deactivations for losses that were indeed marginally significantly different from 0 ($\beta_{Loss,\,Neutral} = -1.81$, SD = 1.97), $t(6) = 2.427$, $P = 0.051$. Hence, greater loss aversion was associated with a tendency towards greater deactivations for losses.

Regarding gains, we observed both increasing activations (e.g., in the striatum) as well as deactivations (e.g., in the vmPFC) with increasing behavioral loss aversion, though these responses were spatially less extended than loss-related correlations (Table S1).

Emotion-Induced Increases in Loss Aversion Are Associated with Greater Neural Activations for Losses. In the previous section, we described how loss aversion in the neutral condition was mediated by positive value coding that displayed greater deactivations for losses relative to activations for gains (i.e., neural loss aversion). In contrast, we hypothesized a shift towards negative value coding in the fearful condition. Specifically, we expected that greater activations for losses would mediate emotion-induced increases in loss aversion. Furthermore, we hypothesized that this shift is triggered by amygdala reactivity to incidental fear cues, which extends to the processing of monetary payoffs.

In line with this hypothesis, we observed a general increase in bilateral amygdala activity following the presentation of fearful faces compared to neutral faces ($\beta_{Gamble,\,Fearful} - \beta_{Gamble,\,Neutral} > 0$, see Fig. 4 *A* and Table S3), but this effect was not linked to emotion-induced changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$, controlling for $\lambda_{neutral}$).

To detect shifts towards negative value coding and in loss processing in particular, we calculated the contrast $\beta_{Loss,\,Fearful} - \beta_{Loss,\,Neutral} > 0$. We found that this contrast becomes significant in a distributed set of regions (Table S3). Please note that this effect could mean either increased activations for losses or reduced deactivations for losses in the fearful condition relative to the neutral condition. To differentiate between these possibilities, we conducted conjunction analyses. First, we calculated a conjunction of the thresholded maps for the contrast $\beta_{Loss,\,Fearful} - \beta_{Loss,\,Neutral} > 0$ and for $\beta_{Loss,\,Fearful} > 0$ with a spatial extent threshold of $k \geq 5$ voxels (Table S3). This revealed clusters for which emotion-induced changes in loss responses were also associated with absolute activations for losses in the fearful condition, e.g., in the bilateral amygdala (Fig. 4 *B* and *C*) and putamen. On average, these regions did not display significant loss-related activity in the neutral condition. Crucially, we also observed that greater emotion-induced activations for losses predicted emotion-induced increases in behavioral loss aversion (Table S3), e.g., in the right superficial and centromedial amygdala (Fig. 4 *B* and *D*), vmPFC (Fig. S1), putamen, and insula. The amygdala cluster overlapped with a cluster that displayed the opposite effect in the neutral condition, i.e., a positive association between neural loss aversion—deactivations for losses, in particular—and behavioral loss aversion. The vmPFC cluster overlapped with a cluster that already displayed activations for losses in the neutral condition (see Fig. 2 *B*).

In contrast, several regions, including the bilateral striatum (Fig. 5 *A* and *B*), paracingulate gyrus/vmPFC, and anterior insula, displayed reduced deactivations for losses in the fearful condition relative to the neutral condition, but on average, there was no change to activations for losses. This was revealed by a conjunction of the thresholded maps for the contrast $\beta_{\text{Loss, Fearful}} - \beta_{\text{Loss, Neutral}} > 0$, $\beta_{\text{Loss, Neutral}} < 0$ and $\beta_{\text{Loss, Fearful}} \leq 0$, with $k \geq 5$ (Table S3). This effect also translated into decreased neural loss aversion in these regions, given that the strength of deactivations for losses strongly contributed to this feature [i.e., $(-\beta_{\text{Loss, Fearful}} - \beta_{\text{Gain, Fearful}}) - (-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}}) < 0$, Table S3]. Reductions in neural loss aversion were also associated with emotion-induced increases in behavioral loss aversion, e.g., in the left caudate (Fig. 5 *A* and *C* and Table S3).

Crucially, we did not observe any emotion-induced increases in neural loss aversion, or enhanced deactivations for losses in particular, across the whole brain, even at a very liberal threshold (uncorrected $P < 0.005$ and $k \geq 20$).

Regarding gains, we observed an emotion-induced switch to deactivations for gains in the fearful condition (Table S3), e.g., in the right superficial and centromedial amygdala (Fig. 4 *C*) and bilateral putamen. We also found small clusters in the bilateral putamen and frontal pole that displayed reduced activations for gains relative to the neutral condition, but that showed no significant deactivations in the fearful condition (Table S3). Similar to the loss-related effects, these changes reflect shifts towards negative value coding in the fearful condition. Emotion-induced increases in loss aversion, however, were only associated with greater activations for gains in the right caudate and left posterior insula (Table S3).

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Discussion

The neural underpinnings of the interactions between affective processing and decision making have recently received increasing attention in the literature (1, 16, 17). However, the neural mechanisms that mediate emotion-induced changes in loss aversion are currently not well understood. In the present study, we replicated the finding that incidental fear cues increase monetary loss aversion (4). At the neural level, we observed a context-dependent employment of distinct valuation processes. Specifically, incidental fear cues induced a fundamental shift from positive towards negative value coding—in particular, from deactivations towards activations for losses—in a distributed set of regions including the amygdala. Furthermore, this shift predicted emotion-induced increases in behavioral loss aversion. Thereby, our study provides a mechanistic explanation of how incidental emotional cues influence decision making.

In the neutral condition, we replicated a previously observed feature termed neural loss aversion, i.e., greater deactivations for losses relative to activations for gains in a set of regions such as the striatum (11, 12, 14, 16). Neural loss aversion, and deactivations for losses in particular, also predicted behavioral loss aversion. We also observed this effect in the amygdala. This is in contrast to the mixed results of some previous reports (11, 12, 15, 16) but in line with a recent study that found neural loss aversion in the amygdala, though unrelated to behavioral loss aversion (14). We also found activations for losses in the left amygdala and in the mOFC/vmPFC, consistent with previous observations (12, 13, 19, 23). However, in contrast to previous findings, loss-related amygdala activations were unrelated to baseline loss aversion (12, 13). Taken together, while we observed that a few brain areas displayed negative value coding, a positive-value coding circuit that exhibits stronger deactivations for losses relative to activations for gains was the predominant source of behavioral loss aversion in a neutral context.

In line with a previous meta-analysis (21), we observed increased amygdala activity following the presentation of fearful relative to neutral faces. Critically, a previous study found that emotion-induced amygdala activity spills over to subsequent processing of unrelated threat-related stimuli (20). We extend this observation to the domain of decision making. Specifically, we found that incidental fear cues induced negative value coding in the amygdala, i.e., activations for losses as well as deactivations for gains. Notably, while loss aversion was associated with greater deactivations for losses in the neutral condition, emotion-induced increases in loss aversion were predicted by stronger emotion-induced amygdala activations for losses. We found these context-dependent effects in the right superficial and centromedial amygdala. Interestingly, the superficial amygdala was previously found to show contextual shifts in the valence processing of famous names, depending on current processing goals (24). We also observed that emotion-induced increases in loss aversion were predicted by emotion-induced increases in activations for losses in the mOFC/vmPFC, which already displayed negative value coding in the neutral condition. The vmPFC is both structurally and functionally connected with the amygdala (25), and this connectivity is critical for the integration of gains and losses during decision making (19).

Remarkably, we did not observe any significant emotion-induced increases in loss-related deactivations. Instead, we observed reduced loss-related deactivations—that is, reduced positive value coding—in the striatum, insula, and vmPFC. These regions were also associated with emotion-induced shifts in valuation in a recent study (17). Specifically, threat of an electric shock also reduced coding of positive subjective expected value in the striatum and vmPFC but induced negative value coding in the insula, relative to a neutral control condition. Our data indicate that these effects might have been due to loss-related effects—a possibility not explored in the threat-of-shock study. Notably, in both our and the threat-of-shock study, reductions in positive value coding may have resulted from a compromised coding of losses in the form of deactivations but also from concurrent activations for losses (i.e., negative value coding) that would partially or fully cancel out deactivations in a summed fMRI signal. Interestingly, the threat-of-shock manipulation neither induced changes in loss aversion nor changes in amygdala activity. A possible explanation for this absence of an effect might be the involvement of different processes, e.g., related to pain. Pain-related processes might also explain the greater shift towards negative value coding in the insula during threat of shock (17) than after fearful faces that more reliably enhance amygdala activity (21). Taken together, our study extends this line of research by linking emotion-induced changes in value coding *and* loss aversion to (predominantly) loss-related effects *and* to the amygdala.

More generally, our study adds to the growing body of evidence for two opposing neural loss (and gain) signals—inhibitory and excitatory—that have been related to distinct, but overlapping motivational systems (8, 9). For instance, consistent with electrophysiological and optogenetic evidence in rodents (26, 27), we found intermingled excitatory *and* inhibitory signals for losses in the human amygdala. We further extend these observations by demonstrating a specific contextual variable that modulates the relative contributions of excitatory and inhibitory loss (but also gain) signals, namely, the presence of incidental fear cues.

We conclude that the amygdala, in concert with other regions, provides a neural substrate for the interaction of incidental affect and valuation. Our findings indicate that emotion-induced increases in loss aversion can be explained by enhanced activations for losses, i.e., a shift towards negative value coding. In contrast, loss aversion in a neutral context was associated with stronger deactivations for losses. Hence, by going beyond behavioral models of choice that are mute to the sources of loss aversion, we provide evidence that loss aversion is mediated by a context-dependent involvement of distinct valuation processes.

Methods

Behavioral Modeling. We set up a two-parameter model—based on Prospect Theory's subjective-value function (5)—in Matlab (v. R2013a; The MathWorks, Inc., Natick, MA, USA). Specifically, we assessed behavioral sensitivity to gains and losses by fitting a logistic regression with a piecewise-linear value function per emotion condition (11, 12). In this regression, each participant's binary choice (accept vs. reject) is the dependent variable (y), and the gain and loss values are the explanatory variables (G and L, respectively). The loss regressor L is associated with the loss-aversion coefficient λ. A value of $\lambda > 1$ indicates that the participant is loss-averse, $\lambda = 1$ indicates that the participant weighs gains and losses equally, and $\lambda < 1$ indicates that the subject weighs gains more strongly than losses. Formally,

$y_{c,s,t} = f\{[(G_{c,s,t} + \lambda_{c,s} L_{c,s,t}) / \sigma_{c,s}] + \varepsilon_{c,s,t}\}$, where f is the logistic link function, c indexes the experimental condition (i.e., neutral or fearful), s indexes subjects, t indexes trials, and ε is the error term. We modeled a potential stochastic component in subjects' choices via a Fechner noise parameter σ (16, 28). Effectively, σ determines the dispersion of the link function f: $\sigma \to \infty$ is equivalent to completely random choice ($f \to ½$), while $\sigma \to 0$ means that no noise is present in participants' choices from the perspective of the model (f approaches a step function). Preference and noise parameters were estimated via maximum likelihood estimation. Crucially, the estimated loss-aversion parameters from our behavioral modeling were included as behavioral covariates in our neuroimaging analysis (see below).

fMRI Acquisition. We acquired functional T_2*-weighted gradient-echo-planar images and structural T_1-weighted images, using a 3-Tesla Siemens Magnetom Trio scanner and a 12-channel head coil. For more details, see *SI Methods*.

fMRI Data Analysis. Data were preprocessed (see *SI Methods*) and analyzed using FMRIB's Software Library [FSL, v. 5.0.7. (29)] on the High-Performance Computing system at Freie Universität Berlin. Statistical time series analyses were performed using FMRIB's improved linear model (FILM) with local autocorrelation correction. We included 9 task-related regressors and their temporal derivatives, denoting:

· face–gamble trials ($\beta_{Gamble,\ Neutral}$ and $\beta_{Gamble,\ Fearful}$),

· parametric modulators representing gains (in euros; 6, 8, …, 20) ($\beta_{Gain,\ Neutral}$ and $\beta_{Gain,\ Fearful}$),

· parametric modulators representing losses (in euros; positively coded, i.e., 6, 8, …, 20) ($\beta_{Loss,\ Neutral}$ and $\beta_{Loss,\ Fearful}$),

· gender recognition trials per condition and for

· missed trials.

Each regressor was convolved with a double-gamma hemodynamic response function (HRF), aligned with the onset of the events of interest, i.e., from face onset or gamble onset (for the parametric modulators representing gains and losses) until the end of the gamble or gender-question presentation.

Statistical inference was performed with higher-level mixed-effects (FLAME 1 and 2) comparisons of the first-level contrasts representing the face–gamble onsets and parametric regressors per condition. Our group-level model was informed by behavioral modeling, as we included baseline loss aversion ($\lambda_{neutral}$) and emotion-induced changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$) as covariates.

For the ROI analysis, a false-discovery rate (FDR) correction with $P < 0.05$ and a minimum cluster extent of 15 voxels ($k \geq 15$) was applied. For details on the construction of our ROI mask, see *SI Methods.* In our whole-brain analysis, we used a cluster-defining threshold of uncorrected $P < 0.001$ (i.e., $Z > 3.1$) and a family-wise error (FWE) cluster correction with $P < 0.05$.

Acknowledgments

This work was supported by the Cluster of Excellence "Languages of Emotion" at Freie Universität Berlin and funded by the Excellence Initiative of the German Federal Ministry of Education and Research through the German Research Foundation (DFG Grant EXC 302).

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SI Methods

Participants. We recruited 30 participants at Freie Universität Berlin. All participants were right-handed and had normal or corrected-to-normal vision. Eligibility was assessed with an fMRI safety and general health screening form. Three subjects had to be excluded from the analysis: one was excluded because she did not understand the rules of the task (as assessed by a questionnaire) and two were excluded because they rejected all or nearly all lotteries, which made the parameter estimation in our behavioral modeling unreliable. Hence, the final analysis sample consisted of 27 participants (15 female; mean age 21.81 years [SD = 3.55 years]). All participants gave written informed consent prior to the experiment, and the ethics committee at Freie Universität Berlin approved all procedures. Participants also completed a self-report questionnaire on psychopathic personality after the experiment (see below and *SI Results).*

Decision-Making Task. Prior to the experiment, participants received an initial endowment of €20 in cash (7, 4) as well as detailed instructions about the experiment and the incentive mechanism (see below). Subsequently, their understanding was assessed through a brief questionnaire. Five training trials allowed subjects to make themselves familiar with the subsequent decision-making task.

The experiment consisted of a pseudo-randomized sequence of 128 gamble trials, distributed equally across two functional runs (i.e., 64 trials per run). In each trial, a different mixed gamble was presented in the form of a pie chart (Fig. 1 *A*). Each gamble consisted of exactly two possible outcomes, one monetary gain and one monetary loss, that were associated with the same probability (i.e., 50%). Each trial was uniquely and pseudo-randomly drawn from a symmetric gains/losses matrix that consisted of potential gains and losses ranging from ±€6 to ±€20 in steps of €2 (8 × 8 = 64 gambles in total). To ensure a sufficient parametric range for subsequent statistical analysis, gains and losses were sampled from all four quadrants within the matrix per run (i.e., both low and high gains and low and high losses). The positioning of the gains and losses on the left and right sides of the pie chart was counterbalanced between subjects. Each decision trial was presented for 3 seconds, and participants were asked to accept or reject the gamble offered by pressing one of two response buttons within this time window. Rejection implied choice of a sure payoff of €0, i.e., the status quo. The last response within the 3-second time window was logged for analysis. At the end of the experimental session, one decision trial was randomly selected for payoff [random-incentive mechanism (28)].

Incentive Mechanism and Penalty for Missed Trials. Rejection of the gamble in the one decision trial that was randomly selected as the pay-off relevant one left the initial endowment of €20 unchanged. Acceptance of the respective gamble could result in a loss that had to be paid/returned to the experimenter or a gain that was paid to the participant on top of the initial endowment. One of these two possibilities was probabilistically determined (i.e., each outcome had a probability of 50%).

Prior to the experiment, participants were also informed that if no key was pressed within the time window of 3000 ms, they would pay a penalty of €1 if this trial was randomly selected for the final payment. This was supposed to incentivize subjects to always make a decision, thereby minimizing missed trials, and to perform the task with sufficient concentration.

Affective Priming. Following the design of our previous behavioral study (4), each gamble in the experiment (but not in the training trials) was presented twice, once preceded by the image of a fearful face and once preceded by a neutral face. The face images served as an emotional or neutral prime, respectively.

The images were taken from the well-validated FACES database (30). We used 64 face images (32 young and middle-aged faces per gender) for priming of decision trials (another 4 male and 4 female faces were used for the gender recognition trials, see below). The combinations of gamble and facial identity were pseudo-randomized per participant and run, but identical in both conditions, i.e., only the emotional expression was manipulated for a specific gamble. Each face was presented once per priming condition (64 face-gamble trials per condition), and face identity was therefore repeated twice in total (within-subject design with 2 × 64 face–gamble combinations in total). Face gender was counterbalanced across conditions.

We displayed the primes for a duration of 250 ms. This is within the 0–300 ms range of stimulus onset asynchronies that has been found to elicit robust affective priming effects in classical priming studies (31). The priming procedure was framed as a gender recognition task. Participants were instructed to silently evaluate the gender of the displayed faces; in 16 pseudo-randomly interspersed explicit gender recognition trials, they were asked to indicate the gender via button press, instead of being shown the lottery choice task (for more details, see below). In sum, there were 144 trials (72 per run): 128 face–gamble trials (64 per run) and 16 face–gender question trials (8 per run). The intertrial interval (ITI) was jittered and ranged from 2 to 8 s (Poisson-distributed; mean 4 s). The sequence of events per trial is depicted in Fig. 1 *A*.

Gender Recognition Task. There are at least two rationales for the use of a gender recognition-framed task. First, processing of emotional faces embedded in a gender recognition task (i.e., relatively implicit emotion processing) has been associated with greater amygdala activation than processing of faces presented in an explicit emotion identification task (32). Second, implicit emotion processing in such a task resembles predominantly automatic or implicit processes in everyday life (33) and thus has high ecological validity.

The explicit gender recognition trials were a combination of a facial prime, followed by a gender-recognition question (i.e., “Gender?” with two response options, “male” and “female”, all presented in German) that was displayed instead of mixed gambles in these trials. Requiring responses to only a few randomly interspersed explicit gender questions ensured continuous performance of gender recognition and implicit emotion processing while at the same time avoiding motoric responses in the majority of trials (i.e., gamble trials) that otherwise may interfere with the subsequent decisions. All participants included in the final sample showed a minimal accuracy of 87.5% (modal value: 100%) in the gender recognition task, indicating that the primes were processed adequately.

Psychopathic Personality. Psychopathic personality was assessed via a 58-item self-report questionnaire, the Triarchic Psychopathy Measure [TriPM (34), German translation by H. Eisenbarth] which was developed to operationalize the triarchic model of psychopathy (35). It consists of three scales that attempt to measure the 3 phenotypic domains of psychopathy postulated by the triarchic model: boldness (19 items, e.g., “I’m afraid of far fewer things than most people”), meanness (19 items, e.g., “How other people feel is important to me” [reverse-coded]) and disinhibition (20 items, e.g., “I often act on immediate needs”). Respondents are required to rate the degree to which each item applies to them using a 4-point Likert scale ranging from 0 (false) to 3 (true).

The TriPM has good convergent and discriminant construct validity with respect to other measures of psychopathy as well as conceptually relevant normal-range and dysfunctional personality traits (36). It has also satisfactory internal consistency. For instance, the same study reported Cronbach’s alphas of .77 for boldness, .88 for meanness, and .84 for disinhibition in a forensic sample. In the present non-forensic, German-speaking sample, Cronbach’s alphas were .78 for boldness, .72 for meanness, .81 for disinhibition, and .75 for the total score. In the present sample, mean scores were 34.19 (SD = 5.71) for boldness, 12.41 (SD = 5.20) for meanness, 15.19 (SD = 6.75) for disinhibition, and 61.78 (SD = 10.28) for the total score.

fMRI Acquisition. Scanning was performed at the Center for Cognitive Neuroscience Berlin (CCNB) at Freie Universität Berlin, Germany, using a 3-Tesla Magnetom Trio scanner (Siemens Healthcare Diagnostics GmbH, Erlangen, Germany) and a 12-channel head coil. Prior to the experiment, a brief structural scan was used to adjust the acquisition planes along the anterior–posterior commissure line for the functional runs. During the experiment, functional images were acquired as T_2*-weighted gradient-echo-planar images (repetition time = 2 s, echo time = 30 ms, matrix = 64 × 64, flip angle = 70°, field of view = 192 mm, interslice gap = 0.6 mm). A total of 37 oblique-axial slices (3 × 3 × 3 mm voxels) parallel to the anterior commissure–posterior commissure line were collected per volume. A total of 270 volumes were collected per experimental run, with 2 runs per participant (each of approximately 9 min duration). Stimuli were presented on LCD goggles and responses were recorded using the software package Presentation (Neurobehavioral Systems, Inc.). Following the experiment, detailed anatomical images were acquired using a T_1-weighted MP-RAGE protocol (256 × 256 matrix, 176 sagittal slices of 1 mm thickness) and served for registration in the preprocessing.

fMRI Preprocessing. Preprocessing included within-run motion correction to the middle volume, slice-timing correction, brain extraction, and spatial smoothing with a Gaussian kernel of 5 mm full-width at half-maximum (FWHM). Subsequently, we used an ICA-based strategy for automatic removal of motion artifacts [ICA-AROMA (37) see below for more details]. After denoising, we applied high-pass temporal filtering with a cutoff of 100 s. Functional images were co-registered to each participant's structural image using boundary-based registration [BBR (38)] and then normalized to the Montreal Neurological Institute (MNI) space (resolution 2 × 2 × 2 mm^3) via nonlinear registration with a warp resolution of 10 mm.

ICA-AROMA. ICA-AROMA (37) is a well-validated procedure to correct for secondary effects of head motion. This toolbox performs data denoising in three steps: First, it runs an independent-component analysis (ICA), i.e., a multivariate exploratory decomposition into independent components [MELODIC (39)]; second, it classifies independent components into signals of interest or motion-related noise based on multiple criteria (i.e., high-frequency content, correlation with motion parameters, edge fraction, and cerebrospinal fraction); at last, it removes noise components from the data via FSL's regfilt function.

ICA-AROMA has been shown to outperform several other motion correction procedures, including a relatively sophisticated Volterra expansion with 24 motion parameters (40).

ROI Mask. For the construction of our ROI mask, we used the Jülich histological atlas (41) to delineate the amygdala, which allows distinguishing between the basolateral, centromedial, and superficial amygdala. The Harvard–Oxford subcortical and cortical structural atlases (42) were used to delineate the insula and striatum ROIs as well as for defining brain regions (other than the amygdala) in our whole-brain results. For these three ROIs, we included only voxels that had 50% or greater probability of belonging to these structures. Given that the vmPFC is not consistently delineated in the literature, we used a meta-analytic vmPFC mask created by Wager et al. (https://canlabweb.colorado.edu/wiki/doku.php/help/core/brain_masks). Specifically, it is based on a reverse-inference map for “vmPFC” from the meta-analytic database “neurosynth” (http://www.neurosynth.org/). Wager et al. then thresholded the map at $P < 0.0001$, after smoothing the Z-map with a 6 mm FWHM kernel and averaging Z-scores across the left and right hemisphere to create a symmetrical map. In total, the complete ROI mask (i.e., amygdala, striatum, vmPFC, and insula) encompassed 50658 mm^3, 6321 voxels.

SI Results

Decision Noise Is Constant Across Conditions. Our regression model also included a parameter for decision noise (σ), which indicates the inconsistency of participants' choices (see *Methods*). Decision noise did not differ significantly between the neutral ($\sigma_{neutral}$ = 1.61, SD = 1.002) and the fearful condition ($\sigma_{fearful}$ = 1.64, SD = 1.003), $t(26) = -0.257$, $P = 0.8$. Thus, emotion-induced changes in risk aversion could not be explained by changes in decision noise. This supports our interpretation that the observed changes in risk aversion were due to changes in loss aversion.

Emotion-Induced Increases in Loss Aversion Are Related to Faster Responses. Mean response times did not differ significantly between the neutral (1190.16 ms, SD = 173.95 ms) and the fearful condition (1189.27 ms, SD = 169.72 ms), $t(26) = -0.082$, $P = 0.935$. However, emotion-induced increases in loss aversion were associated with faster responses in the fearful relative to the neutral condition between-subjects, $r = -.53$, $P = 0.004$. Baseline loss aversion was also associated with faster responses in the neutral condition between-subjects, $r = -.49$, $P = 0.009$. These findings could indicate a greater subjective clarity of the appetitiveness and aversiveness of the gambles with greater loss aversion.

Psychopathic Personality Attenuates Emotion-Induced Effects on Loss Aversion via Altered Amygdalar Value Responses. Psychopathy, or psychopathic personality, is characterized by a range of behavioral and affective-interpersonal features such as antisocial behavior, impulsivity, callousness and lack of empathy (35). Psychopathy is often regarded as a multidimensional construct. For instance, the triarchic model of psychopathy (35) proposes 3 domains—boldness, meanness, and disinhibition—as phenotypic expressions of different etiological-developmental factors. There is strong empirical support for a multidimensional perspective. Several studies in both forensic and community samples found differential effects of psychopathic traits in diverse domains such as emotion processing (43), error monitoring and feedback processing (44, 45).

Using the Psychopathy Personality Inventory-Revised [PPI-R (46)], we found that psychopathic personality moderated the effects of incidental fear cues on loss aversion in our previous behavioral study (4). Specifically, participants scoring high in fearless dominance (i.e., affective-interpersonal features such as social potency and stress immunity) displayed attenuated or even a lack of emotion-induced increases in monetary loss aversion. By contrast, self-centered impulsivity (i.e., impulsive-antisocial features) had no moderating effect.

In the following analysis, we aimed to replicate this observation and explore whether the personality effect is mediated by altered value responses in the amygdala, given that affective-interpersonal features of psychopathy have been related to amygdala hypoactivation during emotion processing (43). Using the Triarchic Personality Measure [TriPM (34), see *SI Methods*], we hypothesized that in particular TriPM boldness and meanness attenuate the influence of incidental fear cues on loss aversion, because boldness and meanness are both thought to reflect an underlying fear-reactivity deficit (35). Moreover, boldness strongly overlaps with PPI-R fearless dominance (35, 36) for which we observed the moderation effect in our previous behavioral study (4). Meanness reflects callousness and low empathy, among others (35, 36), also indicators of reduced affective reactivity and of disregard for others' needs (signaled, e.g., in the face). At the neural level, we hypothesized that psychopathy-related attenuations of emotional effects on loss aversion are mediated by attenuations of emotion-induced amygdala activations for losses.

First, in a multiple regression, we regressed emotion-induced changes in loss aversion ($\lambda_{\mathrm{fearful}} - \lambda_{\mathrm{neutral}}$) on boldness, meanness, and disinhibition simultaneously. The overall model was significant, $R = 0.545$, $R^2_{adjusted} = 0.205$, $F(3,23) = 3.233$, $P = 0.041$. Emotion-induced changes in loss aversion were significantly predicted only by meanness, $\beta = -0.57$ (SE = 0.19), $P = 0.007$, which indicates attenuated or even absent emotion-induced increases in loss aversion in participants that scored higher in meanness (all other Ps > 0.182*).* By contrast, in another model, psychopathic traits did not predict loss aversion in the neutral condition (overall model: $P = 0.686$).

Next, in two separate multiple regressions, we regressed either emotion-induced changes in amygdala activity to losses or to gains on all psychopathic traits simultaneously. For each participant, mean gain/loss-related parameter estimates were extracted for the right superficial-centromedial amygdala cluster (peak: x = 22, y = −8, z = −8) that displayed a positive association between emotion-induced increases in activations for losses and emotion-induced increases in monetary loss aversion. The overall model for loss responses was significant, R = 0.578, $R^2_{adjusted}$ = 0.248, $F(3,23)$ = 3.852, P = 0.023. Emotion-induced changes in loss aversion were significantly predicted only by meanness, β = −0.56 (SE = 0.19), P = 0.006, which indicates attenuated or even absent emotion-induced increases in activations for losses in participants that scored higher in meanness. The other psychopathic traits were no significant predictors (both Ps > 0.115). The overall model for gain responses was not significant, P = 0.168, and neither were its predictors (all Ps > 0.073). Another model which regressed amygdala deactivations in the neutral condition (in the cluster displaying neural loss aversion) on psychopathic traits was also not significant, P = 0.173, and neither were its predictors (all Ps > 0.098).

To test whether attenuated emotion-induced changes in amygdala activations to losses mediated the negative relationship between meanness and emotion-induced changes in loss aversion, we set up a mediation model using the PROCESS macro for SPSS (47) and model variant 4 (for visualizations of all available models, see http://afhayes.com/public/templates.pdf). Specifically, Z-standardized meanness scores served as the independent variable and Z-standardized emotion-induced changes in loss aversion ($\lambda_{\mathrm{fearful}} - \lambda_{\mathrm{neutral}}$) represented the dependent variable. For the mediator variable, we used the same mean loss-related parameter estimates for the right amygdala cluster from above, which displayed a positive association between emotion-induced increases in activations for losses and emotion-induced increases in loss aversion. Furthermore, we controlled for boldness, disinhibition, and baseline loss aversion ($\lambda_{\mathrm{neutral}}$) by adding their Z-standardized values as covariates. Bias-corrected bootstrapping (50,000 samples) was used to generate 95% confidence intervals.

The results of the mediation model are depicted in Figure S2. Again, higher scores in meanness were associated with attenuated emotion-induced increases in loss aversion, β_{total} = −0.67, SE = 0.18, P = 0.001. This effect was reduced, but still significant, when the mediator (i.e., changes in amygdala activations to losses) was taken into account, β_{direct} = −0.42, SE = 0.18, P = 0.03. Crucially, the negative effect of meanness on emotion-induced increases in loss aversion was partially mediated by a negative effect of meanness on emotion-induced increases in amygdala activations to losses, $\beta_{indirect} = -0.24$, SE = 0.15, 95% CI [−0.60, −0.02]. In other words, participants scoring higher in meanness had reduced emotion-induced increases in amygdala activations for losses and, in turn, reduced increases in loss aversion compared to lower-scoring participants.

Our results are consistent with the notion that meanness is a phenotypic expression of deficient fear reactivity (35). Another possibility is that reactivity to fearful faces was reduced due to empathy deficits (35, 36) rather than a general fear deficit. Interestingly, we did not observe a moderation effect for boldness, although it is also thought to reflect reduced fear reactivity (35) and PPI-R fearless dominance (strong overlap with boldness) attenuated emotion-induced changes in loss aversion in our previous behavioral study (4). This difference might be the result of limited statistical power, given the moderate sample size. Alternatively, it might also reflect a true context-dependent effect (e.g., due to stressful scanner environment) or non-shared variance of the TriPM and PPI-R (36). By contrast, in neither study did we observe a moderation effect of TriPM disinhibition or related PPI-R self-centered impulsivity, consistent with their entirely different affective profile [i.e., enhanced and not reduced emotional reactivity (35, 36)].

With regard to the main analysis of the present paper, these findings corroborate the interpretation that the observed effects of incidental fear cues on neural value processing and monetary loss aversion were indeed affective processes. Furthermore, the unique effect of meanness on emotion-induced changes in loss aversion and associated amygdala activations for losses, but not on loss aversion and amygdala deactivations for losses in the neutral condition, provides further support for the idea of context-dependent valuation mechanisms.

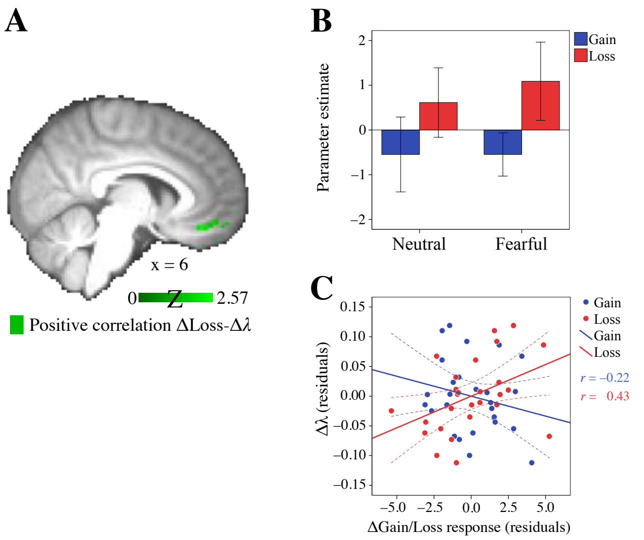

Fig. S1. Emotion-induced changes in vmPFC value coding (*A*) Emotion-induced increases in activations for losses were associated with emotion-induced increases in loss aversion in the vmPFC (green). (*B*) Parameter estimates for the gain and loss regressors per condition for the vmPFC cluster (*C*) Relationships between emotion-induced changes in gain and loss responses and changes in behavioral loss aversion in the vmPFC cluster. Greater activations for losses significantly predicted emotion-induced increases in loss aversion (partial regression plot, i.e., controlling for $\lambda_{neutral}$).

Note: All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 15$. Error bars/lines represent 95% CIs (including between-subject variance).

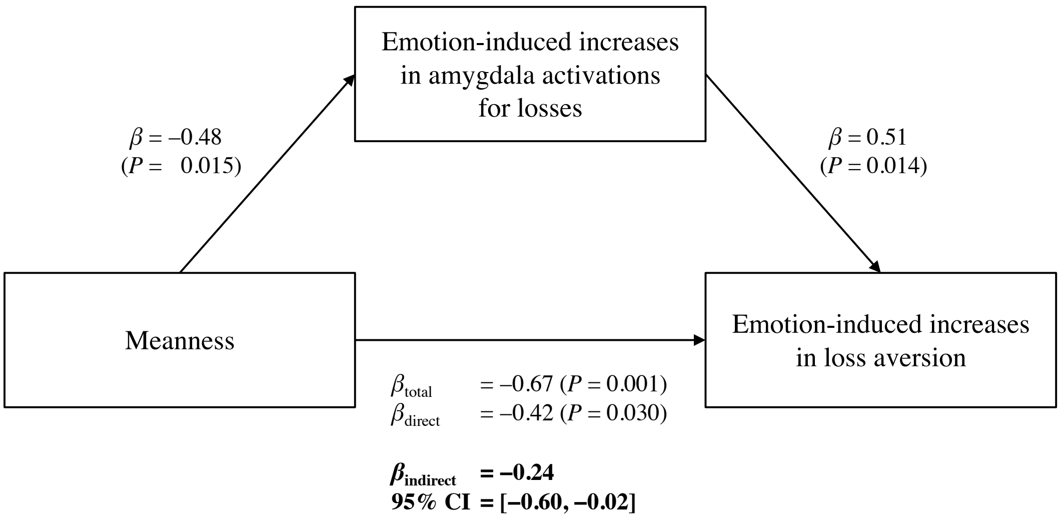

Fig. S2. TriPM meanness attenuated emotion-induced increases in loss aversion, and this effect was partially mediated by attenuated emotion-induced increases in amygdala activations for losses. The mediation model illustrates total, direct, and indirect effects of TriPM meanness on emotion-induced changes in monetary loss aversion. β coefficients represent standardized regression coefficients while controlling for boldness, disinhibition and loss aversion in the neutral condition (not illustrated). β_{total} is the total effect of meanness on emotion-induced changes in loss aversion, β_{direct} is the direct effect after the mediator (i.e., emotion-induced changes in amygdala activations for losses) had been taken into account, and $\beta_{indirect}$ is the indirect effect, i.e., the effect of meanness on emotion-induced changes in loss aversion that was mediated by a change in amygdala activations for losses. For the indirect effect, bias-corrected bootstrapping (50,000 bootstrap samples) provided a 95% confidence interval that did not span 0, indicating a significant partial mediation.

Table S1
Neural responses in the neutral condition - ROI analysis
(small-volume, voxel-wise FDR correction with $P < 0.05$ and spatial extent threshold of $k \geq 15$ voxels):

No. of voxels	Brain region[1]	Hemisphere[2]	MNI (peak) x	y	z	Z-value (peak)
Positive value coding:						
Activations for gains ($\beta_{\text{Gain, Neutral}} > 0$)						
265	Caudate, Nucl. Accumbens, Putamen	R	8	8	2	4.36
223	Caudate, Nucl. Accumbens, Putamen	L	-12	12	0	3.99
120	Insular Cortex	R	34	20	-4	5.36
103	Paracingulate Gyrus	R/L	4	54	2	3.54
94	Insular Cortex	L	-36	18	-8	4.31
26	Putamen	L	-28	6	-2	2.58
20	Putamen	R	28	-4	10	2.68
Greater activations for gains with increasing loss aversion (Positive partial correlation between λ_{Neutral} and $\beta_{\text{Gain, Neutral}}$)						
106	Putamen, Nucleus Accumbens	L	-14	8	-6	3.14
62	Putamen, Caudate	R	22	14	-6	2.51
48	Insular Cortex	L	-34	18	-8	2.77
25	Putamen	L	-24	-2	4	2.81
23	Caudate	L	-8	16	6	2.43
20	Insular Cortex	L	-38	-6	8	2.46
Deactivations for losses ($\beta_{\text{Loss, Neutral}} < 0$)						
561	Caudate, Nucl. Accumbens, Putamen	R	14	18	-4	5.63
503	Caudate, Nucl. Accumbens, Putamen	L	-8	6	4	5.48
276	Paracingulate Gyrus	R/L	2	46	2	4.6
189	Insular Cortex	R	34	22	-4	4.86
137	Insular Cortex	L	-32	20	-6	5.14
Greater deactivations for losses with increasing loss aversion (Negative partial correlation between λ_{Neutral} and $\beta_{\text{Loss, Neutral}}$)						
212	Caudate	L	-10	2	14	4.13
120	Caudate	R	8	8	2	3.74
114	Amygdala (SF, CM, BL), Putamen	R	24	-2	-10	4.06
79	Insular Cortex	L	-40	16	-6	3.15
67	Insular Cortex	R	34	16	0	3.04
61	Putamen	L	-24	4	-8	3.02
23	Putamen	L	-22	6	10	2.41

Activations for gains + deactivations for losses (conjunction of $\beta_{\text{Gain, Neutral}} > 0$ and $\beta_{\text{Loss, Neutral}} < 0$ with $k \geq 5$)[3]						
210	Caudate, Nucl. Accumbens, Putamen	R	-	-	-	-
207	Caudate, Nucl. Accumbens, Putamen	L	-	-	-	-
115	Insular Cortex	L	-	-	-	-
84	Insular Cortex	R	-	-	-	-
81	Paracingulate Cortex, Frontal Pole	R/L	-	-	-	-
9	Putamen	L	-	-	-	-
Neural loss aversion ($-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}} > 0$)						
259	Putamen, Nucl. Accumbens, Caudate	R	22	14	-6	4.04
185	Nucl. Accumbens, Caudate, Putamen	L	-10	10	-12	2.89
30	Insular Cortex	R	42	-2	-8	2.47
19	Insular Cortex	L	-38	10	0	2.26
16	Insular Cortex	R	36	14	0	2.49
Greater neural loss aversion with increasing loss aversion (Positive partial correlation between λ_{Neutral} and $-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}}$)						
104	Caudate	L	-10	2	14	3.25
60	Amygdala (SF, CM), Putamen	R	24	-4	-8	2.94
33	Paracingulate Gyrus, Frontal Medial C.	L/R	-2	36	-14	2.7
17	Insular Cortex	R	38	16	2	2.63
17	Paracingulate Gyrus	R	10	54	-4	2.33
15	Caudate	R	12	18	10	2.43
<u>*Negative value coding:*</u>						
Activations for losses ($\beta_{\text{Loss, Neutral}} > 0$)						
257	Frontal Pole, Frontal Medial Cortex	L/R	-2	58	-14	4.04
16	Amygdala (BL)	L	-30	-4	-24	2.71
Deactivations for gains ($\beta_{\text{Gain, Neutral}} < 0$)						
232	Frontal Pole, Frontal Medial Cortex	R/L	0	56	-12	2.91
17	Insular Cortex	L	-36	-16	10	2.87
Greater deactivations for gains with increasing loss aversion (Negative partial correlation between λ_{Neutral} and $\beta_{\text{Gain, Neutral}}$)						
121	Paracingulate Gyrus, Frontal Med. C.	R/L	10	52	-4	2.54
29	Subcallosal Cortex, rACC	R/L	0	26	-2	2.47
Activations for losses + deactivations for gains (conjunction of $\beta_{\text{Loss, Neutral}} > 0$ and $\beta_{\text{Gain, Neutral}} < 0$ with $k \geq 5$)[3]						
105	Frontal Pole, Frontal Medial Cortex	R/L	-	-	-	-
6	Frontal Medial Cortex	R/L	-	-	-	-

[1] The second column lists the brain regions of all significant voxels based on the Jülich Histological Atlas for the amygdala and the Harvard-Oxford Cortical-Subcortical Atlases for all other regions. [2] Hemispheric localization of the cluster. R = Right hemisphere, L = Left hemisphere. [3] Conjunctions for FDR-based statistics are merely the overlap of significant voxels. Here, peak statistics in the list are left empty, because there exist separate statistics for gain and loss effects.

Table S2
Neural responses in the neutral condition – Whole-brain analysis
(cluster-forming threshold of $P < 0.001$ and FWE-corrected with $P < 0.05$):

No. of voxels	Brain region[1]	Hemisphere[2]	MNI (peak) x	y	z	Z-value (peak)
Positive value coding:						
Activations for gains ($\beta_{\mathrm{Gain,\,Neutral}} > 0$)						
2054	Supramarginal Gyrus	R	52	-36	56	4.89
912	Lateral Occipital Cortex	L	-22	-64	40	4.34
844	Paracingulate Cortex	R/L	2	34	34	4.79
576	Frontal Pole	R	50	40	24	4.49
330	Cerebellum	L	-42	-70	-42	4.34
310	Insular Cortex	R	30	24	8	4.38
195	Frontal Pole	R	44	52	10	4.38
189	Lateral Occipital Cortex	R	14	-78	54	4.22
128	Posterior Cingulate Cortex	R/L	0	-30	36	4.42
124	Lingual Gyrus/Cerebellum	L	-8	-82	-22	4.07
123	Middle Frontal Gyrus	R	32	8	58	4.4
108	Inferior Temporal Gyrus	R	62	-60	-12	3.94
96	Caudate	R	8	8	0	4.05
83	Occipital Pole	R	28	-90	10	3.92
83	Insular Cortex	L	-32	18	-10	3.97
73	Occipital Pole	L	-10	-104	-8	4.11
67	Inferior Temporal Gyrus	L	-54	-62	-14	4
Deactivations for losses ($\beta_{\mathrm{Loss,\,Neutral}} < 0$)						
9379	Lateral Occipital Cortex	R/L	32	-64	52	6.62
1776	Paracingulate Gyrus	R/L	2	22	40	5.99
1418	Frontal Pole	R	44	40	14	5.65
617	Middle Frontal Gyrus	L	-48	10	32	5.31
554	Occipital Fusiform Gyrus/Cerebellum	L/R	-14	-80	-20	4.33
491	Middle Frontal Gyrus	R	34	4	68	4.23
465	Caudate	R	14	18	-2	4.53
461	Caudate	L	-8	10	0	4.48
380	Insular Cortex	L	-30	24	0	4.84
320	Frontal Orbital Cortex	R	42	20	-10	4.9
247	Thalamus	R/L	12	-14	8	4.2
231	Lingual Gyrus	L/R	-2	-82	0	4.25
211	Posterior Cingulate Cortex	R/L	4	-34	28	4.53
181	Brain Stem	R/L	2	-26	-20	4.17
129	Cerebellum	L	38	-62	-40	4.32
111	Inferior Temporal Gyrus	R	56	-54	-10	4.01
90	Supracalcarine Cortex	R	14	-62	14	3.91
81	Superior Frontal Gyrus	L	-24	6	62	4.17
76	Anterior Cingulate Cortex	L/R	-2	2	30	4.09

Greater deactivations for losses with increasing loss aversion (Negative partial correlation between λ_{Neutral} and $\beta_{\text{Loss, Neutral}}$)				
1611	Cerebellum	R/L	8 -80 -24	5.39
525	Lateral Occipital Cortex	R/L	12 -80 44	4.14
444	Superior Parietal Lobule	L	-30 -54 48	4.26
411	Lateral Occipital Cortex	R	26 -64 56	4.27
226	Frontal Pole	R	44 42 14	4.5
218	Paracingulate Gyrus	L/R	-6 28 32	4.56
163	Lateral Occipital Cortex	R	38 -88 0	3.99
151	Cerebellum	R	32 -64 -32	4.5
138	Inferior Frontal Gyrus	L	-42 18 26	3.99
120	Occipital Fusiform Gyrus	L	-28 -82 -12	4.24
93	Caudate	L	-10 2 14	4.13
75	Posterior Cingulate Gyrus	L/R	-2 -30 26	3.93
Activations for gains + deactivations for losses (conjunction of $\beta_{\text{Gain, Neutral}} > 0$ and $\beta_{\text{Loss, Neutral}} < 0$)[3]				
1628	Superior Parietal Lobule	R	40 -44 52	5.46
975	Supramarginal Gyrus	L	-46 -40 48	5.32
667	Paracingulate Gyrus	R/L	2 32 34	5.55
285	Frontal Pole	R	50 40 28	4.92
229	Cerebellum	L	-40 -62 -42	4.59
217	Lateral Occipital Cortex	R	14 -78 54	4.5
205	Frontal Orbital Cortex	R	38 18 -12	4.72
Neural loss aversion ($-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}} > 0$)				
126	Lateral Occipital Cortex	L	-10 -64 56	3.89

[1] The second column lists the brain regions of the peak voxels of significant clusters based on the Harvard-Oxford Cortical-Subcortical Atlases. [2] Hemispheric localization of the cluster. R = Right hemisphere, L = Left hemisphere. [3] We used the script easythresh_conj.sh for a cluster-based conjunction analysis (http://www2.warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/fsl/)

Table S3
Condition differences – ROI analysis
(small-volume, voxel-wise FDR correction with $P < 0.05$ and spatial extent threshold of $k \geq 15$ voxels):

No. of voxels	Brain region[1]	Hemisphere[2]	MNI (peak) x	y	z	Z-value (peak)
Increased activity in prime-gamble trials in fearful condition relative to the neutral condition ($\beta_{\text{Gamble, Fearful}} - \beta_{\text{Gamble, Neutral}} > 0$)						
88	Amygdala (BL, SF)	R	24	-2	-24	2.74
49	Amygdala (BL)	L	-28	-6	-28	3.74
28	Amygdala (SF)	L	-16	-6	-18	2.93
24	Caudate	R	10	16	8	2.46
Emotion-induced shift towards negative value coding:						
Increased activations for losses in the fearful condition relative to the neutral condition $\beta_{\text{Loss, Fearful}} - \beta_{\text{Loss, Neutral}} > 0$						
267	Caudate, Putamen	L	-10	10	6	3.29
203	Paracingulate Gyrus, rACC	R/L	2	48	2	3.49
180	Putamen, Amygdala (SF, CM, BL)	R	20	12	-6	3.34
76	Putamen, Amygdala (SF, CM)	L	-30	-6	2	2.47
68	Caudate	R	14	10	8	3.19
62	Insular Cortex	L	-36	12	0	3.16
38	Putamen	R	30	-8	10	2.99
37	Amygdala (BL)	R	24	-6	-26	2.81
26	Insular Cortex	R	44	2	0	2.95
20	Insular Cortex	R	34	16	4	2.57
16	Insular Cortex	R	34	14	-16	2.82
15	Amygdala (BL)	L	-24	-10	-24	2.5
- Within these regions:						
a) Activations for losses in the fearful condition (conjunction of $\beta_{\text{Loss, Fearful}} - \beta_{\text{Loss, Neutral}} > 0$ and $\beta_{\text{Loss, Fearful}} > 0$ with $k \geq 5$)[3]						
39	Putamen, Amygdala (SF, CM)	L	-30	-6	2	2.47
34	Paracingulate Gyrus, Frontal Medial C.	R/L	4	40	-10	2.5
31	Putamen	R	30	-8	10	2.99
30	Amygdala (BL)	R	24	-6	-26	2.81
5	Amygdala (SF, BL)	R	24	-8	-10	2.04
5	Amygdala (BL)	L	-20	-10	-22	2.17
b) Reduced deactivations for losses in the fearful condition relative to the neutral condition (conjunction of $\beta_{\text{Loss, Fearful}} - \beta_{\text{Loss, Neutral}} > 0$, $\beta_{\text{Loss, Neutral}} < 0$ and $\beta_{\text{Loss, Neutral}} \leq 0$ with $k \geq 5$)[3]						
237	Caudate, Putamen	L	-10	10	6	3.29
149	Putamen	R	20	12	-6	3.34
128	Paracingulate Gyrus, rACC	R/L	2	48	2	3.49
68	Caudate	R	14	10	8	3.19
50	Insular Cortex	L	-36	12	0	3.16
20	Insular Cortex	R	34	16	4	2.57
16	Insular Cortex	R	34	14	-16	2.82

Emotion-induced increases in activations for losses associated with emotion-induced increases in loss aversion (Positive partial correlation between $\lambda_{Fearful} - \lambda_{Neutral}$ and $\beta_{Loss, Fearful} - \beta_{Loss, Neutral} > 0$)						
78	Frontal Medial Cortex	R/L	6	38	-18	2.57
25	Amygdala (SF, CM)	R	22	-8	-8	2.53
20	Frontal Pole	R/L	2	58	-14	2
18	Insular Cortex	R	38	4	2	2.12
16	Putamen	R	26	-8	12	2.64
Reduced activations for gains in the fearful condition relative to the neutral condition $\beta_{Gain, Fearful} - \beta_{Gain, Neutral} < 0$						
79	Putamen, Amygdala (SF, CM, BL)	R	30	4	-6	2.65
74	Frontal Pole	R/L	2	58	2	3.02
64	Putamen	L	-26	12	-4	2.98
43	Putamen	R	28	-2	10	3.15
30	Putamen	L	-26	-2	14	2.37
16	Insular Cortex	L	-38	-6	-2	2.97
14	Putamen	R	28	12	2	2.04
- Within these regions:						
a) Deactivations for gains in the fearful condition (conjunction of $\beta_{Gain, Fearful} - \beta_{Gain, Neutral} < 0$ and $\beta_{Gain, Fearful} < 0$) with $k \geq 5$)[3]						
40	Putamen, Amygdala (CM)	R	30	4	-6	2.65
27	Putamen	L	-26	12	-4	2.98
26	Frontal Pole	R/L	0	60	2	2.85
18	Putamen	L	-26	-2	14	2.37
15	Insular Cortex	L	-38	-6	-2	2.97
14	Amygdala (SF, BL)	R	20	-8	-12	2.1
8	Putamen	R	24	10	4	1.9
5	Putamen	L	-18	12	-2	2.57
b) Weaker activations for gains in the fearful condition relative to the neutral condition (conjunction of $\beta_{Gain, Fearful} - \beta_{Gain, Neutral} < 0$ and $\beta_{Gain, Neutral} > 0$ and $\beta_{Gain, Fearful} \geq 0$ with $k \geq 5$)[3]						
29	Frontal Pole	R/L	2	58	2	3.02
19	Putamen	R	28	-2	10	3.15
15	Putamen	L	-28	8	-2	2.54
9	Putamen	L	-18	10	0	2.33
Emotion-induced increases in activations for gains associated with emotion-induced increases in loss aversion (Positive partial correlation between $\lambda_{Fearful} - \lambda_{Neutral}$ and $\beta_{Gain, Fearful} - \beta_{Gain, Neutral} > 0$)						
43	Caudate	R	14	14	8	2.62
20	Insular Cortex	L	-38	-16	8	2.55

Reduced neural loss aversion in the fearful condition $[(-\beta_{\text{Loss, Fearful}} - \beta_{\text{Gain, Fearful}}) - (-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}}) < 0]$						
122	Caudate	L	-8	6	4	2.77
62	Putamen, Nucl. Accumbens, Caudate	R	22	14	-6	2.74
42	Paracingulate Gyrus, rACC	R/L	0	48	4	3.28
40	Caudate	R	14	10	8	2.16
29	Frontal Medial Cortex	R/L	2	38	-16	2.91
27	Cingulate Cortex	L	-40	14	-2	2.42
19	Amygdala (BL)	R	24	-6	-26	2.98
Emotion-induced decreases in neural loss aversion associated with emotion-induced increases in behavioral loss aversion {Negative partial correlation between $\lambda_{\text{Fearful}} - \lambda_{\text{Neutral}}$ and $[(-\beta_{\text{Loss, Fearful}} - \beta_{\text{Gain, Fearful}}) - (-\beta_{\text{Loss, Neutral}} - \beta_{\text{Gain, Neutral}})]$}						
30	Putamen	L	-32	-14	-6	2.43
22	Insular Cortex	L	-38	-14	6	2.58
22	Frontal Pole	R	2	58	-4	2.37
17	Insular Cortex	R	36	-16	16	2.66
15	Caudate	L	-12	14	12	2.37
15	Putamen	R	28	-8	12	2.63

[1] The second column lists the brain regions of all significant voxels based on the Jülich Histological Atlas for the amygdala and the Harvard-Oxford Cortical-Subcortical Atlases for all other regions. [2] Hemispheric localization of the cluster. R = Right hemisphere, L = Left hemisphere. [3] Conjunctions for FDR-based statistics are merely the overlap of significant voxels. Here, we list peak statistics for the condition differences.