The interaction between emotion and economic decision-making

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Declaration

I, Caroline Charpentier, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

Emotions play an important role in daily life decisions. For example, we are likely to choose, judge, or evaluate things around us in different ways depending on whether we are feeling sad, anxious, or happy. Emotional reactions to life events and outcomes, such as winning an award, or getting a divorce, should also predict individuals' subsequent decisions. However, the mechanisms by which such interactions between emotions and decisions unfold are still poorly understood. The aim of this thesis was two-fold: first, to characterize a computational model of how emotions are integrated into decisions; second, to provide a better understanding of the cognitive and neural mechanisms by which manipulating emotions can alter decisions.

Following the general introduction and methods description, the first experimental chapter shows that integrating emotions (self-report feelings) in a computational model of decision-making could reliably predict people's gambling choices, indicating a unique contribution of feelings to decisions. The second experimental chapter explores the influence of incidental emotional priming on gambling choice and the underlying neural mechanisms, using functional magnetic resonance imaging (fMRI). The findings suggest that how external emotions impact decisions, at both behavioural and neural levels, varied with individual differences in levels of trait anxiety. The third experimental chapter attempts to extend this finding by testing how risky decisions are altered in patients with clinical anxiety, relative to healthy controls; demonstrating a dissociation between sensitivity to risk, which was enhanced in anxiety, and sensitivity to monetary losses, which was not associated with anxiety.

This thesis provides a more complete understanding of the complex interactions between emotions, mood and decision-making. In the final chapter the findings are discussed in light of influential theories in cognitive neuroscience and behavioural economics that posit a central role for emotions in determining the choices we make.

Acknowledgments

The four years of this PhD have been an incredible experience on many aspects, but would not have been the same without the people who have contributed to it and those who I have met along the way. I would first like to thank Jon and Tali for their supervision and guidance throughout the years and different projects. They both gave me wonderful opportunities, from visiting Harvard and MIT with Tali, to the annual lab BAP trip with Jon. Thanks for trusting me with my ideas, for being so supportive and available, and for helping me become a more confident researcher.

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List of Abbreviations

ACC	Anterior Cingulate Cortex
ADHD	Attention Deficit Hyperactivity Disorder
BART	Balloon Analogue Risk Task
BDI	Beck Depression Inventory
BIC	Bayesian Information Criterion
BOLD	Blood Oxygen Level-Dependent
BVR	Basal Vein of Rosenthal
EPI	Echo-Planar Imaging/Image
EV	Expected Value
EUT	Expected Utility Theory
FWE	Family-wise Error
GAD	Generalized Anxiety Disorder
GLM	General Linear Model
IFG	Inferior Frontal Gyrus
IGT	Iowa Gambling Task
MDD	Major Depressive Disorder
MINI	Mini International Neuropsychiatric Interview
MNI	Montreal Neurological Institute
MRI	Magnetic Resonance Imaging
fMRI	functional Magnetic Resonance Imaging
NAcc	Nucleus Accumbens
OCD	Obsessive Compulsive Disorder
PD	Panic Disorder
PFC	Prefrontal Cortex
dlPFC	Dorsolateral Prefrontal Cortex
vmPFC	Ventromedial Prefrontal Cortex
PGT	Probabilistic Gambling Task
PPI	Psycho-Physiological Interaction
PT	Prospect Theory
PTSD	Post-traumatic Stress Disorder
ROI	Region of interest

RTBS	Risk-Taking Behaviors Scale
SAD	Separation Anxiety Disorder
SCR	Skin Conductance Response
SD	Standard Deviation
SocPh	Social Phobia
STAI	State Trait Anxiety Inventory
SVC	Small Volume Correction
ToS	Threat of Shock
VNM	Von Neumann-Morgenstern
WM	Working Memory
WTAR	Wechsler Test of Adult Reading

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Notes to examiners

The findings from Chapters 3 and 4 have been published in two separate peer-reviewed articles:

Charpentier CJ, De Neve J-E, Li X, Roiser JP, Sharot T (2016). Models of affective decision making: How do feelings predict choice? *Psychological Science* 27(6): 763-775.

Charpentier CJ, De Martino B, Sim AL, Sharot T, Roiser JP (2016). Emotion-induced loss aversion and striatal-amygdala coupling in low-anxious individuals. *Social Cognitive and Affective Neuroscience* 11(4): 569-579.

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In Chapter 3, data from the first group of 29 participants (constituting half of the sample used for the main experiment) was collected by two UCL Psychology undergraduate students under my supervision, Eleanor Barley and Joshua Lim, as part of their 2nd year mini-project. Data from the second replication and extension study was collected by a postgraduate intern in the lab, Xinyi Li, also under my supervision. The study benefited from a collaboration and discussions with Jan-Emmanuel De Neve, Associate Professor at the University of Oxford (previously at UCL).

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Chapter 1 General introduction

1.1 Behavioural economics theories of decision-making under risk

This section will first introduce the framework under which economic decision-making was examined over the past few decades in the fields of behavioural economics and psychology. It will describe the models and theories that have been developed, with a specific focus on Prospect Theory, which will be used throughout the different chapters of this thesis.

Economic decisions can be defined as any decision between two or more alternatives, whereby each alternative has to be evaluated by the decision-maker, who will then choose the option to which they assign the highest value. These decisions can encompass a large range of types of alternatives, including everyday goods, food items, investment products, monetary gambles, etc. In particular, many decisions we make on a daily basis involve some level of risk or uncertainty, in the sense that the exact outcome of the decision may not be known with certainty at the time of the decision. In economics, the distinction between risk and uncertainty emerged after seminal work by Frank Knight (Knight, 1921). Risk means that the probabilities of each possible outcome in the decision are fully known, such as decisions to flip a fair coin, or to buy a lottery ticket while knowing the total number of tickets being sold. In contrast, uncertainty means that the underlying probabilities are not fully known and the decision-maker has to assess them, such as when betting on the outcome of a sport event, or deciding on an investment with a variable return.

The decisions used throughout this thesis involved monetary gambles and fall into the description of decisions made under risk, given that the probabilities of each possible outcome in the gambles were always made explicit to the participants.

1.1.1 Expected Utility Theory: a normative model

1.1.1.1 Expected value maximization

Historically, Pascal's Wager in the 17th century laid the ground for decision theory to specify how the expected value of a risky decision option should be calculated. For example, for a risky gamble that offers 90% chance of winning £1 and 10% chance of winning £50, the expected value (EV) can be calculated as the sum of the products between each potential outcome value and its probability:

$$EV = 0.9 * 1 + 0.1 * 50 = £5.9$$

Let us imagine that a participant can choose between playing this gamble or receive a sure amount of £5. According to a theory of expected value maximization, a decision-maker should choose the gamble given that its expected value is higher than the sure outcome of £5. However many people when faced with such a prospect would choose to receive the guaranteed £5. This is because, contrary to what expected value maximization theory would assume, most people do not have a neutral attitude towards risk. Instead most people are risk averse and would avoid a risky prospect in which their chances of earning less than the sure outcome are high (90% here) while their chances of earning more are low (only 10% here). Risk aversion explains many daily life behaviours, in particular decisions to purchase insurance. Yet, it is not accounted for by a decision rule that would only seek to maximize expected value.

1.1.1.2 Expected utility hypothesis

Daniel Bernoulli first offered an account of this problem in the 18th century with Expected Utility Theory (EUT; 1738, later translated in Bernoulli, 1954). In particular, EUT proposes that people do not evaluate prospects by their objective expected value, but instead attribute "utility" to them, in a way that does not vary linearly with value. The main assumption is that as the initial value or wealth of a person increases, the change in utility associated with a one-unit change in value will decrease, a phenomenon also referred to as decreasing marginal utility. For example, this can be illustrated in the observation that winning £100 will matter less to a "wealthy" person, who already has £10,000 in their pocket, than to a "poor" person, who only has £10 in their pocket. Therefore, the change in utility associated with a change in value of +£100 will decrease with higher initial wealth. According to Bernoulli's EUT, expected utility can be calculated as the product between the probability of an outcome and the utility of that outcome. The utility function is assumed to be concave, such that the increase in utility between any given value v and v+1 will be bigger than between v+1 and v+2. A logarithmic shape was first proposed for the utility function, taking into account this concavity and explaining risk aversion. To illustrate that, let us take a slightly simpler example than the one described above, for example a choice between winning £5 for sure and a gamble with 50% chance of winning £10 and 50% of winning nothing. According to expected value maximization theory, a decision-maker should be completely indifferent between these two options because their expected value is the same. EUT, in contrast, predicts than the utility associated with winning £5 will be larger than half (probability of winning = 50%) the utility of winning £10 (**Figure 1-1A**), explaining why most people would choose the sure option in that case.

1.1.1.3 Axiomatization of Expected Utility Theory

It was not before the middle of the 20th century that Von Neumann and Morgenstern (VNM; 1947) provided an axiomatization of EUT (as well as its modern name; expected utility was called "moral expectation" by Bernoulli, to contrast with mathematical expectation), with necessary and sufficient conditions for the theory to hold and explain a decision-maker's choices. VNM posit that such a utility function, the maximization of which would predict a rational agent's decisions, exists provided that the agent's preferences satisfy the following four axioms:

- Completeness: for any two given options L and M, the agent has well-defined preferences, i.e. either prefers L, M, or is indifferent
- Transitivity: the agent's preferences are consistent across any three given options, i.e. if L is preferred over M and M preferred over N, then L should be preferred over N.
- Continuity: preference for an intermediate option is equivalent to a probabilistic compound lottery between the better and worse options, i.e. given $L \leq M \leq N$, there is a probability p such that the agent is indifferent between M and the following lottery: $p*L + (1-p)*N$.

- Independence: an agent's preference for an option over another should hold independently of the presence of a third option. This also implies substitution, or reduction of compound lotteries, such that if L is preferred over M, then any probability mixture p*L should be preferred over p*M.

1.1.1.4 Violations of Expected Utility Theory

However, several violations of these axioms were observed in the following years, making EUT a prescriptive or normative model (explaining what rational agents should do) rather than a descriptive model (actually explaining the way people behave). One of the first and main violations, which came from observing people's decisions, was the certainty effect, also called *Allais paradox* (Allais, 1953). A variation of Allais' example was given by Kahneman & Tversky (1979) to illustrate the violation. Participants were given the following two choice problems:

- Problem 1: Choice between 80% chance of winning £4,000 (A) or £3,000 for sure (B).
- Problem 2: Choice between 20% chance of winning £4,000 (C) or 25% chance of winning £3,000 (D).

Most participants choose B over A, which implies that the utility they associate with winning £3,000 is greater than 0.8 times their utility of winning £4,000 [u(3,000) > 0.8*u(4,000)]. However, when faced with problem 2, most participants choose C over D, which implies the opposite inequality [0.2*u(4,000) > 0.25*u(3,000), equivalent to u(3,000) < 0.8*u(4,000)]. This constitutes a violation of the substitution or independence axiom, in that Problem 2 corresponds to the same choice as Problem 1, with each option weighted by a 0.25 probability. This violation suggests that by removing the certainty of the sure option in Problem 1, reducing the probability of winning from 1 to 0.25 had a stronger effect on choice than a reduction from 0.8 to 0.2. The certainty effect was also demonstrated for non-monetary outcomes.

Another violation of EUT occurs when introducing negative prospects (potential losses) into the decision options. For example, if presented with Problem 1 described above, most people choose B; but if presented with the equivalent problem involving losses – i.e. choice between 80% chance of losing £4,000 (A) or losing £3,000 for sure

(B), most people choose A. This effect was named the reflection effect by Kahneman and Tversky (1979), indicating (i) that the reflection of prospects around zero reverses preferences and (ii) that certainty is not always desirable; instead, certainty is desirable for gains but aversive for losses. This results in risk-seeking in the loss domain (Fishburn and Kochenberger, 1979), an effect not accounted for by EUT.

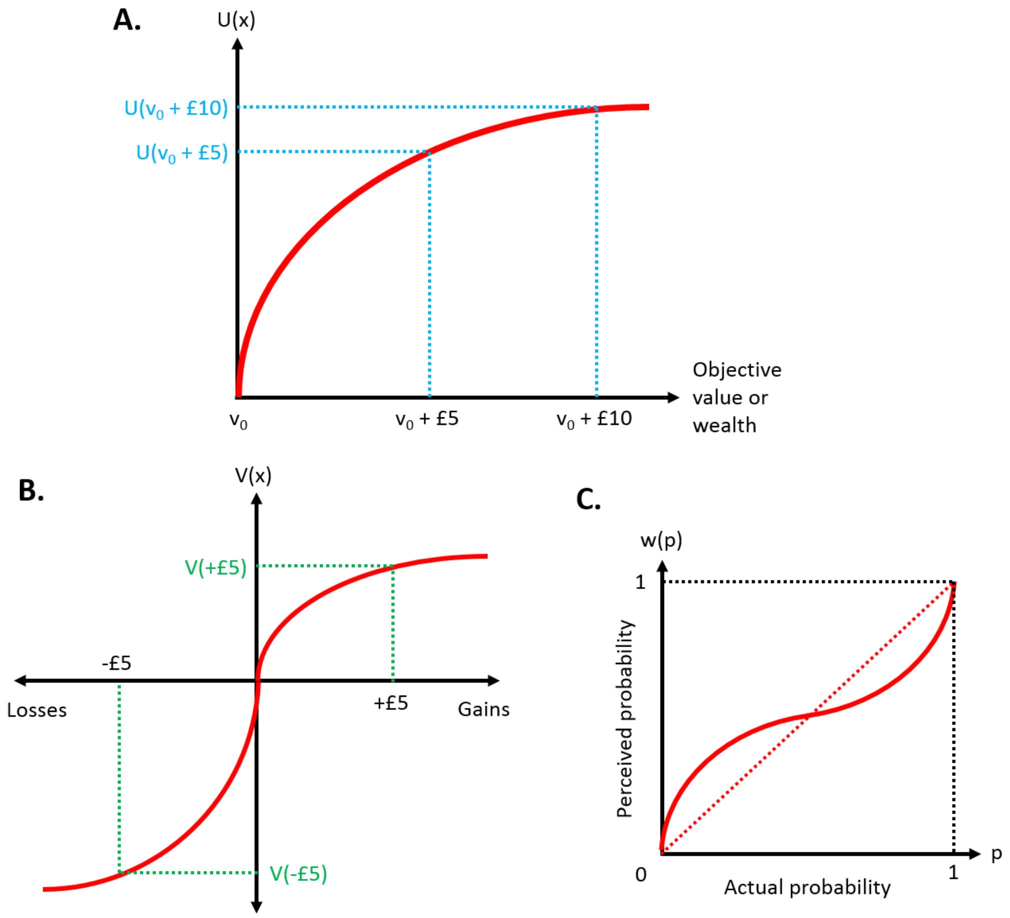


Figure 1-1. Expected Utility Theory (A) and Prospect Theory (B,C) models. A. Schematic representation of the utility function of EUT plotted as a function of objective value or wealth relative to an initial or total state of wealth v_0. The function assumes decreasing marginal utility as value increases, and reflects risk aversion in choice, mainly by the fact that utility associated with a small, sure gain, will be higher than the probability-weighted utility of a risker, higher gain. **B.** Prospect Theory value function is plotted as a function of increase (gains) and decrease (losses) in value relative to a reference point. The S-shape reflects decreasing (absolute) marginal utility for both increasing losses and increasing gains, consistent with risk aversion for gains and risk seeking for losses. The stronger slope of the function in the loss compared to the gain domains [|V(-5)|>|V(+5)|] explains loss aversion. **C.** Prospect Theory probability weighting function associating actual and perceived probabilities of potential outcomes. People tend to overweigh small probabilities and underweigh high probabilities.

1.1.2 Prospect Theory: a descriptive model

Prospect Theory (PT) was proposed by Kahneman and Tversky (1979) to address these violations and provide a descriptive theory of decision-making under risk, which is still used as one of the leading models of choice. In contrast to EUT, which is reference-independent and assumes that utility is applied to changes in wealth relative to an absolute total or initial wealth (v_0 in **Figure 1-1A**), PT introduces the presence of a reference point, relative to which changes in value can be positive or negative, resulting in gains and losses, respectively.

1.1.2.1 Value function

Prospect Theory's value function (**Figure 1-1B**) replaces the utility function from EUT and can be defined by the following properties: it is concave for gains and convex for losses; it is steepest near the reference point, with maximal sensitivity in the first units of gains and losses; and it is steeper in the loss than in the gain domain. Similar to the standard utility function of EUT, the concavity of the value function in the gain domain contributes to risk aversion for gains. On the other hand, its convexity in the loss domain will contribute to risk seeking for losses. This can be easily illustrated with the example of a choice between 50% chance of losing £10 or a sure loss of £5. The convexity of the function will result in the value of a £5-loss being more negative than half the value of a £10-loss, resulting in the risky option being preferred. Finally, the fact that the value function is steeper in the loss relative to the gain domain contributes to loss aversion; the tendency of most people to be more sensitive to losses relative to gains in their decisions (Kahneman et al., 1991; Tversky and Kahneman, 1991; Hardie et al., 1993). This is reflected in the function by the fact that the negative value of losing an amount is greater than the positive value of winning the same amount (see example in **Figure 1-1B** with ±£5).

The parametrization of this value function was established later (Tversky and Kahneman, 1992), with a power function:

$$V(x) = \begin{cases} x^{\alpha} \ if \ x \geq 0 \\ -\lambda(-x)^{\beta} \ if \ x < 0 \end{cases} \qquad \textbf{(Eq. 1-1)}$$

where α and β represent the curvature of the function in the gain and loss domains, respectively, and λ represents the loss aversion coefficient. A decision-maker whose behaviour is consistent with Prospect Theory will exhibit $\alpha<1$ (concavity and risk aversion for gains), $\beta<1$ (convexity and risk seeking for losses), and $\lambda>1$ (loss aversion).

1.1.2.2 Probability weighting

In addition to the value function, Prospect Theory assumes that during decision-making the value of a possible outcome is not directly multiplied by its probability, but by a decision weight w(p). The relationship between actual probabilities and decision weights or perceived probabilities is illustrated in **Figure 1-1C**. This probability weighting function accounts for several violations of the substitution axiom of EUT such as the certainty effect (Allais, 1953; Kahneman and Tversky, 1979). In particular, the examples described above suggest that people are more sensitive to changes in probabilities close to certainty (p=1 or p=0) than intermediate probabilities. This is reflected in the probability weighting function by a steeper slope for more extreme probabilities, close to 0 and 1, and an inflexion point around p=0.5. Similar to diminishing marginal utility, this function represents diminishing sensitivity to changes in probability as probability gets closer to intermediate values. This inverted S-shape results in low probabilities being overweighted and high probabilities underweighted. It can also explain the fourfold pattern of risk attitudes observed in several studies (Fishburn and Kochenberger, 1979; Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), such that people exhibit risk aversion for gains and risk seeking for losses at intermediate to high probabilities (as described above), while at low probabilities the pattern is reversed with risk seeking for gains and risk aversion for losses. An example from Kahneman and Tversky (1979) illustrating the latter effect with low probabilities is that most people choose a 0.1% chance of winning £5,000 over a sure gain of £5 (risk seeking for gains) but choose a sure loss of £5 over a 0.1% chance to lose £5,000 (risk aversion for losses). This is because the 0.1% probability is overestimated, making the gain gamble more attractive than it really is and the loss gamble less attractive than it really is.

The original formulation of Prospect Theory (Kahneman and Tversky, 1979) accounts for decisions made under risk with a maximum of two non-zero potential outcomes. The formulation published in 1992 (Tversky and Kahneman, 1992), Cumulative Prospect Theory, employs separate probability functions for gains and losses as well as cumulative decision weights – applying weights to the cumulative distribution function rather than to separate events. By doing so, the theory can also accommodate decisions under uncertainty (where the probabilities are unknown), as well as prospects with any finite number of potential outcomes.

However, for the purpose of this thesis, given that all the gambling tasks involved decisions under risk (where probabilities are fully known) with a maximum of two non-zero potential outcomes, the original version of Prospect Theory was used. In addition, because the probabilities were never varied and all tasks used 50-50 gambles, I assumed a neutral probability weight – i.e. $w(0.5)=0.5$ – and did not model a probability weighting function. This is a common assumption in many studies focusing on loss and risk aversion rather than probability weighting and using 50-50 gambles (Tom et al., 2007; Sokol-Hessner et al., 2009, 2013; De Martino et al., 2010; Chib et al., 2012).

1.1.3 Decision-making biases and phenomena explained by Prospect Theory

In addition to risk and loss aversion, many decision-making biases can be explained by Prospect Theory, making it a good descriptive model of people's decisions. A few examples will be described in this section.

1.1.3.1 Framing effect

Most normative models of economic decisions, including EUT, assume that decisions should not be influenced by how the options are described to the decision-maker. Prospect Theory, however, predicts that a decision option framed as a potential loss or a potential gain, even though the actual expected value is the same, will impact decisions differently. An example of the framing effect was reported by Tversky and Kahneman (1981), with the Asian disease example. Specifically, participants are told that the outbreak of an Asian disease is expected to kill 600 people and are asked to choose between two possible programmes to combat the disease. With programme A, 200 people will be saved; and with B, there is 1/3 probability that everyone will be saved and 2/3 probability to no one will be saved. When offered this choice, framed in terms of the number of people saved, most participants choose A over B. However when presented with the same choice framed in terms of losses – C (400 people will die) versus D (1/3 probability that nobody will die and 2/3 probability that everyone will die) – participants mostly select D over C. Tversky and Kahneman attribute this bias to the S-shape of the value function, inducing risk aversion (choice of the sure option to save 200 people) when options are framed in terms of gains and risk seeking (choice of the risky programme) when options are framed in terms of losses. The framing effect has also been demonstrated using monetary gambles (Tversky and Kahneman, 1981; De Martino et al., 2006). In De Martino et al. (2006), participants received an initial endowment (e.g. £50) at the beginning of each trial and had to decide between a risky gamble and a sure option. The risky gamble always included a probability (p) to keep all the endowment and a probability (1-p) to lose it all; but depending on the context, the sure option was framed as a gain (e.g. keep £20) or as a loss (e.g. lose £30). Even though the value and final outcome in both cases were exactly the same, participants chose to gamble about 60% of the time in the loss frame and only 40% of the time in the gain frame; framing thus affected about 1/5 of decisions in that study.

1.1.3.2 Endowment effect and status quo bias

Prospect Theory can also be applied to riskless choice (Tversky and Kahneman, 1991) and account for several manifestations of behaviour that are thought to be driven by loss aversion, such as the endowment effect and the status quo bias. The endowment effect was first reported by Thaler (1980), who observed that people require more money to compensate for the loss of a good compared to the amount they would be willing to pay to purchase this same good. This effect was later tested in a series of experiments (Kahneman et al., 1990), showing that students endowed with a mug (worth $5) asked a price of about $7 to sell it, while another group of students not endowed with the mug were only willing to pay $3 to buy it. Similarly, people exhibit a strong preference for options that induce no change of their current situation relative to other options. This is known as the status quo bias and was first introduced by Samuelson and Zeckhauser (1988), who documented the bias using hypothetical daily life decisions about jobs, investments, cars, etc, as well as a field study involving decisions about medical insurance plans. Experimental demonstrations came from Knetsch and Sinden (1984) and Knetsch (1989) who gave participants in their studies different compensation items (e.g. some participants were given a mug and others a chocolate bar). When offered the opportunity to trade their item with a member of the other group, approximately 90% declined and preferred to stick to their initial item.

All the above effects can be explained by shifts in the value function reference point, which then induce preference reversals. In the framing effect, positively framing an option results in placing the reference point below the value of the option, while negatively framing the same option has the effect of shifting the reference point to a higher value than the value of that option. Therefore, the former is perceived as a gain and the latter as a loss. In the endowment effect, subjects endowed with the mug have a higher reference point than subjects without a mug; selling their mug is thus perceived as loss, which has to be compensated to a greater extent given loss aversion. Finally, in the status quo bias, each participant's reference point is at the value of the object they own. When asked to trade that object against another, even though both objects may objectively have the exact same value, loss aversion implies that what will be lost in the trade will loom larger than what will be gained, hence the reluctance to trade.

1.1.4 Neurobiological basis of risk and loss aversion in decision-making

More recently, many studies have focused on characterizing the neurobiological basis economic decision-making under risk, in order to better understand how those biases arise in the brain. Human neuroimaging studies, using functional magnetic resonance imaging (fMRI), have addressed this question by having participants completing a variety of risky decision-making tasks in the MRI scanner, while recording blood oxygen level-dependent (BOLD) signal in their brain. Other studies have used pharmacology in both humans and animals, as well as direct neural recordings in rodents and non-human primates, in order to specifically examine the involvement of neurotransmitters such as dopamine in risk-taking. Despite providing insights into the involvement of brain systems in a cognitive process, these techniques are all correlative, and therefore cannot give a definite answer as to whether these systems are causally involved.

1.1.4.1 Human neuroimaging studies of decisions under risk in humans

Looking at general financial risk-taking, Kuhnen and Knutson (2005) designed a task where participants had to make a choice between a safe bond (always worth $1) and one of two risky stocks. One stock was better than the other and subjects were informed of the underlying probably distributions but were not told which stock was the “good” one and which stock was the “bad” one. The fMRI results showed that pre-choice activity in the nucleus accumbens (NAcc) predicted subsequent risky choices (stock), while pre-choice activity in the anterior insula predicted subsequent risk averse choices (bond). In Christopoulos et al. (2009) participants completed a more explicit task in which they had to choose between a safe option (e.g. 50 points for sure) or a gamble with two equiprobable outcomes (e.g. 50% chance of winning 40 points and 50% chance of winning 60 points). The gamble could either be low risk (40-60) or high risk (10-90, reflecting higher variance), and the value of the sure option was dynamically adjusted across trials using a staircase procedure that took into account the participant’s previous choices, such that the utility of the safe option was closely matched to that of the gamble. This design allowed the authors to demonstrate (i) encoding of expected value or reward magnitude in the ventral striatum, (ii) encoding of objective risk during choice in the dorsal anterior cingulate cortex (dACC), and (iii) individual differences in risk aversion (calculated as the difference in certainty equivalent between low- and high-risk gambles) in the right inferior frontal gyrus (IFG).

Using a similar design combined with a second experiment involving simple responses to visual stimuli associated with different levels of risk and reward values, Tobler et al. (2009) identified a cluster of activation in the lateral prefrontal cortex and suggested that this region integrated value and risk. Specifically, activity in this region tracked value across all participants and was modulated by risk differently depending on individual differences in risk attitudes: activity was enhanced by risk in risk-seeking participants and suppressed by risk in risk-averse participants, suggesting a possible tracking of utility. “Pure” value, independent of risk, was tracked in the ventral striatum. These results are consistent with other studies that have examined the neural basis of decision values between non-risky options (Plassmann et al., 2007; Chib et al., 2009), e.g. goods or food items, suggesting that the utility or subjective value of these options is also encoded in parts of the prefrontal cortex (PFC), namely ventromedial (vmPFC) and dorsolateral (dlPFC). However, other studies suggest that the ventral striatum may also play a key role in integrating several decision variables in a subjective value signal rather than simply coding "pure" objective reward (Hsu et al., 2005; Preuschoff et al., 2006). For example, Preuschoff et al. (2006) found that the ventral striatum encoded both expected reward and risk (calculated as reward variance); however, the two signals were temporally distinct, with immediate encoding of reward and delayed encoding of risk, suggesting a sequential integration process before the decision is made.

1.1.4.2 Human neuroimaging studies of loss processing and loss aversion

Another set of studies has examined the neural basis of loss aversion, with the general hypothesis that, similar to potential losses being overweighted relative to potential gains, some brain systems may be more sensitive to potential losses than potential gains. This is exactly what Tom et al (2007) found in an influential study. Participants in this study had to make a series of decisions to accept or reject mixed gambles offering a 50% chance of winning and a 50% chance of losing. The win and loss amounts were varied parametrically and orthogonally such that their neural signature could be assessed independently. The authors found that a number of brain regions, including ventral striatum and vmPFC, responded to both increasing gains and decreasing losses (no region responded to increasing losses) and exhibited "neural loss aversion", such that the response to decreasing losses was stronger than the response to increasing gains. In addition, this neural loss aversion estimate in the ventral striatum was correlated with behavioural loss aversion (λ parameter estimate) across participants. This study suggests that the ventral striatum may play an important role in representing utility or subjective value rather than simply coding for objective expected value or reward magnitude as suggested by some of the studies described above (Christopoulos et al., 2009; Tobler et al., 2009). In particular, it may constitute the neural signature of the steeper slope observed for losses relative to gains in Prospect Theory's value function. Tom et al had also hypothesized that the amygdala would be involved in loss aversion, given previous evidence of its role in processing losses and negative stimuli (Breiter et al., 2001; Kahn et al., 2002). Even though they failed to evidence such a role for the amygdala, subsequent studies did.

A first strong piece of evidence came from a clinical neuropsychology study in which two patients with amygdala damage failed to exhibit any loss aversion on a similar task to the one used by Tom et al, suggesting that the amygdala is not only involved in, but also necessary for loss aversion (De Martino et al., 2010). In a recent fMRI study (Canessa et al., 2013), the authors replicated Tom et al's finding by demonstrating stronger loss-related deactivations compared to gain-related activations (i.e. "neural loss aversion") in the ventral striatum. They additionally demonstrated a role for the amygdala in specifically processing losses (independent of the processing of gains), as well as in tracking neural loss aversion in a way that correlated with individual differences in behavioural loss aversion. Furthermore, Canessa et al. (2013) also revealed some structural correlates of loss aversion, with increased grey matter volume of amygdalar and para-amygdalar nuclei in individuals with higher loss aversion.

Finally, in another study (Sokol-Hessner et al., 2013), the authors specifically used Prospect Theory's value function equation (**Eq. 1-1** above) to generate each subject's utility value associated with each decision from their individual parameter estimates, including loss aversion. They found a strong neural signature of decision utility in the bilateral striatum consistent with previous studies (Preuschoff et al., 2006; Tom et al., 2007). They analysed the relationship between brain activity and individual differences in loss aversion at the time of outcome (instead of the time of decision, which was examined by previous studies) and found that the extent to which the amygdala responded to loss relative to gain outcomes also correlated with behavioural loss aversion. This role of the amygdala in loss aversion through the enhanced sensitivity to losses, relative to gains, both during decision and outcome stages is consistent with a general role for the amygdala in processing the value of affective and behaviourally relevant stimuli, which has been proposed by recent reviews (Morrison and Salzman, 2010; Pessoa and Adolphs, 2010; Ousdal et al., 2012).

1.1.4.3 Influence of dopamine on risk taking: evidence from pharmacology studies and dopamine neuron recordings

Dopamine is a molecule released by a small number of neurons in the brain, and has been implicated in numerous functions. Dopaminergic neurons' cell bodies are confined to only a few areas, mainly the substantia nigra and the ventral tegmental area, both part of the midbrain. These neurons project to several other brain areas, two of which are the ventral striatum and the prefrontal cortex. As described above, these regions have been implicated in economic decision-making, valuation processes, and risk-taking. It is therefore possible that dopaminergic transmission may play a role in these processes.

To test this hypothesis, several studies have used pharmacological administration of levodopa (L-DOPA), a precursor of dopamine, in human subjects. Cools et al. (2003) found that Parkinson's patients on L-DOPA exhibited increased impulsivity and delay aversion during gambling. More recently Rutledge et al. (2015) have examined the effect of L-DOPA administration in healthy volunteers on a gambling task analysed in a Prospect Theory framework combined with a Pavlovian approach-avoidance bias for gain relative to loss outcomes. They found that L-DOPA increased risky decisions involving potential gains, but not potential losses, and that this effect was best explained by a value-independent Pavlovian approach bias towards risky gains, rather than by an effect of L-DOPA on Prospect Theory parameters (λ, α, or β). Another recent study from the same group (Rigoli et al., 2016) demonstrated a very similar effect using a slightly different paradigm and behavioural model. Specifically, their task did not involve losses, only choices between a sure small gain, and a risky 50-50 gamble between zero and a higher gain; it also included a context manipulation with overall option values varying between low-value context and high-value context blocks. Their model captured behaviour well by distinguishing between subjects' general propensity to gamble, their sensitivity to reward variance (or risk), and the influence of context on their choices. Interestingly, L-DOPA only affected the general propensity to gamble, making subjects more likely to gamble overall, independent of risk or context, consistent with the effect observed in Rutledge et al. (2015).

Finally, animal studies have also provided evidence for a role of dopamine in risk-taking and encoding of subjective value. In rodents, administration of the dopamine releaser amphetamine and stimulation of dopamine D1 and D2 receptors with receptor-selective agonists (St. Onge and Floresco, 2009; Ferenczi et al., 2016), as well as electrical stimulation of midbrain dopamine neurons (Stopper et al., 2014), all increase risky decisions in the animals. Conversely, the blockade of these receptors and the suppression of phasic dopamine bursts induce risk aversion. Optogenetic stimulations of midbrain dopamine neurons have been shown to increase reward-seeking in rodents (Tsai et al., 2009; Witten et al., 2011; Ferenczi et al., 2016), whereas stimulation of D2 receptor-expressing cells in the nucleus accumbens, which are thought to detect pauses and dips in dopamine signalling, increased the animal's sensitivity to past losses and reduced risk taking in subsequent choices (Zalocusky et al., 2016). This provides a causal role for dopamine transmission in controlling risk taking behaviour. Direct neural recording of midbrain dopamine neurons in monkeys demonstrated that dopamine responses scale with the marginal utility of reward (i.e. showing diminishing sensitivity to value) rather than objective reward value (Stauffer et al., 2014) and integrate the subjective value of the reward across multiple attributes, here reward magnitude, risk, and reward type (Lak et al., 2014).

These studies suggest that the dopamine system, through its actions on a distributed network of regions, in particular the striatum, makes an important contribution to the representation of Prospect Theory's value function, and resulting decision-making behaviours under risk.

1.2 Emotions are integral to the decision-making process

The preceding assessment of subjective valuation processes and economic decisions would not be complete without an overview of the role played by emotion and affect. For decades economists have ignored the roles played by emotions, mood, and affective states in economic decisions, which can strongly influence the way people evaluate prospects and choose between them. An extensive part of the literature has examined these roles of emotions during economic decisions, which can broadly be separated into integral and incidental influences, as discussed in the following two sections.

Firstly, integral emotions can be defined as emotions induced by the decision at hand, whether it be the value of potential payoffs, the risk, the presence of a potential loss, the effect of past outcomes, etc. It is important to note that emotion-related processes are referred to by different terms in the literature, such as "emotion", "affect", "mood", or "feelings". Throughout this thesis, I will follow the view of Phelps et al. (2014), recognizing that "emotion is not a unitary construct, but rather a compilation of component affective processes" (Phelps et al., 2014, p.265; see also Lerner et al., 2015). "Affect" is most commonly used as a general term that refers to all of these component processes together. "Emotion" indicates an internal or external discrete reaction to an event, which is usually multifaceted and biologically mediated, and includes physiological responses, facial expressions, action tendencies (approach or avoid), bodily reactions, and subjective feelings. These emotional reactions can usually be measured and examined in the context of their influence on choice, for example. "Feeling" indicates a subjective component of emotion, which can be assessed by self-report questions asking people how they feel in a given context or in response to an event. "Mood", in contrast, refers to feelings that are more diffuse and persist in time without the need for a triggering event.

1.2.1 Somatic marker hypothesis

One early theory of the integral role of emotional responses in economic decision-making was proposed by Antonio Damasio and Antoine Bechara, as the somatic marker hypothesis (see Bechara and Damasio, 2005 for a review). Damasio and Bechara were among the first to suggest that instead of emotions interfering with decision-making by making people irrational, emotions may instead inform and be beneficial to decisions. The key idea behind the theory is that during choice, especially conflicting or difficult choice, bodily emotional reactions arise in response to pleasurable or aversive decision options, as well as thoughts and memories. These responses are encoded in the brain as "somatic markers", somehow informing the brain of the emotional state of the body. These somatic markers then influence decisions by directing the decision-maker towards more advantageous options, an effect that can occur consciously or unconsciously.

Most of the experimental evidence for the theory came from the Iowa Gambling Task (IGT), first introduced in 1994 (Bechara et al., 1994), followed by several variants (Bechara et al., 2000). In the original task, participants are presented with four decks of cards labelled A, B, C and D, and have to pick a card from one of the decks on each trial. The decks are constructed such that A and B always win $100 (high-paying decks) and C and D (low-paying decks) always win $50; however, every so often some cards in each deck are associated with a monetary loss. The frequencies and magnitudes of losses vary across decks, causing high-paying decks A and B to have an overall long-term negative payoff (disadvantageous decks), and low-paying decks C and D a long-term positive payoff (advantageous decks). The other difference between decks is that losses in decks A and C are more frequent, but of smaller magnitude; while losses in decks B and D are less frequent but of much higher magnitude. These probabilities and payoffs asymmetries are not explicitly provided to participants, but must instead be learned over time.

The first study using this task compared the performance of healthy volunteers with that of patients with vmPFC damage (Bechara et al., 1994). The authors found that while healthy volunteers were able to learn the underlying statistics of the task and select more cards from advantageous decks overall, vmPFC patients failed to show such an effect and consistently chose the high-paying but disadvantageous decks throughout, suggesting that their decisions are guided by immediate rewards rather than future losses. Following this result, Bechara et al's hypothesis was that vmPFC may be the neural substrate of somatic markers and that when damaged, patients are not sensitive to the emotional reactions provoked by losses throughout the task and therefore cannot integrate this signal to guide their decisions towards advantageous decks.

To test this hypothesis more precisely, Bechara et al directly measured emotional reactions in a subsequent set of studies by examining anticipatory skin conductance responses (SCRs) in healthy controls and patients with vmPFC (Bechara et al., 1997) or amygdala (Bechara et al., 1999) damage. They found that control subjects exhibited strong SCRs just before selecting a card; and these SCRs were stronger for bad than good decks, even before participants started exhibiting a preference for good decks in their choice behaviour. In contrasts, SCRs in patients with vmPFC and amygdala damage were very low and did not differ for good and bad decks, suggesting an important role for these two areas in processing the emotional value of the decision options and in using them to guide decisions.

However, in the following decade, many criticisms of the somatic marker hypothesis have emerged, mainly driven by potential confounds associated with the IGT (Maia and McClelland, 2004, 2005). In their first study (Maia and McClelland, 2004), the authors ran the IGT using more fine-grained methods to assess what participants know about the decks and about their own strategy at different time points throughout the task, and found that participants report reliable knowledge of the advantageous strategy before showing the effect behaviourally, suggesting that they know what they should do and implement it consciously. This contrasts with Bechara et al's suggestion that emotional responses arise and are used to guide decisions outside of awareness. If Maia and McClelland's claims are true, then the SCRs observed by Bechara et al could constitute a *consequence* of subjects consciously knowing that the bad decks are bad, rather than an unconscious signal that subsequently influences their behaviour (see also Dunn et al., 2006 for a review).

In addition, the design of the task itself presents many confounds that could explain impairments in performance (Hinson et al., 2002; Sanfey et al., 2003; Dalgleish et al., 2004; Fellows and Farah, 2005; Chiu and Lin, 2007; Lin et al., 2007; see Dunn et al., 2006 for a review). Indeed, an increased propensity to choose the disadvantageous decks as observed in the patient populations, and also from a substantial proportion of healthy participants, could arise from deficits in reversal learning (Fellows and Farah, 2005) or working memory (Hinson et al., 2002), from the use of a simple gain-stay-lose-switch strategy (Chiu and Lin, 2007; Lin et al., 2007), from increased impulsivity and risk-taking (Sanfey et al., 2003), reduced sensitivity to losses/reduced loss aversion (Dalgleish et al., 2004), or simply from a lack of motivation (Barrash et al., 2000).

1.2.2 Risk as feelings hypothesis

Loewenstein et al. (2001) proposed the "risk as feelings" hypothesis to account for the effect of emotions directly induced by the decision at hand and experienced at the time of the decision. Specifically, the hypothesis makes a distinction between expected emotions, i.e. what one expects to feel later given the expected outcome of the decision, and current, immediate emotions, felt at the time of decision, which are more visceral reactions to having to make a decision. In the context of a risky decision for example, the level of risk can induce some negative emotions like anxiety or dread (or maybe some positive emotions like excitement for a risk-seeking individual). These emotions are unrelated to the outcome of the decision, but instead derive directly from the decision itself.

Originally, most proposals have considered that such emotions induced by the decision, if any, would simply be a by-product or consequence of the decision, but would not impact the decision in return. Instead, the risk as feeling hypothesis proposes that this interaction is bidirectional: the decision generates feelings which in turn influence the decision; explaining, for example, why an individual who feels more anxious than another at the prospect of a risky decision will more likely to choose a safe option.

In addition, the risk as feeling hypothesis argues that contrary to expected emotions, which usually inform and are beneficial to the decisions (as suggested by the somatic marker hypothesis), the immediate emotional reactions to the decision (e.g. risk-induced fear) usually differ from the more cognitive evaluation of the decision and therefore tend to interfere with people's behaviour and bias their decisions away from the rational course of action. Focusing mainly on the example of fear, Loewenstein et al. (2001) suggest that the following factors are key in making the emotional responses diverge from an objective cognitive evaluation: vividness of the fear response, dependent on past experience and mental imagery; insensitivity of fear responses to probabilities; learning differences varying with the type of risk, etc.

In a recent review (Lerner et al., 2015), the risk as feelings hypothesis was integrated into a more complete model synthesising more recent finding in the literature on emotion-decision interactions. This model, called the emotion-imbued choice (EIC) model generally aims to describe "ways in which emotion permeates choice processes" (Lerner et al., 2015, p.814). The model is reproduced in **Figure 1-2A**. In particular it includes generic processes that form the basis of economic decision-making and come from normative models such as expected value maximization or EUT (black arrows on **Figure 1-2A**). These reflect the fact that (i) several attributes of the decision options, such as potential payoffs, probabilities, delay, etc, are evaluated, compared, and the highest value option is chosen; and (ii) there are individual differences in this process based on people's personality and preference (e.g. high sensation-seekers are likely to take more risks than low sensation-seekers).

A first deviation from the normative models, but accounted for by models such as Prospect Theory or the somatic marker hypothesis, is shown by the green arrow. This represents the influence of emotions about expected potential outcomes on the decision. The main addition of the EIC model, as outlined in the risk as feeling hypothesis, is the presence and influence of current emotions, experienced immediately at the time of the decision. The red arrows show that these current emotions (i) are generated by the evaluation process itself and will in turn influence this evaluation and the subsequent decisions, (ii) can be influenced by the attributes of the decision options, by incidental influences and by individual differences, and (iii) reciprocally interact with expected emotions, such that someone anticipating a painful shock may experience fear now, and the current experience of fear may enhance the negative expected utility of the shock.

1.2.3 Fear processing theory of loss aversion

A similar theory has been proposed about the role of fear in loss aversion, but stemming more from neuroscientific findings (in contrast with the psychological explanation in the risk as feelings hypothesis). An account of loss aversion as an expression of fear (Camerer, 2005), has emerged given the numerous findings indicating a common neural and physiological basis to both fear processing and loss aversion/anticipation.

With respect to fear processing, a network involving the amygdala, insula and striatum has repeatedly been identified. In a study by Phelps et al. (2001), responses in the amygdala and insula tracked the anticipation of an aversive outcome (an electric shock) relative to safe cues (no shock delivered), and correlated across subjects with SCRs, providing evidence for a neural and physiological signature of the expression of fear. The same year, LeDoux and Gorman provided a model of fear processing involving the amygdala and the striatum (LeDoux and Gorman, 2001), mainly drawn from classical fear conditioning paradigm in animals, and depicted in **Figure 1-2B**. The model suggests that fear-arousing stimuli are processed in the lateral nucleus of the amygdala, which is also the area where the conditioned and unconditioned stimuli are integrated initially. Subsequent exposure to the conditioned stimulus will lead to a passive fear response such as freezing, through neurons in the central nucleus of the amygdala, which in turn activates brainstem centres responsible for the different components of the fear response (freezing, hormonal and autonomic responses). However, this model also adds the possibility of an active coping response, whereby, through activation of the basal nucleus of the amygdala and the striatum, the animal can learn to avoid the fear-arousing event in the future. Further work has confirmed that amygdala-striatal interactions also play a key role in the acquisition of avoidance responses in humans (Delgado et al., 2009).

Interestingly, the anticipation of losses as well as loss aversion have been associated with very similar neural correlates. Responses in the amygdala and ventral striatum have been found to track the anticipation of monetary losses during risky decision-making tasks (Kahn et al., 2002; Hahn et al., 2010; Canessa et al., 2013) and to reflect individual differences in loss aversion (Tom et al., 2007; Canessa et al., 2013; Sokol-Hessner et al., 2013). In addition, as discussed above, De Martino et al. (2010) have provided causal evidence for a necessary role of the amygdala in loss aversion. Physiological responses consistent with the expression of fear have also been reported to correlate with loss aversion, such as SCRs, heart rate and pupil dilation (Sokol-Hessner et al., 2009; Hochman and Yechiam, 2011).

Taken together, the studies discussed above point towards the hypothesis that fear processing is likely an integral component of loss aversion.

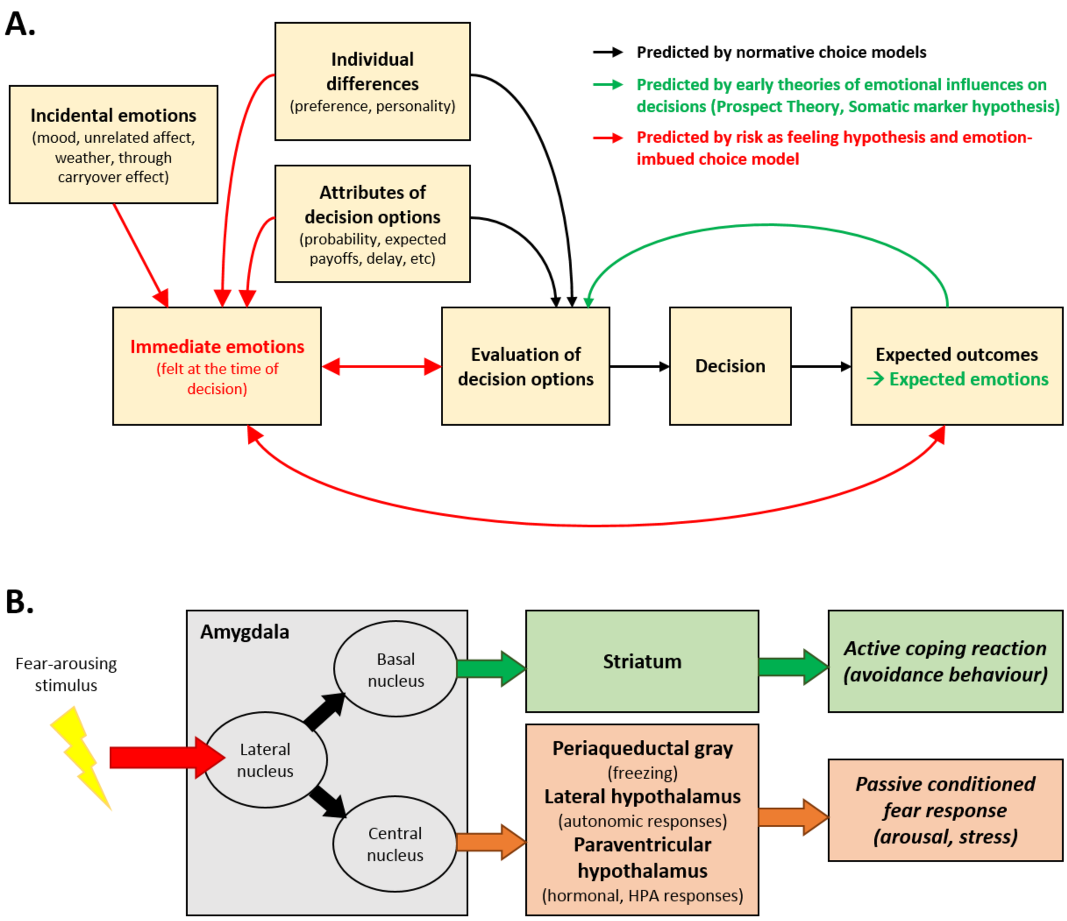


Figure 1-2. Summary of models of integral emotional influences on choice. A. Emotion-imbued choice (EIC) model, drawing on the risk as feelings hypothesis, reproduced from Lerner et al. (2015). **B.** LeDoux's model of fear processing, suggesting that amygdala-striatal interactions underlie active avoidance of aversive stimuli, and may be responsible for the integral effect of fear in loss averse choices. Reproduced from LeDoux and Gorman (2001).

1.2.4 Emotion as a proxy for value / subjective utility

Prospect Theory itself makes key assumptions about an integral role of emotions in choice. Although Prospect Theory was not directly derived by eliciting people's feelings to predict choice, an implicit assumption of the theory is that subjective value or utility is a proxy for feelings, which in turn influence choice. Kahneman expresses this assumption in his book, *Thinking, Fast and Slow*, p.286: "…Humans described by Prospect Theory are guided by the immediate emotional impact of gains and losses" (Kahneman, 2011). He explains this assumption by the interaction between two opposing systems (System 1 and System 2) during the decision-making process. System 1 is the "emotional" system, fast and automatic and requiring no or very little effort or voluntary control to operate. In contrast, the “cognitive” System 2 is more deliberative, reflective and slow and operates via the allocation of cognitive resources and effortful mental computations.

Some early neuroimaging research has tried to separate these two systems in the brain, with regions such as the striatum, amygdala, medial PFC, OFC and insula proposed to constitute the “emotional” brain, and regions such as the dlPFC, rostral PFC, and posterior parietal cortex forming the “cognitive” brain (see Cohen, 2005 for a review applied to economic decisions). However more recent research indicates that there is no clear distinction between these two systems, and in particular, “no clear evidence for a unified system that drives emotion” (Phelps et al., 2014, p.265), suggesting that such a dual-systems view may not hold and that the interaction between emotion and decisions is much more intricate. In this review, Phelps et al argue that emotion *per se* has value, and as such can be encoded in value-related areas such as the vmPFC (Winecoff et al., 2013) and integrated during the decision-making process in the same manner as any other decision variable or attribute. This is consistent with Kahneman’s view that utility is a proxy for emotional associations with decision options. However, this hypothesis has never been empirically tested by explicitly measuring emotions; this is what I set out to do in the study presented in **Chapter 3** of this thesis.

In addition, this assumption that emotion is an integral component of choice suggests that changing emotion should influence decisions. A review of this literature examining the role of external, incidental, influences of emotions on decisions is presented in the next section.

1.3 Incidental effect of emotions on decisions

Previous research has shown that everyday decisions, such as consumption behaviour, indulgence, or assessing risk, are influenced by emotional states. In the laboratory, there are two major ways in which incidental emotions can be experimentally manipulated in order to study their effect on decision-making. The first type of methods includes mood induction procedures, whereby a relatively long-lasting affective state is induced in the participants who are then given a decision-making task to complete while in that state (see section **1.3.1**). The second way includes more subtle trial-by-trial emotional priming procedures, whereby an emotional stimulus is presented to the participant on each trial of the task prior to making a decision (see section **1.3.2**).

1.3.1 Mood and stress induction procedures

1.3.1.1 Behavioural findings

Stress is generally characterized by a short and specific physiological, neural and hormonal response to an event (McEwen, 2007) and may in that sense not fit the criteria for the definition of a mood state, which usually refers to a more long-lasting state than a response to a specific external event. However, I include in this section both effects of stress and other mood induction procedures together, as the methods used to study these effects are usually very similar: an induction procedure followed by the decision-making task.

Mood induction procedures are varied and range from showing participants a short emotional film clip (Lerner et al., 2004; Han et al., 2012; Lee and Andrade, 2014), having them read some emotional scenarios either fictional (Raghunathan and Pham, 1999) or from news report (Johnson and Tversky, 1983), or asking them to write about a past emotional event or about things that make them feel a given emotion (Lerner and Keltner, 2001; Yen and Chuang, 2008). Various stress induction procedures have also been used to induce fear and anxiety, including threat of shock (ToS), the Trier social stress test (TSST), and the cold pressor test (CPT). During the ToS paradigm (Schmitz and Grillon, 2012), subjects typically perform a cognitive task while either at risk of or safe from rare, but unpleasant, electric shocks. The TSST (Kirschbaum et al., 1993) has several variants but usually involves telling the participant that he/she will have to give a presentation and/or perform mental arithmetic in front of a panel of academic judges, followed by an anticipation phase and the actual test phase, often video recorded. Performance on a subsequent decision-making task is usually compared with performance of another group of subjects who perform a sham version of the TSST, in which they are asked to write a short essay or perform some arithmetic task on paper, but they don't have to speak and there is no audience or video recording. In the CPT, participants have to submerge their non-dominant hand in a bucket of ice water (between 0 and 3°C) for 3 minutes, while control participants do the same with a bucket of water at room temperature. Those methods have substantial differences: while ToS induces anticipatory anxiety and participants perform a decision-making task while at threat of receiving a shock at any moment (Engelmann et al., 2015; Robinson et al., 2015a, 2015b), the TSST and CPT are used because they induce a strong stress response, which can be measured physiologically by increased salivary cortisol and heart rate, and during which decision-making is measured (Lighthall et al., 2009; Mather et al., 2009; Porcelli and Delgado, 2009; Pabst et al., 2013; Buckert et al., 2014). Therefore, during ToS paradigms decisions are made under stress, whereas in TSST and CPT the decision-making task occurs during recovery from stress, after the stressful event is over. Because of this difference, these techniques may produce different effects on decision-making behaviour.

A summary of studies that have used either mood or stress induction procedures described above to study their modulatory effect on decision-making under risk is presented in **Table 1-1**, with studies separated into those that used stress induction procedures such as ToS, CPT or TSST (**Table 1-1A**), negative mood induction (**Table 1-1B**) and positive mood induction (**Table 1-1C**). In addition to the variability in the mood and stress induction procedures, the tasks used were also very different. Because the focus of this thesis is the examination of economic decisions in the framework of Prospect Theory's value function, the last column of the table summarizes the effect implied by each study's finding in terms of mood- or stress-induced changes in risk or loss aversion. Note, however, that many of these studies did not directly assess risk and loss aversion, and therefore the observed results could also be explained by other factors.

Table 1-1. Summary of effects of mood and stress induction on decision-making

Study	Task	Mood induced (technique)	Result	Implied effect
A. Stress/anticipatory anxiety induction				
(Lighthall et al., 2009)	BART	***Stress*** (CPT)	↑ risk in men ↓ risk in women	***Depends on gender***
(Mather et al., 2009)	Driving task	***Stress*** (CPT)	↓ risk in older adults (= in younger adults)	↑ ***risk aversion***
(Porcelli and Delgado, 2009)	PGT (lotteries)	***Stress*** (CPT)	↓ risk in gain domain ↑ risk in loss domain	↑ ***reflection effect***
(Putman et al., 2010)	PGT (lotteries)	***Stress*** (Administration of cortisol)	↑ risk for high-risk gamble with large gain (= otherwise)	↓ ***risk aversion***
(Clark et al., 2012)	PGT (lotteries)	***Fear*** (ToS)	↓ risk-taking	↑ ***risk aversion***
(Pabst et al., 2013)	GDT (modified version)	***Stress*** (TSST)	↓ risk in loss domain (= in gain domain)	↑ ***risk aversion***
(Buckert et al., 2014)	PGT (lotteries)	***Stress*** (TSST)	↑ risk in gain domain (= in loss domain)	↓ ***risk aversion***
(Robinson et al., 2015a)	IGT	***Anxiety*** (ToS)	↓ risk in low trait anxious ↑ risk in high trait anxious	***Depends on trait anxiety***
(Robinson et al., 2015b)	Framing effect; Delay discounting	***Anxiety*** (ToS)	No effect	***No effect***
(Engelmann et al., 2015)	PGT (50-50 gambles vs safe option)	***Anxiety*** (ToS)	No effect	***No effect***
B. Negative mood induction				
(Raghunathan and Pham, 1999)	One-shot gamble choice	***Anxiety*** (read scenario)	↓ risk-taking	↑ ***risk aversion***
		Sadness (read scenario)	↑ risk-taking	↓ ***risk aversion***
(Lerner and Keltner, 2001)	Risk perception task	***Fear*** (self-description)	↓ optimistic risk estimates	↑ ***risk aversion***
		Anger (self-description)	↑ optimistic risk estimates	↓ ***risk aversion***
(Lerner et al., 2004)	Endowment effect (EE)	***Disgust*** (film clip)	No EE (↓ selling prices)	↓ ***loss aversion***
		Sadness (film clip)	Reverse EE (buying prices > selling prices)	↓ ***loss aversion***
(Yen and Chuang, 2008)	Status quo bias (3 choices)	***Sadness*** (self-description)	↓ status quo bias	↓ ***loss aversion***
(Han et al., 2012)	Status quo bias	***Disgust*** (film clip)	↓ status quo bias	↓ ***loss aversion***
(Lee and Andrade, 2014)	Cash-out game (stock market simulation)	***Fear*** (film clip)	↓ risk-taking	↑ ***risk aversion***

C. Positive mood induction				
(Isen et al., 1988)	PGT (mixed 50-50 gambles)	***Positive affect*** (giving bag of candy)	↑ negative utility of losses (= for gains, no effect on risk)	↑ ***loss aversion***
(Yen and Chuang, 2008)	Status quo bias (3 choices)	***Happiness*** (self-description)	↑ status quo bias	↑ ***loss aversion***
(Lee and Andrade, 2014)	Cash-out game (stock market simulation)	***Excitement*** (task framing)	↑ risk-taking	↓ ***risk aversion***

↑ means increased; ↓ decreased, = no effect. BART: Balloon Analogue Risk Task, PGT: Probabilistic Gambling Task, GDT: Game of Dice Task, IGT: Iowa Gambling Task. CPT: Cold Pressor Test, ToS: Threat of Shock, TSST: Trier Social Stressor Test.

Instead of describing each study in detail, the main effects that seem to emerge from this literature on the influence of mood and stress on risky decisions are summarized below in four main points, although evidence is overall rather mixed.

First, the induction of fear, stress or anticipatory anxiety tends to decrease people's propensity to take risks (or increase risk aversion). This was found using a one-gamble shot game in a large sample (Raghunathan and Pham, 1999), a computer-based driving game (Mather et al., 2009), a cash-out game framed as a stock market simulation (Lee and Andrade, 2014), and probabilistic gambling tasks (Porcelli and Delgado, 2009; Clark et al., 2012). However, two recent studies, both using the ToS manipulation, failed to evidence any effect of anticipatory anxiety on the framing effect, temporal discounting (Robinson et al., 2015b), risk or loss aversion (Engelmann et al., 2015). Finally, a few studies reported more nuanced effects of fear or stress on risk-taking either due to individual differences based on trait anxiety level (Robinson et al., 2015a), gender (Lighthall et al., 2009), or age (Mather et al., 2009), or differential effects in the gain and loss domains (Putman et al., 2010; Pabst et al., 2013; Buckert et al., 2014). A possible explanation of this fear-induced decrease in risk taking could come from a modulation of the perception of risk, such that when people are afraid or anxious they tend to overestimate the likelihood of negative events and underestimate the likelihood of positive events (Johnson and Tversky, 1983; Lerner and Keltner, 2001), possibly resulting in increased risk aversion in choice. This effect also extends to real-life risky behaviour, such that participants induced with fear (through story telling) and general negative affect (continuous music listening) report a lower inclination to engage in a range of hypothetical risky behaviours such as binge drinking or riding a bike without a helmet (Lindquist and Barrett, 2008).

Second, there is much less evidence for an influence of positive affect on risk-taking than for negative affect. By framing their task as an exciting game to the participants, Lee and Andrade (2014) found that their original effect of fear in reducing risk taking was reversed, such that the excitement induced by the framing of the game resulted in an increase in risk taking. In an earlier study (Isen et al., 1988), inducing positive affect by giving participants a bag of candy before the start of the experiment had no effect on people's sensitivity to gains and risk taking, leaving open the question of whether positive affect increases risk taking. Even though this question still needs investigating, it has important implications for the financial domain, since a recent study has suggested that excitement-induced increases in risk-taking could contribute to financial market bubbles (Andrade et al., 2016).

Third, a small body of evidence using paradigms in which task performance is assumed to be driven by loss aversion seems to converge towards an effect of mood valence on loss aversion, but in the opposite direction from the effect on risk aversion, with positive affect increasing loss aversion and negative affect decreasing loss aversion. Using positive affect induction, Isen et al. (1988) found that subjects under positive affect were more sensitive to losses and exhibited a greater negative utility of high losses than subjects under neutral affect. Similarly, using a status quo bias task, Yen and Chuang (2008) found that the preference for the status quo option increased with happiness induction, but decreased with sadness induction, consistent with increased and decreased loss aversion, respectively. Finally, the endowment effect, which is also thought to result from loss aversion, was found to be eliminated following disgust induction, and even reversed following sadness induction (Lerner et al., 2004), consistent with reduced loss aversion. However, only one study to date has directly examined how loss aversion is affected by emotion induction, in this case anticipatory anxiety using ToS, and found no effect (Engelmann et al., 2015), possibly calling into question the interpretation of fear processing as an integral driver of loss aversion, as described in section **1.2.3** above. Instead a possible alternative could come from an emotion-induced shift in reference points. Positive affect induction may move someone's reference point higher, making losses loom even larger, and vice versa for negative affect induction. However, such an interpretation, taken alone, would also imply increased risk aversion following positive affect and increased risk-taking following negative affect, which does not seem supported by the current literature, suggesting that other processes are at play.

Finally, a valence-driven dichotomy appears too simplistic, as several studies have demonstrated opposite effects of two emotions within the same valence on risk taking. Raghunathan and Pham (1999) found that while anxiety induction increased risk aversion, sadness induction in contrast increased risk seeking. Similarly, Lerner and Keltner (2001) induced fear and anger in separate groups of participants by asking them to describe three to five things, as well as the details of one particular situation, that make or has made them most afraid/angry. When examining optimistic risk estimates (the subjective perception of risk associated with positive events), they showed a fear-induced decrease and an anger-induced increase in optimistic risk estimates. A theory that could account for these effects is the appraisal-tendency framework (ATF; Lerner and Keltner, 2000, 2001; Lerner et al., 2015). Specifically, the "ATF posits that emotions predispose individuals to appraise the environment in specific ways toward similar functional ends" (Lerner et al., 2015, p.805). Different dimensions, such as certainty, pleasantness, or individual control, will influence the appraisal tendency attributed to the emotion and affect behaviour in a goal-directed manner. A dimension on which an emotion scores high will be more likely to influence behaviour by activating the corresponding appraisal tendency. For example the differential effect of fear and anger on risk-taking may be driven by the certainty dimension, which is high for anger and low for fear, inducing an appraisal tendency towards risk in angry individuals and away from risk in afraid individuals.

1.3.1.2 Neuroimaging findings

Only a handful of studies to date have attempted to examine the neural correlates of such mood effects on decision-making under risk. In the case of stress or anxiety, obvious candidate regions include the amygdala and striatum, which play an important role in adaptive fear responses (LeDoux and Gorman, 2001), as well as parts of the prefrontal cortex, such as the OFC, vmPFC, or dmPFC, whose activity and connectivity with the amygdala have been shown to be modulated by stress (Arnsten, 2009; Roozendaal et al., 2009; Robinson et al., 2012).

In 2012, Lighthall et al adapted their version of the Balloon Analog Risk Task (BART) for fMRI. In this task, participants are required to inflate a balloon as much as possible but stop before it explodes. They thus face sequential choices where they have to decide whether to pump the balloon one more time (therefore gaining more money) or collect their current reward and moving to the next balloon. The behavioural findings from the original study (Lighthall et al., 2009) revealed no main effect of stress on risk taking but an exploratory post-hoc analysis demonstrated a gender difference in the effect of stress (induced by CPT) on risk taking: stress increased risk taking in men but decreased risk taking in women. In the fMRI version of the task (Lighthall et al., 2012), which had to be adapted to fit the constraints of scanning, the authors failed to replicate their gender-by-stress interaction on risk-taking, with overall low risk-taking in all participant groups (stressed men, non-stressed men, stressed women, non-stressed women). However, they found a post-hoc interaction on reward collection rates and decision times, such that male participants under stress made faster decisions and collected more rewards than non-stressed male participants, while female participants under stress made slower decisions and collected fewer rewards than non-stressed female participants. These interactions were reflected in the activity of the insula and dorsal striatum (putamen) during decisions, such that stress increased activity in these regions for men but decreased it for women, potentially reflecting increased (decreased) motivation to cash out money and sensitivity to rewards in stressed male (female) participants.

In a recent study (Engelmann et al., 2015), participants completed a gambling task in which they had to choose between a sure option and a risky 50-50 gamble. Stress was manipulated by having some blocks performed under threat of strong electric shocks, while other blocks were only associated with weak shocks. The authors did not find any effect of stress on gambling propensity, risk or loss aversion. However, stress induced significant task-related changes in the brain, namely a reduction in the tracking of expected subjective value and prediction of choice in the ventral striatum and vmPFC, as well as a reduction in connectivity between these two regions. These results suggest that even though choices were not affected, subjects may rely on different processes when under stress, relying less on (complex) subjective value computations and maybe more on more simple heuristics, both strategies resulting in similar choices in the specific task used.

Overall this absence of mood or stress induction behavioural effects when tested in fMRI may question the efficacy of these procedures in the MRI scanner, possibly due to the design constraints and the impossibility of adapting a mood induction procedure into a more flexible event-related design. In addition, except for the ToS manipulation, which can easily be implemented within subjects over different blocks, most studies described in this section had to employ between-subjects designs, where negative mood was typically induced in one group of participants, and positive or neutral mood in another. These procedures also raise the possibility that participants may easily infer the purpose of the experiment, and purposefully adapt their behaviour to fit with that purpose – known as the "good subject" effect in demand characteristics (Orne, 2009).

1.3.2 Emotional priming techniques

In order to address these issues, trial-by-trial emotional priming methods have also been used to examine emotional effects on economic decisions in a more controlled and automatic way.

One technique that ensures emotional priming occurs outside of the participant's awareness is subliminal priming, in which emotional pictures, such as faces portraying various emotions, are shown to the participant for a very short duration (usually less than 30ms). Even though participants do not consciously report the presence of faces, these are still processed in the brain, notably in the amygdala (Whalen, 1998; Morris et al., 1999), and can influence preference judgments of unrelated visual stimuli (Niedenthal, 1990; Murphy and Zajonc, 1993). In the context of consumer-related behaviour, Winkielman et al. (2005) found that priming thirsty participants with subliminal happy faces, relative to angry faces, made them pour and drink more beverage and increased their willingess to pay for the drink, suggesting a possible interaction between emotional priming and valuation processes. Another study found opposite effects of subliminal priming with guilt- and sadness-related words on indulgence and helping behaviour (Zemack-Rugar et al., 2007). Specifically guilt priming decreased indulgence decisions (money allotted to purchasing a CD/DVD instead of school supply) and increased helping behaviour (time alloted to charity), while sadness priming had the reverse effect. However, there is no evidence to date about a possible effect of subliminal emotional primes on economic decision-making under risk.

A few studies have examined this using supraliminal priming. Knutson et al. (2008) primed participants by showing them erotic pictures (positive primes), pictures of household appliances (neutral primes) or pictures of snakes and spiders (negative primes) for 2 seconds before having them choose between a high-risk (e.g. 50% chance to win and 50% chance to lose $10) and a low-risk (e.g. 50% chance to win and 50% chance to lose $1) gamble. Similar to some of the effects observed with positive affect induction above, participants chose the high-risk option more often when primed with positive pictures relative to neutral ones. However, negative primes had no effect on choice. In addition, participants performed this task during fMRI, and a conjunction analysis showed that the same voxels in the ventral striatum (nucleus accumbens) responded to both the presentation of positive (versus negative) primes and the anticipation of shifting to the high-risk option (versus shifting to the low-risk option). In addition, activity in the ventral striatum partially mediated the effect of positive primes on risk taking. This suggests a potential role for the ventral striatum in integrating emotional and risk signals into a decision variable. A few years later, a very similar priming paradigm was used in a financial investment task, in which subjects had to decide between investing in a safe bond or a risky stock (Kuhnen and Knutson, 2011). Relative to neutral primes, negative pictures overall made people more risk averse (i.e. more likely to choose the safe bond), especially if their prior choice was already for the safe option. Overall, positive pictures did not have an effect on risky choice; however, they tended to make people more risk seeking in trials where their previous choice was already the risky stock. The authors speculated that the differences from the earlier study (Knutson et al., 2008) may have resulted from the use of more potent and arousing negative pictures in the second study.

Using the framing effect task developed by De Martino et al. (2006), Cassotti et al. (2012) added an emotional priming procedure to study the effect of incidental emotions on the framing effect. Before each choice, participants were presented with a picture from the International Affective Picture System database (IAPS; Lang et al., 1997) for 5 seconds. A between-subjects design was used, such that a third of participants were primed with pleasant pictures, a third with unpleasant pictures, and a third were not primed (control group). Positive pictures abolished the framing effect, specifically by decreasing risk seeking in the loss frame, while negative pictures had no effect. However, the negative pictures did not distinguish between different emotions and consisted of a mix of fearful and sad images. These two emotions have been shown to have opposite effects on risk taking using mood induction in previous work (Raghunathan and Pham, 1999); it is therefore possible that the effects in Cassotti et al. (2012) cancelled each other out.

At the time when the experiments in this thesis were planned, there was no evidence for a possible influence of incidental emotional primes on loss aversion, which is what I set out to examine in **Chapter 4** of this thesis. However, a very recent study provided preliminary evidence that incidental fear cues, presented either during the decision or just before, increase monetary loss aversion (Schulreich et al., 2016). This result would be consistent with the hypothesis that loss aversion reflects the expression of fear (Camerer, 2005) and relies on fear processing systems in the brain (LeDoux and Gorman, 2001). Interestingly, this study may point towards some differences between effects of long-lasting mood induction procedures and of transient emotional primes. A transient fearful cue may trigger rapid fear processing and increase Pavlovian avoidance of losses (Seymour and Dolan, 2008; Ly et al., 2014); whereas a more long-lasting change in mood may recruit different systems in the brain and possibly result in opposite effects on behaviour.

In summary, trial-by-trial emotional priming methods have the advantage, relative to mood induction procedures, of being better adapted for event-related fMRI designs, as they allow for within-subjects manipulations, and are probably less susceptible to demand characteristics. One downside, however, is that the emotional experience is likely to be less intense and vivid than during a mood induction procedure. Even though the evidence for an effect of incidental emotional cues on risky decision-making is still limited, and the low number of studies do not yet allow one to draw general conclusions on the specific components of emotion (valence, arousal, certainty, etc) that may drive such effects, they help pave the way for some of the work presented in this thesis, as well as future investigations.

1.4 Emotion and decision-making in anxiety

Anxiety disorders constitute a major global heath burden (Beddington et al., 2008), and are characterized by negative emotional processing biases as well as decision-making impairments (Hartley and Phelps, 2012; Robinson et al., 2013). Anxiety is therefore a relevant psychiatric construct to study in relation to this thesis given that the interaction between emotion and decision-making may vary with anxiety levels. In addition, studying emotion and decision-making processes in anxiety is important and could provide a better understanding of cognitive impairments in anxiety and potential insights into the development of psychological interventions.

Anxiety can be examined in two ways: first as a vulnerability factor within healthy individuals, by studying individual difference in dispositional levels of anxiety or trait anxiety as measured by self-report questionnaires (Sandi and Richter-Levin, 2009; Bishop and Forster, 2013); and secondly as a clinical pathology, by comparing patients diagnosed with an anxiety disorder with healthy controls. This section examines the literature on emotional processing and decision-making in anxiety from both perspectives.

1.4.1 Anxiety and disrupted emotional processing

Anxiety states are sustained anticipatory responses to unpredictable threats, including affective, physiological and cognitive changes, and can in that sense de distinguished from fear, which encompasses responses to predictable threats (Grillon et al., 1991; Grillon, 2008; Davis et al., 2010). In many situations, anxiety defined as such is adaptive because it allows avoidance of potential threats in uncertain environments as well as increased vigilance and alertness. However, there are strong individual differences in the deployment of these harm-avoidance processes, with some people more prone to anxiety than others (high versus low level of dispositional anxiety). Clinical anxiety is thought to emerge through a dysregulation of such "adaptive" anxious response, whereby these harm-avoidance processes become permanent rather than deployed in potentially threatening situations, and as a result start interfering with the patient's daily life and ability to concentrate (Bishop and Forster, 2013; Robinson et al., 2013).

Both dispositional and clinical anxiety have been associated with enhanced detection and processing of negative emotional information, particularly threat-related stimuli. In two similar studies (MacLeod et al., 1986; MacLeod and Mathews, 1988), subjects were presented with pairs of words, one threat-related and one neutral. On some trials a dot probe replaced one of the words, and subjects were instructed to press a button as quickly as possible when the probe appeared. High trait anxious individuals were faster to detect the probe when it replaced a threat word than a neutral word, while low trait anxious individuals showed no difference (MacLeod and Mathews, 1988). In MacLeod et al. (1986), the same effect was found between clinically anxious patients and healthy controls. This suggests an attentional bias towards threat-related stimuli in anxious individuals. Similarly, the same authors have demonstrated that unattended threat-related stimuli, presented outside the participants' awareness, act as distractors and impair performance of anxious individuals, but not control, in a reaction time task (Mathews and MacLeod, 1986). This attentional bias towards threat was also demonstrated in younger anxious populations (children and adolescents), both clinical (Roy et al., 2008) and dispositional (Telzer et al., 2008), using angry (threatening) versus neutral faces. A meta-analysis of 172 studies confirmed the robustness of this threat-related attentional bias, both in different clinical anxiety disorders and high trait anxious individuals, with a medium effect size (Cohen's d=0.45; Bar-Haim et al., 2007; see also Cisler and Koster, 2010 for a review). Despite this specific threat-induced facilitation effect on attention, it is important to note that anxiety is generally associated with attentional deficits, mainly poor attentional control and ability to flexibly allocate attention to relevant parts of changing environments (Derryberry and Reed, 2002; Eysenck et al., 2007).

Neuroimaging studies have also provided converging evidence that anxious individuals exhibit increased neural responses, particularly in the amygdala and PFC, to fearful and angry faces. This has been shown both in high trait versus low trait anxious individuals (Etkin et al., 2004; Stein et al., 2007; Telzer et al., 2008), as well as in clinically anxious patients relative to non-anxious controls (Monk et al., 2006;

Blair et al., 2008). A recent study has also provided evidence of increased functional connectivity between the amygdala and dmPFC during processing of fearful versus happy faces in patients with anxiety relative to healthy controls (Robinson et al., 2014).

Finally, anxiety is also associated with difficulties in regulating emotions; both implicitly, as demonstrated using a task that creates emotional conflict and requires adaptation to that conflict to perform accurately (Etkin et al., 2010; Etkin and Schatzberg, 2011), and in daily life, with difficulties in deploying cognitive reappraisal to regulate emotions (Farmer and Kashdan, 2012). Using fMRI, impairments in emotional conflict adaptation in anxious individuals were shown to be associated with reduced connectivity between the pregenual or ventral anterior cingulate cortex (ACC) and the amygdala, a mechanism thought to play a central role in emotion regulation, with ACC hypothesized to dampen the emotional response in the amygdala (Etkin et al., 2010; Etkin and Schatzberg, 2011).

1.4.2 Anxiety and economic decision-making

An early model of anxiety suggested that intolerance to uncertainty is a pivotal feature of generalized anxiety disorder (GAD; Dugas et al., 1998). Anxious individuals find uncertain situations particularly aversive and distressing, possibly because they exhibit a deficit in learning about the outcomes of their actions in very uncertain environments (Browning et al., 2015). This deficit, and resulting intolerance to uncertainty, are likely to play a key role in the development and maintenance of pathological anxiety.

In addition, such intolerance for uncertainty should have important consequences on economic decisions in which uncertainty and risk are involved. The results of studies that have investigated risk perception and risk taking in anxious individuals are summarized in **Table 1-2**, with studies separated according to whether they examine the effect of dispositional (**Table 1-2A**) or clinical (**Table 1-2B**) anxiety.

Table 1-2. Summary of effects of dispositional and clinical anxiety on risky decision-making.

Study	Task	Manifestation Population	Effect of anxiety	Implied effect
A. Dispositional anxiety in normal population				
(Maner and Schmidt, 2006)	RTBS & Optimism Scale (risk appraisals)	Trait anxiety	↓ risky behaviours ↑ pessimistic risk estimates	↑ ***risk aversion***
(Maner et al., 2007) studies 1 and 2	BART	Trait and social anxiety	↓ risk-taking	↑ ***risk aversion***
(Miu et al., 2008)	IGT	Trait anxiety	↓ performance	***unclear***
(Lorian and Grisham, 2010)	RTBS (30-item version) & BART	Social anxiety	↓ risky behaviours ↓ risk-taking	↑ ***risk aversion***
(Xu et al., 2013)	Framing effect task	Trait anxiety	↑ framing effect	↑ ***risk aversion for gains & risk-seeking for losses***
B. Clinical anxiety (compared with healthy controls)				
(Butler and Mathews, 1983)	Risk estimation questionnaire	Adults	↑ pessimistic risk estimates	↑ ***risk aversion***
(Maner et al., 2007) study 3	RTBS (14-item version)	Adults	↓ risky behaviours	↑ ***risk aversion***
(Mueller et al., 2010)	IGT (modified)	Adults	↓ decisions leading small but consistent losses	***unclear***
(Giorgetta et al., 2012)	PGT (lotteries)	Adults	↓ risky choices	↑ ***risk and/or loss aversion***
(Galván and Peris, 2014)	Cups Task (choice of safe vs risky option)	Adolescents	↓ risk for losses = for gains	↑ ***risk aversion for losses or*** ↑ ***loss aversion***
(Ernst et al., 2014)	Accept/Reject 50-50 mixed gambles	Adolescents	No effect	= ***loss aversion***

↑ means increase, ↓ means decrease, = means no effect. RTBS: Risk-Taking Behaviors Scale (Weber et al., 2002), BART: Balloon Analogue Risk Task, IGT: Iowa Gambling Task, PGT: Probabilistic Gambling Task.

Specifically, there is clear evidence that anxious individuals, relative to their non-anxious counterparts, (i) overestimate the risk associated with negative events (Butler and Mathews, 1983; Maner and Schmidt, 2006), (ii) report a lower inclination to engage in everyday risky behaviours (Maner and Schmidt, 2006; Maner et al., 2007; Lorian and Grisham, 2010), and (iii) avoid risky options during decision-making tasks under risk (Maner et al., 2007; Lorian and Grisham, 2010; Giorgetta et al., 2012). This suggests that anxiety is associated with exacerbated risk aversion (see also Hartley and Phelps, 2012; Paulus and Yu, 2012; Robinson et al., 2013 for reviews), which is consistent with a model of anxiety based on the intolerance of uncertainty.

Interestingly, Maner et al. (2007) also collected reports of people's willingness to engage in risky everyday behaviour in other patient groups, including patients with mood disorders and patients with learning disorders and/or no formal axis I diagnosis. They found that group differences in reported risky behaviours were driven specifically by a reduction in the anxious patient group. By contrast, the level of reported risk-taking in the other patient groups was similar to that of healthy controls, suggesting that increased risk avoidance may be specific to anxiety, rather than driven by negative affect in general.

Another piece of evidence for the role of anxiety in decision making comes from a study that showed increased susceptibility to the framing effect with trait anxiety (Xu et al., 2013), suggesting an increased propensity to both choose the sure option when framed as a gain (decreased risk taking in the gain domain) and avoid the sure option when framed as a loss (increased risk taking in the loss domain). Interestingly, this was the first study to also examine the neural basis of these individual differences. Their results show that high trait anxious individuals exhibit increased amygdala activity and amygdala-vmPFC connectivity during decisions consistent with the frame, but decreased dorsal ACC activity and ACC-vmPFC connectivity during decisions counter to the frame. This is consistent with previous reports of enhanced amygdala responses and amygdala-prefrontal connectivity in anxiety (Etkin et al., 2004; Stein et al., 2007; Robinson et al., 2014), suggesting a role for this amygdala-prefrontal brain network.

Interestingly, this increased susceptibility to the framing effect in anxiety may be mediated by genetic differences in the promoter region of the serotonin transporter gene (5-HTTLPR). Carriers of the short allele at this locus, which results in reduced serotonin transporter expression and function, relative to carriers of the long allele, exhibit enhanced dispositional anxiety (Lesch et al., 1996; Crişan et al., 2009), are more susceptible to the framing effect (Crişan et al., 2009; Roiser et al., 2009), and show increased amygdala responses during decisions made in accord with the frame but fail to engage amygdala-PFC coupling mechanisms during decisions made counter to the frame (Roiser et al., 2009).

However, these studies focusing on the framing effect did not directly examine the neural basis of increased risk avoidance in anxiety. A recent study in adolescents with or without an anxiety disorder did so (Galván and Peris, 2014), using a decision-making task where participants had to choose between a safe and a risky option both matched in expected value (e.g. $2 for sure or 1/5 chance of $10). Half the trials used gains, and half used losses. The behavioural results showed reduced risk taking in anxious adolescents compared to controls, but only in the loss domain. The neuroimaging findings revealed that anxiety was associated with decreased ventral striatum response during risky choice involving gains and increased amygdala response during risky choice involving losses. Although these responses were not directly associated with the behavioural effect, they suggest that non-anxious individuals may make decisions mainly by processing gains in the ventral striatum, while anxious individuals may more heavily rely on an amygdala-mediated influence of losses.

Finally, a possible link between anxiety and loss aversion has not been established. There is a strong hypothesis that loss aversion should increase with anxiety, given the associated negative biases in emotional and attentional processes, as well as the heightened sensitivity to large negative outcomes (Hartley and Phelps, 2012; Paulus and Yu, 2012). However, there has been no study to date examining loss aversion in relation to anxiety in adult participants. One study looked at this question in adolescents (Ernst et al., 2014) and found no difference in loss aversion between anxious and healthy adolescents. In two other studies (Giorgetta et al., 2012; Galván and Peris, 2014), the gambling tasks used involved potential losses as well as gains, but did not allow differentiating between risk and loss aversion, such that the observed decreased propensity to choose the risky options in those tasks could be driven by increased risk aversion, increased loss aversion or a combination of both. Similarly, the increased susceptibility to the framing effect observed in high trait anxious individuals (Xu et al., 2013) could be driven by increased loss aversion, but also by increased risk aversion for gains and decreased risk aversion for losses. No study to date has examined risk and loss aversion parameters in anxiety using a Prospect Theory framework – this is what I address in **Chapter 5** of this thesis.

1.5 Thesis aims and summary of chapters

The overall aim of this thesis is to contribute a mechanistic account of the computational and neural processes by which emotion influence economic decisions, both from an integral and incidental perspective. From the evidence discussed in this introductory chapter it seems clear that emotion plays a key role in decision-making, and that decisions can be altered by manipulating emotions. However, how exactly these processes unfold is still largely unknown and represents the focus of this thesis over three main questions addressed in the three separate experimental chapters.

1.5.1 Chapter 3: how are feelings integrated into economic decisions?

Chapter 3 provides a computational account of the integral influence of emotion on economic choices. In particular, it aims to examine how self-report feelings are integrated during the decision-making process and to develop a computational model of choice that integrates both feelings and value and by doing so performs better than traditional models. This model may also explain how the integration of feelings during choice results in loss aversion.

1.5.2 Chapter 4: how do incidental emotional cues modulate loss aversion?

With a focus on loss aversion, the aim of the study presented in Chapter 4 was to examine whether and how incidental emotional cues alter loss aversion, with the hypothesis, given the (limited) literature detailed in section **1.3.2**, that fearful cues may increase loss aversion while happy cues may instead reduce loss aversion. In addition, Chapter 4 also examined the neural mechanisms involved in this incidental influence of emotions on loss aversion, with a particular focus on the amygdala and the ventral striatum, as well as individual differences in these processes due to trait anxiety.

1.5.3 Chapter 5: how does anxiety affect the relative contribution of risk and loss aversion to economic choice?

Finally, given the association between trait anxiety and emotion-induced changes in loss aversion described in Chapter 4, as well as the lack of studies to date examining separate contributions of risk and loss aversion to choice in anxiety disorders, the study presented in Chapter 5 aimed to address these two points. It details the results of a behavioural study comparing a group of clinically anxious patients with matched healthy controls on a Prospect Theory-derived gambling task that allows separating risk and loss aversion within the same model of choice. In addition, it aims to expand the results of Chapter 4 observed in high trait anxious, but non-clinical, individuals, to a sample of clinically anxious patients.

Chapter 2 Experimental methods

This chapter will describe the common methods that were used in the experimental chapters of this thesis. Specifically the Prospect Theory framework under which economic decisions were studied and modelled is described, followed by the detail of two pilot studies that were run to develop a reliable emotional priming procedure together with a sensitive gambling task.

2.1 Participant screening: Mini International Neuropsychiatric Interview (MINI)

For the studies presented in **Chapter 4** and **Chapter 5**, as well as pilot work presented in section **2.5** below, participants were screened using the Mini International Neuropsychiatric Interview (MINI; Sheehan et al., 1998). The MINI is a short, structured diagnostic interview to clinically assess symptoms of neuropsychiatric disorders, in accordance with the Diagnostic and Statistical Manual of Mental Disorder-IV (DSM-IV) and the International Classification of Diseases (ICD) 10th revision for psychiatric disorders. The complete version of the MINI contains 16 sections; however, for screening purposes and because some sections are redundant, I used a version that was reduced to 12 sections, assessing the following: major depressive episode, (hypo) manic episode, panic disorder (PD), agoraphobia, obsessive-compulsive disorder (OCD), post-traumatic stress disorder (PTSD), alcohol abuse and dependence, non-alcohol psychoactive substance use disorders, psychotic disorders (and mood disorder with psychotic features), anorexia nervosa, bulimia nervosa, and generalized anxiety disorder (GAD). The following four sections were not included: dysthymia, suicidality, social phobia, and antisocial personality disorder.

Healthy volunteers (pilot studies, Chapter 4, and healthy controls in Chapter 5) were included only if they did not meet criteria for any of the aforementioned sections of the MINI. GAD patients (Chapter 5) had to meet criteria for GAD to be included in the study and were excluded if they met criteria for manic or hypomanic episodes (past or current), psychotic disorders, alcohol or substance abuse (in the last 6 months) or dependence. Given that their comorbidity with GAD is high, the other disorders such as depression and other anxiety disorders did not constitute exclusion criteria.

2.2 Self-report questionnaires and verbal IQ measure

Both emotional processing and economic decision-making are subjective and highly likely to vary across individuals. In order to examine such individual differences in the studies presented in this thesis, participants completed self-report mood and personality questionnaires at the end of each study.

The first questionnaire that was systematically administered is the State Trait Anxiety Inventory (STAI, Spielberger et al., 1983). The STAI contains 40 questions, divided into two sub-groups. The first 20 questions assess state anxiety, asking people to evaluate their current state of anxiety by rating the intensity of their feelings *"right now, at this moment"*. The 20 questions are statements that people have to rate with one of the following four answers: "Not at all", "Somewhat", "Moderately so", "Very much so". Ten of these statements, such as "I am tense" or "I feel nervous" are directly coded, with a score ranging from 1 (Not at all) to 4 (Very much so). The other 10 statements, such as "I am relaxed" or "I feel secure" are reverse coded, with a score ranging from 4 (Not at all) to 1 (Very much so). The next 20 questions assess trait anxiety – the more stable proneness to anxiety – by asking people to indicate how they *generally* feel using the following four answers: "Almost never", "Sometimes", "Often", "Almost always". Again, scores on 11 of the questions are directly coded from 1 to 4, such as "I worry too much about something that doesn't really matter" or "I lack self-confidence"; while the other 9 questions, such as "I am a steady person" or "I am satisfied with myself", are reverse coded. Overall state and trait anxiety scores are obtained by adding scores of the 20 questions for each subscale. Both scores can range from 20 (low anxiety) to 80 (high anxiety). With respect to trait anxiety, previous studies have found that most people from a healthy population will score between 20 and 50 (mean score around 35; Knight et al., 1983; Crawford et al., 2011); while a score above 50 may indicate some clinical relevance for an anxiety disorder (Kvaal et al., 2005; Julian, 2011). In this thesis individual differences in trait anxiety were examined in pilot studies (see sections **2.5.1** and **2.5.2** below), as well as **Chapter 4** and **Chapter 5**, either by including trait anxiety scores as a covariate in the analyses, running a Pearson's correlation between trait anxiety scores and a dependent variable of interest, or performing a median split on trait anxiety scores and comparing participants with high versus low anxiety.

The second questionnaire that participants completed was the Beck Depression Inventory (BDI, Beck et al., 1961) to assess depressive symptoms. The questionnaire contains 21 questions corresponding to different symptoms. For each question, participants have to pick one of four statements best corresponding to how they have been feeling *over the past few days*. The four statements are presented in order of increasing severity, with the first statement corresponding to a score of 0 (e.g. "I do not feel sad"), then a score of 1 (e.g. "I feel sad"), 2 (e.g. "I am sad all the time and can't snap out of it"), or 3 (e.g. "I am so sad or unhappy that I can't stand it"). The overall BDI score is obtained by summing each individual question's score, and can range from 0 to 63, with a score above 15 typically considered clinically relevant (Sprinkle et al., 2002). Because the distribution of BDI scores is often positively skewed in the general population (Lasa et al., 2000), with a majority of people scoring very low (below 10 – Beck et al., 1988), it is difficult to use BDI scores as a covariate in analyses, except for studies in patient populations. Therefore, I primarily used BDI scores for screening purposes, excluding participants who scored above 15.

Participants in all studies except for Chapter 3 were also administered the Wechsler Test of Adult Reading (WTAR; Wechsler, 2001). In this test, the participant is presented with a list of 50 words and asked to read them out loud to the experimenter in the order from 1 to 50. There is no time limit, and one point is scored for each word read correctly. The final score out of 50 can then be converted to an IQ score according to standard score conversion tables and age, averaging 100 in the population. The WTAR was mainly used to match anxious patients and healthy controls in the study presented in Chapter 5, and to ensure no participant exhibited a strong IQ deficit.

2.3 Gambling tasks

All experimental chapters of this thesis used gambling tasks to assess decision-making biases such as loss and risk aversion. All versions of the task used 50/50 gambles, in which participants have 50% chance of winning a monetary amount and 50% chance of losing a monetary amount. These gambles are referred to as mixed gambles throughout. Based on expected value (EV) calculation, one should accept the gamble whenever the win amount is higher than the loss amount. However, in reality, most people reject gambles when the win and loss amounts are close and only start accepting gambles when the win amount is about twice as big as the loss. This is thought to be driven by loss aversion.

In the pilot studies (section **2.5** below) and in **Chapter 4**, which focused on loss aversion and its modulation by emotional cues, all trials of the task involved mixed gambles as described above and participants had to decide whether to accept or reject such gambles. In **Chapter 5**, however, in order to estimate both loss and risk aversion, gain-only trials were added to the task; they involved choosing between a sure win and a 50/50 gamble between a higher win and £0. This allowed to assess sensitivity to risk separately from sensitivity to losses. In order to have a consistent trial presentation, the mixed gamble trials in Chapter 5 were also presented as a choice between a sure option (always £0) and the mixed gamble between a win and a loss (instead of a choice to accept or reject the mixed gamble). Finally, in **Chapter 3**, given that the gambling task was run on its own and independent from priming with emotional cues, trials did not need to be repeated for each emotion condition and more trials could be included in the task, allowing the addition of loss-only trials. Those were symmetrical to the gain-only trials, in that they involved a choice between a sure loss and a 50/50 gamble between a higher loss and £0. Adding these trials was useful to be able to estimate risk attitudes separately in the gain and loss domains.

A key point to take into account when designing such gambling tasks is the range of monetary amounts to use throughout the task. Because all the experiments were incentive-compatible, only relatively small amounts (lower than £30) were used, so that it was believable for participants that some of these amounts (or the average amount over several randomly-selected trials) would be paid to them for real at the end of the experiment. In addition, amounts needed to be paired (a win and a loss in the mixed gambles, a small win and a high win in the gain-only trials, a small loss and a high loss in the loss-only trials), such that the range of pairs would cover the range of indifference points (the gamble expected value at which a participant would accept or reject the gamble with a probability of 0.5) across subjects. For example, let us imagine a set of mixed gambles consisting of all possible pairing between wins ranging from £5 to £10 and losses also ranging from £5 to £10. With such a set, where the highest-value gamble is win £10/lose £5, it is likely that participants with a high degree of loss aversion will not accept any gamble of the set. If this happens, it will be impossible to estimate loss aversion reliably for these participants as their indifference point will be unknown. In order to reliably estimate decision-making parameters, such as risk and loss aversion, one needs to make sure that there are enough trials where the participant decides to gamble and enough trials where they decide not to. Two solutions are possible to ensure this.

First, gamble EVs may encompass a large range of values, such that every participant's indifference point will be included in that range. This is what was implemented in **Chapter 3**, where the gamble set was built using combinations of amounts ranging from £0.20 to £12. However, the drawback of this method is that it requires a lot of trials in order to include all possible gain/loss combinations. This was a problem for all the other studies presented in this thesis, which used emotional priming and required all gamble trials to be repeated identically for each emotion condition.

Therefore, the other option, which allowed reducing the number of trials per emotion condition in **Chapter 4** and **Chapter 5**, was to build a gamble matrix centred on each participant's indifference point. Therefore, participants completed a practice session of the gambling task, which included a staircase procedure and during which potential wins and losses were varied parametrically as follows. The gamble EV (EV = 0.5*win amount + 0.5*loss amount) was adjusted every 2 trials in order to reach the participant's indifference point (the EV for which gambles were accepted half of the time on average). Each set of 2 trials contained one "high" EV gamble and one "low" EV gamble. The EV of accepted gambles was decreased by 0.5 while the EV of rejected gambles was increased by 0.5. Potential gains ranged between £6 and £24 and potential losses between £1 and £12. For each trial, the gain/loss pair was chosen randomly among all pairs with the same desired EV. Once the indifference point for mixed gambles (and for gain-only gambles in **Chapter 5**) were determined, gamble matrices could be build centred on this indifference point with a relatively low number of trials (49 trials for mixed gambles, 25 trials for gain-only gambles), allowing repetition of the gamble set across the different emotional conditions.

A potential risk with using such a staircase procedure during practice is that participants could learn to "play" the staircase; i.e. accept very few gambles during practice to make the gamble expected value increase, then accept most gambles during the main task to maximize their outcome. Therefore, subjects whose gamble acceptance rate was less than 10% during practice and more than 90% in the main task were excluded. However this did not occur for any of the participants in Chapters 4 and 5. Other exclusion criteria based on participants' data from the gambling task included very high (>95%) or very low (>5%) gamble acceptance rate throughout the entire task (practice and main task), suggestive of insensitivity to value; inconsistent choices as reflected by values of the μ parameter (see **Eq. 2-6** below) close to 0 and aberrant parameter estimates (e.g. negative loss aversion values), suggestive of bad understanding of the task; or a high number of missed trials (>10%) throughout the task.

2.4 Modelling of economic decisions

2.4.1 Model definition and estimation

The different models of gambling decisions used throughout this thesis were all derived from Prospect Theory's subjective value function equation.

Utility or subjective value (u) of monetary gains (x>0) is defined as:

$$u(x) = x^{\rho_{gain}} \qquad \textbf{(Eq. 2-1)}$$

where ρ_{gain} represents the curvature of the function (or diminishing marginal utility) in the gain domain: a ρ_{gain} value lower than 1 indicates diminishing sensitivity to changes in gain value as gain value increases and results in risk aversion in the gain domain, while a ρ_{gain} value higher than 1 indicates risk seeking for gains.

Utility or subjective value (u) of losses (x<0) is defined as:

$$u(x) = -\boldsymbol{\lambda} \cdot (-x)^{\rho_{loss}} \qquad \textbf{(Eq. 2-2)}$$

where λ represents loss aversion: a λ value higher than 1 indicates overweighting of gains relative to losses during decision-making and a λ value lower than 1 the converse; and ρ_{loss} represents the curvature of the function (or diminishing marginal utility) in the loss domain: a ρ_{loss} value lower than 1 indicates diminishing sensitivity to changes in loss value as loss value increases and results in risk seeking in the loss domain, while a ρ_{loss} value higher than 1 indicates risk aversion for losses.

Using the above equations the utility of each gamble can then be calculated as follows:

$$u(gamble) = u(mixed) = 0.5 \cdot G^{\boldsymbol{\rho_{gain}}} - 0.5 \cdot \boldsymbol{\lambda} \cdot |L|^{\boldsymbol{\rho_{loss}}} \qquad \textbf{(Eq. 2-3)}$$

for mixed gamble trials, with G the value of the gain and L the value of the loss, and:

$$u(gamble) = u(gain\ only) = 0.5 \cdot G^{\boldsymbol{\rho_{gain}}} - S^{\boldsymbol{\rho_{gain}}} \qquad \textbf{(Eq. 2-4)}$$

for gain-only trials, with G the value of the high, risky gain and S the value of the sure gain, and:

$$u(gamble) = u(loss\ only) = -0.5 \cdot \boldsymbol{\lambda} \cdot |L|^{\boldsymbol{\rho_{loss}}} + \boldsymbol{\lambda} \cdot |S|^{\boldsymbol{\rho_{loss}}} \qquad \textbf{(Eq. 2-5)}$$

for loss-only trials, with L the value of the high, risky loss and S the value of the sure loss.

These utility values are then entered in a softmax function to estimate the probability of accepting or choosing each gamble (coded as 1 if the gamble was chosen and 0 if the gamble was rejected or the sure option chosen):

$$P(gamble) = \frac{1}{1 + e^{-\mu \cdot u(gamble)}} \qquad \textbf{(Eq. 2-6)}$$

where μ is the logit sensitivity or "inverse temperature" parameter, an index of choice consistency for repeated identical gambles, equivalent to the maximal slope of a logistic regression curve: higher μ values indicate more consistent choices. Best-fitting parameters were estimated using a maximum likelihood estimation procedure in Matlab.

According to the literature, most people exhibit a λ parameter greater than 1, indicative of loss aversion, and ρ parameters lower than 1, indicative of risk aversion in the gain domains and risk seeking in the loss domain (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992; Fox and Poldrack, 2014). Whether ρ_{gain} and ρ_{loss} are different or can be estimated as a single parameter is unclear, as many studies failed to demonstrate a difference (for a review see Fox and Poldrack, 2014). In **Chapter 3** of this thesis, which is the only study where the gambling task included both gain-only and loss-only trials, allowing ρ_{gain} and ρ_{loss} to be estimated separately, there was no significant difference, and the model with a single ρ parameter performed better.

In summary, for **Chapter 3**, equations **2-3**, **2-4** and **2-5** were used to calculate gamble utility for mixed, gain-only, and loss-only trials, respectively, except that a single ρ parameter ($\rho_{gain} = \rho_{loss} = \rho$) was estimated. For **Chapter 4**, as well as pilot studies (section **2.5** below), given that the task contained only mixed gambles, only equation **2-3** was used to estimate λ, with the assumption that $\rho_{gain} = \rho_{loss} = 1$ (because the curvature of the utility function could not be estimated without the inclusion of at least some gain-only trials in the task). For **Chapter 5**, equations **2-3** and **2-4** were used given that the task included a combination of mixed and gain-only gambles, again with a single ρ parameter ($\rho_{gain} = \rho_{loss} = \rho$).

2.4.2 Model comparison: Bayesian Information Criterion (BIC)

In order to perform model comparison, BIC scores (Schwartz, 1978) were calculated for each model and each participant using the following equation:

$$BIC = -2 \cdot LL + k \cdot \ln(N) \qquad \textbf{(Eq. 2-7)}$$

where k represents the number of parameters in the model, N the number of trials used to estimate the parameters, and LL the loglikehood of the model calculated using the estimated best fit parameters. Comparing BICs is similar to a loglikelihood ratio test with the addition that the number of parameters in the model is taken into account and, therefore, models with more parameters are penalised.

BIC scores were then summed across participants before being compared between models. Lower BICs represent better model fits.

2.5 Development of the emotional priming procedure and loss aversion task

The face stimuli used as emotional primes throughout this thesis consisted of pictures from the NimStim Face Stimulus Set (http://www.macbrain.org/resources.htm). A set of 40 identities was chosen (20 male faces and 20 female faces), and each face stimulus was presented depicting either a neutral, happy, or fearful expression, resulting in a set of 120 face stimuli (primes). Surprised faces were also included in the pilot studies but were then discarded to reduce the task duration for the fMRI study (**Chapter 4**). For the object control condition, used in pilot study 2, Chapter 4 and Chapter 5, 20 pictures of light bulbs, obtained from the internet, were selected as a non-face control.

2.5.1 Pilot study 1: subliminal priming

In order to study the emotional modulation of loss aversion without the participant realising the goal of the study, the first pilot study used subliminal emotional primes as a procedure to manipulate emotions outside of the participants' awareness.

2.5.1.1 Methods

The design of an example trial is presented in **Figure 2-1**. Each trial of the task started with the presentation of a prime for 16.7ms (unknown to the participant), corresponding to the duration of one refresh of the screen for a refresh rate of 60 Hz. This was immediately followed by the presentation of a mask (scrambled face image) for 283ms. Participants were then presented with a mixed gamble and had to decide whether to accept or reject it (no time limit). There was a 1s fixation cross presented before the start of the next trial.

The primes belonged to one of the following 5 conditions: happy face, fearful face, surprised face, neutral face (no emotion control), scrambled image (no face control). For each face condition, the mask was a scrambled image of the face presented immediately before. When there was no prime, a scrambled image of a neutral face was presented for 300ms (combined duration of prime and mask). Images were all resized to 462 (width) x 588 (height) pixels. Scrambled images were created using

Matlab, dividing the original image into 33 x 42 squares of 14 x 14 pixels each, and then randomising the position of each square on the image.

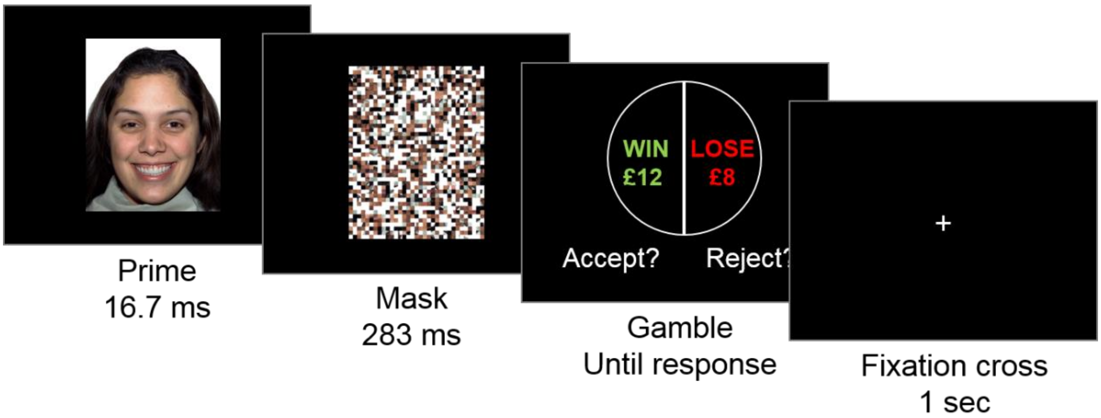


Figure 2-1. Task design – pilot study 1. Participants completed 450 trials of this task, with 90 trials for each of the following 5 emotion prime conditions: happy face, fearful face, neutral face, surprised face, and scrambled image like the mask. On each trial, the prime was presented subliminally for 16.7ms, immediately followed by a mask consisting of a scrambled image of the prime for 283ms. The gamble was then presented on the screen and participants had to press the left or right arrow button to indicate their choice to accept or reject the gamble.

Psychtoolbox (version 3; http://psychtoolbox.org/; Brainard, 1997; Kleiner et al., 2007) was used for visual presentation of stimuli. The reliability of timings was tested using a photodiode, which detected the presence of a white square shown at the top-left corner of the screen at the same time as the prime (the white square was only present during preliminary tests and was removed when participants performed the task). The current produced by the photodiode could then be recorded and analysed with precise temporal resolution, confirming that the stimuli were indeed on the screen for the duration of one refresh (16.7 ms).

Participants completed 90 trials per condition, randomly interspersed, leading to a total of 450 trials, presented in 3 blocks of 150 trials each with short breaks in between. Each set of 90 trials was constructed as follows: 81 gambles from all possible gain/loss pairs with gains ranging from £8 to £24 in £2 increments and losses ranging from -£6 to -£14 in £1 increments, as well as 9 catch trials with all possible gains and a “loss” of zero. Those catch trials were added to ensure participants paid attention to the task, as the obvious choice on these trials should be to accept the gamble.

Participants were not instructed about the presence of faces in the task. They were simply told that the aim of the task was to study their gambling behaviour. The presence of the scrambled image was explained as follows: *"A scrambled image, made of squares filled with different colours (see below, left picture), will appear quickly at the beginning of each trial. This is to indicate you that the trial is about to start and that you should get ready to evaluate the upcoming gamble and decide to accept or reject it as quickly as possible."*

After the task participants completed a short debriefing questionnaire designed to assess whether they noticed the presence of the primes and asking them to guess the purpose of the study. After that they completed a follow-up task. They were explained that on some trials of the first task, a face was flashed very quickly before the presentation of the scrambled image and had to complete a recognition task. Specifically, two faces were presented on each trial, one that was used as a prime in the first task and one that was novel, and they had to indicate which one they thought they saw during the first task. In addition, valence and arousal ratings were collected for all the faces. At the end of the study, participants completed mood questionnaires (BDI, STAI – see section **2.2** above).

2.5.1.2 Participants and payment

Thirty-five participants were recruited from the University College London subject pool to participate in the study. Two subjects had to be excluded because they made random choices and only accepted the gamble at chance level on catch trials; three additional subjects were excluded because they accepted the gamble on less than 3% of the trials, making their loss aversion impossible to estimate by the model. The final sample had 30 participants (13 males, 17 females, mean age = 26 years ± 7.40, age range: 19 to 52). The study was approved by the UCL departmental ethics committee and all subjects were paid for their participation in an incentive compatible manner. Specifically, they started the task with £20 and the average outcome of 10 randomly selected trials was added or removed to this initial endowment.

2.5.1.3 Results

Loss aversion (λ) was estimated using the Prospect Theory model described in section **2.4.1** above. Specifically, equation **2-3** was used to estimate λ, with the assumption that $\rho_{gain} = \rho_{loss} = 1$. When estimated across all trials independent of emotion condition, average loss aversion was 2.099 ± SD 0.60, significantly greater than 1 ($t(29)=10.03$, $P<0.001$). When estimated separately for each of the 5 emotion conditions and analysed in a repeated-measures ANOVA, there was no main effect of emotion condition on loss aversion ($F(4,116)=1.172$, $P=0.327$, for details see **Table 2-1** below). However, when trait anxiety scores were added in the ANOVA as a covariate, a significant emotion*trait anxiety interaction emerged ($F(4,112)=3.188$, $P=0.016$). To investigate which effects were driving the interaction, all pairwise differences in loss aversion between two emotion conditions were calculated and correlated with trait anxiety. This revealed that the interaction was primarily driven by a negative correlation between trait anxiety and the change in loss aversion from neutral to surprised faces ($r(30)=-0.544$, $P=0.002$) and a trend for a negative correlation between trait anxiety and the change in loss aversion from neutral to fearful faces ($r(30)=-0.310$, $P=0.095$), but no association between trait anxiety and the change in loss aversion from neutral to happy faces ($r(30)=-0.091$, $P=0.634$).

2.5.1.4 Limitations and changes for subsequent studies

Examining the recognition task data revealed that participants were not able to perform above chance in recognizing the faces that were used in the main task (mean performance = 50.09% ± SD 7.01), suggesting that primes were not consciously remembered. However, based on the debriefing questionnaires, six participants (20%) were able to correctly guess the purpose of the experiment; 14 participants (46.67%) spontaneously noticed the presence of faces flashed before the prime without being prompted for it, and an additional seven participants (21 participants total – 70%) reported the presence of a face when prompted about the content of something appearing before the scrambled image. Although the results were promising and participants were not able to identify the specific emotions associated with the faces, these answers from the debriefing questionnaires indicated that the priming procedure was not completely subliminal. For this reason, I decided to next pilot a version of the task where the primes were presented supraliminally, but with a cover story to avoid participants deducing the true goal of the experiment (demand characteristics; Orne, 2009).

Table 2-1. Emotional modulation of task variables and interaction with trait anxiety – pilot study 1.

	Happy	Fearful	Surpr.	Neutral	Scrbl.	One-way repeated-measures ANOVA	Interaction with trait anxiety
P_{accept}	0.361 (0.189)	0.350 (0.180)	0.356 (0.180)	0.357 (0.176)	0.350 (0.189)	$F(4,116)=0.86$ $P=0.49$	$F(4,112)=2.50$ $P=0.047$*
Loss aversion	2.077 (0.644)	2.121 (0.596)	2.087 (0.566)	2.091 (0.593)	2.125 (0.641)	$F(4,116)=1.17$ $P=0.33$	$F(4,112)=3.19$ $P=0.016$*
RT_{gamble} (s)	1.422 (0.613)	1.387 (0.543)	1.398 (0.553)	1.370 (0.560)	1.370 (0.532)	$F(4,116)=0.79$ $P=0.53$	$F(4,112)=0.58$ $P=0.68$

For each condition, means and standard deviations across participants are reported, for the following variables: probability to accept the gamble (P_{accept}), loss aversion parameter (λ), and reaction time to decide whether to accept or reject the gamble in seconds (RT_{gamble}). The main effect of condition and its interaction with trait anxiety were assessed and the corresponding statistics are reported in the last two columns. None of these variables were modulated by emotional condition. The emotional modulation of gamble acceptance and loss aversion (λ), but not of reaction times, varied according to trait anxiety. Surpr. stands for Surprise and Scrbl. for Scrambled.

2.5.2 Pilot study 2: supraliminal priming with cover story

In the next pilot study, the gambling task was embedded in a working memory task and participants were told that the aim of the study was to investigate how memory was affected by emotions.

2.5.2.1 Methods

All stimuli used in this pilot study, as well as in **Chapter 4** and **Chapter 5**, were resized to a resolution of 200 (width) x 300 (height) pixels and were displayed on a black background using Cogent 2000 (www.vislab.ucl.ac.uk/cogent.php) running under Matlab.

Participants started the study with a practice memory task (20 trials) where an array of 2, 4, or 6 faces or objects were presented on the screen for 3 seconds. All stimuli from a given array always pertained to the same condition: happy faces, fearful faces, surprised faces, neutral faces, or objects. The objects were pictures of light bulbs added as a non-face control instead of the scrambled images in pilot study 1. After a 1.5s fixation cross, one of the stimuli was shown in the centre of the screen surrounded by empty boxes at the 2, 4, or 6 locations from the original array, and participants had to click on the box where that stimuli was previously located in the array. Participants were then told that in order to make the memory task more challenging, they would have to perform a distracting gambling task while holding the stimuli in memory. They were then given a practice gambling task to complete. This practice gambling task contained 20 trials and corresponded to the start of a double staircase procedure. Specifically, the first 10 trials included 5 gambles with an EV of 10 (which are usually always accepted), and 5 gambles with an EV of -2 (which are usually always rejected). Gain and loss values were chosen at random within combinations of values that gave the desired expected value, with gains not exceeding £30 and losses not exceeding £15. If at least 3 gambles of a given EV (e.g. 10) were accepted, the EV for the following 5 trials was decreased by 1; while if at least 3 gambles out of 5 were rejected (e.g. in the case of an expected value of -2) then the EV was increased by 1.

During the main task, participants completed 180 trials with a similar double staircase procedure. The 180 trials were divided into 18 mini-blocks of 10 trials each; 5 trials with a "low" (subjective) expected value and 5 trials with a "high" (subjective) expected value, both determined by increasing or decreasing expected value depending on the choices from the previous mini-block. This time, the adjustments in EV were ±0.5 (instead of ±1 during the practice), which allowed more sensitivity in determining the indifference point. In addition, each of the 5 trials belonged to one of the 5 emotion conditions, and the adjustment in EV from one mini-block to the next was done separately for each emotion condition (rather than based on the average choice of the 5 trials as in the practice). In summary, participants completed 36 trials of each condition.

Each trial of the main task (**Figure 2-2**) started with the presentation of an array of 2, 4, or 6 stimuli for 3s (the size of the array was randomly determined at the beginning of each trial) that participants had to memorise. They were then presented with the mixed gamble and had to decide (with no time limit) whether to accept or reject it by clicking on the "Accept?" or "Reject?" box. Finally one stimulus from the array was shown on the centre of the screen and participants had to click on the box where the stimuli was originally located.

After the end of the task participants completed a rating task to rate all the face stimuli on valence and arousal, mood questionnaires (BDI, STAI) and a debriefing that assessed their perception of the goal of the study, their strategy on both the memory and the gambling parts of the task, and a final question asking whether they thought the emotional content of the faces may have impacted their gambling decisions.

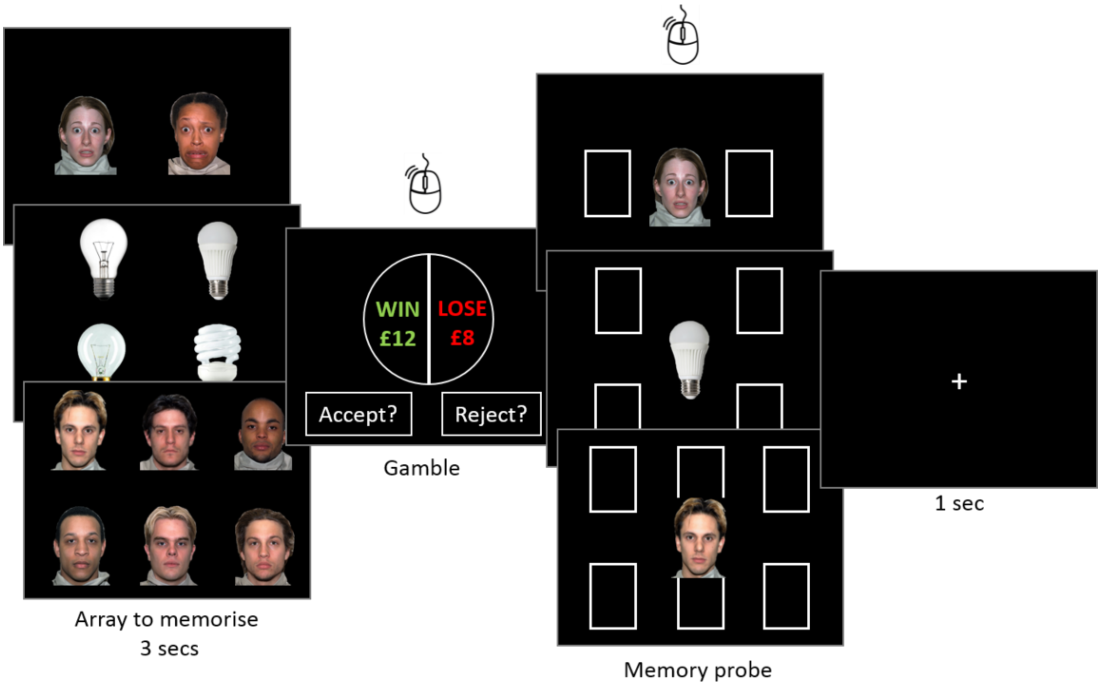


Figure 2-2. Task design – pilot study 2. Participants completed 180 trials of this task, with 36 trials for each of the following 5 emotion prime conditions: happy face, fearful face, neutral face, surprised face, and object (light bulb). On each trial, an array of 2, 4, or 6 primes, all pertaining to the same condition, was presented for 3s and subjects were instructed to memorise the location of each stimulus on the screen. The gamble was then presented and participants had to decide whether to accept or reject it. After making their choice, one of the stimuli presented in the initial array was shown at the centre of the screen and participants had to remember where it was located in the initial array. For both gambling and memory responses, participants used the mouse to click on the corresponding box (accept or reject for the gamble, location on the screen for the memory probe), and had no time limit to make those responses.

2.5.2.2 *Participants and payment*

Thirty-seven participants were recruited from the University College London subject pool to participate in the study. One subject was excluded because of past alcohol dependence and psychotic symptoms; one because of high BDI score of 31 and borderline past depressive episode. One subject's data was lost because of a Matlab error. Two additional subjects had to be excluded because of very inconsistent choices in the gambling task, making their loss aversion parameter impossible to reliably estimate (and reflected in low values for the consistency parameter μ: 0.084 and 0.00012). The final sample consisted of 32 participants (14 males, 18 females, mean age = 25.41 years ±9.19, age range: 18 to 57). The study was approved by the UCL departmental ethics committee and all subjects were paid for their participation in an incentive compatible manner. Specifically, they started the task with £15 and the average outcome of 10 randomly selected trials was added or removed to this initial endowment.

2.5.2.3 *Results*

Analyses were conducted similarly to pilot study 1 (see section **2.5.1** above). Average loss aversion, estimated across all trials, was 2.024 ± SD 1.11, significantly greater than 1 ($t(31)=5.218$, $P<0.001$), and very close to the mean loss aversion estimate from pilot study 1. There was also no difference in loss aversion between the five emotion conditions (one-way repeated-measures ANOVA: $F(4,124)=0.796$, $P=0.530$; for details see **Table 2-2** below). However, when trait anxiety scores were added in the ANOVA as a covariate, a significant emotion*trait anxiety interaction emerged ($F(4,120)=2.945$, $P=0.023$), consistent with pilot study 1. Examining correlations between trait anxiety scores and pairwise differences in loss aversion, the interaction was primarily driven by a negative correlation between trait anxiety and the change in loss aversion from neutral to fearful faces ($r(32)=-0.381$, $P=0.031$), which did not achieve significance in pilot study 1. The correlation between trait anxiety and the change in loss aversion from neutral to surprised faces was also negative, but not significant ($r(32)=-0.277$, $P=0.12$). Similar to pilot study 1, trait anxiety was not associated with differences in loss aversion between neutral and happy faces ($r(32)=-0.100$, $P=0.587$).

Table 2-2. Emotional modulation of task variables and interaction with trait anxiety – pilot study 2.

	Happy	Fearful	Surprise	Neutral	Object	One-way repeated-measures ANOVA	Interaction with trait anxiety
P_{accept}	0.547 (0.176)	0.556 (0.157)	0.545 (0.169)	0.545 (0.171)	0.556 (0.159)	$F(4,124)=0.24$ $P=0.91$	$F(4,120)=2.88$ $P=0.026$*
λ (loss aversion)	1.992 (1.092)	2.020 (1.107)	2.053 (1.117)	2.048 (1.224)	1.994 (1.074)	$F(4,124)=0.80$ $P=0.53$	$F(4,120)=2.95$ $P=0.023$*
RT_{gamble} (s)	1.987 (0.736)	1.983 (0.820)	1.998 (0.706)	1.954 (0.685)	1.958 (0.630)	$F(4,124)=0.18$ $P=0.95$	$F(4,120)=0.07$ $P=0.99$
WM accuracy	0.642 (0.130)	0.624 (0.126)	0.610 (0.139)	0.642 (0.133)	0.608 (0.136)	$F(4,124)=1.39$ $P=0.24$	$F(4,120)=0.14$ $P=0.97$

For each condition, means and standard deviations across participants are reported, for the following variables: probability to accept the gamble (P_{accept}), loss aversion parameter (λ), reaction time to decide whether to accept or reject the gamble in seconds (RT_{gamble}), and working memory (WM) accuracy collapsed across the 3 difficulty levels. The main effect of condition and its interaction with trait anxiety were assessed and the corresponding statistics are reported in the last two columns. None of these variables were modulated by emotional condition. The emotional modulation of gamble acceptance and loss aversion (λ), but not of reaction times or working memory accuracy, varied according to trait anxiety.

2.5.2.4 Conclusions, limitations, and changes for subsequent studies

No participant guessed the actual goal of the study when asked in the debriefing, suggesting that this new design was better adapted to account for demand characteristics than the subliminal priming procedure. In addition, the memory task has the advantage to ensure that participants are paying attention and actually encoding the prime stimuli.

However, this second design still suffered from a few limitations that needed to be addressed. First, the fact that the staircase procedure was implemented throughout the entire task meant that participants could potentially learn to "play" the staircase and make the gamble EV increase over time, thus maximising their outcome and moving away from their real indifference point. Moreover, because the adjustment in EV from one mini-block to the next was allowed to vary separately for each emotion condition, the final set of gambles on which analyses were run may have been different for each emotion condition, making them harder to compare. To address this issue, I decided for studies presented in Chapters 4 and 5 to have a longer practice gambling task running through the entire staircase, allowing to estimate the participant's indifference point right after the practice session. I was then able to build a gamble set for the main task centred on this indifference point and repeated identically for each emotion condition.

Second, people did not perform very well in the 6-stimulus memory task. Even though most participants performed above chance (average memory accuracy for 6 stimuli: 0.381 ±0.123; 4 stimuli: 0.605 ±0.155, 2 stimuli: 0.919 ±0.0897), they reported in the debriefing finding it difficult to encode 6 stimuli in such a short time, especially with the interference of the gambling task. In addition, when adapting this task for the fMRI (**Chapter 4**), the inclusion of jitters between the different onsets increased the duration of the period between encoding and retrieval from 1.5s to 10s, thus making the memory task more challenging because of this extra delay. Therefore, the 6-stimulus condition was dropped for subsequent versions of this task.

Finally, because of timing considerations in the scanner, and because fearful and surprised face seemed to have a very similar effect in both pilot studies, the surprise condition was also dropped for subsequent versions of the task in order to focus on the comparison between the effects of a positive emotion (happy faces), a negative emotion (fearful faces), no emotion control (neutral faces) and no emotion-no face control (objects).

In conclusion, these pilot studies allowed the development of an emotional priming procedure that was (i) not subject to the technical limitations of subliminal priming, and (ii) embedded in a cover story to effectively conceal the real goal of the experiment and prevent demand characteristics. In addition, they helped to optimise the determination of gain/loss matrices for the gambling task: using a staircase to target each participants' indifference point then building a matrix centred on that indifference point. Such a design improved sensitivity whilst minimizing the total number of trials and duration of the task to use in the scanner (**Chapter 4**) and with a patient population (**Chapter 5**).

Chapter 3 How feelings predict economic choice: models of affective decision-making

3.1 Abstract

Intuitively, how we feel about potential outcomes will determine our decisions. Indeed, one of the most influential theories in psychology, Prospect Theory, implicitly assumes that feelings govern choice. Surprisingly, however, very little is known about the rules by which feelings are transformed into decisions. Here, we characterize a computational model that uses feelings to predict choice, and reveal that this model predicts choice better than existing value-based models, showing a unique contribution of feelings to decisions, over and above value. Similar to Prospect Theory value function, feelings showed diminished sensitivity to outcomes as value increased. However, loss aversion in choice was explained by an asymmetry in how feelings about losses and gains were weighted when making a decision, not by an asymmetry in the feelings themselves. The results provide new insights into how feelings are utilized to reach a decision.

3.2 Introduction

How would you feel if you won an award for outstanding professional achievement? How would you feel if your marriage broke apart? Intuitively, answers to these questions are important, as they should predict your actions. If the prospect of losing your spouse does not fill you with negative feelings you may not attempt to keep the unit intact. But how exactly do feelings associated with possible outcomes relate to actual choices? What are the computational rules by which feelings are transformed into decisions? While an expanding body of literature has been dedicated to answering the reverse question, namely how decision outcomes affect feelings (Mellers et al., 1997; Kermer et al., 2006; McGraw et al., 2010; Kassam et al., 2011; Carter and McBride, 2013; Rutledge et al., 2014; Yechiam et al., 2014), little is known of how feelings drive decisions about potential outcomes.

Here, we examine whether feelings predict choice and build a computational model that characterizes this relationship. We turn to Prospect Theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) as a starting point in this research. The assumptions of Prospect Theory (see section **1.2.4** in general introduction for details) suggest that if we measure a person's feelings associated with different outcomes, we should be able to generate that person's utility function and use it to predict their choices. While Prospect Theory is one of the most influential theories in economics and psychology, this implicit assumption has never been empirically tested. Thus, if and how feelings guide choice is still unknown.

To address this question, in three separate studies, participants reported how they felt, or expected to feel, after winning or losing different amounts of money. Those self-reported feelings were used to form a "feeling function"; a function that best relates feelings (expected and/or experienced) to objective value. Next, this function was used to predict participants' choices in a different decision-making task. The findings were replicated in all three studies.

An intriguing question is what such a "feeling function" would look like. One possibility is that it resembles Prospect Theory's value function, which relates the subjective value estimated from choice data to objective value. First, for most people, the value function is steeper for losses in comparison to gains, resulting in loss aversion (Kahneman and Tversky, 1979; Kahneman et al., 1991; Tversky and Kahneman, 1991). Yet whether the impact of a loss on feelings is greater than the impact of an equivalent gain is still unknown. Alternatively, it is possible that the impact of gains and losses on feelings is similar, but that the weight given to those feelings differs when making a choice. Second, we examined whether, similar to Prospect Theory's value function, the "feeling function" was also concave for gains and convex for losses, implying that feelings associated with gains and losses would become less sensitive to outcome value as gains and losses increase. That is, the impact of winning (or losing) ten dollars on feelings is less than twice the impact of winning (or losing) five dollars.

Once feelings were modelled using this "feeling function" the next aim was to examine whether they can predict choice. There were two main complementary hypotheses about the shape of the "feeling function" and its relation to choice behaviour. The first hypothesis was that feelings would be related to value with the same properties as Prospect Theory's value function: stronger impact of losses than gains on feelings, and diminishing impact of value on feelings as value increases. In turn such "feeling function" would predict choice at least as well as Prospect Theory's value function, if not better. The second hypothesis was that if feelings do not relate to value with the properties described above, by being symmetrical for gains and losses and/or by varying linearly with value, then choice behaviour may be best explained by how these feelings are weighted and combined during the choice process, rather than by how potential outcome value influences feelings in the first place.

3.3 Materials and methods

3.3.1 Participants

Fifty-nine healthy volunteers (24 males, mean age 23.94y, age range 19-35y) were recruited to take part in the experiment via the UCL Subject Pool. Sample size was determined using a power analysis (G*power version 3.1.9.2; Faul et al., 2007), based on previous studies that have investigated the link between decision outcomes and self-report feelings using within-subjects designs. Effect sizes (Cohen's d) in those studies ranged from .245 to .798, with a mean at .401 (Kermer et al., 2006; Harinck et al., 2007; Yechiam et al., 2014). A sample size of 59 subjects would achieve 85% power of detecting an effect size of .401 with an alpha of 0.05. Three subjects were excluded: one who showed no variation at all in their feelings ratings, one whose data from the gambling task were lost, and one who missed more than 50% of the trials in the gambling task. Final analyses were run on 56 subjects (22 males, mean age 23.91y, age range 19-35y). All participants gave written informed consent and were paid for their participation. The study was approved by the departmental ethics committee at UCL.

3.3.2 Behavioural tasks

Participants completed two tasks, the order of which was counterbalanced.

1. Feelings Task. In the feelings task, subjects completed 4 blocks of 40 to 48 trials each, in which they reported either expected (**Figure 3-1A**) or experienced (**Figure 3-1B**) feelings associated with a range of wins and losses (between £0.2 and £12), or no change in monetary amount (£0). At the beginning of each trial participants were told how much was at stake and whether it was a win trial (e.g., if you choose the "good" picture, you will win £10) or a loss trial (e.g., if you choose the "bad" picture, you will lose £10). Their task was then to make a simple arbitrary choice between two geometrical shapes, associated with a 50% chance of winning versus not winning (on win trials) or of losing versus not losing (on loss trials). On each trial participants were told that one novel stimulus was randomly associated with a gain or loss (between £0.2 and £12) and the other novel stimulus with no gain and no loss (£0). Each stimulus was presented once so learning was not possible. There was no way for the participants to know which abstract stimulus was associated with a better outcome. The probability of sampling each amount was controlled to ensure that each gain and each loss from the range was sampled twice in each block: on one instance the outcome was the amount at stake (win/loss) and on the other one the outcome was £0 (no win/no loss). Participants reported their feelings by answering the questions "How do you feel now?" (experienced feelings, after a choice) or "How will you feel if you win/lose/don't win/don't lose?" (expected feelings, before a choice), using a subjective rating scale ranging from "Extremely unhappy" to "Extremely happy". In two of the four blocks (counterbalanced order) they reported their expected feelings (**Figure 3-1A**), and in the other two blocks, they reported their experienced feelings (**Figure 3-1B**). Expected and experienced feelings were collected in different blocks to avoid subjects simply remembering and repeating the same rating. The choice between the two geometrical shapes was simply instrumental and implemented in order to have subjects actively involved with the outcomes. This instrumental choice also allowed manipulating agency: on two of the blocks (one with expected feelings and one with experienced feelings) the participant made the choice between the two stimuli, and in the other two blocks the computer made the choice for the participant who had to indicate the computer choice with a button press after it was made. There were no differences in the data between own choice and computer choice blocks, therefore data was collapsed. Even when making their own choices subjects had no control over the outcome, thus it may not be surprising that feelings did not differ between own choice

and computer choice. Note, that the above relates only to the task eliciting feelings associated with outcomes and not, obviously, to the gambling task.

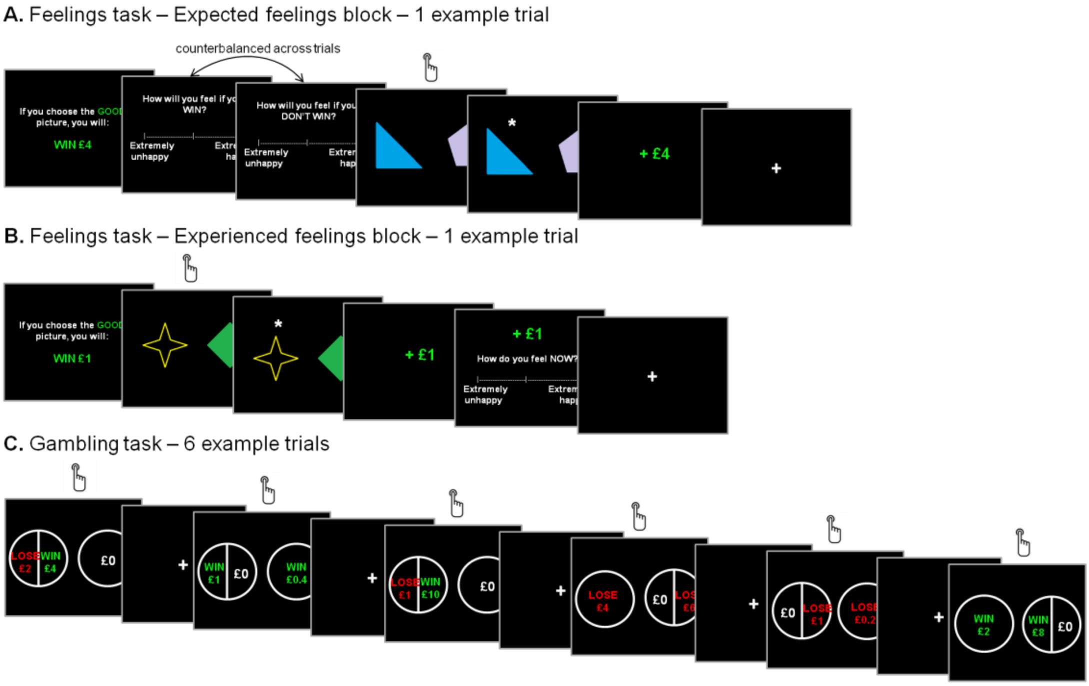


Figure 3-1. Experimental design. Participants completed two tasks in a counterbalanced order (**A,B**): a feelings task where they reported (in different blocks) expected (**A**) or experienced (**B**) feelings associated with winning, losing, not winning or not losing a range of monetary amounts; and (**C**) a gambling task where they selected between a sure option and a gamble involving the same amounts as those used in the feelings task. Feelings were modeled as a function of value and this resulting feelings function F was used to predict choice in the gambling task. For each trial, feelings associated with the sure option, the risky gain, and the risky loss were extracted and entered in a cross-trials within-subject logistic regression model.

<u>2. Gambling Task.</u> Participants completed a probabilistic choice task (**Figure 3-1C**) in which they made 288-322 choices between a risky 50/50 gamble and a sure option. Importantly, all the amounts used in the gambling task were the same as those used in the feelings task (between £0.2 and £12), such that feelings associated with these outcomes could be combined to predict gamble choice. There were 3 gamble types: mixed (subjects had to choose between a gamble with 50% chance of a gain and 50% of a loss, or sure option of £0), gain-only (subjects had to choose between a gamble with 50% chance of a high gain and 50% chance of £0, or a sure, smaller, gain) and loss-only (subjects had to choose between a gamble with 50% chance of a high loss and 50% chance of £0, or a sure, smaller, loss). In Prospect Theory, these 3 types of

choices are essential to estimate loss aversion, risk preference for gains, and risk preference for losses, respectively.

3.3.3 Study groups

Participants were recruited in two different groups that were then collapsed in the analyses. A group of 29 participants (20 females, mean age=23.2y) was tested on a first version of the task, where each of the four blocks had 48 trials with 12 different amounts (£0.2, £0.4, £0.6, £0.8, £1, £1.2, £2, £4, £6, £8, £10, £12) that could be won, lost, not won or not lost. For expected feelings participants were asked "how will you feel if you win/lose?"; and for experienced feelings "how do you feel now?". The rating scale ranged from 1 (extremely unhappy) to 10 (extremely happy) and participants had to press a key (1 to 9 for ratings 1 to 9 and 0 for rating 10) to indicate their feelings. A second group of 30 participants (15 females, mean age=24.5y) completed a slightly shorter version of the feelings task that had 40 trials per block (10 amounts instead of 12: £0.2, £0.5, £0.7, £1, £1.2, £2, £5, £7, £10, £12) and indicated their ratings by moving a cursor on a symmetrical rating scale, in which 0 was used as a reference point. Specifically, for expected feelings they were asked "if 0 is how you feel now, how will you feel if you win/lose?"; and for experienced feelings "if 0 is how you felt just before the choice, how do you feel now?". Ratings ranged from -5 (extremely less happy) to +5 (extremely more happy). The first group of participants completed the feelings task first, while the second group completed the gambling task first. The results (parameters and model fits from the feelings function models, and from the regression models to predict choice) did not differ between the two study groups, indicating that those features of the design that varied between the two groups were not a significant factor. Data were therefore collapsed for all the analyses reported in the main text, and study group was controlled for by adding a dummy variable as a between-subject factor in all the analyses.

3.3.4 Feelings function models

3.3.4.1 Description of models

The impact of outcome on feelings was calculated relative to three different baselines: difference from the mid-point of the rating scale, difference from rating reported on the previous trial (for experienced feelings only), difference from corresponding zero outcome. These were calculated for each win and loss amount, for expected and experienced feelings separately. For each subject, for each of the above methods, feelings function models were then fit (ten for expected feelings and ten for experienced feelings) to explain how feelings best relate to value outcomes:

Feeling Model 1: $$F(x) = \boldsymbol{\beta} x$$

Feeling Model 2: $$F(x) = \begin{cases} \boldsymbol{\beta_{gain}} x, & x > 0 \\ \boldsymbol{\beta_{loss}} x, & x < 0 \end{cases}$$

Feeling Model 3: $$F(x) = \begin{cases} \boldsymbol{\beta}(|x|)^{\boldsymbol{\gamma}}, & x > 0 \\ -\boldsymbol{\beta}(|x|)^{\boldsymbol{\gamma}}, & x < 0 \end{cases}$$

Feeling Model 4: $$F(x) = \begin{cases} \boldsymbol{\beta_{gain}}(|x|)^{\boldsymbol{\gamma}}, & x > 0 \\ -\boldsymbol{\beta_{loss}}(|x|)^{\boldsymbol{\gamma}}, & x < 0 \end{cases}$$

Feeling Model 5: $$F(x) = \begin{cases} \boldsymbol{\beta}(|x|)^{\boldsymbol{\gamma_{gain}}}, & x > 0 \\ -\boldsymbol{\beta}(|x|)^{\boldsymbol{\gamma_{loss}}}, & x < 0 \end{cases}$$

Feeling Model 6: $$F(x) = \begin{cases} \boldsymbol{\beta_{gain}}(|x|)^{\boldsymbol{\gamma_{gain}}}, & x > 0 \\ -\boldsymbol{\beta_{loss}}(|x|)^{\boldsymbol{\gamma_{loss}}}, & x < 0 \end{cases}$$

Feeling Model 7: $$F(x) = \begin{cases} \boldsymbol{\beta} x + \boldsymbol{\varepsilon}, & x > 0 \\ \boldsymbol{\beta} x - \boldsymbol{\varepsilon}, & x < 0 \end{cases}$$

Feeling Model 8: $$F(x) = \begin{cases} \boldsymbol{\beta_{gain}} x + \boldsymbol{\varepsilon}, & x > 0 \\ \boldsymbol{\beta_{loss}} x - \boldsymbol{\varepsilon}, & x < 0 \end{cases}$$

Feeling Model 9: $$F(x) = \begin{cases} \boldsymbol{\beta} x + \boldsymbol{\varepsilon_{gain}}, & x > 0 \\ \boldsymbol{\beta} x - \boldsymbol{\varepsilon_{loss}}, & x < 0 \end{cases}$$

Feeling Model 10: $$F(x) = \begin{cases} \boldsymbol{\beta_{gain}} x + \boldsymbol{\varepsilon_{gain}}, & x > 0 \\ \boldsymbol{\beta_{loss}} x - \boldsymbol{\varepsilon_{loss}}, & x < 0 \end{cases}$$

In all these models, x represents the value (from -12 to -0.2 for losses and from 0.2 to 12 for gains) and F the associated feeling. The slope between feelings and values is represented by the parameter $\boldsymbol{\beta}$ estimated as a single parameter in all odd-numbered models, or separately for losses and gains in all even-numbered models. If loss aversion is reflected in feelings, $\boldsymbol{\beta_{loss}}$ should be significantly greater than $\boldsymbol{\beta_{gain}}$ and even-numbered models should perform better overall. Similar to the curvature parameter of Prospect Theory value function, $\boldsymbol{\gamma}$ reflects the curvature of the feeling function, i.e. the fact that feelings become more or less sensitive to changes in value as absolute value increases (Feeling Models 3 to 6). In Feeling Models 5 and 6, the curvature is estimated separately in the gain and loss domains. If the "feeling function" is S-shaped (function concave for gains and convex for losses) $\boldsymbol{\gamma}$ values should be significantly smaller than 1. To ensure that a function with curvature fit the feelings data better than a simple linear function with an intercept, Feeling Models 7 to 10 were defined (as respective comparisons for Feeling Models 3 to 6), where $\boldsymbol{\varepsilon}$ represents the intercept, or the offset (positive for gains, negative for losses) where feelings start for values close to £0.

3.3.4.2 Model estimation

All these models were estimated in Matlab (www.mathworks.com) using a maximum-likelihood estimation procedure (Myung, 2003). Given a Feeling Model $f(x, \theta)$ with θ the set of parameters, x the range of outcome values, and y the feelings data to be modelled, the residuals from the model can be written as:

$$\mathcal{E} = y - f(x, \theta) \qquad \textbf{(Eq. 3-1)}$$

Assuming an appropriate normal distribution for the residuals, the likelihood of a given residual $\mathcal{E}_i$ is:

$$\mathcal{L}(\mathcal{E}_i|\theta, \sigma) = \frac{e^{\frac{-\mathcal{E}_i^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \qquad \textbf{(Eq. 3-2)}$$

where σ represents the standard deviation of the residuals (an additional parameter to be estimated). Then the *fmincon* function was used to find the optimal set of parameters (θ, σ) that minimizes the negative log likelihood (thereby maximizing the likelihood):

$$-\log \mathcal{L} = -\log[\mathcal{L}(\mathcal{E}|\theta,\sigma)] = \sum_i \left[\frac{\mathcal{E}_i^2}{2\sigma^2} + 0.5\log(2\pi\sigma^2)\right] \qquad \textbf{(Eq. 3-3)}$$

BIC scores were then calculated for each subject using the following equation that penalizes additional parameters in the model:

$$BIC = -2\log\hat{\mathcal{L}} + k\log(n) \qquad \textbf{(Eq. 3-4)}$$

where $\log\hat{\mathcal{L}}$ represents the maximum of loglikelihood $\mathcal{L}$ (estimated using equation **3-3** above), k the number of parameters in the model (including σ as an extra parameter), and n the number of data points (trials) that were fitted. BIC scores were calculated for each subject and model, and then summed across subjects. Lower sum of BICs for a given model compared to another indicates better model fit.

3.3.5 Prediction of gambling choice

3.3.5.1 Estimation of logistic regression models

Feeling values from Feeling Model 3 (found to be the most parsimonious model overall) were then used to predict choices in the gambling task. Specifically, for each participant, the feeling associated with each amount was calculated using Feeling Model 3 with that participant's estimated parameters ($\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$). Thus, for each trial of the gambling task, a feelings value was obtained for the sure option, the gain and the loss presented on that trial. A feelings value of 0 was used when the amount in the gamble trial was £0. The probability of choosing the gamble on each trial, coded as 1 if the gamble was chosen and 0 if the sure option was chosen, was then entered as the dependent variable of a logistic regression (Choice Model), with feelings associated with the sure option (S, coded negatively in order to obtain a positive weight), the gain (G, multiplied by its probability 0.5), and the loss (L, multiplied by its probability 0.5) entered as the 3 predictor variables:

$$P(gamble) = \frac{1}{1 + e^{-[\boldsymbol{\omega_S} F(S) + \boldsymbol{\omega_G} F(G) + \boldsymbol{\omega_L} F(L)]}}$$

Logistic regressions were run on Matlab using the *glmfit* function, using either expected feelings (Choice Model 1) or experienced feelings (Choice Model 2). To determine whether those modelled feelings predicted choice better than value-based models, 5 other comparisons models were used to predict choice from values (Choice Models 3 to 7; see section **3.3.5.3** below for details).

In order to be compared across conditions and subjects, weight values ω were standardized using the following equation (Menard, 2004; Schielzeth, 2010):

$$\omega'_x = \omega_x \times \frac{s_x}{s_y}$$

where ω'_x is the standardized weight value, ω_x the original weight for predictor variable x obtained from the regression, s_x the standard deviation of variable x, and s_y the standard deviation of the dependent variable y, here the binary choice values. Standardized weight values were extracted from each regression and compared using repeated-measures ANOVA and paired t-tests.

3.3.5.2 Loss and risk aversion modelling

Loss and risk aversion were estimated for each subject using choice data from the gambling task and based on Prospect Theory equations (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992; Sokol-Hessner et al., 2009; Fox and Poldrack, 2014). The model was estimated as explained in **Chapter 2** (section **2.4.1**) using equations **2-3** to **2-6**, resulting in a loss aversion parameter λ for each subject, as well as estimates of risk preference ρ and logit sensitivity μ.

In particular, the model was used to estimate risk and loss aversion on half the choice data, and to predict choice from subjective utility on the other half of choice data (see section **3.3.5.3** below).

To predict individual differences in loss aversion from feelings, λ values were extracted for each subject on the entire set of gambling choices. They were then log-transformed [ln(λ+1)] to ensure positive values and normal distributions, and correlated across subjects with the difference in how feelings about losses and feelings about gains are weighted during choice (**Figure 3-8**).

3.3.5.3 Comparison models

Choices were predicted from feelings using the previously built feelings function (Choice Models 1 and 2). In order to examine whether this feelings function does a better job at predicting choice than objective value, or choice-derived subjective utility, five other models were tested (Choice Models 3 to 7).

First a simple "Value" model (Choice Model 3) tried to predict choice simply by entering the amounts available multiplied by probability, regardless of associated feelings parameters β and γ or subjective utility parameters such as loss and risk aversion. For example, if the choice is a mixed gamble between winning £10 and losing £6, the three predictors will be £0*1 (sure option), £10*0.5 (gain), and -£6*0.5 (loss).

The second comparison model included log(Value) as predictors (Choice Model 4). Most standard economic models account for the curvature of the utility function by taking the logarithm of linear values. In this model and with the example above, the three predictors would be computed as: 0 (sure option), log(10)*0.5 (gain), and -log(6)*0.5 (loss).

The three additional models predicted choice from Prospect Theory-derived subjective utility. To do so, risk and loss aversion parameters were estimated on half the choice data using the model described above (section **2.4.1** and equations **2-3** to **2-6**) for each subject. One model included value weighted with the loss aversion parameter $\boldsymbol{\lambda}$ ($£0 \times 1$, $£10 \times 0.5$, $-\boldsymbol{\lambda} \times £6 \times 0.5$; Choice Model 5); one included value parameterized with the risk attitude parameter $\boldsymbol{\rho}$ ($£0 \times 1$, $(£10)^{\boldsymbol{\rho}} \times 0.5$, $-(£6)^{\boldsymbol{\rho}} \times 0.5$; Choice Model 6); and the last model included both parameters to compute subjective values ($£0 \times 1$, $(£10)^{\boldsymbol{\rho}} \times 0.5$, $-\boldsymbol{\lambda} \times (£6)^{\boldsymbol{\rho}} \times 0.5$; Choice Model 7).

All seven logistic regression choice models were run on the other half of the choice data, in order to be comparable and to avoid circularity for the utility-based models. The gambling task was designed such that each gamble was repeated twice; therefore, one occurrence of each gamble was present in each half of the data. In addition, in order to ensure the reliability of this split-half analysis, 100 iterations were run with a different data splitting on every iteration. The loglikelihood of each model was extracted from the logistic regression and BIC scores were calculated for each subject (see Model comparison section **2.4.2**). The sum of BIC scores across subjects was then calculated for each model and each iteration, in order to report the number of simulations where the two feelings model performed better than the five comparison models.

3.3.6 Replication and extension studies

Two separate studies were conducted to replicate the findings and extend them to cases where the impact of a loss and a gain on feelings is evaluated (i) within the same trial (see Replication and extension study 1, section **3.4.7**) and (ii) on the same unipolar rating scale (see Replication and extension study 2, section **3.4.8**).

3.4 Results

The analysis followed two main steps. First participants' reported feelings associated with different monetary outcomes were used to build a "feeling function". Specifically, we found the best fitting computational model to characterize how feelings associated with different amounts of gains and losses relate to the objective value of these amounts. Second, we tested whether that model of feelings predicted participants' choices on a separate task.

3.4.1 Characterizing a "feeling function"

The first aim was to characterize a model that best fit feelings to outcome value. To that end, for each subject ten models (see **section 3.3.4** above for equations and details) were run to fit data of expected feelings to outcome value and ten equivalent models to fit experienced feelings to outcome value. The models differed from each other in two ways: with respects to their slope parameter (β) and to their curvature parameter (γ). If models with one β parameter fit better than models with two (one for gains (β_{gain}) and one for losses (β_{loss})) that would indicate that gains and losses do not affect feelings to different extents. If two β fit better that would indicate a difference in the magnitude of influence. If models with a curvature (γ) fit better than linear models with an intercept (ε) that would suggest that the sensitivity of feelings varies as outcomes increase, such that the feeling of winning/losing £10 is more or less intense than twice the feeling of winning/losing £5. BIC values, which penalise for additional parameters, showed that the best fitting model (i.e. the lowest BIC value) for both expected (**Figure 3-2A**) and experienced (**Figure 3-2B**) feelings was Feeling Model 3 (see **Table 3-1** for BIC and R^2 values), which has one γ and one β:

$$F(x) = \begin{cases} \boldsymbol{\beta}(|x|)^{\gamma}, \ x > 0 \\ -\boldsymbol{\beta}(|x|)^{\gamma}, \ x < 0 \end{cases}$$

where x is the gain/loss amount (positive for gains and negative for losses) and F the corresponding feeling.

This suggests that:

(i) feelings' sensitivity to outcomes gradually decreased as outcomes increased. Similar to Prospect Theory's value function, γ was significantly smaller than 1 (expected feelings: γ=0.512 ± SD 0.26, t(55)=-14.05, P<0.001, Cohen's d=1.88, 95% CI=[0.418;0.558]; experienced feelings: γ=0.425 ± SD 0.23, t(55)=-18.52, P<0.001, Cohen's d=2.5, 95% CI=[0.513;0.637]), indicating that the "feeling function" was concave in the gain domain and convex in the loss domain. Graphically, **Figure 3-3** shows that the magnitude of feelings associated with £10 for example was less than twice the magnitude of feelings associated with £5.

(ii) neither sensitivity (β) nor curvature (γ) differed between gains and losses. Equal sensitivity suggests that when feelings associated with losses and gains are evaluated separately their impact is symmetrical, such that losses are not experienced more intensely than gains. On the surface, these findings contradict the notion of "loss aversion" as proposed by Prospect Theory (Kahneman and Tversky, 1979; Kahneman et al., 1991; Tversky and Kahneman, 1991, 1992). However, what will be showed later is that while here losses do not necessarily impact feelings more than gains they are weighted to a greater extent when making a choice (see **section 3.4.6** below). With regards to curvature, a single γ was more parsimonious than two separate ones for gains and losses, suggesting that the extent of concavity for gains was equivalent to the extent of convexity for losses.

Further support for point (i) came from the fact that all models with a curvature parameter γ (Feeling Models 3-6) were better fits, as indicated by lower BIC values, than corresponding linear models with an intercept (Feeling Models 7-10). This was true both when comparing BICs for models fitting expected feelings (BIC difference < -112) and experienced feelings (BIC difference < -37) (**Table 3-1**). Further support for point (ii) came from the fact that Feeling Model 3 had lower BICs than other curved functions with additional parameters that fit gains and losses with separate parameters

(Feeling Models 4-6, see **Table 3-2**) for both expected and experienced feelings. In addition, the absolute impact of losses and gains on ratings of feelings relative to a zero outcome revealed no difference ($F(1,55)=0.01$, $P=0.92$, $\eta_p^2=0.00018$).

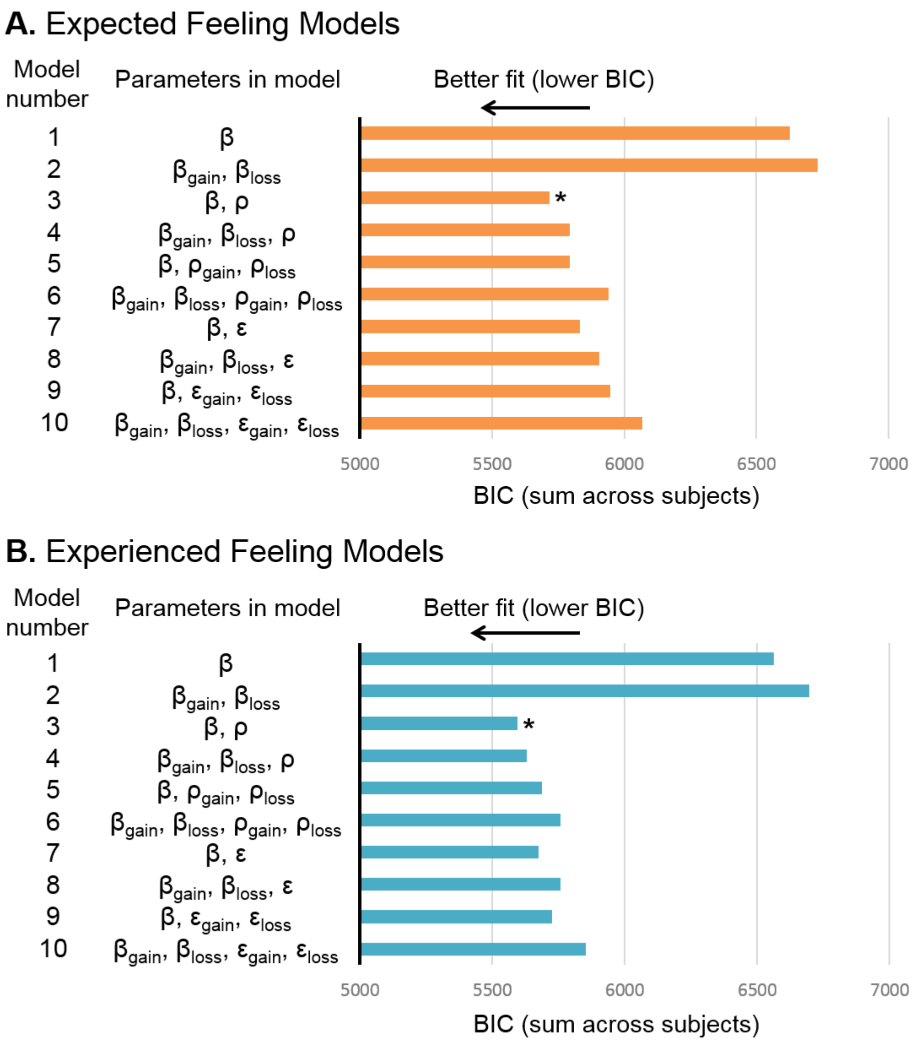


Figure 3-2. Feeling Models. BIC values, summed across all subjects, are plotted for the ten models fitting feelings to outcome value (see **section 3.3.4.1** above for equations), separately for (**A**) Expected feelings ratings and (**B**) Experienced feelings ratings. Feeling Model 3 was the most parsimonious model, as indicated by lower BIC values for both expected and experienced feelings.

Table 3-1. Feeling Models

Model #	Number of parameters	Name of parameters	Expected feelings		Experienced feelings	
			Sum of BICs	Mean R^2	Sum of BICs	Mean R^2
1	1	β	6625.7	0.720	6561.1	0.637
2	2	β_{gain}, β_{loss}	6731.5	0.731	6695.0	0.648
3	2	β, γ	**5716.1**	0.804	**5594.0**	0.744
4	3	β_{gain}, β_{loss}, γ	5792.2	0.814	5628.4	0.758
5	3	β, γ_{gain}, γ_{loss}	5793.4	0.814	5685.6	0.753
6	4	β_{gain}, β_{loss}, γ_{gain}, γ_{loss}	5938.8	0.819	5758.4	0.764
7	2	β, ε	5833.3	0.800	5674.7	0.742
8	3	β_{gain}, β_{loss}, ε	5905.1	0.811	5757.2	0.752
9	3	β, ε_{gain}, ε_{loss}	5947.7	0.808	5723.9	0.755
10	4	β_{gain}, β_{loss}, ε_{gain}, ε_{loss}	6069.4	0.814	5851.3	0.761

Ten different models were fit to the feelings data in order to best explain its relationship to amount lost and gained (see **section 3.3.4.1** above for exact equations). All models were run separately on expected and experienced feelings. BIC scores were summed across subjects and R^2 values averaged across subjects. Smaller BIC values and higher R^2 values are indicative of better model fit. Note that BIC values cannot be directly compared between expected and experienced feelings models because the numerical values of the dependent variables are different. R^2 alone cannot be used to determine the best fitting model as it does not account for the number of parameters.

Table 3-2. Comparison between Feeling Model 3 and Feelings Models 4 to 6

	Expected feelings		Experienced feelings	
	Number of subjects (/56)	BIC difference	Number of subjects (/56)	BIC difference
Model 3 > Model 4	46	-76.1	42	-34.4
Model 3 > Model 5	46	-77.3	44	-92.2
Model 3 > Model 6	50	-222.6	47	-163.1

Feeling Model 3 performed better than Feeling Models 4, 5, and 6 with additional parameters. The table shows the number of subjects for which Model 3 performed better than the compared model, as well as the statistics for the BIC difference between the two models ($BIC_{model3} - BIC_{comparison\ model}$). Negative values indicate that Feeling Model 3 was more parsimonious (had a lower BIC).

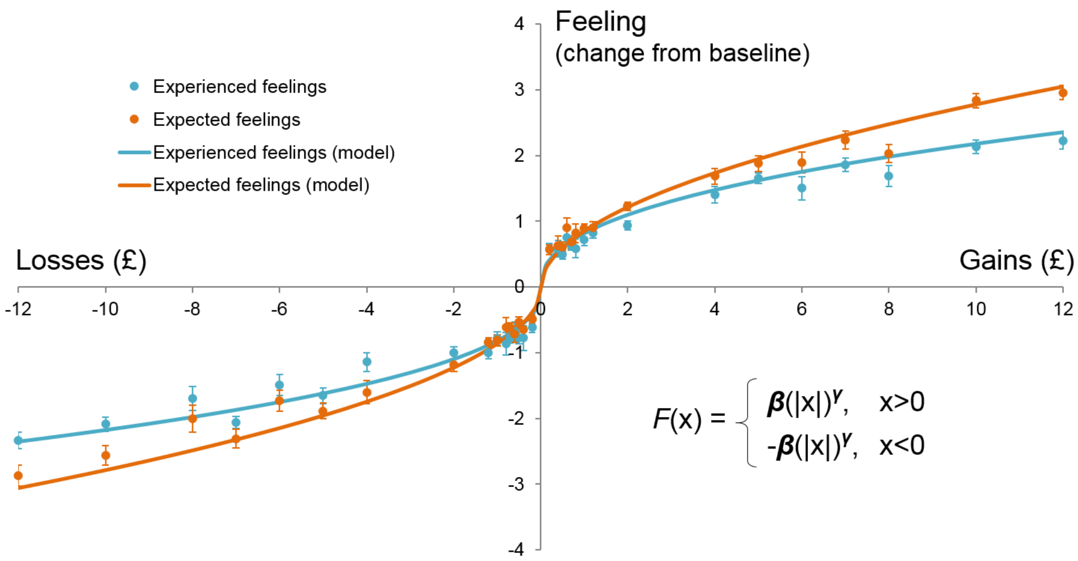


Figure 3-3. "Feeling function". Plotted are expected and experienced feelings ratings averaged across participants for each outcome value, as well as best fitting Feeling Model 3. Average slope (β) across participants was 0.857 ± SD 0.36 for expected feelings and 0.819 ± SD 0.37 for experienced feelings (paired t-test revealed no significant difference between them: $t(55)=0.65$, $P=0.52$, Cohen's $d=0.087$, 95% CI=[-0.079;0.155]). Average curvature (γ) was 0.512 ± SD 0.26 for expected feelings and 0.425 ± SD 0.23 for experienced feelings. Both γ values were significantly smaller than 1 ($t(55)>14$, $P<0.001$, Cohen's $d>1.87$), consistent with an S-shaped function and indicating diminishing sensitivity of feelings to increasing outcome values. γ was also significantly smaller for experienced relative to expected feelings (paired t-test: $t(55)=3.31$, $P=0.002$, Cohen's $d=0.442$, 95% CI=[0.034;0.138]), suggesting that the "impact bias" grows with increasing outcomes. Error bars represent SEM.

3.4.2 Controlling for different methods of calculating feelings

Feelings associated with losses and gains were elicited using one of two different scales and the impact of losses and gains on feelings were computed using three different methods: as the change from the mid-point of the rating scale, as the change from the previous rating, and as the change from the rating associated with zero outcome (i.e., the rating associated with not winning or not losing the equivalent amount). For all the Feeling Models the latter baseline resulted in the best fit (**Table 3-3**). Thus only results using this baseline are reported; however, the results were the same when using the other two methods of calculating feelings, suggesting that the findings do not depend on the method of calculating feelings.

Table 3-3. Mean R^2 values associated with each Feeling Model, separately for each method of calculating feelings

Model #	Parameters	Rating baseline used:	Expected feelings: Zero baseline	Expected feelings: Mid-scale point	Experienced feelings: Zero baseline	Experienced feelings: Mid-scale point	Experienced feelings: Previous trial feeling
1	β		**0.72**	0.66	**0.64**	0.37	0.45
2	β_{gain}, β_{loss}		**0.73**	0.68	**0.65**	0.47	0.46
3	β, ρ		**0.80**	0.74	**0.74**	0.49	0.53
4	β_{gain}, β_{loss}, γ		**0.81**	0.77	**0.76**	0.68	0.54
5	β, γ_{gain}, γ_{loss}		**0.81**	0.76	**0.75**	0.55	0.54
6	β_{gain}, β_{loss}, γ_{gain}, γ_{loss}		**0.82**	0.79	**0.76**	0.69	0.55
7	β, ε		**0.80**	0.74	**0.74**	0.49	0.52
8	β_{gain}, β_{loss}, ε		**0.81**	0.76	**0.75**	0.57	0.54
9	β, ε_{gain}, ε_{loss}		**0.81**	0.77	**0.75**	0.68	0.53
10	β_{gain}, β_{loss}, ε_{gain}, ε_{loss}		**0.81**	0.78	**0.76**	0.69	0.54

The impact of outcomes on feelings was computed using three different methods: as the change from the rating associated with zero outcome (i.e., the rating associated with not winning or not losing the equivalent amount – zero baseline), as the change from the mid-point of the rating scale, or as the change from the previous rating. All feeling models were then fit to these feelings data. For all feeling models the zero baseline resulted in the best fit. Note, feeling change compared to previous trial feeling could only be computed for experienced feelings, as actual feelings are not measured during expected feelings blocks. Bold indicates the best fitting model.

3.4.3 Impact bias increases with the amount at stake

Interestingly, comparing the functions for experienced and expected feelings revealed an "impact bias" that increased with amounts lost/gained. The "impact bias" is the tendency to expect losses/gains to impact our feelings more than they actually do (Gilbert et al., 1998). Specifically, the curvature (γ) was smaller for experienced relative to expected "feeling function" (paired t-test: $t(55)=3.31$, $P=0.002$, Cohen's $d=0.442$, 95% CI=[0.034;0.138]), while there was no difference in sensitivity values (β) ($t(55)=0.65$, $P=0.52$, Cohen's $d=0.087$, 95% CI=[-0.079;0.155]). Thus, although both expected and experienced feelings became less sensitive to outcomes as absolute values of loss/gain increased, this diminished sensitivity was more pronounced in experience than in expectation. As a result, for small amounts of money gained/lost people's expectations of how they will feel were more likely to align with their experience. However, as amounts gained/lost increased, people were more likely to overestimate the effect of outcomes on their feelings, expecting to be affected more by gains and losses than they actually were (i.e., the impact bias; Gilbert et al., 1998). Graphically, the growth of the impact bias can be observed in **Figure 3-3** as the increase in separation between the blue line (experienced feelings) and the more extreme orange line (expected feelings).

3.4.4 Feeling function predicts choice better than value-based models

Once the function that fit feelings to outcome value was established, the next question was to examine how well those feelings predict choices, in particular how they are combined and weighted to make a decision.

To answer this question, the Feeling Model built above from the data recorded in the first task was used to predict decisions made in a separate gambling task. To do so two logistic regressions were conducted for each participant (one using expected feelings – Choice Model 1 – and one using experienced feelings – Choice Model 2), where choice on the gambling task was entered as the dependent variable (either 1 if the subject selected the gamble or 0 if the subject selected the sure option) and feelings (predicted by Feeling Model 3) associated with the options were entered as the independent variable. Specifically, using the participant's β and γ from Feeling Model 3, the feelings associated with each available option were computed and multiplied by their probability. For example, if a participant was offered a mixed gamble trial where s/he could either choose a gamble that offered a 50% chance of gaining £10 and a 50% chance of losing £6 or a sure option of £0, the feelings associated with these three elements were multiplied by their probability: the feeling associated with gaining £10 $[F(£10) = \beta \times 10^{\gamma} \times 0.5]$; the feeling associated with losing £6 $[F(-£6) = \beta \times (-6)^{\gamma} \times 0.5]$ and the feeling associated with getting £0: $[F(£0) = 0 \times 1 = 0]$. These were entered in the logistic regression to predict choice (Choice Model). Each logistic regression thus resulted in three weight parameters ω, which reflected the weight assigned to feelings when making a choice; one for gains (ω_G), one for losses (ω_L) and one for sure options (ω_S).

Importantly, choice models using feelings as predictors (Choice Models 1 and 2) were compared to five other regression models which predicted choice using: objective values (Choice Model 3), log of objective values (consistent with standard economics models to account for the curvature of utility – Choice Model 4), as well as three models derived from Prospect Theory, where value was weighted for each subject with their loss aversion parameter (Choice Model 5), risk aversion parameter (Choice Model 6), or both (Choice Model 7) (see section **3.3.5.3** above for more details). To avoid circularity and ensure all Choice Models were run on the same set of choice data, loss and risk aversion parameters were estimated using half the choice data; then, all seven Choice Models, including those in which extracted feelings were used rather than values, were run on the other half of the choice data.

Choice Models 1 and 2 , in which choice is predicted from feelings extracted from the expected and experienced "feeling function" respectively, predicted choice better than all value-based comparison models (Choice Models 3-7), as indicated by lower BIC scores (**Figure 3-4**), and higher R^2 values (**Table 3-4**). Running the split-half analysis 100 times, with a different way to split the data on every simulation, revealed that models using feelings predicted choice better than all 5 comparison models in 99 simulations out of 100, thus confirming the reliability of this finding.

In addition, the results were the same when using the feeling functions computed with the other two methods of calculating feelings, as explained in section **3.4.2** above. Indeed, when estimating Choice Models to predict gambling choice from these feeling functions varying in their reference point, the finding that these feelings predicted choice better than the five other value-based Choice Models was replicated (Choice Model using expected feelings from scale mid-point: BIC=8884, R^2=0.30; Choice Model using experienced feelings from scale mid-point: BIC=8915, R^2=0.30; Choice Model using experienced feelings from previous trial feeling: BIC=8924, R^2=0.30; value-based Choice Models: BIC>9025, R^2<0.29).

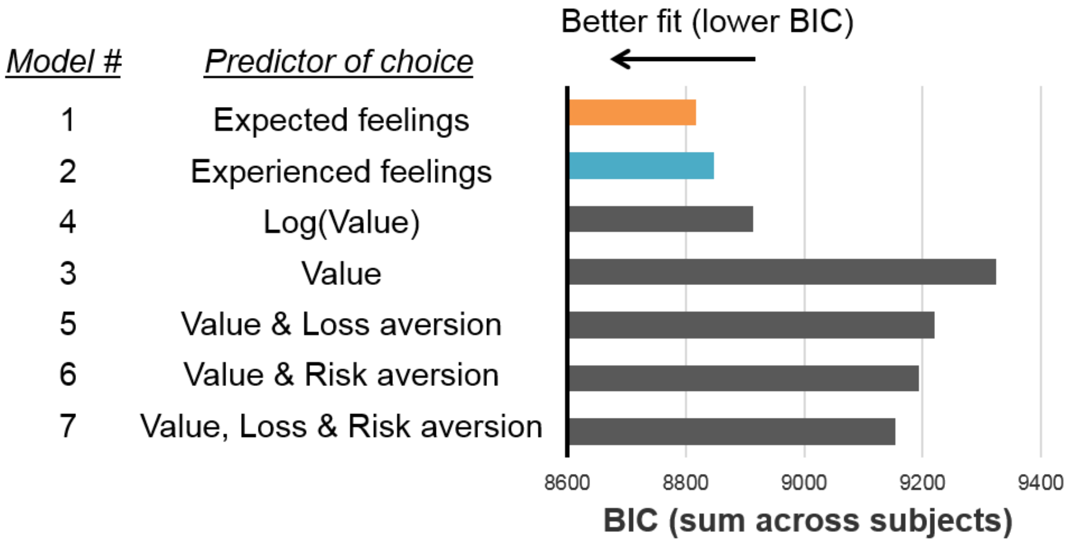


Figure 3-4. Choice Models. Seven logistic regressions (Choice Models) were run to predict choices on the gambling task, using either feelings derived from the "feeling function" build using expected (Choice Model 1) or experienced (Choice Model 2) feelings as predictors, or using value-based comparison models (Choice Models 3-7). BIC scores summed across subjects (smaller BIC scores indicate a better fit) show that derived feelings (both expected and experienced) predict choice significantly better than all other value-based models.

Table 3-4. Predictive value of Choice Models

Model #	Predictor of choice	Pseudo R^2
1	Expected feelings	**0.31**
2	Experienced feelings	**0.31**
3	Log(Value)	**0.30**
4	Value	**0.26**
5	Value & Loss aversion	**0.27**
6	Value & Risk aversion	**0.27**
7	Value, Loss & Risk aversion	**0.28**

Choice Models using feelings derived from each subject's "feeling function" predicted choice better than Choice Models using value or value-derived functions. Note that all Choice Models were run on the exact same half of the choice data and that feeling and value functions were extracted from separate, independent data. Therefore, these Choice Models are directly comparable. Given that all models have the same number of parameters ($\boldsymbol{\omega_G}$, $\boldsymbol{\omega_L}$ and $\boldsymbol{\omega_S}$, representing the weights associated with gain, loss and sure option on choice, respectively), higher pseudo R^2 value indicates better model fit.

3.4.5 Loss aversion in gambling choice

Across all participants in the main study, mean loss aversion (λ), estimated from the gambling task date (**Figure 3-1C**), was 2.38 (±SD=2.19), significantly greater than 1 (t(55)=4.72, P<0.001, Cohen's d=0.63, 95% CI=[1.80;2.97]). In the replication and extension studies, mean loss aversion was 2.49 (±SD=2.10, t(19)=3.17, P=0.005, Cohen's d=0.71, 95% CI=[1.51;3.48]) and 2.38 (±SD=2.14, t(29)=3.54, P=0.001, Cohen's d=0.65, 95% CI=[1.58;3.18]) for study 1 and 2, respectively. However, because the distribution of this loss aversion parameter is often positively skewed, an average parameter greater than 1 may be driven by few highly loss averse subjects; therefore, the median loss aversion was also calculated to ensure it was above 1 (similar to Tom et al., 2007). This was the case in all three studies, with median λ values of 1.64, 2.17 and 1.47 for the main study, replication and extension studies 1 and 2, respectively. Finally, gambling choices on mixed gamble trials can also be indicative of loss aversion. To investigate this, the proportion of risky choices was calculated across all subjects for each study group. Results are shown in **Figure 3-5** and reveal that participants reliably avoid gambling when the loss and gain amounts are the same (shown by a proportion of risky choice between 20-40% along the diagonal of the matrices in **Figure 3-5**). Across all studies their indifference point (gambles for which the proportion of risky choice is 50%) was shifted towards gambles with a positive expected value (i.e. gain value>loss value), such that the gain value needs to be about twice as big as the loss value for participants to start gambling more than 50% of the time. This indicates that loss aversion was reliably present in choice and across the whole range of gambles.

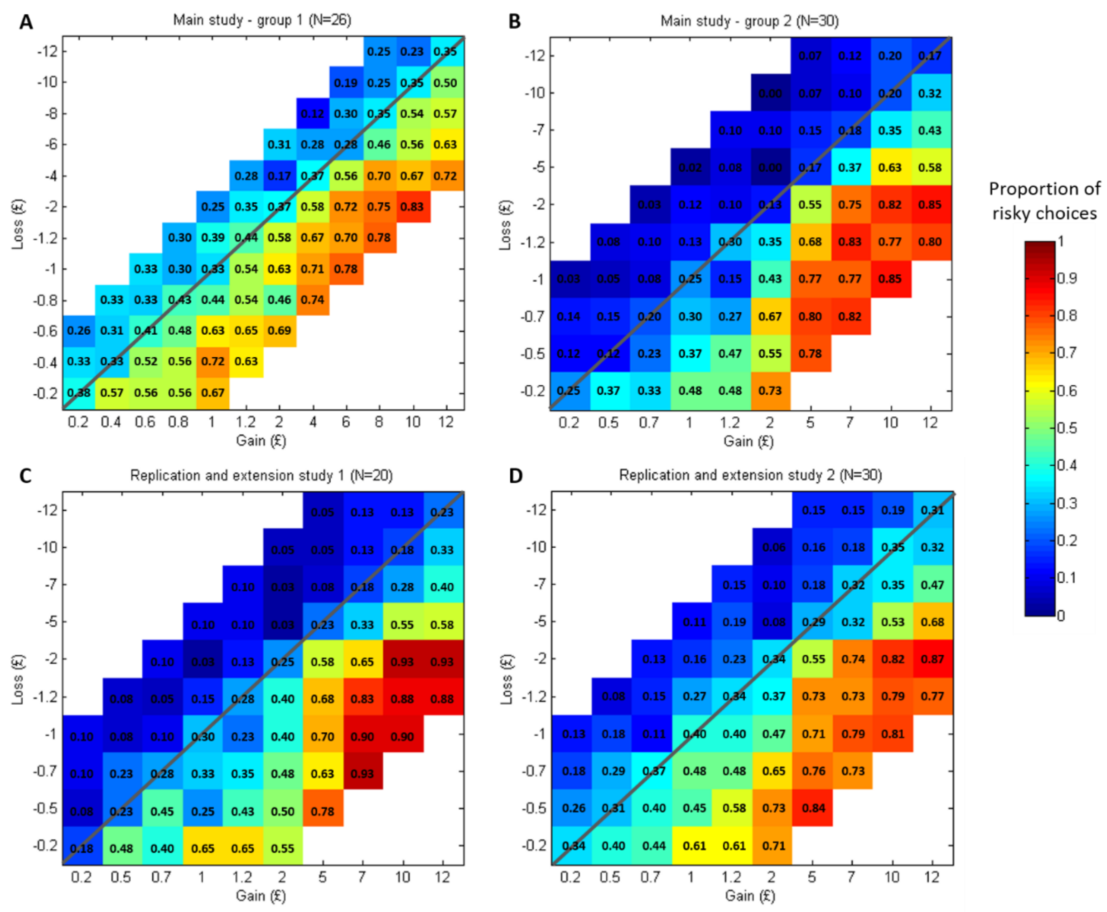


Figure 3-5. Proportion of risky choices detailed for each mixed gamble trial from the choice task. Each table shows the gain and loss values used to create the range of mixed gambles. Each gamble consisted of 50% chance to win the gain amount and 50% chance to lose the loss amount. As detailed in section **3.3.3** above ('Study groups' paragraph), a slightly different range of values were used for the first (**A**) and second (**B**) groups of the main study, resulting in 71 and 69 gamble types, respectively. Both replication and extension studies (**C** and **D**) used the same gambles as **B**. Each gamble was presented twice. For each subject, the propensity of choosing each of these gambles over the sure option of £0 was calculated by averaging over the 2 trials where the specific gamble was shown, then the mean proportion of risky choices was calculated by averaging that probability across all subjects in each group. The number and colour inside each cell both indicate that mean proportion of risky choices. Loss aversion is reflected in each group by reliable avoidance of gambles with the same gain and loss value (proportion of risky choices always <50% along the diagonal) and participants starting to choose the gamble more than 50% of the time only when the gain value was about twice as big as the loss value.

3.4.6 Feelings associated with losses are weighted more than feelings associated with gains when making a decision

Are feelings about potential losses and gains given equal weights when we deliberate on a decision? The "feeling function" indicated that the impact of a loss on feelings was symmetrical to the impact of an equivalent gain. Yet, while losses and gains may impact explicit feelings similarly, these feelings were weighted differently when making a choice.

Specifically, ω parameters from the choice models, which predicted choices from feelings, demonstrated a greater weight for feelings associated with losses (ω_L) relative to gains (ω_G) in predicting choice (for expected feelings: t(55)=3.04, *P*=0.004, Cohen's d=0.406, 95% CI=[0.684;3.33]; for experienced feelings: t(55)=2.93, *P*=0.005, Cohen's d=0.392, 95% CI=[0.599;3.19]; **Figure 3-6**). Models that allowed different weights for losses and gains performed significantly better than models that did not (**Table 3-5**).

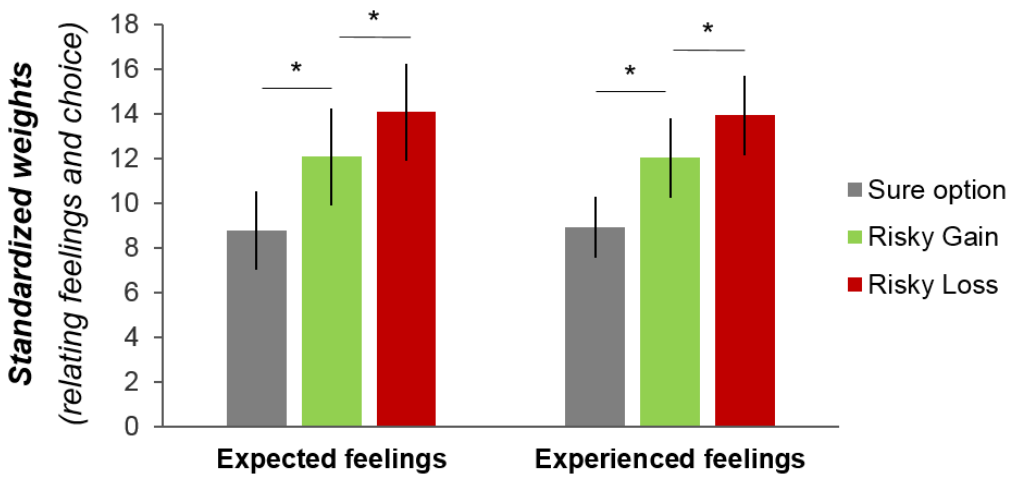


Figure 3-6. Standardized weight parameters from Choice Models. The resulting standardized parameters from Choice Model 1 (expected feelings) and Choice Model 2 (experienced feelings) show that the weight of feelings associated with losses is largest, followed by the weight of feelings associated with gains, with the weight of feelings associated with sure options smallest. This suggests that feelings associated with losses are weighted more than feelings associated with gains when making a choice. Error bars represent SEM. Two-tailed paired t-tests: * *P*<0.05.

Table 3-5. Choice Models in which losses and gains are weighted differently perform better

	Expected Feelings		Experienced Feelings	
	BIC	R^2	BIC	R^2
Losses and gains weighted differently (ω_S, ω_G, ω_L)	17092	0.30	17156	0.30
Losses and gains weighted together (ω_S, ω_{GL})	19594	0.18	19519	0.18

Separate logistic regressions models were run on all choice trials to predict choice from feelings (either expected or experienced). Specifically, to demonstrate that feelings for losses and feelings for gains had a different weight on choice, choice models where losses and gains are weighted differently were compared to choice models where both losses and gains are given the same weight ω_{GL}. This revealed that choices are predicted significantly better when feelings for losses and feelings for gains are assigned different weights.

The results were replicated when examining the data obtained with the other two methods of calculating feelings (see section **3.4.2** above). Indeed, feelings about losses were found to be weighted more than feelings about gains in predicting choice, independent of the baseline used to calculate feelings (expected feelings from scale mid-point: t(55)=3.38, P=0.001; experienced feelings from scale mid-point: t(55)=3.33, P=0.002; experienced feelings from previous trial feeling: t(55)=3.20, P=0.002).

Follow-up analysis revealed that this increased weighting of feelings about losses relative to gains was true only in mixed-gamble trials, where losses and gains are weighted simultaneously, but not when comparing gain-only and loss-only trials, in which gains and losses are evaluated at different time points (different trials). Specifically, logistic regressions were run to predict choice from feelings separately for each trial type, and weight of feelings parameters were entered into a two (trial type: mixed/non-mixed) by two (outcome: loss/gain) repeated-measures ANOVA. This revealed a significant interaction (expected feelings: F(1,55)=6.54, *P*=0.013, η_p^2=0.106; experienced feelings: F(1,55)=7.46, *P*=0.008, η_p^2=0.119; **Figure 3-7**), driven by a greater weight put on feelings associated with losses relative to gains during mixed-gamble choices (expected feelings: t(55)=3.66, *P*=0.001, Cohen's d=0.489, 95% CI=[1.67;5.71]; experienced feelings: t(55)=2.45, *P*=0.018, Cohen's d=0.327, 95% CI=[0.91;9.10]) but not during loss- versus gain-only trials (expected feelings: t(55)=0.82, P=0.42, Cohen's d=0.109, 95% CI=[-3.25;7.71]; experienced feelings: t(55)=0.79, P=0.43, Cohen's d=0.105, 95% CI=[-2.75;6.32]). In other words, only when potential losses and gains are evaluated simultaneously (i.e. in the same gamble) are feelings about losses weighted more strongly during choice than feelings about gains. Results of the first replication and extension study further show that even when gains and losses are evaluated in the same trial during the feelings task, their impact on feelings does not differ, but their weight on gamble choice does (see section **3.4.7** below for details).

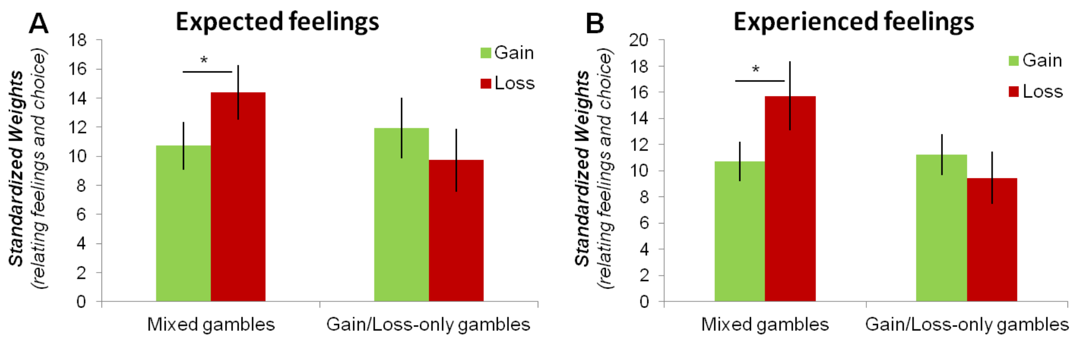


Figure 3-7. Influence of gamble type on differential weighting of feelings associated with losses versus gains. Logistic regressions were run to predict choice from feelings separately for each trial type. Standardized parameter estimates representing the decision weight of feelings were analyzed in a two (trial type: mixed/non-mixed gambles) by two (outcome: loss/gain) repeated-measures ANOVA. Significant interactions for both expected (**A**) and experienced (**B**) feelings indicate that more weight is given to feelings about a loss relative to a gain only when the loss and the gain are evaluated simultaneously (i.e. in the same gamble). Error bars denote SEM. Paired t-tests: * P<0.05.

To further tease apart the asymmetrical use of feelings associated with gains and losses in shaping choice from the use of value alone, another logistic regression was run (Choice Model 8) in which raw feelings (i.e. reported feelings relative to baseline rather than those derived from the feeling function) were added as predictors of choice in the same logistic regression as objective values themselves. This was done to reveal the weight assigned to feelings in making a choice over and beyond the effect of value *per se*, when the two compete. The results showed no difference in the weight assigned to the value of losses and gains *per se* (t(55)<1.2, P>0.23, Cohen's d<.17), only to the weight assigned to the associated feelings (expected feelings: t(55)=3.59, P=0.001, Cohen's d=0.479, 95% CI=[1.29;4.55]; experienced feelings: t(55)=2.28, P=0.027, Cohen’s d=0.307, 95% CI=[0.197;2.89]). Again, this was only true for mixed gamble choices, not for gain-only or loss-only trials where neither feelings nor values were weighted differently between losses and gains (**Table 3-6**). This suggests that losses are not weighted differently from gains; rather feelings associated with losses are weighted differently from feelings associated with gains, emphasizing the importance of feelings in decision making.

Table 3-6. Weight of feelings on choice, while controlling for value, separated by gamble type

		Expected feelings		Experienced feelings	
		Mixed gambles	Gain/Loss-only gambles	Mixed gambles	Gain/Loss-only gambles
Weight of feelings about **gains** on choice, controlling for value (±SD)		-0.202 (±6.01)	1.976 (±5.92)	0.388 (±4.25)	3.045 (±13.51)
Weight of feelings about **losses** on choice, controlling for value (±SD)		4.017 (±8.11)	2.246 (±4.43)	2.671 (±5.14)	0.029 (±6.34)
T-test Loss vs Gain	t(53)=	2.843	0.302	2.709	1.522
	P=	0.006	0.763	0.009	0.134

Both raw feelings (i.e. reported feelings relative to baseline rather than those derived from the feeling function) and objective values were added as predictor of gambling choice in the same logistic regression, separately for each gamble type. The weights of feelings about gains and losses were extracted from each regression, averaged across subjects, and compared using a paired t-test. Data from two participants were excluded because the logistic regression models could not be fit and resulted in aberrant parameter values.

This last conclusion raises the possibility that individual differences in decision-making could be explained by how people weigh feelings when making a choice. Indeed, using the weights from the above Choice Model 8 showed that individual differences in both loss aversion and the propensity to choose gambles were directly correlated with the extent to which feelings associated with losses were overweighted compared to gains while controlling for value (correlation between loss aversion and loss-gain weight difference for expected feelings: r(56)=0.56, *P*<0.001; for experienced feelings: r(56)=0.34, *P*=0.012; correlation between propensity to gamble and loss-gain weight difference for expected feelings: r(56)=-0.61, *P*<0.001; for experienced feelings: r(56)=-0.46, *P*<0.001; **Figure 3-8**). Specifically, subjects who weighted feelings about losses more than feelings about gains were more loss averse and less likely to gamble.

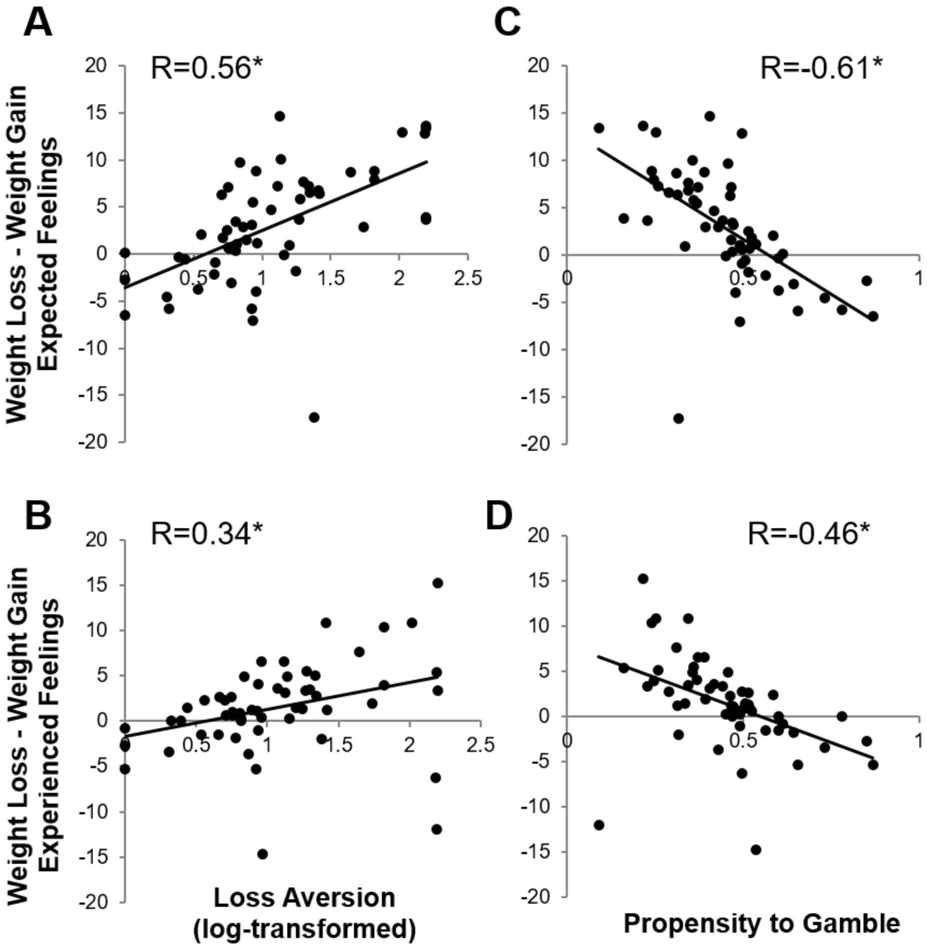


Figure 3-8. Individual differences in choice are driven by the relative weights of feelings. Raw feelings (i.e. reported feelings relative to baseline) and objective values were combined in the same regression model (Choice Model 8) to examine the extent to which feelings predict choice while controlling for value. Each regression used either Expected (**A**,**C**) or Experienced (**B**,**D**) raw feelings together with objective values of each of the 3 decision options (Gain, Loss, Sure option), leading to 6 weight parameters in each regression ($\omega_G^{feelings}, \omega_L^{feelings}, \omega_S^{feelings}, \omega_G^{value}, \omega_L^{value}, \omega_S^{value}$). The difference between the weight of feelings about losses ($\omega_L^{feelings}$) and the weight of feelings about gains ($\omega_G^{feelings}$) was then calculated for each individual and each regression and plotted against ln Loss Aversion (**A**,**B**) (parameter estimated for each individual from the choice data and log-transformed as ln[Loss Aversion +1] before running the correlation) and proportion of chosen gambles (**C**,**D**). These correlations indicate that the greater weight a participant puts on feelings associated with a loss relative to a gain when making a decision, the more loss averse (and less likely to gamble) they are. Note that loss aversion and propensity to gamble are highly correlated, therefore correlations in **C** and **D** are not independent from **A** and **B**, respectively, and are displayed for illustrations purposes.

This set of results suggests that the asymmetric influence of gains and losses on decision-making, as suggested by Prospect Theory, is not necessarily reflected in expected nor experienced feelings, nor in different weights assigned to value *per se*, but rather in the extent to which feelings associated with losses and gains are taken into account when making a decision.

3.4.7 Replication and extension study 1

3.4.7.1 Rationale

Because the feelings task reported in the main text elicited feeling ratings about gains and about losses on separate trials, this design does not rule out the possibility that losses and gains may impact feelings differently when they are evaluated at the same time.

3.4.7.2 Methods

Thus, a follow-up study was run using exactly the same procedure as before, except that on each trial of the feelings task (**Figure 3-9**), the outcomes at stake included a gain, a loss, and £0 (rather than gain versus £0 on some trials, and loss versus £0 on different trials). Twenty participants were recruited and tested on this paradigm (12 males, 8 females, mean age: 23.8 years, age range: 19-33). Ten participants completed the feelings task first, and the remaining completed the gambling task first. Block order within the feelings task was also counterbalanced across subjects. The range of amounts and rating scale used were the same as in the second study group of the main study (see "Study groups" paragraph above). Participants were told that each picture from the pair was associated with a certain probability to win, lose, or get £0, and that these probabilities were different for each picture and not shown to them. Therefore participants had to rate their feelings on every trial knowing that each picture chosen could result in a gain, a loss, or a null outcome (£0). To maintain consistency with the previous design, participants were only asked to rate their expected feelings about two of the three potential outcomes on each trial. These were determined such that each amount from £0.2 to £12 (win or lose) had at least one expected feeling rating associated with it; then the other rating was selected randomly from the other two options. The order of the two ratings was randomized. The impact of losses and gains on feelings were computed using three different baselines as in the main experiment. For all ten feelings models, using the change from the mid-point of the rating scale resulted in best fit of both expected and experienced feelings data as indicated by higher R^2 values and lower BIC values, and was therefore used for all the analyses below. Note that in contrast with the main experiment the zero baseline did not result in the best fit of feelings data. This is because in the replication study the zero outcome was always associated with two possible outcomes instead of one. Thus, the zero baseline was calculated differently – for each amount (for example £2), the ratings associated with £0 were averaged across all trials where that specific amount (£2) was at stake, regardless of third amount presented (which could be for example -£1, or -£10) – this conceptually and mathematically different approach resulted in different model fits.

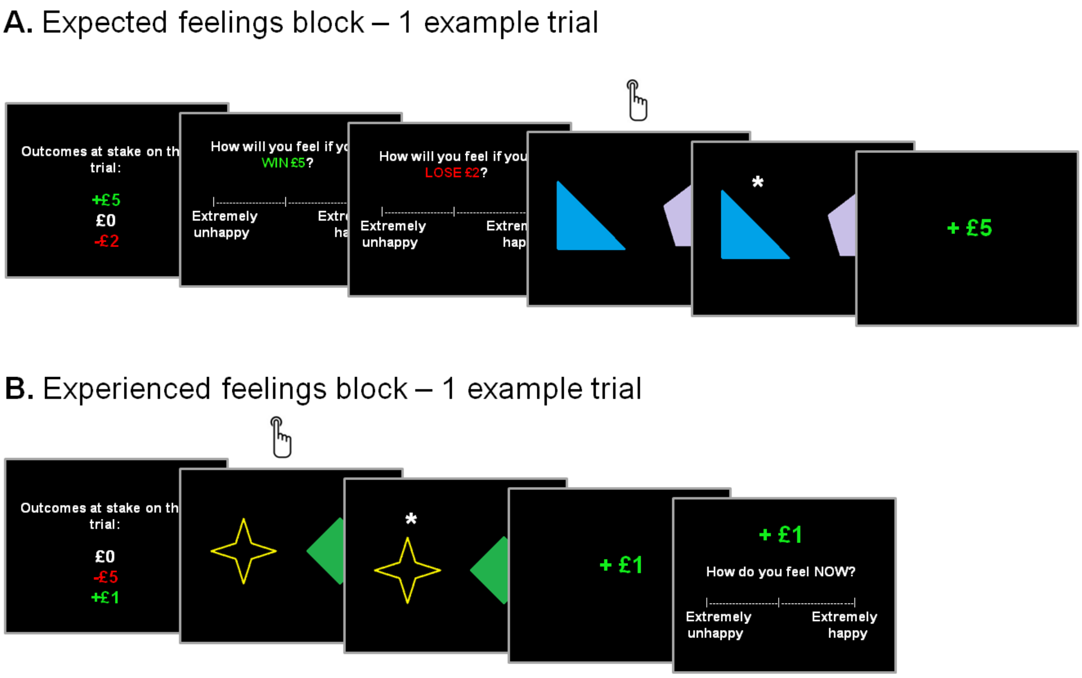


Figure 3-9. Replication and extension study 1 – design of the feelings task. An additional study was run to replicate the findings and test whether gains and losses impact feelings differently when they are evaluated in the same trial. The task structure was similar to the main study (**Figure 3-1**), except that on each trial of the feelings task, three potential outcomes were presented to the subject, always including a gain, a loss, and a null outcome (£0). The design of the gambling task (**Figure 3-1C**) remained the same.

3.4.7.3 Results

Feeling Models. Feelings were fit with the ten Feeling Models described in the main Methods to determine which function best relates feelings to value. If gains and losses impact feelings differently when evaluated at the same time, then a Feeling Model with different parameters (for example, a different slope β) for gains and losses, such as Feeling Model 4 or 6, should fit the feelings data better. However, this was not the case; instead the previous finding was replicated, showing that Feeling Model 3, with a single slope (β) and single curvature (γ) parameter for gains and losses, was the most parsimonious function that explains how feelings relate to value (**Figure 3-10**). This result replicates the previous finding that gains and losses impact feelings similarly and extends to cases where the loss and the gain are evaluated together.

Choice Models. To examine whether and how these feelings are weighted to predict choice, feelings extracted from best fitting Feelings Model 3 were entered in a logistic regression to predict choice on the gambling task. The same seven Choice Models were run as in the main data, again replicating the finding that feelings predicted choice better than value-based models (as indicated by lower BIC scores and higher R^2 values for Choice Models 1 and 2; **Figure 3-11A**). Importantly, during choice, participants also weighted their feelings about losses more than their feelings about gains (expected feelings: $t(19)=2.41$, $P=0.027$; experienced feelings: $t(19)=2.32$, $P=0.032$; **Figure 3-11B**). Finally, the extent to which feelings about losses were weighted more than feelings about gains (in a separate Choice Model controlling for the effect of value) was positively associated with individual estimates of behavioural loss aversion (expected feelings: $r(20)=0.54$, $P=0.014$; experienced feelings: $r(20)=0.44$, $P=0.052$; **Figure 3-11C**).

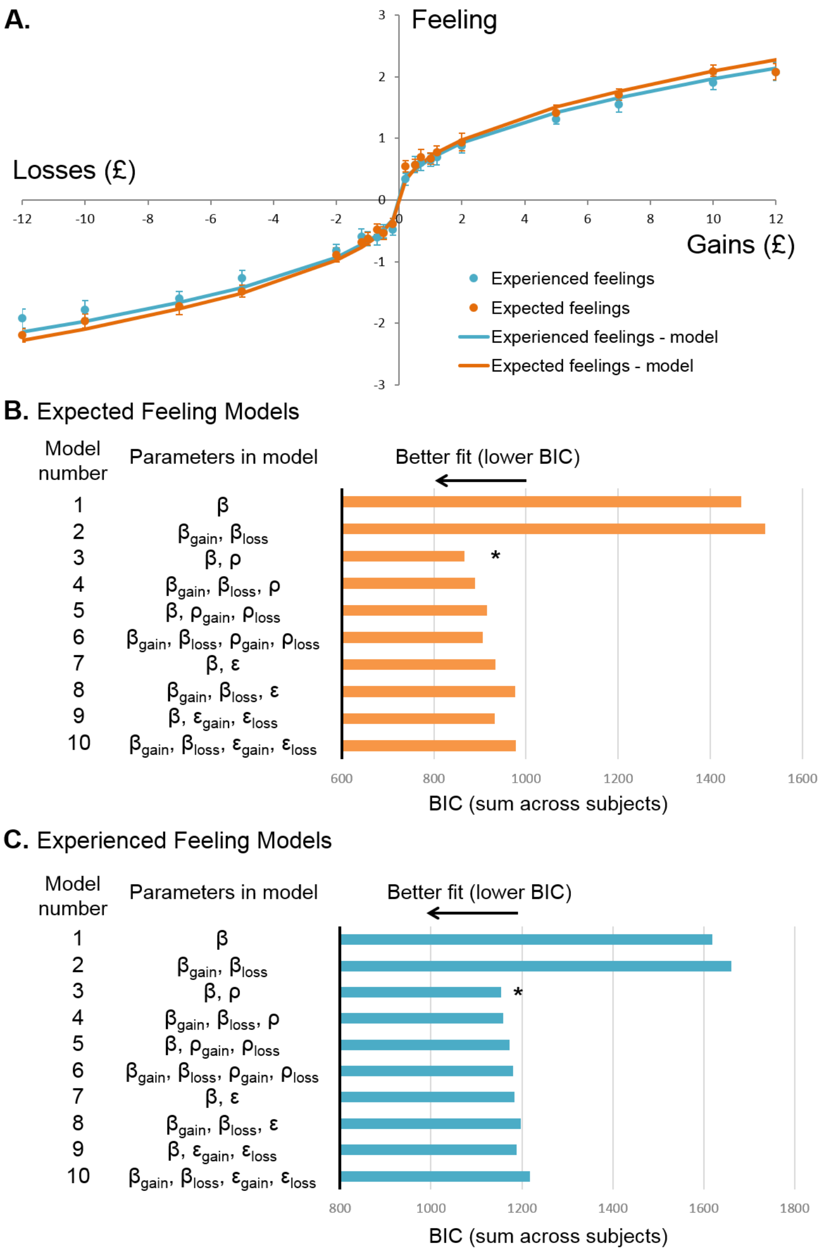


Figure 3-10. Replication and extension study 1 – "Feeling function" and Feeling Model fits. Feelings data collected on the replication and extension study were fit using the same procedure as the main study. (**A**) Expected and Experienced feelings ratings are plotted for each outcome value as the average rating across participant. Error bars represent SEM. The line representing best fitting Feeling Model 3 is also plotted. Average slope ($\boldsymbol{\beta}$) across participants was 0.702 ± SD 0.24 for expected feelings and 0.669 ± SD 0.25 for experienced feelings. Average curvature ($\boldsymbol{\gamma}$) was 0.474 ± SD 0.17 for expected feelings and 0.469 ± SD 0.23 for experienced feelings (both significantly smaller than 1, consistent with diminishing sensitivity of feelings to increasing outcome values: t(19)>10, P<0.001). BIC values, summed across all subjects, for each of ten Feeling Models are plotted separately for (**B**) Expected feelings ratings and (**C**) Experienced feelings ratings. This replicates the finding of the main study (**Figure 3-2** and **Figure 3-3**) that Feeling Model 3 was the most parsimonious model and extends it to a situation in which the impact of gains and losses on feelings is evaluated during the same trial.

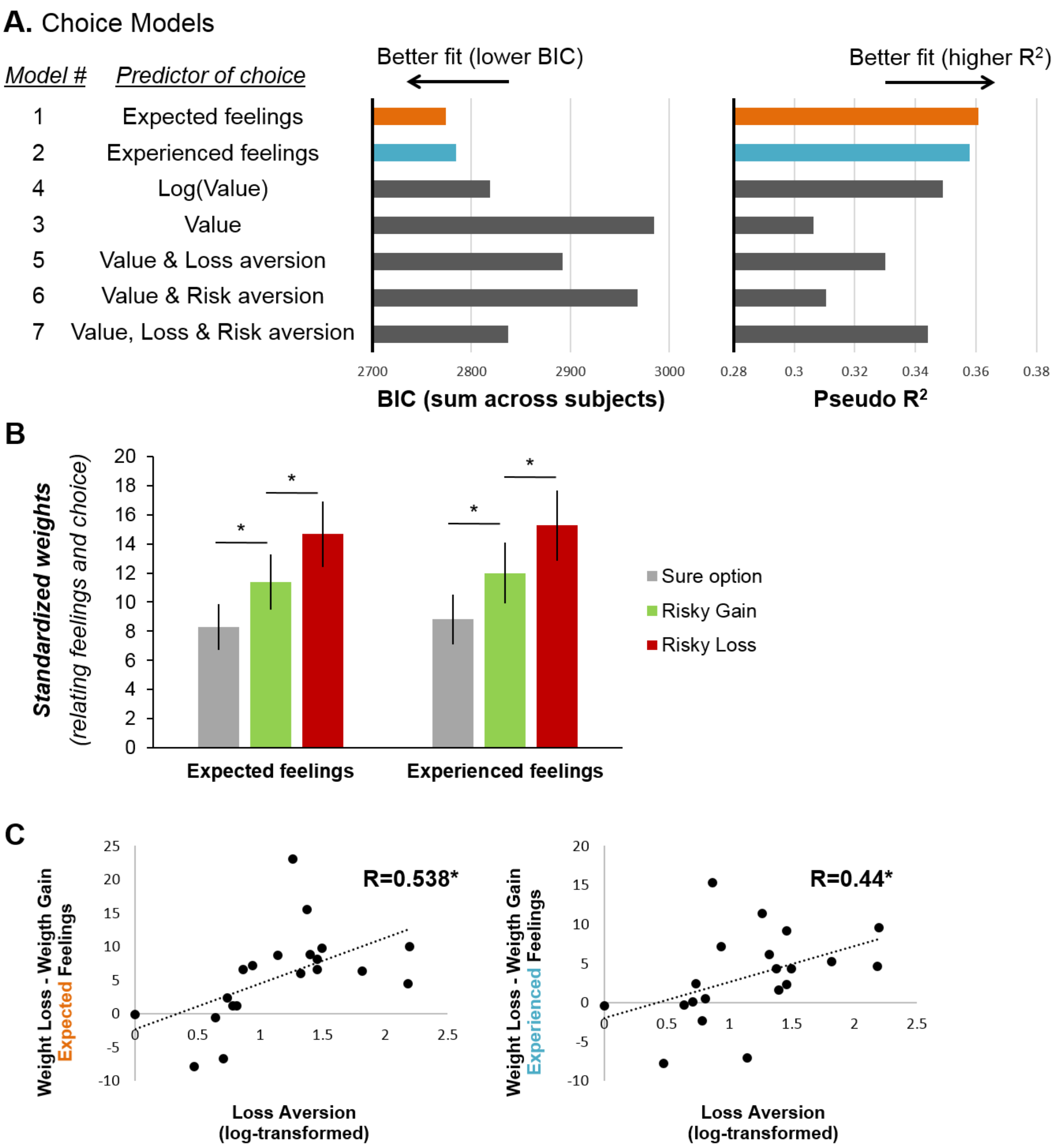


Figure 3-11. Replication and extension study 1 – Choice Models. Using the same procedure as in the main study (**Figure 3-4**), choices on the gambling task were entered in logistic regression models with expected feelings, experienced feelings, or various value-based regressors as predictors. Replicating the findings, BIC scores indicated that derived feelings predicted choice better than all other value-based models (**A**), with feelings about losses weighted more during a decision than feelings about gains (**B**). When running an additional Choice Model where both raw feelings and values were added as predictor of choice (similar to **Figure 3-8**), thereby allowing to examine the predictive weight of feelings on choice while controlling for value, we replicated the finding that the extent to which participants overweigh their feelings about losses relative to gains during choice predict individual differences in loss aversion (**C**). Two-tailed paired t-tests: * P<0.05.

3.4.8 Replication and extension study 2

3.4.8.1 Rationale

A recent study (McGraw et al., 2010) has reported that measuring feelings on a bipolar scale, like the main experiment did, resulted in no gain/loss asymmetry in feelings, consistent with the main findings, while using a unipolar scale (which represents the magnitude of feelings only) does result in an asymmetry. The suggestion is that a unipolar scale allows positive and negative feelings to be directly evaluated and scaled relative to one another. The experiment was thus rerun using a unipolar scale.

3.4.8.2 Methods

Data were collected on an independent group of 30 participants (15 males, 15 females, mean age = 24 years, age range = 18-35). The procedure was the same as in the main study, except that a unipolar rating scale was used in the feelings task. A power analysis indicated that a sample size of 30 would give 99% power to detect an effect size similar to the one observed in McGraw et al. ($d=0.76$ for the difference between feelings for gains and losses using the unipolar scale) at a threshold of $p<0.05$. Even if the true effect size is lower ($d=0.5$), achieved power would be 85%.

On experienced feelings trials the question was "How is this outcome affecting your feelings now?". On expected feelings gain trials subjects were asked "How would winning £X affect your feelings?" and "How would not winning £X affect your feelings?", and on expected feelings loss trials "How would losing £X affect your feelings?" and "How would not losing £X affect your feelings?". Participants responded by moving a cursor on a scale ranging from 0 ("No effect") to 5 ("Very large effect"). For analysis, ratings associated with losing and with not winning were coded negatively. Analysis then proceeded exactly as in the main experiment.

3.4.8.3 Results

Feeling Models. As in the main experiment Feeling Model 3, with a single slope (β) and single curvature (γ) parameter for gains and losses, was the best model of the ten in explaining how feelings relate to value (**Figure 3-12**). This suggests that even when using the same unipolar scale that allows scaling positive and negative feelings relative to each other regardless of valence, gains and losses have a symmetrical impact on feelings.

Bayes Factor analysis. In addition, a Bayes Factor analysis was run on the feelings data using JASP (version 0.7.1; Love et al., 2015; Morey and Rouder, 2015). A Bayesian repeated-measures ANOVA was conducted with domain (gain/loss) and amount (the range of 10 amount values from £0.2 to £12) as within-subject factors. The winning Bayesian ANOVA model included a main effect of amount, but no effect of domain or domain*amount interaction, consistent with the Feeling Models result. In particular, adding a main effect of domain made the model about 11 times worse (BF[Amount Model over Amount & Domain Model]=10.87 for expected feelings and 10.62 for experienced feelings), offering strong evidence for an absence of feelings asymmetry between gains and losses (for correspondence between BF magnitude and strength of evidence, see Jeffreys, 1961; Jarosz and Wiley, 2014).

Choice Models. As in the main experiment, feelings extracted from best fitting Feeling Model 3 predicted choice better than value-based models (as indicated by lower BIC scores and higher R^2 values for Choice Models 1 and 2; **Figure 3-13A**). During choice, participants weighted their feelings about losses more than their feelings about gains (expected feelings: t(29)=2.29, P=0.030; experienced feelings: t(29)=2.08, P=0.047; **Figure 3-13B**). Finally, the extent to which participants overweighted their feelings about losses relative to gains (in an additional Choice Model where the effect of value per se is accounted for) also predicted individual differences in behavioural loss aversion (expected feelings: r(30)=0.62, P<0.001; experienced feelings: r(30)=0.63, P<0.001; **Figure 3-13C**).

With these additional studies, the findings from the main study were replicated in two further independent samples, thereby confirming and strengthening the results.

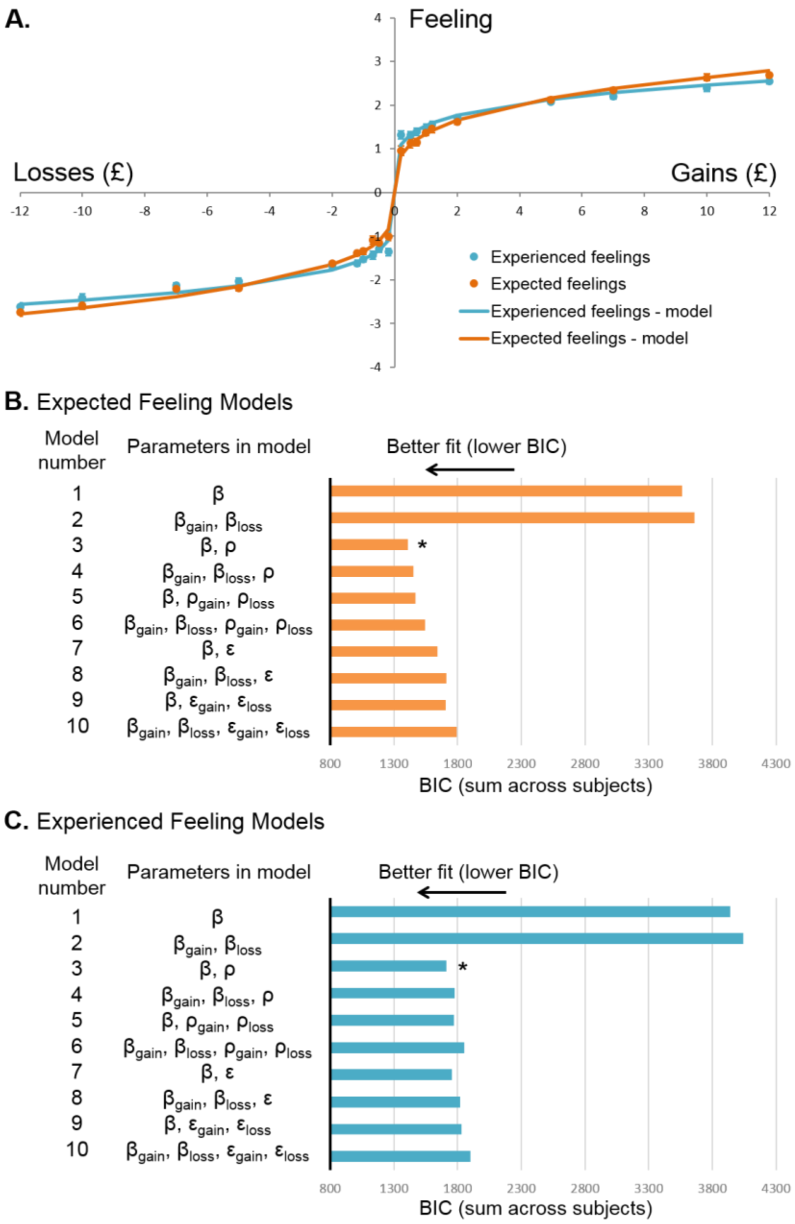


Figure 3-12. Replication and extension study 2 – "Feeling function" and Feeling Model fits. Feelings data collected on the second replication and extension study were fit using the same procedure as the main study. The only difference from the main study was the use of a unipolar rating scale to measure reported feelings. (**A**) Expected and Experienced feelings ratings are plotted for each outcome value. Error bars represent SEM. The line representing best fitting Feeling Model 3 is also plotted. Average slope ($\boldsymbol{\beta}$) across participants was 1.339 ± SD 0.36 for expected feelings and 1.509 ± SD 0.34 for experienced feelings. Average curvature ($\boldsymbol{\gamma}$) was 0.299 ± SD 0.18 for expected feelings and 0.215 ± SD 0.16 for experienced feelings (both significantly smaller than 1, consistent with diminishing sensitivity of feelings to increasing outcome values: t(29)>20, P<0.001). BIC values, summed across all subjects, for each of ten Feeling Models are plotted separately for (**B**) Expected feelings ratings and (**C**) Experienced feelings ratings. This replicates the finding of the main study (**Figure 3-2** and **Figure 3-3**) that Feeling Model 3 was the most parsimonious model and extends the finding to cases where the impact of losses and gains on feelings is reported on a unipolar rating scale.

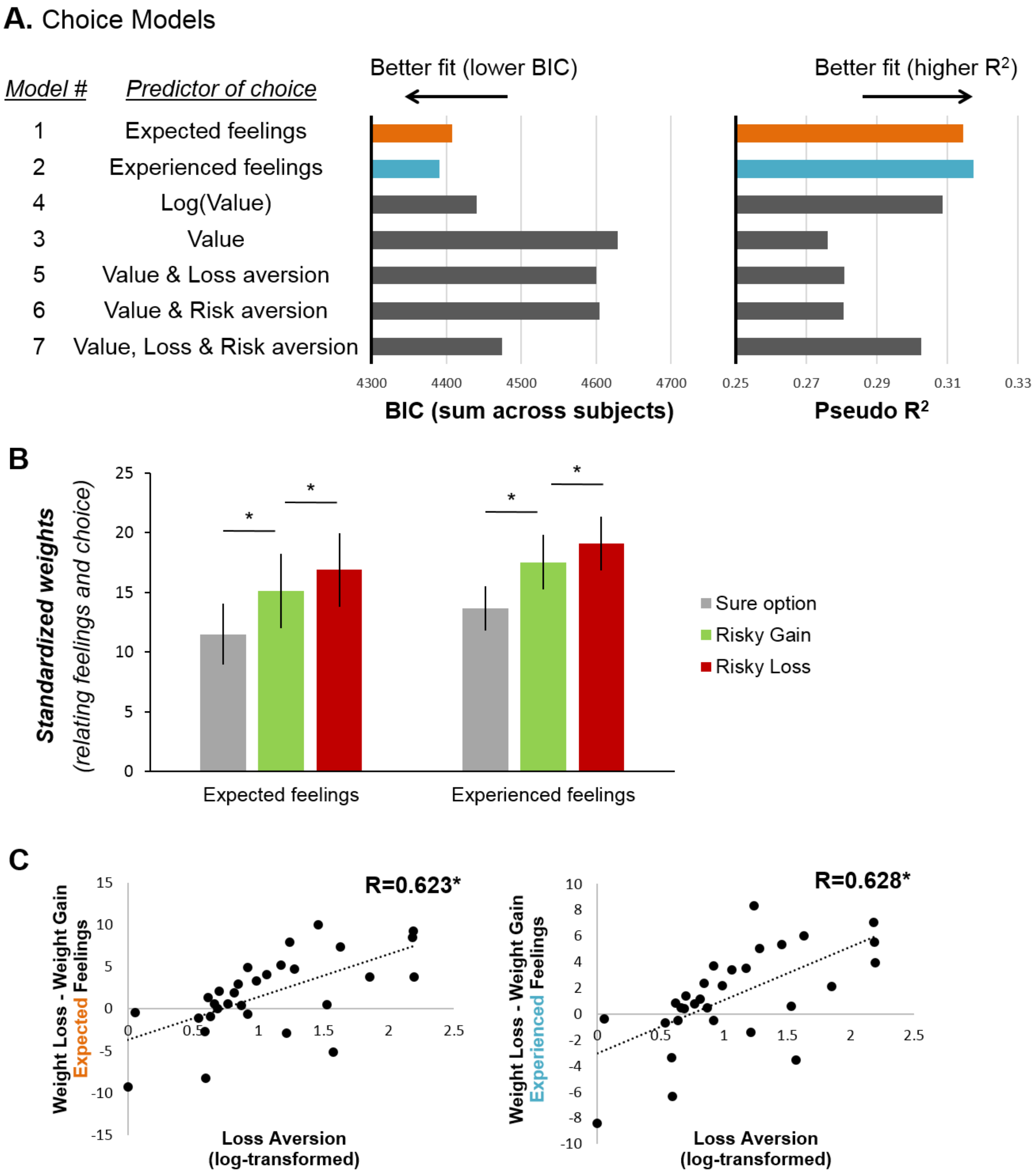


Figure 3-13. Replication and extension study 2 – Choice Models. Using the same procedure as in the main study (**Figure 3-4**), choices on the gambling task were entered in logistic regression models with expected feelings, experienced feelings, or various value-based regressors as predictors. Replicating the main findings, BIC scores indicated that derived feelings predicted choice better than all other value-based models (**A**), with feelings about losses weighted more during a decision than feelings about gains (**B**). When running an additional Choice Model where both raw feelings and values were added as predictor of choice (similar to **Figure 3-8**), thereby examining the predictive weight of feelings on choice while controlling for value, we replicated the finding that the extent to which participants overweigh their feelings about losses relative to gains during choice predict individual differences in loss aversion (**C**). Two-tailed paired t-tests: * *P*<0.05.

3.5 Discussion

The relationship between human feelings and the choices they make has occupied scientists, policymakers and philosophers for decades. Indeed, in recent years numerous studies have investigated how decisions and outcomes impact people's feelings (Mellers et al., 1997; Kermer et al., 2006; McGraw et al., 2010; Kassam et al., 2011; Carter and McBride, 2013; Rutledge et al., 2014; Yechiam et al., 2014) and life satisfaction (Boyce et al., 2013; De Neve et al., 2015). Yet, the equally critical question of how people's explicit feelings impact their decisions has been relatively neglected. This study addressed this important question in a controlled laboratory setting and modelled how feelings are integrated into decisions. The results demonstrate that feelings drive the decisions people make. However, the rules by which they do so differ from previously assumed.

Feelings were first modelled in a "feeling function" (Feeling Model), which was then used to predict choices (Choice Model). The Feeling Model predicted choice better than objective values, and a unique contribution of feelings in the decision process was demonstrated. The initial hypothesis outlined in the introduction was that the "feeling function" would exhibit the same properties as Prospect Theory's value function, namely diminishing sensitivity to increasing outcome values and stronger impact of losses relative to gains. However, only the first part of this hypothesis was confirmed.

Indeed, the "feeling function" that best related feelings to value was found to be concave for gains and convex for losses, similar to Prospect Theory value function (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) and other non-linear utility functions (Von Neumann and Morgenstern, 1947; Bernoulli, 1954; Fox and Poldrack, 2014; Stauffer et al., 2014). This curvature suggests that explicit feelings, similar to subjective value or utility, show diminishing sensitivity to outcomes as the value of these outcomes increases (Carter and McBride, 2013). In other words, the impact of winning or losing ten dollars on feelings is less than twice that of winning or losing five dollars.

However, the Feeling Model revealed no asymmetry between gains and losses, suggesting that the impact of a loss on feelings is not necessarily greater than the impact of an equivalent gain. This was replicated in two additional studies where a gain and a loss were evaluated at the same time and where the associated feelings about gains and losses were reported using the same unipolar scale. These findings do not suggest that the feelings associated with losses and gains would always be symmetrical. To the contrary, different stimuli and context may result in varying asymmetric effects (Harinck et al., 2007; McGraw et al., 2010). In particular, in contrast to the findings reported here, a loss-gain asymmetry in feelings has been previously reported in a study using a one-shot game, where the stakes consisted of large ($200) hypothetical amounts (McGraw et al., 2010). The study examines responses to incentive-compatible, but relatively small, gains and losses. It is possible that for higher amounts an asymmetry in feelings would emerge. However, a speculation is that even for large stakes the "feeling function" may do a better job at predicting choice than value alone. That question awaits testing.

Despite this absence of asymmetry in feelings, loss aversion was still present in choice, consistent with Prospect Theory. Importantly, when making a decision a greater weight was put on feelings associated with losses relative to gains. Therefore, the finding suggests that even when losses do not impact feelings more strongly than gains, those feelings are weighted more when making a choice than feelings about gains, consistent with the second hypothesis outlined in the introduction. Moreover, the amount by which feelings associated with losses are over-weighted relative to gains in making a decision relates to individual differences in loss aversion and propensity to gamble.

This finding resolves a long-standing puzzle by which loss aversion is often observed in choice, but not necessarily in explicit feelings (Mellers et al., 1997; Kermer et al., 2006; Harinck et al., 2007; McGraw et al., 2010). It suggests that the asymmetric influence of gains and losses on decision making, as suggested by Prospect Theory, is not reflected in expected or experienced feelings directly, neither in different weights assigned to value per se, but in the extent to which feelings about losses and gains are taken into account when making a decision. This result is consistent with the interpretation of an increased attention to losses when making a choice (Yechiam and Hochman, 2013). When losses and gains are presented separately in a decision their associated feelings are weighted in a symmetrical way. However, when they compete for attention, as is the case in mixed gambles, people may allocate more attention to the feelings they would derive from the loss than from the gain, leading them to choose in a loss averse manner. It is also possible that people implicitly experience losses to a greater extent than gains (Sokol-Hessner et al., 2009; Hochman and Yechiam, 2011), but this difference is not exhibited in explicit reports.

The findings also provide the first demonstration of an increasing impact bias with value. Specifically, there was a general impact bias in feelings (also called affective forecasting error), where people expect the emotional impact of an event to be greater than their actual experience (Gilbert et al., 1998; Kermer et al., 2006; Kwong et al., 2013; Levine et al., 2013; Morewedge and Buechel, 2013; Wilson and Gilbert, 2013). Interestingly, this impact bias was not constant, but increased with value. This was due to a stronger curvature of experienced feelings relative to expected feelings. In other words, as absolute value increases, sensitivity to value diminished more quickly for experienced relative to expected feelings. This suggests that as people win or lose more money, they are more and more biased towards overestimating the emotional impact of these outcomes.

Our modelling approach provides novel insight into how explicit feelings relate to choice. Such understanding is both of theoretical importance and has practical implications for policy-makers, economists and clinicians who often measure explicit feelings to predict choice (Benjamin et al., 2012, 2014).

Chapter 4 Emotional modulation of loss aversion: an fMRI study

4.1 Abstract

Adapting behaviour to changes in the environment is a crucial ability for survival, but such adaptation varies widely across individuals. Here we asked how humans alter their economic decision-making in response to emotional cues, and whether this is related to trait anxiety. Developing an emotional decision-making task for functional magnetic resonance imaging (fMRI), in which gambling decisions were preceded by emotional and non-emotional primes, allowed assessing emotional influences on loss aversion, the tendency to overweigh potential monetary losses relative to gains. The behavioural results revealed that only low-anxious individuals exhibited increased loss aversion under emotional conditions, and that this was similar for positive (happy faces) and negative (fearful faces) emotions. This emotional modulation of decision-making was accompanied by a corresponding emotion-elicited increase in amygdala-striatal functional connectivity, which correlated with the behavioural effect across participants. Consistent with prior reports of 'neural loss aversion', both amygdala and ventral striatum tracked losses more strongly than gains, and amygdala loss aversion signals were exaggerated by emotion, suggesting a potential role for this structure in integrating value and emotion cues. Increased loss aversion and striatal-amygdala coupling induced by emotional cues may reflect the engagement of adaptive harm-avoidance mechanisms in low-anxious individuals, possibly promoting resilience to psychopathology.

4.2 Introduction

The previous chapter of this thesis demonstrated that emotions play an integral role in driving people's decisions, confirming the assumptions of Prospect Theory. This suggests that externally manipulating a person's emotions should alter their decisions.

Detecting and processing such changes in our environment, and adapting our decisions in response to those changes, are important features of human behaviour. For example, we are likely to behave and make choices differently if we receive positive or negative social feedback (Sip et al., 2015), or if threatening and emotionally arousing cues appear in our surroundings (Mobbs et al., 2007, 2009). However, such behavioural adaptation varies substantially across individuals, and the factors that influence how people alter their decision-making in emotional situations remain poorly understood.

Trait anxiety is likely to be an important factor in people's tendency to alter their decisions in response to emotional cues. Rodent studies have reported that low levels of anxiety are associated with adaptive stress-coping and learning behaviour (Landgraf and Wigger, 2002; Herrero et al., 2006). Highly anxious humans exhibit difficulty in modulating learning in volatile environments (Browning et al., 2015), cognitive control (Derryberry and Reed, 2002; Bishop, 2007, 2009) and emotion regulation (Etkin et al., 2010; Farmer and Kashdan, 2012); and it has been suggested that the flexible modulation of behaviour in response to anxiogenic environmental changes may be an important mechanism by which further exposure to stress can be avoided (Mathews and Mackintosh, 1998; Robinson et al., 2013, 2015a). Therefore it is possible that highly anxious individuals may fail to adapt their decision-making under emotional conditions. On the other hand, high anxiety is also associated with exaggerated responses to emotional stimuli (Etkin et al., 2004; Fox et al., 2007; Stein et al., 2007; Sehlmeyer et al., 2011), raising the possibility that decision-making in highly anxious individuals may be disproportionately influenced by emotion.

Therefore, whether decision-making is influenced by emotional cues to a greater extent in low anxious individuals (potentially driven by greater behavioural flexibility), or in high anxious individuals (potentially driven by greater emotional reactivity) is unknown. To disambiguate between these hypotheses, a functional magnetic resonance imaging (fMRI) paradigm was developed, in which each decision (accepting or rejecting a gamble) was preceded by emotional or non-emotional primes. People's decisions were examined in the framework of Prospect Theory (Kahneman and Tversky, 1979), and their loss aversion (the tendency to overweigh potential losses relative to gains; Kahneman et al., 1991; Tversky and Kahneman, 1991; Hardie et al., 1993) was modelled under emotional relative to non-emotional conditions. To investigate whether avoidance of potential losses is altered specifically under threat, or under emotional arousal in general, both negative and positive emotional cues were used.

Based on prior work implicating the amygdala and ventral striatum in both loss aversion (Tom et al., 2007; De Martino et al., 2010; Canessa et al., 2013; Sokol-Hessner et al., 2013) and the processing of emotional cues (Adolphs, 2002; Glascher and Adolphs, 2003; Dalgleish, 2004; Mobbs et al., 2006; Phelps, 2006; Pessoa and Adolphs, 2010; Wang et al., 2014), these regions were hypothesized to drive the influence of emotion on economic decisions. Specifically, two mechanistic hypotheses were tested: 1) that enhanced amygdala and striatum responses to potential losses relative to gains ("neural loss aversion") may be directly modulated by emotion in a manner that drives changes in behaviour; 2) that the amygdala and ventral striatum play complementary roles in this modulation of decision-making, and it is their functional integration (as opposed to their activation) that underlies changes in loss aversion.

4.3 Materials and methods

4.3.1 Participants

Thirty healthy volunteers were recruited by advertisement. Data from two participants were excluded because of a lack of behavioural consistency in the gambling task, making loss aversion impossible to model. Final analyses included 28 participants (15 males, 13 females, age range 19-47 years, mean 26.5 years). Participants gave written informed consent and were paid for their participation in an incentive-compatible manner. The study was approved by the local departmental ethics committee.

4.3.2 Procedure

Participants attended the laboratory on two different days. On Day 1 (screening session), participants were administered the MINI (Sheehan et al., 1998; see section **2.1**), BDI and an MRI safety questionnaire. Eligibility for the study required: no past or present psychiatric disorders, including alcohol/substance dependence/abuse, BDI<15 and no MRI contraindications.

They first practiced the 20 trials of the memory task, with no gambles, thus ensuring that they were able to perform the task correctly and were familiar with the response buttons. Specifically, on each trial participants memorized the positions of two or four faces or objects presented on the screen for 3 s, and, after a delay of 10 s, reported the previous location of one of the stimuli, displayed at the centre of the screen. The stimuli displayed on each trial were chosen randomly among all pictures from the same emotion condition (all happy, all fearful, all neutral, or all objects) and (for faces) from the same gender (all males or all females). Difficulty and condition were randomized across trials.

After this practice memory task, participants were instructed that in order to make this memory task more challenging, they would perform a distracting gambling task while holding the stimuli in memory. They next completed a training block of gamble-only trials. The design of the gambling task to assess loss aversion was adapted from a previous study (Tom et al., 2007). On each trial participants were presented with a mixed gamble in which there was a 50% probability of winning the amount of money written in green (e.g. “WIN £12”) and a 50% probability of losing the amount written in red (e.g. “LOSE £8”). The left/right positions of the win and loss amounts were randomly assigned. Participants had 2 seconds to decide whether they wanted to take (accept) or pass on (reject) the gamble, and indicated their choice by a button press.

At the screening session, loss aversion was estimated in a training block of 49 trials (without the concurrent memory task) using a double staircase procedure to adjust the gambles for each participant, allowing to build a gamble matrix centred on each participant’s indifference point (see section **2.3** for details).

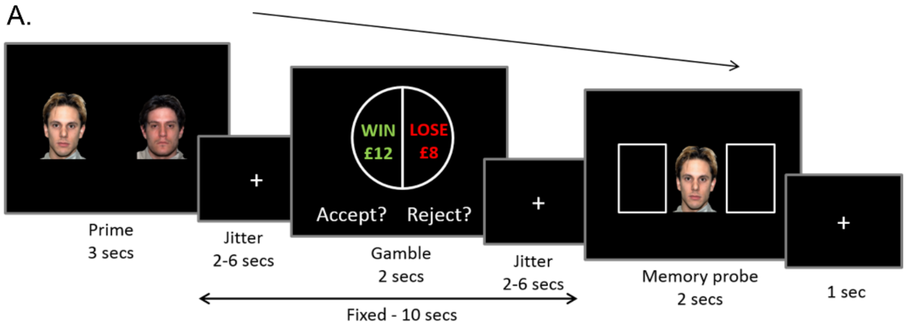
Participants finished the training session with 40 trials of the combined memory/loss aversion task, in which gambles were determined using a similar staircase procedure to the training gambling task above. These data ensured that participants still scored above chance on the memory task despite interference from the gambling task, and that their choices on the gambles were consistent with their previously estimated indifference point.

Participants returned to the laboratory for Day 2 (scanning session) after the screening session (mean delay=17.92 days, range=1-44 days). During this session, they initially completed one block of trials of the combined emotional decision-making task (**Figure 4-1A**) before entering the scanner, and four further 11-min blocks during fMRI scanning. Since there is large variability in loss aversion across individuals, each participant's indifference point on the loss aversion task from Day 1 was used on Day 2 to individually tailor the gamble matrix (**Figure 4-1B-C**).

After the scan, participants completed the BDI and the STAI. None of the 28 participants scored above 15 on the BDI (mean=1.68, SD±2.09, range 0-10). Mean trait anxiety was 31.2 (SD±6.34). Trait anxiety was used as a covariate in the analyses; in addition, a median split was performed, with 14 participants in a "low" trait anxiety group (mean=25.9, SD±3.03, range 20-30) and 14 in a "high" trait anxiety group (mean=36.5, SD±3.65, range 33-44).

4.3.3 Emotional decision-making task

Each trial started with the presentation of either two or four prime stimuli from the same condition (happy/fearful/neutral/object) for 3s (prime: **Figure 4-1A**). Participants were instructed to memorize their location. After a jittered delay of 2-6s, the gamble appeared for 2s and participants decided whether to accept or reject this gamble. There was another 2-6s jittered delay before the probe face/object appeared. Participants had 2s to indicate the location where the probe had been displayed in the first screen, followed by a 1s fixation cross between trials. Gamble outcomes were not revealed. The two delays were jittered in order to decorrelate the prime stimuli from the gamble presentation time, but always summed to 8s, such that the inter-trial interval was maintained at a constant 16s throughout the task. Participants completed 196 trials of this combined task (49 trials of each of the four conditions: happy, fearful, neutral, object). Gambles were randomly sampled from a 7*7 gain-loss matrix centred on each participant's own indifference point (example matrices: **Figure 4-1B-C**). This was done to ensure that the same ranges of wins and losses were presented for each emotion condition, and to optimize sensitivity to detect emotion-driven changes in loss aversion with a majority of gambles close to the participant's indifference point.



B.

Potential losses							
-10	-4	-3.5	-3	-2.5	-2	-1	0
-8	-3	-2.5	-2	-1.5	-1	0	1
-6	-2	-1.5	-1	-0.5	0	1	2
-5	-1.5	-1	-0.5	0	0.5	1.5	2.5
-4	-1	-0.5	0	0.5	1	2	3
-3	-0.5	0	0.5	1	1.5	2.5	3.5
-2	0	0.5	1	1.5	2	3	4
IP=0	2	3	4	5	6	8	10
	Potential gains						

C.

Potential losses							
-10	0.5	1	1.5	2	2.5	3.5	4.5
-8	1.5	2	2.5	3	3.5	4.5	5.5
-6	2.5	3	3.5	4	4.5	5.5	6.5
-5	3	3.5	4	4.5	5	6	7
-4	3.5	4	4.5	5	5.5	6.5	7.5
-3	4	4.5	5	5.5	6	7	8
-2	4.5	5	5.5	6	6.5	7.5	8.5
IP=4.5	11	12	13	14	15	17	19
	Potential gains						

Figure 4-1. Experimental design. A. On each trial, participants were first presented with an array (prime) of two or four faces (all happy, all fearful, or all neutral) or objects (light bulbs) and had 3 s to memorise it. They then had to decide whether to accept or reject a mixed gamble in which there was a 50% chance of winning the amount in green, and a 50% chance of losing the amount in red. Finally, a probe from the first array was presented and participants had to report its position. **B, C.** In order to optimize model fitting and sensitivity to emotional context, an estimate of each participant's indifference point (IP) was obtained from the practice session, and used to define the gamble gain/loss matrix. Each matrix was formed by combining seven potential gains with seven potential losses, leading to 49 gambles, repeated across each of the four conditions. Example matrices are shown with the resulting gamble expected value (EV=0.5*gain + 0.5*loss), centred on an indifference point of 0 (**B**, non-loss averse participant), or 4.5 (**C**, highly loss averse participant).

4.3.4 Incentive-compatible payment procedure

Participants were endowed with an initial amount of £15, to which the average outcome of 10 randomly selected choices was added or removed. They were explained this payment procedure carefully before starting the task. Participants earned an average of £17.41 on the task (i.e. extra win of £2.41 on top of the initial £15 endowment), and payments ranged from £11 to £22.90. They also received £7 for their time on the screening session and £10 on the scanning session.

4.3.5 Post-scanning tasks

Immediately after scanning, participants completed a final block of 49 trials of the task, in which all the memory stimuli were objects. This block was added to control for the fact that during the main task objects were presented on only one-quarter of trials and might therefore be perceived as oddballs (relative to faces) and could potentially influence loss aversion purely on the basis of novelty. To control for this, the change in gambling propensity was additionally calculated using the data from the object-only block completed by participants immediately after scanning, instead of the object trials presented during the scan. The results were the same irrespective of which object condition was used for comparison in the non-emotional trials. The change in propensity to gamble between emotional and non-emotional trial significantly correlated with trait anxiety in both cases (object trials presented during the scan: $r(28)=0.437$, $P=0.020$; object trials from post-scan object-only block: $r(28)=0.413$, $P=0.029$). This argues against a possible oddball effect from the object trials.

Participants then rated each of the 120 faces used inside the scanner for emotional content and arousal, from very negative to very positive, and from not at all arousing to very arousing, respectively.

Finally they completed a debriefing questionnaire in order to determine whether they suspected the true purpose of the experiment. Only one participant indicated that he suspected the actual purpose, but also stated that this thought occurred to him while answering the debriefing questions and not while he was performing the task; therefore, his data were included in the analysis.

4.3.6 Behavioural data analysis

Behavioural data were analysed using IBM SPSS Statistics (v.21) and Matlab. Missed gamble trials were excluded. For each participant, the probability of accepting the gamble (P_{accept}), mean reaction time (RT) to accept or reject the gamble, number of missed trials, and working memory accuracy were calculated separately for the different emotion conditions and submitted to repeated-measures analysis of variance (ANOVA) in order to assess the impact of emotion on behaviour. Trait anxiety scores were added as covariates in the analyses (**Table 4-1**).

In order to assess loss aversion a two-parameter model was estimated based on Prospect Theory's subjective utility function (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992; Sokol-Hessner et al., 2009; Chib et al., 2012), following the methods described in section **2.4** (**Chapter 2**). Specifically, for each trial, the subjective utility (u) of each gamble was estimated using equation **2.3**, assuming that $\rho_{gain} = \rho_{loss} = 1$, resulting in:

$$u(gamble) = 0.5 \cdot G + 0.5 \cdot \lambda \cdot L \qquad \textbf{(Eq. 4-1)}$$

(with losses L entered as negative values). These utility values were then used in a softmax function (**Eq. 2-6**) to estimate the probability of accepting each gamble (coded as 0 or 1 for each rejected or accepted gamble, respectively).

Different models were run using this procedure, where loss aversion (λ) and choice consistency (μ) parameters were estimated. A first Prospect Theory model (**Eq. 4-1** and **2-6** as above) was estimated with all trials included independently of emotion condition (Model 1). Both parameters were successfully estimated by the model in 28 out of 30 participants. The remaining two participants' choice behaviour was very inconsistent ($\mu<0.8$ and $\lambda<0$), resulting in poor model fits, and their data were excluded from the analyses. The mean loss aversion parameter (λ) was 1.56 (SD±0.92, range 0.63–5.44), significantly greater than 1 (one-sample t-test: $t(27)=3.21$, $P=0.003$).

In order to assess the impact of emotion on loss aversion and choice consistency, four further models were estimated:

- Model 2: λ and μ estimated separately for trials with emotional (happy and fearful faces) and non-emotional (neutral faces and objects) primes: 4-parameter model

- Model 3: λ and μ estimated separately for each of the four conditions (happy, fearful, neutral, and objects): 8-parameter model

- Model 4: λ estimated separately for emotion and no emotion trials; μ estimated separately for each of the four conditions: 6-parameter model

- Model 5: λ estimated separately for each of the four conditions; μ estimated separately for emotion and no emotion trials: 6-parameter model

To assess whether estimating λ and μ for emotional versus non-emotional contexts was more parsimonious than estimating them separately for each of the four conditions, BIC scores (Schwartz, 1978) were calculated for each model and each participant (see section **2.4.2** for details). Sum of BIC scores across all participants for the two-condition model (emotional & non-emotional – Model 2) was 3,212 while sum of BICs for the other models including one or both parameters estimated separately for the four conditions (happy, fearful, neutral & object) were 3,646, 3,400 and 3,460 for Models 3, 4 and 5, respectively. BIC was lower for Model 2 than for all the other models; therefore, the two-condition model was used preferentially in all analyses, other than to verify that the effects obtained were independent of valence or face processing per se.

The percentage change in λ and in μ between emotional and non-emotional conditions was calculated from this two-condition model. Both variables were normally distributed with Skewness values smaller than 1 and Kurtosis values smaller than 3 (percentage change in λ: Skewness=-0.252, Kurtosis=0.669; percentage change in μ: Skewness=0.672, Kurtosis=2.033). However, the distribution of the loss aversion parameter λ was positively skewed, so when analyses where run on this parameter per se (e.g. correlation between loss aversion and trait anxiety), λ values were log-transformed before running statistical tests.

To estimate risk aversion a procedure reported previously was used (De Martino et al., 2010), based on the behavioural sensitivity to gamble variance (O'Neill and Schultz, 2010). When gamble variance is high (e.g. win £10/lose £10 relative to win £2/lose £2), the risk is high; therefore, risk averse individuals will exhibit a stronger reduction in gamble acceptance as gamble variance increases. To calculate this sensitivity to gamble variance, a linear regression was run between gamble variance (calculated for each gamble as $[0.5*\text{gain}–0.5*\text{loss}]^2$, with losses entered as negative values) and the probability of gamble acceptance (calculated for groups of gambles with the same variance). For each subject, risk aversion was approximated by the negative value of this regression slope, separately for emotional and non-emotional conditions. Note that the design of the task did not allow to concurrently estimate loss and risk aversion in the same utility model. To do so, the task could have included a subset of trials where risk is present, but losses do not need to be weighted against gains, so that the model can distinguish between risk and loss aversion. However, because of fMRI time constraints, it was not possible to add these trials to the task. Risk aversion was therefore estimated separately and added as a covariate in the analyses to ensure it did not affect the results. In particular, to ensure that the influence of trait anxiety was specific to the change in loss aversion, partial correlations were conducted, in which emotion-driven change in loss aversion was correlated with trait anxiety while controlling for changes in risk aversion and choice consistency.

4.3.7 MRI data acquisition

Neuroimaging data were collected on a Siemens Avanto 1.5T MRI scanner using a 32-channel head coil. To correct for inhomogeneities of the static magnetic field, fieldmaps were acquired and used in the unwarping stage of data preprocessing. Four functional scanning sessions, composed of 4 dummy and 203 functional volumes, were acquired using a pre-scan normalized gradient echo-planar imaging (EPI) sequence with the following parameters: volume repetition time=3.132s, echo time=50ms, flip angle=90^{o}, matrix=64x64, voxel size=3x3x3mm^3, 36 axial slices sampled for whole brain coverage, tilt=-30^{o}. A T1-weighted MPRAGE anatomical scan was acquired at the end of the session (176 sagittal slices, repetition time=2.73s, echo time=3.57ms, flip angle=7^{o}, matrix=224x256, voxel size=1x1x1mm^3).

4.3.8 MRI data processing and analysis

MRI data preprocessing and analysis was performed using SPM8 software (Wellcome Trust Centre for Neuroimaging, London, UK, http://www.fil.ion.ucl.ac.uk/spm) in Matlab. The first four volumes of each functional session were discarded from the analyses to allow for T1 equilibration. A field map was then created for each functional session using the SPM FieldMap toolbox. Using this field map file for phase correction, images were realigned to the first functional volume of each session and unwarped using 7th degree B-spline interpolation. Movement plots were checked to ensure that any scan-to-scan translations greater than one-half of a voxel (1.5 mm) or rotations greater than 1 degree did not cause artifacts in the corresponding scan(s). If artifacts were detected, the corrupted scans were removed and replaced by an average of the previous and following scans and the corrupted scan was added as a regressor of no interest in the design matrix. The anatomical scan was coregistered to the unwarped mean functional image. All images were then reoriented such that the anterior commissure lay at coordinates [x=0, y=0, z=0]. Functional images were spatially normalized to the standard MNI EPI template using 7th degree B-spline interpolation, and smoothed using a 4 mm3 full-width at half maximum (FWHM) Gaussian kernel. After defining and estimating contrasts, the resulting contrast images were smoothed again using a 7 mm FWHM kernel, such that the final images included in the second level models were smoothed by $\sqrt{(4^2+7^2)} \approx 8$ mm.

For each participant, the GLM was used to model BOLD signals during the task, incorporating an AR(1) model of serial correlations and a high-pass filter at 1/128s. Two first-level models were defined. The first model identified brain regions tracking gain and loss value independent of emotion (similar to Tom et al., 2007). It included the following regressors (and associated durations), collapsed across all memory conditions and convolved with the SPM synthetic hemodynamic response function: prime onset (3s); gamble onset (2s) with gain value, loss value (coded as negative values), and choice difficulty (distance between gamble expected value and participant's indifference point) as parametric modulators; memory probe onset (stick function); missed gamble onset (if any: stick function). The 6 movement parameters were also included in the model.

To assess whether these responses were modulated by emotion, another model contained the same regressors as above, but separately for emotional trials (happy and fearful faces) and non-emotional trials (neutral faces and objects). This constituted the primary analysis based on the behavioural results suggesting that grouping trials into emotional and non-emotional ones was most parsimonious. However, to ensure that the effects were not driven by face processing *per se* and to contrast emotional with neutral faces, a further model was estimated in which neutral face and object trials were modelled separately.

First-level contrasts were created through linear combinations of the resulting beta images, and analysed at the group level with one-sample t-tests, using the standard summary-statistics approach to random-effects analysis in SPM. A cluster-forming threshold of $P<0.001$ uncorrected was applied, followed by FWE correction at $P<0.05$, using SVC in a priori ROIs. These were: bilateral ventral striatum (caudate and putamen, left and right combined) given its role in loss aversion (Tom et al., 2007; Canessa et al., 2013), and bilateral amygdala, given its role in processing emotion (Adolphs, 2002; Glascher and Adolphs, 2003; Dalgleish, 2004; Phelps, 2006; Pessoa and Adolphs, 2010; Wang et al., 2014). ROIs were anatomically defined using the Automated Anatomical Labeling (AAL) atlas in the SPM WfuPickAtlas toolbox (Tzourio-Mazoyer et al., 2002).

4.3.9 Functional connectivity analyses

Amygdala-striatum functional connectivity was analysed using PPI in SPM8. First, the ventral striatum cluster found to track value (using a $P<0.001$ (uncorrected) threshold and masked with the anatomical ROI) was used as the seed region. BOLD timeseries was extracted across all voxels in this mask, and adjusted for all effects of interest. A first-level model was created for each participant including the deconvolved striatal BOLD timeseries (physiological regressor), the emotional context (contrast between emotional and non-emotional trials at the time of the gamble: psychological regressor) and their cross-product (PPI regressor). This model also included the following regressors: prime onset, memory probe onset, parametric modulators for gains and losses at gamble onset, all split by emotion condition, as well as missed gamble onset (if any) and movement regressors. Two nuisance timeseries were also added, from a white-matter voxel (corpus callosum body, MNI coordinates: 0,14,19) and from a cerebrospinal fluid voxel (centre of right lateral ventricle, MNI coordinates: 4,14,18); both in the same y-plane as the ventral striatum peak voxel. Finally, contrasts were defined on the striatal timeseries (physiological) regressor, modelling "main effect" functional connectivity, and on the PPI regressor, modelling the modulation of functional connectivity by emotional context, which were analysed at the second level. Again, in order to make sure that the observed effects were driven by emotional faces rather than faces in general, the PPI analysis was repeated for emotional versus neutral faces trials at the time of the gamble (excluding the object condition).

4.4 Results

4.4.1 Emotional modulation of loss aversion depends on trait anxiety

Emotional stimuli increased loss aversion (λ) in individuals with low trait anxiety. The percentage change in loss aversion was calculated for each participant between emotional and non-emotional trials, thus removing inter-individual variability due to loss aversion values *per se*, and related to trait anxiety scores across participants. There was a significant negative relationship between emotion-driven change in loss aversion and trait anxiety ($r(28)=-0.524$, $P=0.004$, **Figure 4-2A**), such that low anxious individuals showed the greatest increase in loss aversion induced by emotional cues. Importantly, baseline loss aversion (modelled across all trials independent of emotion condition and log-transformed because positively skewed) was not correlated with trait anxiety ($r(28)=-0.031$, $P=0.88$; after removing one outlier with very high λ: $r(28)=0.043$, $P=0.83$), suggesting that the effect of trait anxiety on loss aversion change is not simply driven by regression to the mean.

The percentage change in risk aversion between emotional and non-emotional trials, although highly correlated with change in loss aversion ($r(28)=0.65$, $P<0.001$; expected given that loss and risk aversion were estimated separately; see De Martino et al., 2010; Canessa et al., 2013), was not correlated with trait anxiety ($r(28)=-0.23$, $P=0.24$). Finally, the correlation between emotion-induced change in loss aversion and trait anxiety was unchanged when controlling for change in risk aversion and change in choice consistency (partial correlation, $r(28)=-0.51$, $P=0.008$). Note that most participants exhibited a negative sensitivity to gamble variance (mean beta = -0.0014 ± 0.0026, significantly negative: $t(27)=-2.80$, $P=0.009$), meaning that their propensity to choose the gamble decreased as gamble variance increased, consistent with risk aversion. There was no correlation between risk aversion and trait anxiety ($r(28)=-0.22$, $P=0.26$).

Table 4-1. Emotional modulation of task variables and interaction with trait anxiety.

	Emotion (Fearful + Happy)	**No Emotion** (Neutral + Object)	**Paired t-test**	**Interaction with trait anxiety**
P_{accept}	0.607 (0.171)	0.607 (0.165)	t(27)=0.009 P=0.99	F(1,26)=6.12 P=0.02*
λ (loss aversion)	1.563 (0.953)	1.553 (0.894)	t(27)=0.623 P=0.54	F(1,26)=4.53 P=0.04*
μ (choice consistency)	2.486 (1.83)	2.020 (1.274)	t(27)=2.244 P=0.033*	F(1,26)=1.81 P=0.19
Sensitivity to gamble variance (risk-seeking)	-0.0014 (0.0025)	-0.0016 (0.0027)	t(27)=0.951 P=0.35	F(1,26)=1.73 P=0.20
RT_{accept} (s)	1.081 (0.156)	1.072 (0.143)	t(27)=0.934 P=0.36	F(1,26)=0.001 P=0.98
RT_{reject} (s)	1.216 (0.183)	1.224 (0.187)	t(27)=-0.582 P=0.57	F(1,26)=0.199 P=0.66
Missed gamble responses (% trials)	2.81 (3.51)	3.21 (3.61)	t(27)=-0.869 P=0.39	F(1,26)=2.395 P=0.13
WM accuracy (2 stimuli)	0.935 (0.057)	0.938 (0.045)	t(27)=-0.278 P=0.78	F(1,26)=1.89 P=0.18
WM accuracy (4 stimuli)	0.665 (0.129)	0.662 (0.134)	t(27)=0.141 P=0.89	F(1,26)=2.137 P=0.16
Missed WM responses (% trials)	3.43 (5.05)	3.68 (4.76)	t(27)=-0.893 P=0.38	F(1,26)=1.319 P=0.26
Mean arousal rating (scale from 1 to 100)	50.8 (20.3)	30.66 (14.2)	t(27)=5.345 P<0.001*	F(1,26)=1.815 P=0.19
Mean valence rating (scale from 1 to 100)	48.5 (7.17)	42.3 (8.23)	t(27)=4.105 P<0.001*	F(1,26)=0.258 P=0.62

For each condition, means and standard deviations across participants are reported, for the following variables: probability to accept the gamble (P_{accept}), loss aversion parameter (λ), reaction time to accept and reject the gamble in seconds (RT_{accept} and RT_{reject}), number of missed gamble responses, working memory (WM) accuracy for the 2- and 4-stimulus conditions, number of missed memory responses, mean arousal and valence ratings (on a scale from 0 to 100). The main effect of condition and its interaction with trait anxiety were assessed and the corresponding statistics are reported in the last two columns. Apart from arousal and valence ratings, none of these variables were modulated by emotional stimuli. Only the emotional modulation of gamble acceptance and loss aversion (λ) varied according to trait anxiety. Averaged across all participants, the percentage change in loss aversion was not significantly different from zero (mean=1.01%, SD=7.8%, range=-18.08%-16.21%, one-sample t-test: t(27)=0.685, P=0.499).

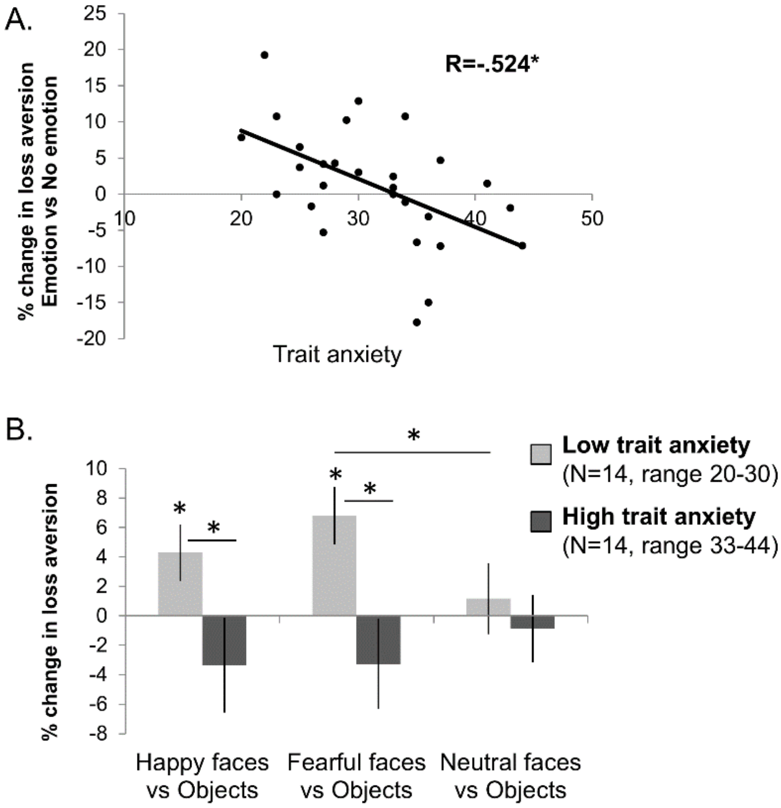


Figure 4-2. Emotional cues increase loss aversion in low-anxious individuals. A. The change in loss aversion following emotional relative to non-emotional primes was negatively correlated with trait anxiety across participants. **B.** Participants with low trait anxiety (median-split, N=14 per group) showed a significant increase in loss aversion following both happy and fearful stimuli. Collapsing fearful and happy trials into an emotional condition and neutral and object trials into a non-emotional condition was justified by the fact that there was no valence effect, and no differences between neutral faces relative to object stimuli. Two-tailed *P*-values: * *P*<0.05. Error bars represent SEM.

Performing a median split on trait anxiety scores confirmed the emotional modulation of loss aversion, revealing a significant condition (emotion/no emotion) * trait anxiety (low/high) interaction ($F(1,26)=6.96$, $P=0.014$). While the "low" anxious group showed a significant increase in loss aversion following emotional relative to non-emotional stimuli (+5.49%, SD=6.38%, $t(13)=3.22$, $P=0.007$), there was no significant effect of emotion on loss aversion in the "high" trait anxiety group (-2.81%, SD=7.52%, $t(13)=-1.40$, $P=0.18$).

To check that collapsing emotional (happy/fearful) and non-emotional (neutral/object) conditions together did not alter the results, the change in loss aversion was examined separately for each condition (happy, fearful and neutral) relative to object (**Figure**

4-2B). First, there was no difference between positive and negative emotion: the valence (happy/fearful)*trait anxiety group (low/high) interaction was non-significant ($F(1,26)=0.24$, $P=0.63$) and the effect of trait anxiety group on emotionally-driven changes in loss aversion was significant for happy and fearful faces separately (happy: $t(26)=2.04$, $P=0.05$; fearful: $t(26)=2.75$, $P=0.01$). Second, the effect of neutral faces relative to object stimuli on loss aversion did not differ between trait anxiety groups ($t(26)=0.6$, $P=0.55$). Third, model comparison analyses showed that estimating loss aversion for emotional and non-emotional trials (i.e. collapsing happy and fearful together, and neutral and object together) was more parsimonious than estimating loss aversion separately for all conditions.

Increased loss aversion following emotional cues, as identified in low anxious individuals (**Figure 4-2A**) should be accompanied by a corresponding decrease in the propensity to gamble, as subjective utilities will be perceived as lower when losses loom larger. Consistent with this, there was a significant positive relationship between trait anxiety and the increase in the proportion of accepted gambles from non-emotional to emotional trials ($r(28)=0.437$, $P=0.020$).

Analyses of the choice consistency parameter (μ) revealed that participants were more consistent in their gambling choices on emotional than on non-emotional trials ($t(27)=2.24$, $P=0.033$, **Figure 4-3** and **Table 4-1**), though this effect did not correlate significantly with trait anxiety ($r(28)=-0.31$, $P=0.12$). Similarly, only the emotional modulation of gamble acceptance and loss aversion correlated significantly with trait anxiety, ruling out the possibility that differences in memory, RTs or missed trials may have driven the observed effects (**Table 4-1**).

Taken together, the behavioural results suggest that emotional cues trigger changes in loss aversion as a function of trait anxiety, such that low anxious individuals show the greatest emotionally-induced increase in loss aversion. In addition, this effect is not driven by risk aversion, or by choice consistency. Finally, and surprisingly, both positive and negative emotional stimuli have a similar effect.

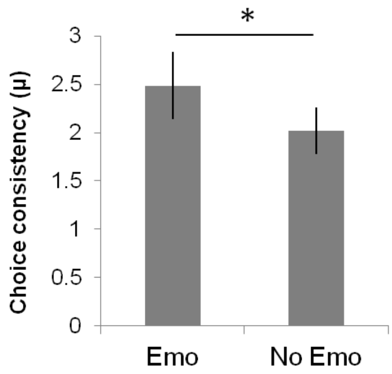


Figure 4-3. Choice consistency increases under emotion. Choice consistency parameter (inverse temperature) μ was significantly higher on emotional relative to non-emotional trials. Two-tailed *P*-values: * *P*<0.05. Error bars represent SEM.

4.4.2 Neural responses to decreasing losses are greater than to increasing gains

The first step in the fMRI data analysis was to verify that expected value signals were observed in the brain at the time of gamble, with exaggerated responses to losses ("neural loss aversion") in the ventral striatum. Next, responses to emotional primes were examined, as well as emotional modulation of value signals in the amygdala. Finally, the interaction between these two regions was investigated using functional connectivity. For all analyses the relationship with trait anxiety was also assessed.

A whole-brain analysis was first conducted to identify clusters with a parametric response to decreasing losses and increasing gains, time-locked to the presentation of the decision and independent of emotion condition. This "gain & loss" contrast is equivalent to a single parametric modulator representing the expected value of the gamble (0.5*gain+0.5*loss, with losses coded as negative values). Three clusters surviving whole-brain correction for multiple comparisons were found to track gamble value (**Table 4-2A**), located in the right ventral striatum (**Figure 4-4A**), right amygdala/hippocampus (**Figure 4-4B**), and anterior cingulate/orbitofrontal cortex (**Figure 4-4C**), confirming previous reports of generic value signals in these regions (Gottfried et al., 2003; Tom et al., 2007; Kable and Glimcher, 2009; Morrison and Salzman, 2010).

Parameter estimates (betas) were extracted for each region, separately for losses and gains. There was a greater parametric response to decreasing losses relative to increasing gains in each of these three regions (significant in the ventral striatum, t(27)=3.52, P=0.002; and amygdala, t(27)=3.16, P=0.004; marginally significant in the ACC/OFC, t(27)=1.95, P=0.06; **Figure 4-4D-F**), consistent with previous reports of loss-biased value signals in these regions (Tom et al., 2007; Canessa et al., 2013; Sokol-Hessner et al., 2013).

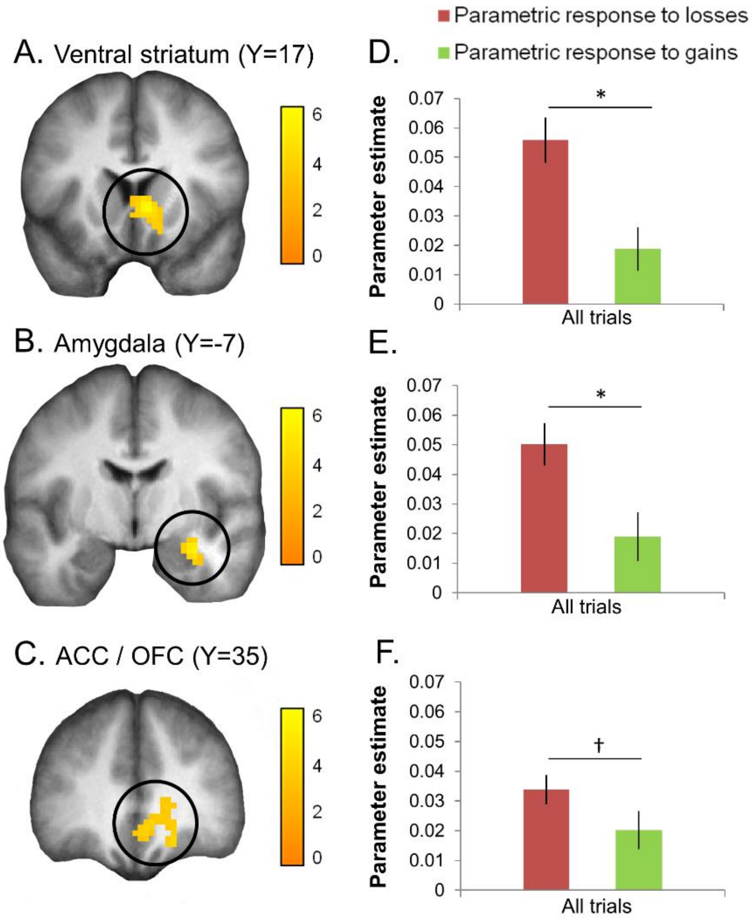


Figure 4-4. Brain regions tracking gamble expected values. A whole-brain analysis was conducted to identify regions showing a parametric response to decreasing losses and to increasing gains. Clusters surviving whole-brain FWE correction were found in the ventral striatum (**A**), the amygdala extending into the hippocampus (**B**), and the anterior cingulate (ACC)/orbitofrontal cortex (OFC) (**C**). Activations are displayed at P<0.001 (uncorrected) on the average anatomical scan from all 28 participants. Colour bars represent T-values. (**D-F**) Parameter estimates (betas) extracted from the parametric response to losses (red bars) and to gains (green bars) separately revealed greater tracking of losses relative to gains in these regions (at trend level in the ACC). Note that the latter contrasts are orthogonal to that used for voxel identification and therefore do not require correction for a voxel-wise search. Two-tailed P-values: * P<0.05, † P<0.1. Error bars represent SEM.

Table 4-2. Brain regions exhibiting an expected value signal (A) and a neural loss aversion signal (B) at the time of gamble.

A. Parametric response to decreasing losses and increasing gains (expected value signal)								
All p(unc)<0.001, k>10		**size**	**T**	**x**	**y**	**z**	**Type of FWE correction**	**P(FWE-corr)**
Ventral striatum (**Figure 4-4A**)	R	144	6.14	9	17	-2	Whole-brain, cluster-level	0.0017
Amygdala / Hippocampus (**Figure 4-4B**)	R	184	5.63	33	-7	-20	Whole-brain, cluster-level	<0.001
ACC / OFC (**Figure 4-4C**)	med/ R	106	4.75	21	38	-14	Whole-brain, cluster-level	0.008
Precuneus	R	21	5.01	18	-55	43		
Cerebellum	med	25	4.73	0	-67	-29		
Fusiform gyrus / Cerebellum	L	12	4.38	-21	-55	-20		
Superior frontal gyrus	R	14	4.24	21	50	10		
Caudate head	L	21	4.05	-18	26	1		
B. Parametric response to decreasing losses > Parametric response to increasing gains (neural loss aversion signal)								
All p(unc)<0.001, k>10		**size**	**T**	**x**	**y**	**z**	**Type of FWE correction**	**P(FWE-corr)**
Precuneus / Occipital gyri	R&L	328	5.17	24	-64	19	Whole-brain, cluster-level	<0.001
Ventral striatum (**Figure 4-5A**)	R	42	4.61	12	14	-8	SVC, peak-level	0.026
Precuneus / Superior parietal	R	11	4.57	18	-49	46		
Hippocampus	R	28	4.50	24	-25	-17		
Occipital gyrus	L	36	4.43	-15	-76	-8		
Cerebellum	R	13	4.26	6	-52	-17		

The analysis was initially thresholded at P<0.001 (uncorrected), cluster size ≥10. For completeness, clusters of at least 10 contiguous voxels that did not survive FWE correction are also reported. ACC – anterior cingulate cortex. OFC – orbitofrontal cortex.

The result in the ventral striatum was confirmed by creating a loss minus gain contrast (similar to Tom et al., 2007). Specifically, to identify regions in the brain where the parametric response to decreasing losses was greater than the parametric response to increasing gains, the contrast [parametric response to losses > parametric response to gains] was explored across the whole brain, independent of emotion condition. This voxel-wise search yielded a cluster in the ventral striatum that responded more strongly to decreasing losses than increasing gains, overlapping with that reported above, as well as a cluster in bilateral precuneus/occipital cortex (**Figure 4-5A** and **Table 4-2B**). In other words, responses in these regions tracked decreasing losses significantly more strongly than increasing gains (equivalent to the "neural loss aversion" signal identified by Tom et al., 2007). However, none of these activations was related to loss aversion behaviourally across participants, even when excluding an outlier with a very high loss aversion value (all r<0.25 and P>0.2).

Interestingly, biased striatal parametric responses to losses relative to gains (contrast estimate averaged across the cluster) were negatively correlated with trait anxiety (r(28)=-0.392, P=0.039, **Figure 4-5B**). Further analysis showed that this effect was primarily driven by parametric response to losses: ventral striatum response to decreasing losses correlated significantly negatively with trait anxiety (r(28)=-0.478, P=0.01, **Figure 4-5C**), whereas the response to gains did not (r(28)=-0.016, P=0.94). These two correlations were significantly different (Steiger's Z=1.98, P<0.05).

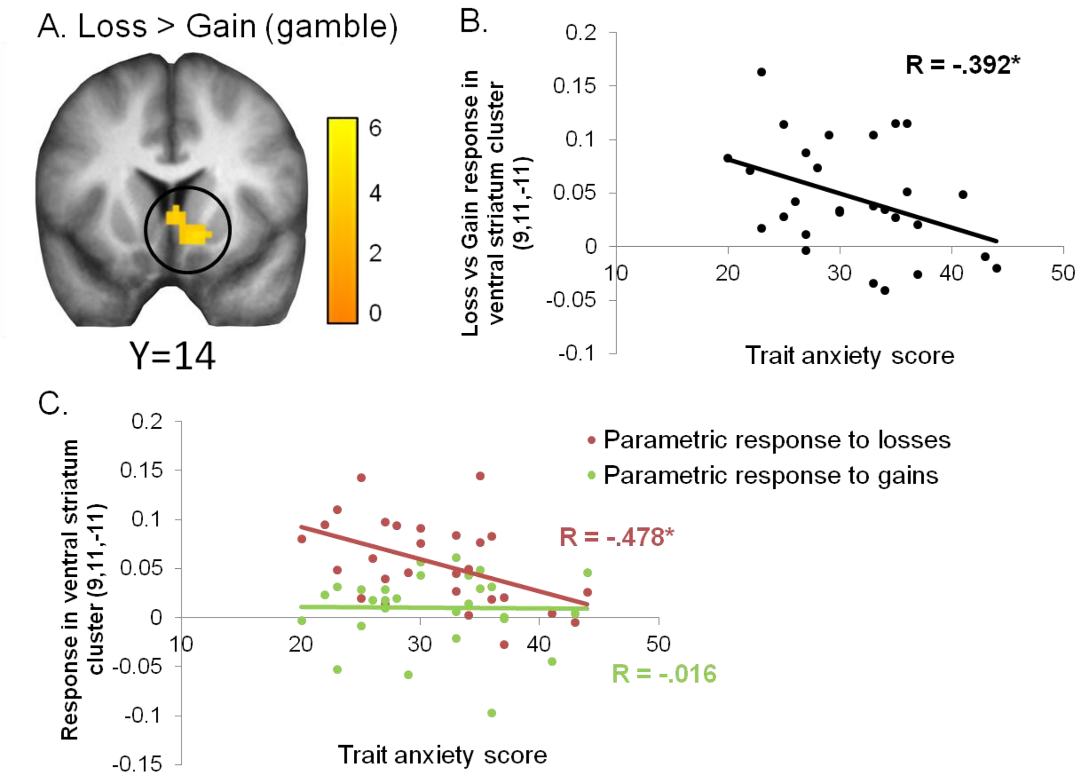


Figure 4-5. Striatal loss aversion signals. A. A cluster in the right ventral striatum showed a greater parametric response to decreasing losses than to gains. Activation is displayed at P<0.001 (uncorrected), but survived small volume correction (P_{SVC}<0.05) in the anatomically defined striatal ROI (bilateral caudate + putamen). The colour bar represents T-values and voxels are overlaid on the average anatomical scan from all 28 participants. **B.** Trait anxiety was negatively associated with the magnitude of this biased loss vs gain signal in the ventral striatum. **C.** Specifically, the parametric response to losses, but not to gains, was negatively correlated with trait anxiety: the less anxious the participant, the greater the response to decreasing losses, but not to increasing gains, in the ventral striatum.

4.4.3 Amygdala response to emotional cues correlates positively with trait anxiety

In a second analysis, time-locked to the presentation of the prime, the contrast between emotion (happy and fearful faces) and non-emotion (neutral faces and objects) trials was explored. Consistent with prior reports (Sabatinelli et al., 2011) this revealed a widespread pattern of activation, with whole-brain corrected results in the fusiform gyrus, occipital gyrus, OFC/medial PFC, posterior cingulate cortex, middle temporal gyrus, anterior insula, inferior temporal gyrus extending into frontal gyrus, and amygdala extending into bilateral hippocampus (**Table 4-3**). Given previous literature suggesting that amygdala responses vary with anxiety (Etkin et al., 2004; Stein et al., 2007; Sehlmeyer et al., 2011), signal from the right amygdala cluster was extracted (peak voxel MNI coordinates: 33, -1, -26; **Figure 4-6A**), showing a significant positive relationship with trait anxiety ($r(28)=0.417$, $P=0.027$; **Figure 4-6B**). This relationship was not driven by responses to faces in general – while amygdala responses to emotional relative to neutral faces correlated with trait anxiety ($r(28)=0.39$, $P=0.04$), amygdala responses to neutral faces relative to objects did not ($r(28)=-0.042$, $P=0.83$; marginally significant difference between the two correlations: Steiger's $Z=1.83$, $P=0.067$).

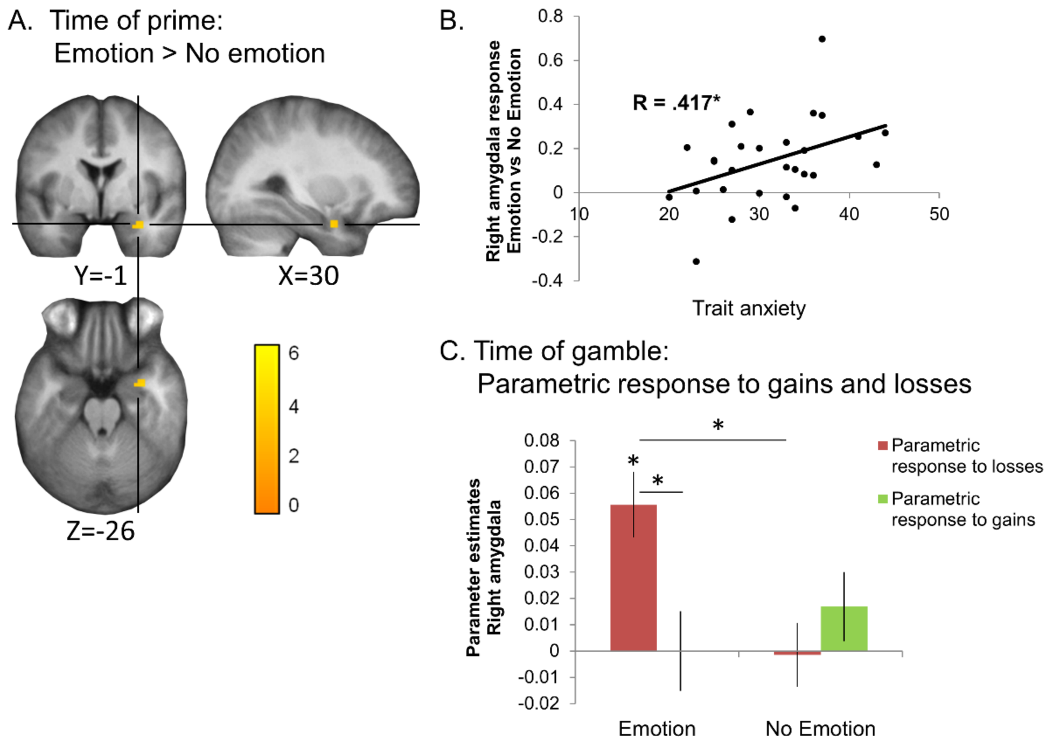


Figure 4-6. Modulation of amygdala responses by emotional cues. A. A cluster in the right amygdala showed greater response to emotional versus non-emotional primes (i.e. at initial stimulus presentation). Activation is displayed at P<0.001 (uncorrected), but survived FWE voxel-level small volume correction (P_{SVC}<0.05) in the anatomically defined bilateral amygdala ROI. The colour bar represents T-values and voxels are overlaid on the average anatomical scan from all 28 participants. **B.** Amygdala response to emotional primes was positively correlated with trait anxiety. **C.** Extracting parametric response to losses and to gains in this amygdala cluster at the time of gamble, separately for emotion and no emotion trials, revealed that the amygdala only tracks decreasing losses following emotional cues. Two-tailed P-values: * P<0.05. Error bars represent SEM.

Table 4-3. Brain regions showing response to emotional relative to non-emotional stimuli during presentation of the prime.

Emotion>No Emotion during stimuli presentation. All p(unc)<0.001		size	T	x	y	z	Type of FWE correction	P(FWE-corr)
Fusiform gyrus	R	208	12.55	42	-52	-23	Whole-brain, cluster-level	<0.001
	L	133	8.14	-42	-58	-26		0.002
Occipital gyrus	R	349	8.38	24	-94	-8	Whole-brain, cluster-level	<0.001
	L	354	8.10	-30	-91	-17		<0.001
OFC / mPFC	med	901	7.94	0	56	-8	Whole-brain, cluster-level	<0.001
PCC	med	273	6.47	-3	-49	28	Whole-brain, cluster-level	<0.001
Middle temporal gyrus	L	258	6.28	-57	-13	-20	Whole-brain, cluster-level	<0.001
	R	125	5.86	57	-10	-26		0.003
	R	105	5.08	66	-49	1		0.007
Anterior insula	L	160	5.96	-39	20	-17	Whole-brain, cluster-level	0.001
Inferior temporal / frontal gyrus	R	116	5.18	33	23	-29	Whole-brain, cluster-level	0.005
Hippocampus / Amygdala	L	65	5.45	-21	-13	-20	Whole-brain, cluster-level	0.049
	R	51	5.72	21	-10	-20		0.10
Amygdala ROI	L	2	4.19	-18	-7	-17	SVC, peak-level	0.011
	R	9	4.17	33	-1	-26		0.011

The analysis was initially thresholded at P<0.001 (uncorrected), cluster size ≥10. To identify effects in the amygdala, a bilateral anatomical ROI was used to perform small volume correction without a cluster size criterion.

4.4.4 Emotional cues modulate loss aversion signals in the amygdala

To test whether the above amygdala responses play a role in the observed emotion-driven changes in loss aversion, parametric responses to losses and to gains (at the time of the gamble) were extracted separately for emotional and non-emotional trials, from the right amygdala cluster identified above (responding to emotional primes - MNI: 33, -1, -26). The resulting parameter estimates (betas) were submitted to a 2-(gamble component: loss/gain) by-2 (prime: emotional/non-emotional) repeated-measures ANOVA. There was a significant interaction (F(1,27)=7.998, P=0.009, **Figure 4-6C**), driven by a positive amygdala parametric modulation, on emotional trials only, by decreasing losses (t(27)=3.61, P=0.001) but not increasing gains (t(27)=-0.88, P=0.39). However, there were no relationships with trait anxiety or emotion-elicited change in loss aversion (added as covariates: all P>0.25).

The above modulation of amygdala value signal was specific to emotional cues, rather than faces in general. When extracting the response to losses separately for emotion, neutral and object conditions, and submitting the resulting betas to a one-way ANOVA (emotion/neutral/object), there was a significant main effect of emotion ($F(2,54)=3.49$, $P=0.038$). The amygdala parametric response to losses was higher on emotional face relative to neutral face trials ($t(27)=3.08$, $P=0.005$), but not on neutral face relative to object trials ($t(27)=-0.6$, $P=0.55$).

4.4.5 Striatal-amygdala functional connectivity is associated with changes in loss aversion

Are emotionally-induced changes in loss aversion driven by ventral striatum-amygdala interactions during emotional decision-making? To test this hypothesis, a PPI analysis was conducted, with emotion versus no-emotion (at the time of the decision) as the psychological factor (**Figure 4-7A**). The ventral striatum cluster (shown in **Figure 4-4A**) was defined as the seed region, and beta estimates for the physiological and PPI effects were extracted from the right amygdala cluster that responded to emotional cues (the target region: shown in **Figure 4-6A**). The increase in ventral striatum-amygdala connectivity between non-emotional and emotional trials was negatively correlated with trait anxiety ($r(28)=-0.47$, $P=0.012$, **Figure 4-7B**), and positively correlated with emotion-elicited change in loss aversion ($r(28)=0.42$, $P=0.025$, **Figure 4-7C**). In other words, low anxious individuals exhibited an increase in striatal-amygdala functional connectivity on emotional trials, which in turn was associated with emotion-elicited loss aversion.

Again, this pattern of results held when examining the emotion-driven change in striatal-amygdala connectivity, excluding the object condition (negative correlation between PPI and trait anxiety: $r(28)=-0.38$, $P=0.047$), suggesting that trait anxiety modulates functional connectivity changes specifically in response to emotional stimuli.

Functional connectivity across the entire fMRI time series (or “main effect” functional connectivity) was estimated from the physiological (striatal) regressor in the PPI model. The “main effect” connectivity between ventral striatum and amygdala was significantly positive (mean beta=0.111, SD=0.017, $t(27)=6.60$, $P<0.0001$), thus confirming pronounced coupling between ventral striatum and amygdala (Roy et al., 2009). There was no correlation between this "main effect" coupling and trait anxiety (r(28)=-0.14, P=0.48). The emotional modulation of this functional connectivity between the ventral striatum and the amygdala (the PPI effect) was non-significant across all subjects (t(27)=0.76, P=0.46). In addition, an exploratory whole-brain analysis of the PPI effect (P<0.001 uncorrected, k>10 voxels) revealed no supra-threshold clusters where the connectivity with the ventral striatum seed region was modulated by emotion.

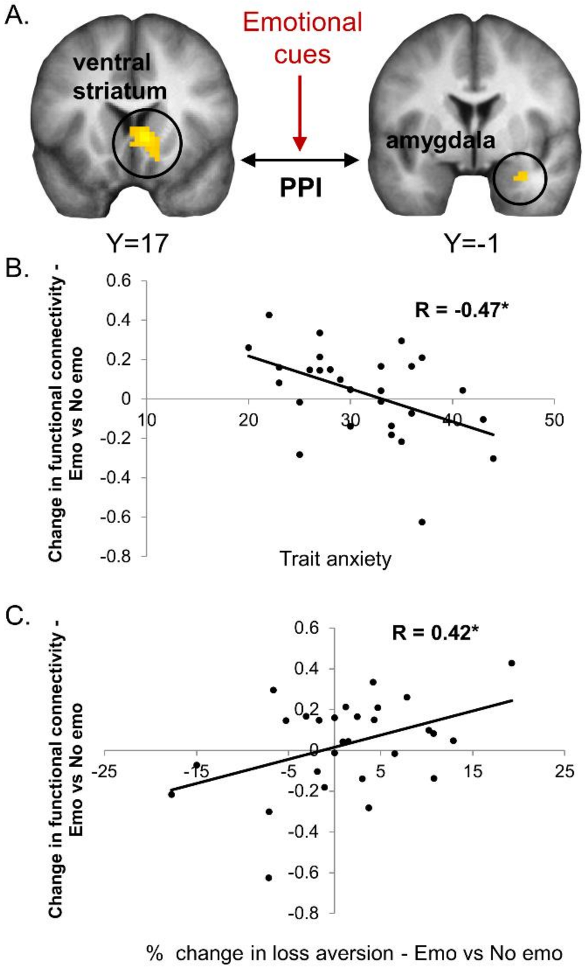


Figure 4-7. Emotional modulation of striatum-amygdala functional connectivity is related to trait anxiety and loss aversion change. A. Psychophysiological interaction (PPI) analysis was conducted to assess how ventral amygdala-striatum functional connectivity was modulated by emotional relative to non-emotional cues, using the ventral striatum cluster as a seed (**Figure 4-4A**). **B.** The PPI effect (i.e. emotion-driven increased connectivity) in the amygdala was negatively correlated with trait anxiety. In other words, low anxious individuals exhibited increased ventral striatum-amygdala connectivity following emotional relative to non-emotional stimuli. **C.** This increased functional connectivity was associated with emotion-elicited increase in loss aversion across participants.

4.5 Discussion

How people alter their decisions in response to emotional cues, and the neural mechanisms underlying such changes, vary with their level of trait anxiety. Specifically, low-anxious individuals exhibit increased loss aversion when primed with emotional cues. This was accompanied by and associated with increased functional coupling between the striatum and amygdala, regions that have been implicated in loss aversion (Tom et al., 2007; De Martino et al., 2010; Canessa et al., 2013; Sokol-Hessner et al., 2013).

One of the main aims was to establish whether loss aversion would be modulated by emotional cues to a greater extent in low-anxious individuals (which would be predicted by greater behavioural flexibility), or in high-anxious individuals (which would be predicted by emotional hypersensitivity). The data support the first hypothesis. This is consistent with a recent study in which only low-anxious individuals decreased risk-taking under stress (Robinson et al., 2015a). This finding may reflect an adaptive ability of individuals with low anxiety to deploy harm-avoidance strategies (avoiding potential harm from monetary losses) in response to emotionally-arousing cues. This could be linked with the reduced sensitivity to pathological anxiety disorders in this low-anxiety group (Robinson et al., 2013, 2015a), and with previous reports of anxiety-related impairments in the ability to adapt behaviour to changes in the environment (Blanchette and Richards, 2003; Farmer and Kashdan, 2012; Robinson et al., 2013, 2015a; Browning et al., 2015).

An alternative interpretation of the findings could be that high anxious individuals may in fact exhibit greater attentional control than low anxious individuals and be better at ignoring the emotional primes, which are irrelevant to the gambling task. Although this interpretation is inconsistent with the theory of impaired attentional control in anxiety (Eysenck et al., 2007; Bishop, 2009), it remains possible that such superior attentional control is a feature of non-clinical anxiety (i.e. high trait anxiety in healthy individuals; see Robinson et al., 2013 for a review), and that dysfunctional attentional control only emerges in clinical anxiety. Further work is needed to distinguish between these explanations.

Recent literature has shown a growing interest in the link between anxiety and decision-making (for a review see Hartley and Phelps, 2012), and provided evidence for heightened sensitivity to uncertainty and ambiguity in high anxiety. A recent study demonstrated an increased framing effect in high anxious individuals (Xu et al., 2013). According to Prospect Theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1981, 1986), framing effects on choice could be driven both by loss aversion and by diminishing sensitivity to changes in value as value increases (resulting in risk avoidance in the gain domain and risk seeking in the loss domain). There was no direct relationship between trait anxiety and loss aversion in the data, suggesting that the increased framing effect observed in Xu et al. (2013) may be driven by stronger diminishing sensitivity to value changes in high trait anxious individuals, rather than by increased loss aversion. Similarly, the results are in line with a recent study in adolescents showing that clinically anxious and healthy adolescents did not differ in their level of loss aversion (Ernst et al., 2014). Note that the sample of healthy volunteers included a relatively constrained range of anxiety scores; it would therefore be interesting to examine loss aversion (and its modulation by emotion) in clinically anxious individuals, which was the aim of the study presented in **Chapter 5**.

The findings also indicate that positive and negative emotional expressions induced similar changes in decision-making. This supports the hypothesis that increased avoidance of potential losses is recruited under general emotional arousal, rather than specifically under incidental threat. Previous work, using a pharmacological manipulation of autonomic arousal, suggests that arousal responses specifically drive loss aversion, but not risk aversion (Sokol-Hessner et al., 2015b). Although speculative, this hypothesis of an arousal-driven loss aversion could explain the findings that (i) manipulating emotional arousal influenced loss aversion in the same direction regardless of valence and (ii) this effect was specific to loss aversion, with risk aversion (estimated separately) not altered by emotional manipulation.

However, due to time constraints in the scanner, a limitation of the task design was that it was not possible to include additional trials necessary to estimate risk aversion together with loss aversion in the same utility model. Typically this would be done by adding choices between a sure gain and a gamble (featuring a chance of a higher gain or zero); on such gain-only trials only risk aversion (but not loss aversion) should contribute to safe choices. Without these trials, the Prospect Theory-derived model could not distinguish between risk and loss aversion. Estimating risk aversion separately, using an approach that has been used before (De Martino et al., 2010; Canessa et al., 2013), and ensuring it did not contribute to the results by adding it as a covariate in the analyses was the best alternative to overcome this limitation.

Our fMRI results shed light on a potential mechanism underlying the emotional modulation of economic behaviour, related to amygdala-striatum functional connectivity. Consistent with previous studies both amygdala and ventral striatum tracked losses more strongly than gains (Tom et al., 2007; De Martino et al., 2010; Canessa et al., 2013; Sokol-Hessner et al., 2013); however, the modulation of these signals by emotional cues was not associated with emotionally-driven changes in loss aversion.

Instead, the interaction between amygdala and ventral striatum was the neural metric most related to the observed behavioural effects. Emotionally-induced changes in functional connectivity between ventral striatum and amygdala correlated negatively with trait anxiety and were associated with behavioural changes in loss aversion, with low-anxious individuals showing increased loss aversion together with increased amygdala-striatum functional connectivity in response to emotional cues. According to a recent study, a potential concern is that amygdala activations could be driven by drainage from nearby vessels such as the basal vein of Rosenthal (BVR; Boubela et al., 2015). However, in the present fMRI data there was no observed patterns consistent with BVR signals, even at a very liberal threshold (data not shown). In particular, the amygdala cluster responding to emotional relative to non-emotional primes (MNI coordinates [30,-1,-24]) did not extend to the posterior amygdala, and instead was located in the lateral anterior amygdala on the opposite side to the BVR (MNI coordinates [14.6,-7.7,-15.5] according to Boubela et al., 2015) with voxels adjacent to the BVR not activated. Therefore the amygdala activations reported in this study are unlikely to be confounded by a contribution from the BVR.

Amygdala-striatum connectivity is well established in both animal and human fMRI work and has been suggested to play a role in motivated behaviour (Price, 2003; Zorrilla and Koob, 2013), emotional memory (Ferreira et al., 2008; Paz and Pare, 2013), reward-related processes (Everitt and Robbins, 1992; Camara et al., 2008) and learning to avoid harmful negative outcomes (Delgado et al., 2009). The results provide a further insight into a potential function of amygdala-striatum interactions, suggesting that changes in functional connectivity between these two regions, as opposed to responses in each region per se, may drive the tendency towards more conservative decisions under emotionally arousing conditions.

In summary, incidental emotional cues can modulate loss averse behaviour and associated neural responses, shedding light on a potential mechanistic account of emotional influences on economic decisions (Phelps et al., 2014). A speculation resulting from the findings is that the amygdala may integrate emotional information about external cues together with value information from the ventral striatum, in order to produce a decision signal. Individual differences in amygdala-striatal coupling are related to trait anxiety, possibly reflecting improved functional integration between these regions in low anxious individuals, and greater flexibility to adapt decision-making in emotionally volatile environments.

Chapter 5 Risk and loss aversion in clinical anxiety

5.1 Abstract

Anxiety disorders are associated with disruptions in both emotional processing and decision-making. In healthy individuals these processes are known to strongly interact, such that decisions are influenced by emotional cues and states and vice versa. However, whether these interactions are altered in clinical anxiety remains an unresolved and important question with the potential to provide a better cognitive understanding of anxiety disorders. To address this question, patients with Generalized Anxiety Disorder (GAD) and matched healthy controls completed a gambling task, featuring a decision between a gamble and a safe (certain) option on every trial. Each decision was preceded by happy, fearful, or neutral faces, or object primes. One type of gamble featured only wins ("gain-only"); the other type involved weighing a potential win against a potential loss ("mixed"); allowing to assess risk and loss aversion respectively by fitting a computational Prospect Theory model to participants' choice data. Relative to healthy controls, GAD patients exhibited enhanced risk aversion, but equivalent levels of loss aversion. However, both risk and loss aversion seemed robust to priming by emotional cues. These findings suggest that economic decision-making in clinical anxiety is characterized by a reduced propensity to take risks, not by a stronger aversion to losses.

5.2 Introduction

Anxiety disorders constitute a major global health burden (Beddington et al., 2008), and are characterized by negative emotional processing biases, as well as disrupted working memory and decision-making (Hartley and Phelps, 2012; Paulus and Yu, 2012; Robinson et al., 2013). Understanding impaired cognitive processing in anxiety disorders is important as it could help to improve cognitive-based therapies for anxiety by better targeting the specific processes that are disrupted.

In particular, patients with anxiety frequently report difficulties concentrating and making decisions. When faced with risky economic decisions, individuals with an anxiety disorder (Butler and Mathews, 1983; Maner et al., 2007; Mueller et al., 2010; Giorgetta et al., 2012; Ernst et al., 2014) or healthy individuals with high dispositional anxiety (Maner and Schmidt, 2006; Maner et al., 2007; Lorian and Grisham, 2010; Mueller et al., 2010) exhibit increased risk avoidant behaviour.

For example, in Maner et al. (2007), different groups of patients (anxiety disorder, mood disorder, learning disorder) and a group of healthy controls were administered a risk-taking questionnaire. Only anxious patients exhibited reduced risk-taking relative to controls, suggesting that increased risk avoidance may be specific to anxiety. However, the main limitation of this study is that patients did not perform a task designed to directly assess risk-taking: questionnaires are non-objective and subject to well-established limitations including demand characteristics (Orne, 2009). In a modified version of the IGT (Mueller et al., 2010), GAD patients exhibited increased avoidance of decks with accumulated low magnitude but consistent losses. However, the main limitation of the IGT is that many processes contribute to behaviour on the task and it becomes hard to disentangle what drives the observed effect; in this case, possible explanations include increased risk aversion in GAD patients, increased loss aversion, improved learning of negative outcomes, or improved learning in general. Finally, in Giorgetta et al. (2012), the authors addressed some of these concerns by administering a probabilistic gambling task, which does not involve learning, to anxious patients and matched controls. Anxious patient exhibited a strong reduction in their propensity to choose the riskier gambles relative to controls. However, once again, it cannot be determined from this design whether avoidance of these gambles is driven by enhanced aversion to risk, aversion to losses, or a combination of the two. Finally, patients with anxiety tend to overestimate the risk of negative events (Butler and Mathews, 1983); however, it is unclear whether this might also extend to the positive domain. If not, such an imbalance in risk processing could result in increased loss aversion in clinical anxiety, with patients overestimating the risk of negative events (or losses) more so than that of positive events (or gains); in other words resulting in increased weighting of losses relative to gains. In sum, prior work assessing risk-taking behaviour in anxiety is unclear.

There is a strong hypothesis that loss aversion should increase with anxiety, given the associated negative biases in emotional and attentional processes, as well as the heightened sensitivity to large negative outcomes (Hartley and Phelps, 2012; Paulus and Yu, 2012). However, somewhat surprisingly, there are no published studies to date examining loss aversion in relation to anxiety in adult participants. One study examined this question in adolescents (Ernst et al., 2014) and found no difference in loss aversion between anxious and healthy adolescents. In other studies (Giorgetta et al., 2012; Galván and Peris, 2014), the gambling tasks used involved potential losses as well as gains, but did not allow dissociating between risk and loss aversion.

Therefore, the primary aim of this study was to test the hypothesis that both risk and loss aversion are higher in unmedicated anxious patients relative to healthy controls. By using a task that clearly separates risk and loss aversion and does not involve learning, these processes were adequately separated. A secondary aim of this study was to replicate and extend the findings presented in the previous chapter (**Chapter 4**), in which healthy individuals with low anxiety exhibited an emotion-induced increase in loss aversion. A first prediction was that healthy controls, or at least those with relatively low levels of trait anxiety (between 20 and 30 on the STAI), would exhibit increased loss aversion following the presentation of emotional relative to non-emotional primes. A second hypothesis was that clinically anxious patients would fail to adapt their decision-making behaviour in response to emotional cues – therefore showing no emotional modulation of risk or loss aversion – or would adapt it in a "non-optimal" direction, engaging harm-seeking rather than harm-avoidant behaviours – therefore showing reduced risk or loss aversion in response to emotional cues.

5.3 Materials and Methods

5.3.1 Participants

Twenty-nine unmedicated patients with Generalized Anxiety Disorder (GAD) and 26 matched healthy volunteers were recruited by advertisement. Data from four patients and three controls were excluded because of insensitivity to value in the gambling task (3 patients, 1 controls) or more than 10% of missed trials (1 patient, 2 controls), making loss and risk aversion impossible to model. Final analyses included 25 GAD patients (20 females, 5 males, mean age 25.2 years ± SD 4.90) and 23 healthy controls (18 females, 5 males, mean age 25.74 years ± SD 6.55) (see **Table 5-1** for details).

Participants gave written informed consent and were paid for their participation in an incentive-compatible manner. The study was approved by University College London research ethics committee.

5.3.2 Procedure

Participants were pre-screened by completing an online trait anxiety questionnaire after expressing interest in participating in the study. High trait anxiety has been shown to constitute a vulnerability factor for anxiety disorders, with clinically anxious individuals usually scoring above 50 on the scale (Kvaal et al., 2005; Julian, 2011). A short phone screening was then conducted on participants scoring under 35 (prospective healthy controls) or above 50 (prospective anxious patients) on the trait anxiety scale to ensure they did not meet any exclusion criteria: diagnosis of schizophrenia, bipolar disorder, attention deficit hyperactivity disorder (ADHD), or learning disability, medication for psychiatric disorder (e.g. antidepressants) in the last 30 days, consumption of cannabis in the last 30 days, consumption of any other recreational drug in the last week, recent (<6 months) alcohol or drug abuse, current or past neurological disorder. Any other past or present psychiatric diagnosis was also an exclusion criterion for the control group. All participants were fluent in English (native language or at least some secondary school education in English).

On the day of their visit to the laboratory, all participants were first administered the MINI (Sheehan et al., 1998) to confirm that healthy controls had no past or present psychiatric disorders, and that patients met MINI criteria for GAD. Because of their high comorbidity with GAD (Cloninger, 1990; Hirschfeld, 2001), major depressive disorder (MDD; current or past), as well as other anxiety disorders, did not constitute an exclusion criterion for the GAD group as long as criteria for current GAD were met. However, while most GAD patients (24 out of 25) had experienced at least one depressive episode in the past, only about half (13 out of 25) met criteria for current MDD at the time of the study, thereby making it possible to examine the role of anxiety disorder in the presence or absence of depressive symptoms (see section **5.4.4** below). Participants then completed the WTAR, providing an estimate of IQ.

Table 5-1. Demographics, questionnaire scores, and GAD patients' clinical characteristics

	GAD patients (N=25)	Healthy controls (N=23)	T(46)	P-value
N female : N male	20 : 5	18 : 5	-	-
Age in years (s.d.)	25.20 (4.90)	25.74 (6.55)	-0.33	0.75
IQ score (predicted from WTAR score) (s.d.)	109.60 (5.32)	108.13 (6.30)	0.88	0.39
STAI Trait anxiety score (s.d.)	55.24 (8.10)	30.00 (5.01)	12.85	<0.001
BDI score (s.d.)	16.96 (9.19)	1.57 (3.17)	7.62	<0.001
Age of onset of anxiety (s.d.)	18.08 (5.99)	-	-	-
Average number of years with anxiety (s.d.)	7.12 (5.85)	-	-	-
Number (%) with current major depressive episode	13 (52%)	-	-	-
Number (%) with past medication (anxiolytic or antidepressant)	2 (8%)	-	-	-
Number (%) hospitalized for anxiety or depression	1 (4%)	-	-	-
Number (%) with past suicide attempts	1 (4%)	-	-	-

Participants then completed the practice for the emotional decision-making task as described in the general methods chapter (**Chapter 2**) of this thesis (first practice on the emotional memory task alone, then practice on the gambling task alone, then practice on the combined task). A slight variation was used in the design of the task. For the memory part, only 2 stimuli were included in the memorisation array (instead of 2 and 4 in the fMRI version of the task). This is because the 4-stimuli condition was challenging, with several subjects in the fMRI study performing close to chance, and because the relationship between trait anxiety and emotional modulation of loss aversion in that previous study was stronger in the 2-stimuli condition (correlation between trait anxiety and emotion-induced change in loss aversion from fMRI study: $r(28)=-0.465$ for the 2-stimuli condition; $r(28)=-0.175$ for the 4-stimuli condition), which may be because fewer cognitive resources were taken up by the memory task. For the gambling part of the task, some gain-only gambles were added to the mixed (gain/loss) gambles in order to estimate both loss and risk aversion in the same model. The gain-only gambles involved a choice between a sure gain (ranging from £3 to £7) and a risky gamble with 50% chance of winning a higher amount and 50% chance of not winning anything (£0). The range of higher amounts for the gamble was determined based on each participant's indifference point from the practice trials. To maintain consistency across trials, the presentation of the mixed gambles was slightly altered from the task in the previous chapter (**Chapter 4**) such that participants were presented with a choice between the mixed gamble and a sure option of £0, instead of a choice between accepting and rejecting the mixed gamble (see **Figure 5-1** for an example). In each condition (happy, fearful, neutral, objects), there were 49 mixed gambles (7*7 matrix built exactly as before), as well as 25 gain-only gambles (5*5 matrix, centred on the participant's indifference point estimated from the practice gambling task), leading to a total of 296 trials, all randomly interleaved and split into 4 blocks of equal length.

After the task, participants completed the STAI and the BDI (see trait anxiety and BDI scores in **Table 5-1**). As expected, both measures were significantly higher in patients than in controls (trait anxiety: $t(46)=7.62$, $P<0.001$; BDI: $t(46)=12.85$, $P<0.001$).

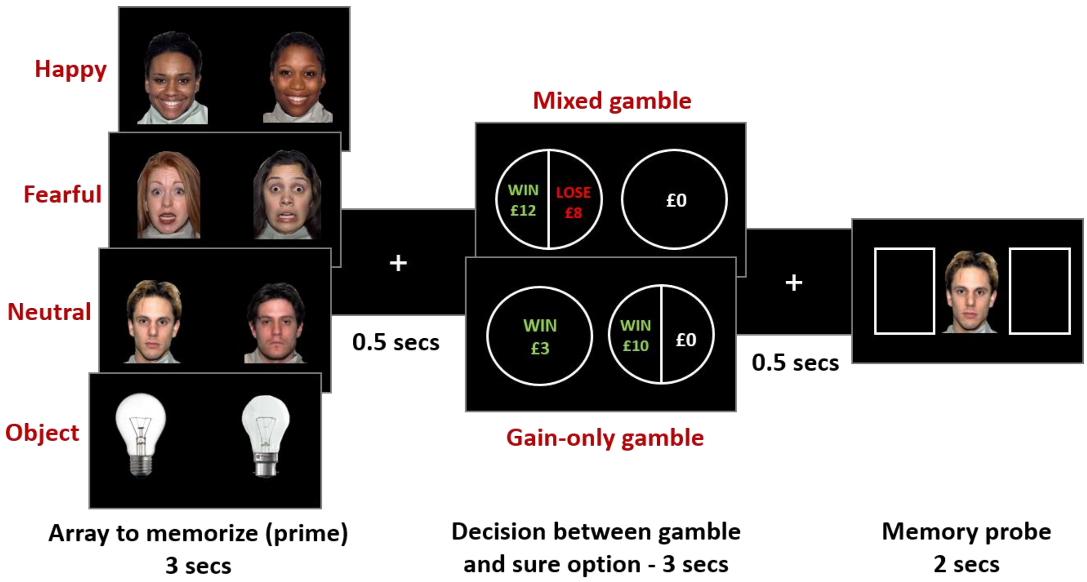


Figure 5-1. Trial design - clinical anxiety study. The design was similar to that of the fMRI study (**Chapter 4, Figure 4-1A**) except that (i) the array to memorize always contained 2 primes (instead of 2 and 4), and (ii) gain-only gambles were added to the mixed gambles in order to estimate risk and loss aversion in the same model.

5.3.3 Behavioural data analysis

The propensity to choose the gamble over the sure option was calculated separately for healthy controls and GAD patients and in three different ways for analysis purposes. First, the overall propensity to gamble was calculated across all trials and compared between controls and patients using an independent two-sample t-test. Second, it was calculated separately for mixed and gain-only gambles, and analysed in a 2-by-2 ANOVA with gamble type as a within-subjects factor and group as a between-subjects factor. Finally, to investigate the role of emotional primes on gambling decisions, the propensity to gamble was calculated separately for each emotion condition and analysed in a 4 (emotion condition) by 2 (group) ANOVA. Other variables, such as reaction times, working memory accuracy, and missed trials, were analysed in a similar way (see **Table 5-2** for a summary of all outcome variables).

In order to simultaneously estimate loss and risk aversion within the same model, an extra parameter ρ was added to the model (as described in **Chapter 2**, section **2.4.1**). Specifically for each trial, the subjective utilities (u) of the gamble and of the sure option were estimated using equations **2-3** and **2-4**, with the assumption that $\rho_{gain} = \rho_{loss} = \rho$ and with losses coded as negative values, resulting in:

$$u(gamble) = 0.5 \cdot G^{\boldsymbol{\rho}} + 0.5 \cdot \boldsymbol{\lambda} \cdot |L|^{\boldsymbol{\rho}} \qquad \textbf{(Eq. 5-1)}$$

$$u(sure) = 0.5 \cdot S^{\boldsymbol{\rho}} \qquad \textbf{(Eq. 5-2)}$$

λ again represents loss aversion: $\lambda>1$ indicates an overweighting of losses relative to gains and $\lambda<1$ the converse. The ρ parameter represents the curvature of the utility function, which reflects varying sensitivity to changes in values as value increases. In particular, if $\rho<1$, the utility function is concave for gains and convex for losses, resulting in risk aversion on gain-only trials (greater utility for a sure gain than for a risky 50/50 gamble with the same expected value); $\rho>1$ indicates risk-seeking.

Similar to the previous chapters and to equation **2-6**, these subjective utility values were used in a softmax function to estimate the probability of choosing the gamble on each trial (coded as 1 or 0 for choosing the gamble or the sure option, respectively), with the inverse temperature parameter μ:

$$P(gamble) = \frac{1}{1 + e^{-\mu[u(gamble) - u(sure)]}} \qquad \textbf{(Eq. 5-3)}$$

Different models were run using this procedure, where the three parameters (λ, ρ, and μ) were estimated: (i) across all trials; (ii) separately for emotional (happy and fearful faces) and non-emotional (neutral faces and objects) trials; or (iii) separately for each of the four emotion conditions. In the latter case, the model with 12 parameters could not be reliably estimated; therefore, only λ and ρ were estimated separately for each of the four emotions conditions, with a single μ across all trials, resulting in a model with 9 parameters instead of 12.

The distribution of both λ and ρ parameters was positively skewed, so they were log-transformed before running statistical tests. In addition, because risk aversion is highest for lowest values of ρ, the negative value –log(ρ) was taken as the final index of risk aversion. This allowed both risk and loss aversion to be similarly distributed, with positive values of log(λ) and of –log(ρ) indicating loss aversion and risk aversion, respectively.

To test whether the difference between patient and control groups were indeed specific to anxiety or may be driven by depression, which is known to be highly comorbid with anxiety, two analyses were run. First the anxious patients were divided into two groups according to whether they met criteria for current MDD in addition to GAD. A one-way ANOVA was then run on risk and loss aversion estimates, comparing the following three groups: patients with GAD and MDD, patients with GAD only, and controls. Means were then compared with post-hoc t-tests using the least significant difference (LSD) test.

5.4 Results

A summary of all outcome variables, calculated separately for healthy controls and GAD patients, is presented in **Table 5-2** below.

Table 5-2. Summary of outcome variables

	GAD patients	Healthy controls	T(46)	P-value	Cohen's d
P_{gamble}	0.325 (0.161)	0.394 (0.174)	-1.426	0.161	0.412
P_{gamble} mixed gambles	0.354 (0.204)	0.376 (0.173)	-0.393	0.696	0.114
P_{gamble} gain-only gambles	0.268 (0.145)	0.430 (0.257)	-2.728	0.009*	0.788
λ (loss aversion)	2.013 (0.494)	2.067 (0.752)	0.141 (log)	0.889	0.041
ρ (risk preference)	0.564 (0.313)	0.875 (0.537)	-2.491 (log)	0.016*	0.720
μ (inverse temperature)	5.120 (4.124)	3.858 (4.502)	1.014	0.316	0.293
RT_{gamble} (s)	1.294 (0.229)	1.319 (0.209)	-0.390	0.699	0.113
$RT_{sure\ option}$ (s)	1.134 (0.193)	1.250 (0.228)	-1.914	0.062	0.553
Missed gamble responses (% trials)	0.514 (0.787)	0.646 (1.125)	-0.477	0.636	0.138
WM accuracy (% correct)	90.78 (11.11)	92.15 (4.675)	-0.547	0.587	0.158
Missed WM responses (% trials)	2.203 (2.717)	1.983 (2.183)	0.307	0.760	0.089

Note that for comparing λ and ρ parameters between groups, their values were log-transformed before running statistical tests.

5.4.1 Propensity to gamble

Across all participants, the average propensity to choose the gamble was 35.8%. Although healthy controls tended to gamble slightly more than GAD patients (39.4% versus 32.5%, respectively), this difference was not significant (t(46)=-1.426, P=0.161, Cohen's d=0.412). However, when the type of gamble – mixed versus gain-only – was added as a within-subjects factor, a significant gamble type*group interaction emerged (F(1,46)=5.196, P=0.027, η_p^2=0.101, **Figure 5-2**), such that propensity to gamble on mixed gamble trials did not differ between controls and patients (t(46)=-0.393, P=0.696, Cohen's d=0.114) but patients gambled significantly less than controls on gain-only trials (t(46)=-2.728, P=0.009, Cohen's d=0.788). Note, however, that due to the tailoring process during the practice gambling task, the range of values used to build the gambles for the main task varied across participants; therefore, examining the proportion of chosen gambles may not reflect actual levels of risk-taking given that values may be different between subjects. To do so, risk and loss aversion parameters were estimated from the Prospect Theory model, taking into account the specific range of values for each participant.

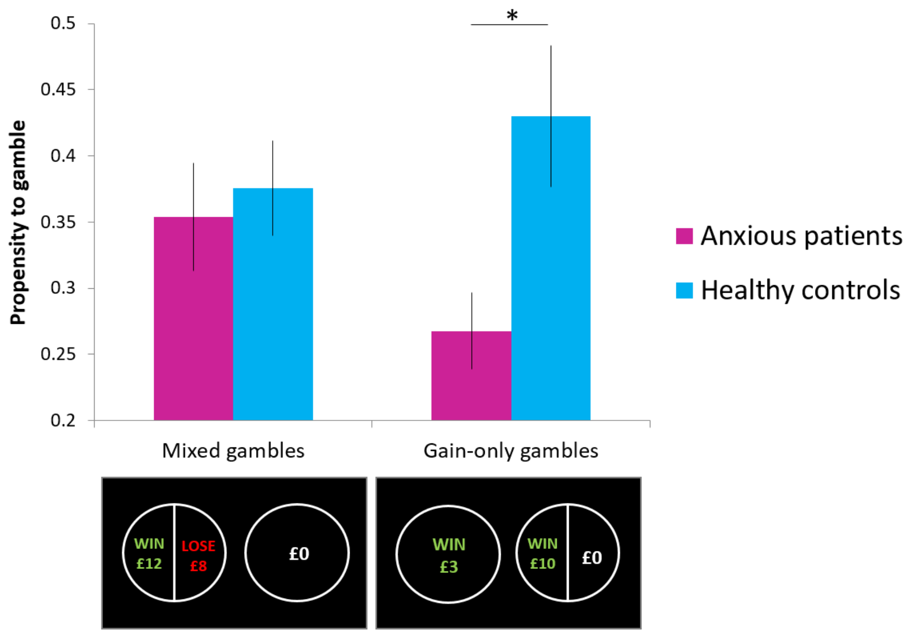


Figure 5-2. Propensity to gamble. The proportion of trials in which the gamble was chosen was calculated for each participant and each gamble type (mixed, gain-only), then averaged separately for healthy controls and GAD patients. Error bars represent SEM. * p<0.05, two-tailed t-test.

5.4.2 Risk and loss aversion

Estimated across all trials independent of emotion condition, the average λ parameter across all participants was 2.039 (±SD 0.625), greater than 1 and consistent with loss averse decisions, and with previous literature suggesting that people weigh losses about twice as much as gains (Tversky and Kahneman, 1992; Tom et al., 2007; De Martino et al., 2010; Chib et al., 2012). Risk aversion was also evident in people's choices, with an average ρ parameter of 0.713 (±SD 0.458), lower than 1 and indicative of diminishing sensitivity to changes in value as value increases. Statistically, these were confirmed by one-sample t-tests (against zero) on the log-transformed parameters, with loss aversion [log(λ)] and risk aversion [-log(ρ)], both significantly positive (loss aversion: $t(47)=14.81$, $P<0.001$, Cohen's d=2.14; risk aversion: $t(47)=6.261$, $P<0.001$, Cohen's d=0.904). The distribution of each parameter across individuals is depicted in **Figure 5-3A**. This graph additionally reveals that loss and risk aversion are not correlated across individuals ($r(48)=0.107$, $P=0.469$), suggesting that distinct processes underlie risk and loss aversion and that the parameters are not trading off against each other in the model.

In order to examine group differences in risk and loss aversion, both log-transformed parameters were analysed separately and compared between patients and controls (**Figure 5-3B**). Risk aversion was significantly higher in anxious patients relative to controls (t(46)=2.491, P=0.016, Cohen's d=0.720), but there was no difference in loss aversion between groups (t(46)=0.141, P=0.889, Cohen's d=0.041).

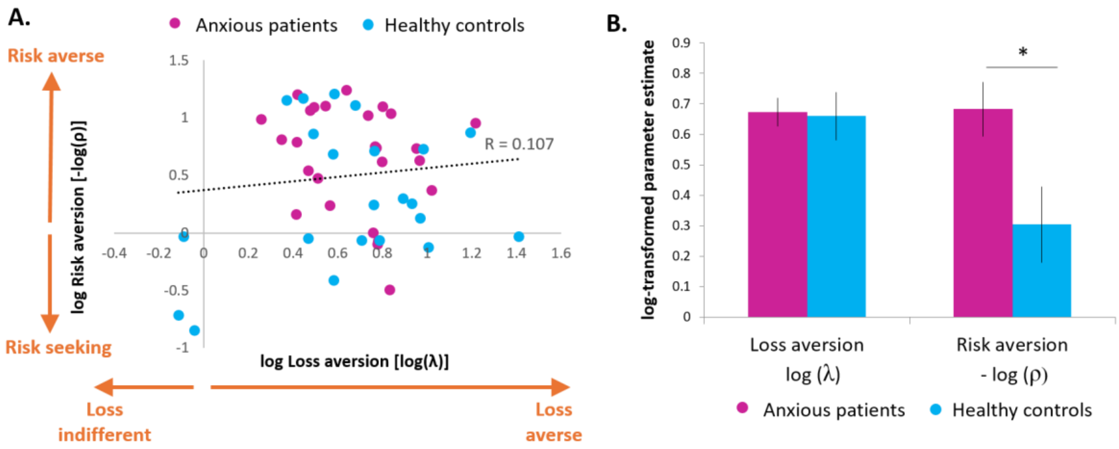


Figure 5-3. Risk and loss aversion parameter estimates. A. Distribution of log-transformed parameter estimates. Positive values indicate risk aversion and loss aversion, respectively. **B.** Mean estimates of loss and risk aversion, plotted separately for GAD patients and healthy controls. Error bars represent SEM. * P<0.05, two-tailed.

5.4.3 Impact of incidental emotions on decision-making

The effect of emotional primes on subsequent gambling decisions was analysed in a 4 (Prime: Happy, Fearful, Neutral, Object) by 2 (Group: GAD patients, healthy controls) ANOVA on the following dependent variables: propensity to choose the gamble over the sure option (calculated across all trials), loss aversion, and risk aversion. None of these variables was influenced by the content of the prime (main effect of prime on propensity to gamble: F(3,138)=1.459, P=0.228, η_p^2=0.031, **Figure 5-4A left panel**; on loss aversion: F(3,138)=1.034, P=0.379, η_p^2=0.022, **Figure 5-4B left panel**; on risk aversion: F(3,138)=0.877, P=0.455, η_p^2=0.019, **Figure 5-4C left panel**). There was also no interaction between emotional prime and group on these variables (propensity to gamble: F(3,138)=0.069, P=0.977, η_p^2=0.001; loss aversion: F(3,138)=1.653, P=0.180, η_p^2=0.035; risk aversion: F(3,138)=0.602, P=0.615, η_p^2=0.013). Note that the increased risk aversion observed in anxious patients relative to controls was present for each prime condition (**Figure 5-4C left panel**).

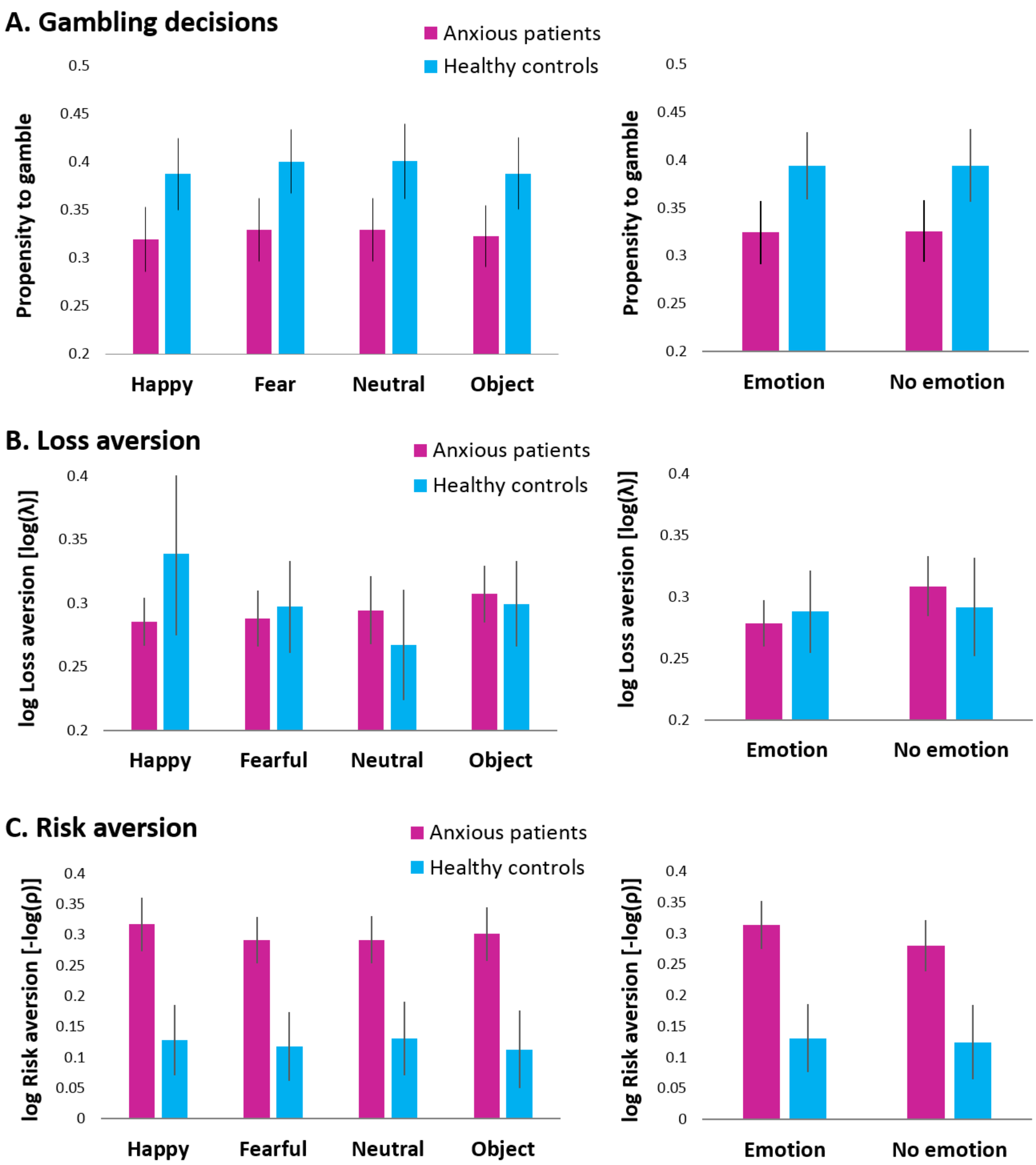


Figure 5-4. Impact of incidental emotional primes on economic decisions. The impact of emotional manipulation, through incidental presentation of visual primes prior to making a gambling decision, was examined on three variables: proportion of trials where the gamble is chosen (**A**), loss aversion (**B**) and risk aversion (**C**), calculated separately for each prime condition (happy faces, fearful faces, neutral faces, and objects – **left panels**) or collapsed across emotion conditions (happy and fearful) and across non-emotion conditions (neutral and object) – **right panels** – and averaged across GAD patients and healthy controls.

For consistency with the analyses reported in **Chapter 4**, loss and risk aversion parameters were also estimated collapsing across both emotional conditions (Happy and Fearful) and across both non-emotional conditions (Neutral and Object) to compare the effect of emotional versus non-emotional cues on decisions. However, none of the decision variables were affected by emotion (propensity to gamble: $F(1,46)=0.037$, $P=0.848$, $\eta_p^2=0.0008$, **Figure 5-4A right panel**; loss aversion $F(1,46)=2.227$, $P=0.142$, $\eta_p^2=0.046$, **Figure 5-4B right panel**; risk aversion: $F(1,46)=2.014$, $P=0.163$, $\eta_p^2=0.042$, **Figure 5-4C right panel**) or by an interaction between emotion and group (propensity to gamble: $F(1,46)=0.011$, $P=0.919$, $\eta_p^2=0.0002$; loss aversion: $F(1,46)=1.365$, $P=0.249$, $\eta_p^2=0.029$; risk aversion: $F(1,46)=0.897$, $P=0.349$, $\eta_p^2=0.019$).

5.4.4 Controlling for depression scores

Because anxiety and depression are highly comorbid, it is possible that the higher risk aversion observed in GAD patients relative to controls could be due to higher depressive scores or higher occurrence of MDD diagnoses in the patient group (see **Table 5-1**), rather than higher anxiety. Trait anxiety and BDI were indeed highly correlated across the entire sample ($r(48)=0.836$, $P<0.001$, **Figure 5-5A**). Therefore, in order to control for depression diagnosis, GAD patients were split according to current MDD diagnosis (at the time of study), resulting in two sub-groups: patients with GAD and MDD (N=13) and patients with GAD but no current MDD (N=12). A one-way ANOVA was then run on log-transformed risk and loss aversion estimates of these two patient sub-groups as well as the control group, revealing a significant effect of group on risk aversion ($F(2,45)=3.853$, $P=0.029$, $\eta_p^2=0.146$, **Figure 5-5B**) but no effect on loss aversion ($F(2,45)=0.012$, $P=0.988$, $\eta_p^2=0.0005$). For risk aversion, post-hoc least significant difference (LSD) tests revealed increased risk aversion in patients with GAD only (no MDD) relative to controls (mean difference = 0.509; 95% confidence interval = [0.134,0.885], P=0.009), and no difference between the two patients groups (mean difference = 0.252; 95% confidence interval = [-0.170,0.674], P=0.24). There was also no difference between patients with GAD and MDD relative to controls (mean difference = 0.258; 95% confidence interval = [-0.108,0.624], P=0.16). This suggests that if anything the increased risk aversion observed in anxious patients relative to controls is driven by those patients who do not exhibit comorbid depressive disorder, arguing against an effect of depression in enhancing risk aversion.

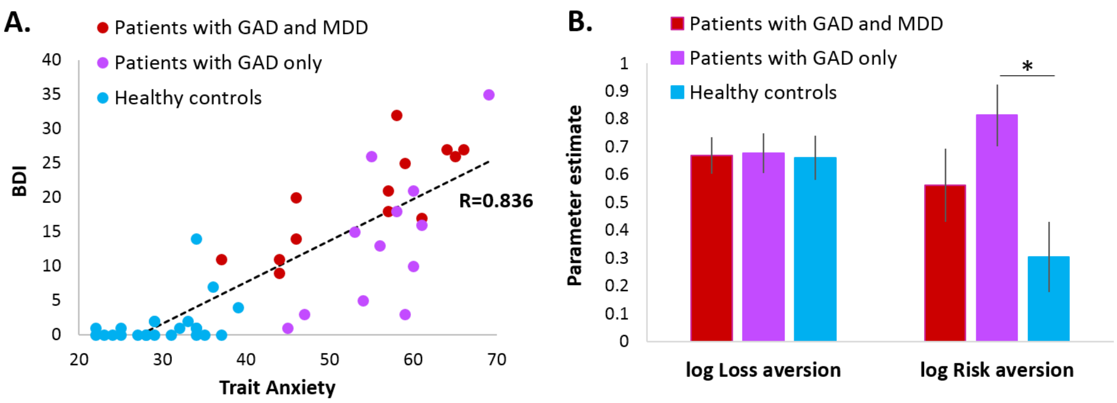


Figure 5-5. Controlling for depression levels in risk and loss aversion estimates. A. Despite their correlation with trait anxiety scores, variability in BDI scores and MDD diagnosis within the patient group allowed examining differences in risk and loss aversion between GAD patients who met MDD criteria and those who did not. **B.** Anxious patients with and without a current diagnosis of MDD did not differ in their level of loss and risk aversion; however, only GAD patients without MDD exhibited significantly higher risk aversion than controls, confirming that increased risk aversion is driven by anxiety rather than depressive symptoms. Error bars represent SEM; post-hoc LSD tests: * P<0.05.

5.5 Discussion

This study demonstrated that relative to healthy individuals, patients with clinical anxiety exhibit an enhanced degree of risk aversion, but similar levels of loss aversion. Originally, given the broad literature associating anxiety with a more conservative decision-making style (see Hartley and Phelps, 2012; Robinson et al., 2013 for reviews), the main hypotheses were that both risk and loss aversion would increase in clinical anxiety. Interestingly, however, only the first hypothesis was confirmed.

Increased risk aversion means that clinically anxious individuals are less likely to take risks when making decisions, consistent with reduced general tendency to engage in risky daily-life behaviours observed in anxious individuals (Maner et al., 2007) as well as previous studies using gambling tasks (Mueller et al., 2010; Giorgetta et al., 2012). Psychologically, a possible explanation for this increased risk-avoidance bias could stem from a bias in the evaluation of risk, with anxious individuals overestimating the risk of negative events happening to them (Butler and Mathews, 1983), which would result in an overestimation of the probabilities of not winning the gamble, and in a stronger disengagement from risky decisions and behaviours relative to healthy individuals.

The hypothesis that loss aversion would also be enhanced in anxiety was, however, not confirmed in the present study. Despite the myriad of studies suggesting negative attentional and emotional biases in anxiety (Mogg and Bradley, 2005; Bar-Haim et al., 2007; Cisler and Koster, 2010; Etkin et al., 2010; MacLeod and Mathews, 2012; Robinson et al., 2014), leading to the assumption that anxious individuals may give more weight to negative outcomes (in this case monetary losses) compared to healthy individuals, this had never been investigated by directly examining loss aversion. It is important to note that loss aversion was present in both healthy controls and clinically anxious individuals: on average participants weighted monetary losses approximately twice as much as monetary gains. However, this ratio was the same across both groups, and anxious patients did not overweigh losses in comparison to the control group. This is consistent with a recent study in adolescents, which did not find any loss aversion difference between anxious and healthy adolescents (Ernst et al., 2014). Although surprising, this result may suggest that when the prospect of a loss or negative outcome is evaluated on its own, anxious patients may be more sensitive than controls and report more negative judgments and affect; however, when they have to weight this prospective loss against a prospective gain in order to make a decision, the degree by which they do so is similar to controls.

Results from the emotional priming procedure additionally showed that both risk and loss aversion seem robust to manipulation by incidental emotional cues. In particular, the original effect described in **Chapter 4** (section **4.4.1**, **Figure 4-2**), namely an increase in loss aversion for emotional relative to non-emotional primes in low anxious individuals, was not replicated. A possible explanation could be that trait anxiety scores in the control group of the present study were not as low as those of the low anxious group showing the effect in Chapter 4. A more detailed examination of this results, combining data of Chapters 4 and 5 is presented in the general discussion (**Chapter 6**, section **6.2**).

Finally the general effect of anxiety on risk aversion (independent of emotional priming) was found to be specific to anxiety and not driven by higher depression, known to be comorbid with anxiety. Within the anxious patient group, current MDD diagnosis was not associated with any variation in risk or loss aversion. If anything, the enhanced risk aversion in anxious patients relative to controls was exclusively driven by those patients who did not meet criteria for MDD, arguing against a role for depressive symptoms in increasing risk-avoidant decisions. Even though the present results suggest that reduced risk-taking seems to be a specific feature of anxiety disorders, very little is known about economic decision-making biases in depression and this warrants further investigation.

This study addressed a significant omission in previous designs of risky decision-making tasks (Mueller et al., 2010; Giorgetta et al., 2012), as well as the loss aversion task used in **Chapter 4**, in which safe choices could be driven both by risk or loss aversion. Here, both decision parameters were reliably estimated within the same task and computational framework. The study of economic decisions, and their interaction with emotions, was also expanded to a clinical group in which affect and emotional processes are disrupted. Clinically, these results may be of importance given that patients with anxiety frequently report difficulties making decisions in their everyday life. In particular, they may help pave the way for the development of future cognitive-based interventions to better target this specific symptom, for example by focusing on reducing patients' sensitivity to risk, rather than to negative outcome, when they have to make decisions.

Chapter 6 General Discussion

This discussion will first summarise the findings of experimental Chapters 3-5, giving a brief overview of the results and conclusions of each study. It will then provide a unifying analysis combining the behavioural data from Chapters 4 and 5 to examine the link between anxiety and the emotional modulation of loss aversion across both studies. The findings of this thesis will then be discussed in light of their implications for models of the role of emotion in economic decision-making and for future research. The limitations associated with each study will then be presented, followed by a conclusion on the possible development of therapeutic interventions.

6.1 Summary of experimental findings

6.1.1 Chapter 3: how are feelings integrated into economic decisions?

The aim of the studies presented in **Chapter 3** was to test the implicit assumption of Prospect Theory that emotions govern our decisions and to provide a computational account of how they do so. Emotions were measured as subjective, self-report, feelings in a task that elicited such feelings in response to winning or losing a range of monetary amounts. These feelings were then incorporated in a "feeling function" that reflected the best relationship between feelings and monetary values. Finally this function was used to predict participants' gambling decisions in a separate risky decision-making task involving choices between a sure option and a risky gamble. The findings can be summarised in three main points. First, feelings show diminishing sensitivity to monetary value as value increases, similar to Prospect Theory's value function, but importantly do not show an asymmetry between gains and losses. Second, the "feeling function" predicts gambling decisions better than existing models of economic choice, showing a unique contribution of feelings to decisions. Third, individual differences in loss aversion were driven by an overweighting of feelings about losses, relative to feelings about gains, at the time of the decision. Importantly, these findings indicate that loss aversion does not arise from a greater impact of losses relative to equivalent gains on feelings, but instead from a greater influence of feelings about losses relative to feelings about gains when weighting up the decision options.

6.1.2 Chapter 4: how do incidental emotional cues modulate loss aversion?

After showing in Chapter 3 that an asymmetric integration of feelings into choice explains loss aversion, my aim in **Chapter 4** was to show that by manipulating emotions, loss aversion could be altered. In addition, I aimed to investigate the underlying neural mechanisms of this effect, using fMRI, as well as to understand sources of individual differences in this process, given that people react and adapt to changes in the environment, and in particular changes in emotional cues, in very different ways. Participants completed a loss aversion task during fMRI while being primed before each decision by emotional (fearful or happy faces) or non-emotional cues (neutral faces or objects). The behavioural finding was that relative to non-emotional cues, emotional cues increased loss aversion, but only in individuals with low trait anxiety, which was hypothesized to be driven by a greater ability to flexibly engage harm-avoidance mechanisms in response to changes in their environment. The neuroimaging results were three-fold. First, previous accounts of "neural loss aversion" in the ventral striatum were replicated, with activity in the ventral striatum found to track decreasing losses more strongly than increasing gains. Second, the amygdala responded to the presentation of emotional cues relative to non-emotional cues, and tracked monetary losses but only following emotional cues, suggesting a potential role for the amygdala in integrating emotion and value signals. Finally, the behavioural effect observed (emotion-induced risk aversion) was associated with an emotion-induced increase in amygdala functional connectivity with the ventral striatum; an effect that also decreased with trait anxiety levels. These findings provide new insights into the key role played by the amygdala and ventral striatum, as well as their functional interaction, in loss aversion and its modulation by emotion.

6.1.3 Chapter 5: how does anxiety affect the relative contribution of risk and loss aversion to economic choice?

My aim in **Chapter 5** was two-fold; first, to formally examine risk and loss aversion in clinical anxiety, as previous studies suggesting increased risk avoidance in anxiety have not been able to separate the contributions of risk and loss aversion to choice; and second, to replicate the behavioural finding from Chapter 4 and extend it to clinical anxiety. I was successful with the first aim, showing that reduced propensity to choose risky gambles over safe options in clinical anxiety was driven specifically by increased risk aversion; while loss aversion did not differ between anxious patients and healthy controls. However, the behavioural finding of Chapter 4, namely an increase in loss aversion for emotional relative to non-emotional primes in low anxious individuals, failed to replicate. In fact, individuals in the control, non-anxious group in Chapter 5 did not exhibit any change in loss or risk aversion in response to emotional cues. There was also no difference between anxious patients and healthy controls in how emotional cues modulated loss or risk aversion. Some possible explanations, as well as an analysis of data combined from Chapters 4 and 5 is presented in the next section.

6.2 Emotional modulation of loss aversion: integrated findings from Chapters 4 and 5

Several possibilities could explain the absence of effect of emotional cues on loss aversion in low anxious individuals in Chapter 5, relative to Chapter 4 (see section **4.4.1**, **Figure 4-2**). A first potentially important difference between the participant groups from the two studies was that the range of trait anxiety scores from the low anxious individuals in Chapter 4 (between 20 and 30) was lower than the range of scores from the control group in Chapter 5 (between 22 and 39). One possibility could be that this effect is specific to individuals with extremely low levels of anxiety, consistent with the hypothesis of a link with resilience to anxiety. This might also reflect a sampling bias for the fMRI study (Chapter 4), such that those who are prepared to volunteer for a brain scanning study are generally less anxious. Another explanation could come from a difference in timings between the two tasks. Because the study presented in Chapter 4 was adapted for fMRI, the inter-trial interval was longer: the delay between the presentation of the emotional faces and the gamble varied between 2 and 6 seconds, whereas in Chapter 5 this delay was reduced to 0.5 seconds to allow the addition of gain-only trials to the design. However, if anything one would expect the influence of the emotional prime to be greater when presented closer to the decision, so this factor is unlikely to explain the difference in findings. Finally, another possibility is that the conditions inside the fMRI scanner, such as noise, enclosed space, less opportunity for visual distraction, may interact with the emotional manipulation to make it more potent.

Interestingly, despite the absence of a significant interaction between emotion and group (anxious patients vs controls) on loss aversion in Chapter 5, I noted the presence of an emotion-induced decrease in loss aversion in the patient group (**Figure 5-4B right panel**; t(24)=2.161, P=0.041), which could expand the finding of Chapter 4. In order to examine this possibility in more detail, the data from Chapters 4 and 5 were combined into one sample of N=76 participants. Similar to Chapter 4's methods, the percentage change in loss aversion (λ parameter) between emotional cues (fearful and happy faces) and non-emotional cues (neutral faces and objects) was calculated for each participant. However this variable was not normally distributed (Kolmogorov-Smirnov test for normality with Lilliefors significance correction: statistic=0.129, P=0.003), due to a heavy-tailed distribution (on both sides of the distribution; Kurtosis value = 3.415) and the presence of 4 outliers, defined by asterisks in SPSS. After these outliers were removed the variable was normally distributed (Kolmogorov-Smirnov test: P=0.2; Kurtosis = 0.851; N=72). Partial correlations were then run between trait anxiety and the percentage change in loss aversion from non-emotional to emotional cues, controlling for study group (dummy coded variable categorising participants into studies from Chapter 4 or 5).

Across all 72 participants, this correlation was significantly negative (partial correlation r(69)=-0.307, P=0.009; **Figure 6-1A**), suggesting that the significant effect observed in Chapter 4 holds when adding the data from Chapter 5. This negative correlation remained significant when including only the data from non-clinically anxious participants (N=48, partial correlation r(45)=-0.372, P=0.010, **Figure 6-1B**). I next examined group differences and within-group effects by splitting participants into three groups: a low anxious group with trait anxiety scores ranging from 20 to 30 similar to the low anxious group in Chapter 4 (N=23, including 14 participants from Chapter 4 and 9 participants from Chapter 5); a clinically anxious group consisting of all the GAD patients from Chapter 5 (N=24); and a mild-anxious group with the remaining participants, with trait anxiety scores ranging from 31 to 44 similar to the high anxious group in Chapter 4 (N=25, including 14 participants from Chapter 4 and 11 participants from Chapter 5). The average emotion-induced change in loss aversion is plotted separately for each of these three groups in **Figure 6-1C**. A univariate ANOVA, controlling for Study, revealed a significant main effect of anxiety group (F(2,68)=6.183, P=0.003). Post-hoc t-tests using the least significant difference test showed that this effect was driven by a significant difference between the low and mild-anxious groups (mean difference = 5.70; 95% CI = [0.486, 10.91], P=0.033) and between the low and clinically anxious groups (mean difference = 9.14; 95% CI = [3.88, 14.41], P=0.001), but not between the mild- and clinically anxious groups (mean difference = 3.45; 95% CI = [-1.71, 8.60], P=0.19). In addition, one-sample t-tests performed on each group mean demonstrated a significant emotion-induced increase in loss aversion in low anxious individuals (t(22)=3.57, P=0.002), consistent with the finding of Chapter 4, no change in loss aversion in mild-anxious individuals (t(24)=0.27, P=0.79), and a marginally significant decrease in loss aversion following emotional cues in clinically anxious participants (t(23)=1.83, P=0.08). Note that the difference between this latter t-test and the one reported above (corresponding to the decrease in loss aversion for anxious individuals depicted in **Chapter 5**, **Figure 5-4B right panel**; t(24)=2.161, P=0.041) is driven by the fact that the statistical test in Chapter 5 was run on the difference between loss aversion in the emotional relative to non-emotional conditions, whereas the variable reported here in **Figure 6-1C** is the percentage change in loss aversion (rather than the difference). In addition, one outlier was removed from the patient group, resulting in the newer test being run on 24 subjects instead of 25. Because the loss aversion variables (during emotional and non-emotional conditions) reported in **Figure 5-4B right panel** were normally distributed, all participants were included in the analyses. It is only when calculating the percentage change in loss aversion for the current analysis to be consistent with Chapter 4 that outliers emerged and had to be removed from the data.

Finally, despite the suggestion that the findings from Chapter 4 hold when adding the data from Chapter 5, this pattern of results has to be taken with caution given the distribution of trait anxiety scores across the whole sample, which is more consistent with a bimodal rather than normal distribution, resulting in very few data points for trait anxiety scores between 45 and 55. As mentioned in the limitations section **6.4** below, replications of these results will be needed in future investigations.

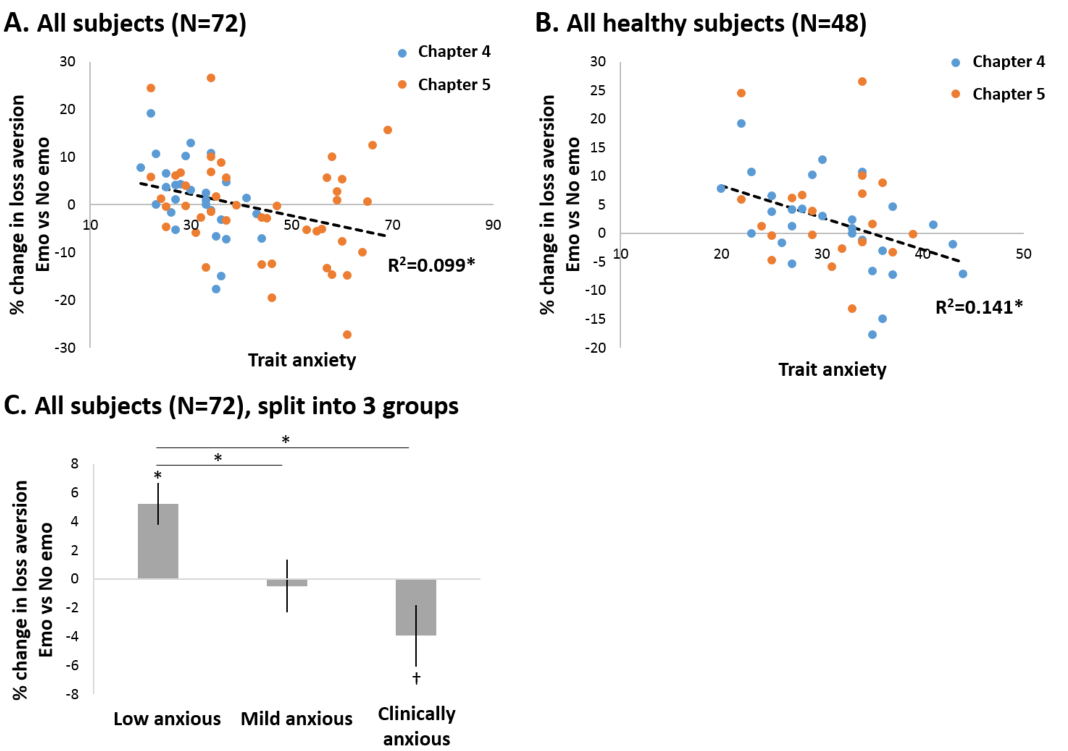


Figure 6-1. Combined analysis of data from Chapters 4 and 5. Data from studies presented in Chapters 4 and 5 of this thesis were combined to analyse how individual differences in anxiety levels relate to emotion-induced changes in loss aversion across the whole sample (N=72, following the exclusion of 4 outliers). The percentage change in loss aversion between emotional and non-emotional cues was calculated for each participant and correlated with trait anxiety (**A**) across all subjects and (**B**) across all healthy subjects excluding clinically anxious participants from Chapter 5. **C.** The mean emotion-induced change in loss aversion is plotted for each of three groups: low anxious subjects (trait anxiety between 20 and 30, N=23), mild-anxious subjects (trait anxiety between 31 and 44, N=25) and clinically anxious subjects (patient group from Chapter 5, N=24). Error bars represent ± 1 SEM. Two-tailed t-tests: * P<0.05; † P<0.1.

6.3 How these findings pave the way for new mechanistic accounts of the role of emotion in decision-making

6.3.1 A model of choice based on the integration of subjective feelings: implications of Chapter 3

The findings of Chapter 3 provide a novel account and computational model of how emotions are utilized to predict choice. Specifically, the model incorporates how people's feelings relate to objective value then uses this relationship to predict choice by adding a greater weight to feelings about losses than to feelings about gains. It confirms the assumption of Prospect Theory that emotions mediate the influence of objective value on choice. The non-linear, S-shaped, relationship between emotion and objective value also suggests that emotion can be viewed as a utility signal.

However, the two components of the model point towards some differences with the assumptions of Prospect Theory. First, contrary to Prospect Theory's value function, the function that relates emotion and objective value is not steeper for losses than for gains, suggesting that losses do not impact subjective feelings to a greater extent than gains. Second, it is when these feelings are incorporated into a decision variable at the time of choice that the gain-loss asymmetry appears. Therefore, the model suggests that the utility signal that ultimately determines an agent's decisions (or decision utility) can be decomposed into an early component based on the emotional evaluation of each potential outcome separately ("emotion utility"), followed by a later component formed of the asymmetrically-weighted integration of these emotion utilities, with a greater weight attributed to negative than positive utilities. Note that in this framework, what I call "emotion utility" is conceptually very similar to Kahneman's proposed "experienced utility" (Kahneman et al., 1997).

Crucially, the model incorporating a "feeling function" performed better in predicting an independent set of choices than traditional models based on expected value maximization, expected utility (modelled as log[expected value]) maximization, or maximization of Prospect Theory-derived utility (calculated using subject-specific estimates of risk aversion only, loss aversion only, or both). Therefore, by directly measuring emotions, instead of estimating the role of emotion from people's choices as assumed by Prospect Theory and reflected in estimates of risk and loss aversion, the model's ability to predict choice can be reliably improved.

This idea suggests that measuring more components of emotions than only subjective feelings may provide an even better model of people's decisions. In particular, these other measures could include physiological emotional responses, such as SCRs, heart rate, pupil dilation, brain responses, or subjective reports of different emotions (e.g. fear, anger, sadness, excitement, etc) or emotional dimensions (e.g. valence, arousal, etc). With these measures, it may be possible to dissect how the different components of emotions lead to a decision, and provide a better descriptive account of economic decision-making.

6.3.2 An improved understanding of loss aversion: an expression of autonomic arousal, rather than fear?

Previous work has suggested, as described in **Chapter 1** (section **1.2.3**), that loss aversion may be an expression of fear, given the common neural and physiological signatures of both fear processing and the anticipation of losses or loss aversion. Although the neuroimaging findings from **Chapter 4**, involving amygdala-striatum interactions and amygdala tracking of losses only following an emotional prime, may be consistent with LeDoux's model of fear processing (LeDoux and Gorman, 2001), most of the behavioural findings of this thesis do not support this account, especially in terms of specificity to fear processing. Instead, they might be more consistent with other models of amygdala function that emphasise its role in arousal, emotional intensity or affective significance, instead of simply processing fear or negative emotions (Morrison and Salzman, 2010; Pessoa and Adolphs, 2010; Wang et al., 2014; Seara-Cardoso et al., 2016).

First, the findings of **Chapter 3** suggest that loss aversion arises from increased weighting of feelings about potential losses relative to feelings about potential gains, rather than feelings about losses being more intense per se. If the fear of losing was the main driver of loss aversion, then one could expect negative feelings about losses to be bigger in magnitude than positive feelings about gains; but the results presented in Chapter 3 suggest that there is no such asymmetry in people's reported feelings. To test this hypothesis more specifically, however, one possibility would be to collect subjective reports of different emotions, one of them being fear. If loss aversion results from the expression of fear, then it should be specifically reflected in ratings of fear, but not other emotions (which could also be one of the reasons why asymmetry is not observed in the data).

Second, if fear drives loss aversion, then manipulating fear should alter loss aversion. This is what a recent study has found, such that increasing fear with the presentation of fearful faces resulted in an increase in loss aversion (Schulreich et al., 2016). However, this study did not test for the specificity of fear relative to other emotions, as fear was the only emotion used. In the study presented in **Chapter 4**, findings suggest that even though fearful faces seemed to have the strongest effect on increasing loss aversion in low anxious individuals, happy faces also had a significant effect in the same direction (**Figure 4-2B**), suggesting a potential role for emotional arousal, rather than fear, in modulating loss aversion.

Finally, anxious individuals are known to exhibit exacerbated fear responses, mainly reflected by increased behavioural and neural responses to threat-related stimuli (Bar-Haim et al., 2007; Robinson et al., 2013, 2014). Therefore, a fear-related account of loss aversion should predict increased loss aversion in anxious individuals, which is not supported by the results of **Chapter 5** showing no difference in loss aversion between anxious patients and healthy controls.

A more recent account of loss aversion suggests a key role for autonomic arousal (Sokol-Hessner et al., 2009, 2015b; Sokol-Hessner and Phelps, 2016). Specifically, Sokol-Hessner et al propose a mechanistic account by which "amygdala-mediated arousal responses [to decision outcomes] may drive striatally mediated decisions to avoid losses" (Sokol-Hessner and Phelps, 2016; p.12); an account consistent with the possible function of the amygdala in encoding arousal more generally (Glascher and Adolphs, 2003; Pessoa and Adolphs, 2010; Seara-Cardoso et al., 2016). Sokol-Hessner et al provide preliminary evidence that adrenergic responses may relay this arousal response (Sokol-Hessner et al., 2015b), to a greater extent for losses than for gains, which in turn induces avoidance of subsequent losses and loss aversion. In addition, they hypothesized that such an effect should be greater in individuals who are more sensitive or better able to perceive their own internal states, including states of arousal. They found support for their hypothesis in a recent study showing that participants with increased interoceptive abilities in a heartbeat-detection task exhibit higher loss aversion (Sokol-Hessner et al., 2015a). I suggest that the results of this thesis, in particular of **Chapter 4**, can be interpreted in light of this account: both fearful and happy faces increase arousal, and as such induce an increase in loss aversion; in addition, low anxious individuals may have a greater ability to perceive and react to this internal state of arousal than high anxious individuals, which could explain why emotion-induced changes in loss aversion are only observed in the low anxious group. However, this latter hypothesis awaits testing. Examining loss aversion in alexithymia would be interesting for that purpose. Alexithymia is characterized by a deficit in identifying, experiencing and describing one's own emotion (Sifneos, 1973; Taylor et al., 1999) and may in that sense be associated with difficulties in monitoring internal bodily states. Predictions would include lower loss aversion in subjects with high alexithymia, as well as reduced or no emotion-induced changes in loss aversion, compared to subjects with no alexithymia.

Finally, while past studies have suggested a role for dopamine in promoting risk seeking (thus reducing risk aversion; St. Onge and Floresco, 2009; Stopper et al., 2014; Rutledge et al., 2015; Ferenczi et al., 2016; Rigoli et al., 2016); whether dopamine also influence loss aversion, perhaps by changing the relative contribution of losses and gains to decisions, remains unknown. It would therefore be interesting for future studies to examine whether and how loss aversion is changed by the administration of a dopamine agonist such as L-DOPA.

6.3.3 Interaction between emotion and decision-making phenomena not accounted for by Prospect Theory's value function

All the studies presented in this thesis focused exclusively on estimating Prospect Theory's value function parameters, namely loss aversion (λ) and curvature (ρ), an index of risk preference. However, an important component of Prospect Theory as described in **Chapter 1** (section **1.1.2.2**) is the probability weighting function, which suggests that during risky decisions, people overweigh low probabilities and underweigh high probabilities. Because all the experimental designs in this thesis used gambles with 50% chance of each outcome, and probabilities were never varied to a range that encompassed low and high probabilities, it was not possible to estimate such probability weighting function in the data collected in this thesis.

However, similar to the findings of this thesis that indicate both an integral and incidental influence of emotions on risk and loss aversion, emotions may also play a key role in the probability weighting process. The following two studies would therefore be useful to conduct in the future to address this point. First, by measuring emotional reactions to probabilistic potential outcomes, one could examine whether these emotional reactions relate to outcome probabilities in a similar way as Prospect Theory-derived probability weights do. Second, if this influence is established, one could use emotional induction or priming methods to manipulate emotions and examine the consequences on the probability weighting function.

A recent study has provided preliminary evidence for the latter (Schulreich et al., 2014). The authors used a within-subject emotion induction procedure using music. Participants completed four blocks of a probabilistic gambling task (50 trials per block) where they had to decide between two lotteries (e.g. 75% chance of $3 and 25% chance of $15 versus 90% chance of $5 and 10% chance of $10). All the amounts were potential gains (no losses were involved), and magnitude and probability were varied parametrically across the 50 trials of each block, such that one lottery was always riskier than the other (wider spread in magnitude and/or probability). Before each block a 6-min emotion induction procedure was performed by having the participant listen to either happy music, sad music, random tones, or no music. Relative to sad music or random tones, happy music made participants more likely to choose the risky option, consistent with some of the studies reviewed in **Chapter 1** (Knutson et al., 2008; Lee and Andrade, 2014). However, their model of participants' choices, which included two parameters from the probability weighting function (sensitivity and elevation) as well as a curvature parameter for the value function (ρ, similar to risk aversion estimates throughout this thesis), revealed that the effect of happy music on risky choice was not driven by a reduction in the curvature of the value function, but by an increase in the elevation parameter. This increase results in overall higher probability weights following happy music relative to sad music or random tones, such that people will overall perceive the probabilities of winning as slightly higher when they are happy, in turn increasing risk taking.

Finally, there are also several other decision-making phenomena that are not accounted for by Prospect Theory value or probability weighting functions, and for which the role played by emotions is still poorly understood. One example includes context effects on decision-making, in particular the similarity, compromise and attraction effects, which occur when a third option is added to a binary choice. To illustrate these context effects, the common example concerns the choice between two cars A and B, A being cheap but lower quality and B more expensive but high quality, to the extent that the decision-maker is indifferent between A and B. The similarity effect is caused by the addition of another car S that is very similar to A, which biases the decision towards car B over car A (Tversky, 1972). The compromise effect occurs when a car C is added. Car C is extremely expensive but also extremely high quality, thus making car B a compromise between A and C; this increases the probability of car B to be chosen over car A (Simonson, 1989). Finally, the attraction effect results from adding a decoy car D that is close to car B but both more expensive and lower quality. Car D should therefore be discarded altogether in the choice process; instead it makes car B more likely to be chosen than car A (Huber et al., 1982). Several models have been developed to explain all three context effects (see Noguchi and Stewart, 2014, for a review), such as multi-alternative decision field theory (Roe et al., 2001) or the leaky competing accumulator model (Usher and McClelland, 2001). In particular, these models are dynamic models, whereby one attribute (e.g. car price) will be attended to at one moment, then all alternatives will be evaluated simultaneously on that attribute. Then at the next moment, a different attribute will be attended. Evaluation of the alternatives at every moment in time depends on which attribute is attended to. An alternative is chosen once this evaluation reaches a threshold. To my knowledge integral and incidental influences of emotions on these context effects have not been investigated, so future research questions could aim to examine such emotion effects on the dynamic allocation of attention to attributes of decision options; and thus provide a better understanding of which parameters of these models incorporate integral components of emotions and can be modulated by incidental emotions.

6.4 Limitations of studies within this thesis and directions for future research

6.4.1 Chapter 3

One limitation of the study from Chapter 3 is that the assessment of emotions was limited to one subjective feelings question about the subject's self-reported happiness. Even though the findings were replicated in three independent samples, including one where the rating scale was changed to ask subjects to rate the impact of the monetary outcome on their feelings (rather than the valence on a scale from very unhappy to very happy), it is still possible that the findings might have differed if a different assessment was used, in particular asking about negative emotions.

In addition, previous studies that have measured more implicit emotional responses to decision outcomes (in particular monetary gains and losses) have generally shown an asymmetry between gains and losses; an effect that the studies of Chapter 3 of this thesis and other studies (Mellers et al., 1997; Kermer et al., 2006; Harinck et al., 2007; McGraw et al., 2010) have failed to demonstrate using self-report feelings. For example, Sokol-Hessner et al. (2009) showed that the average SCR per dollar lost was greater than the average SCR per dollar won. Pupil dilation and heart rate (Hochman and Yechiam, 2011), as well as amygdala responses (Sokol-Hessner et al., 2013), were also found to be greater in response to losses than to equivalent gains. This suggests again that using different methods of assessing emotions may lead to different results and interpretations. In particular here, it is possible that participants do experience losses to a greater extent than gains, but that this difference is (deliberately or not) not reflected in explicit reports. It is important that future studies assess the consistency between implicit and explicit reports of emotions, in order to improve models of how such emotions influence decisions.

Another limitation of this study comes from the fact that feelings were not measured at the exact time of choice. The risk as feelings hypothesis presented in **Chapter 1** (section **1.2.2**; Loewenstein et al., 2001; Lerner et al., 2015) suggests that feelings induced by the decision at hand, for example by the level of risk independent of the potential outcomes, influence the decision. The results of Chapter 3 make the assumption that the decisions are determined by a weighted combination of the feelings about potential outcomes. Two potential caveats could contradict that claim. First, it is possible that feelings about potential outcomes are different at the time of choice than when evaluated in a different context (here a different task). If so, an alternative explanation to the results could be that loss aversion is actually reflected in a gain-loss asymmetry in feelings experienced at the time of choice, rather than by an asymmetry in the weight of feelings experienced in a different contexts. Second, because feelings induced by the decision itself were not directly measured (with a question such as "how do you feel about making this decision?"), a component of emotion (the current or immediate emotions suggested by the risk as feelings hypothesis) and its influence on choice were neglected. Future directions would therefore involve developing a task and a model of emotional decision-making that can account for the influence of both immediate and expected emotions at the time of choice.

Finally, whether expected and experienced feelings contribute differently to decisions is still not established by the data. Even though the findings suggest that both predict choice better than traditional value-based models, they were both strongly correlated with each other, making it impossible to include them in the same model to examine their unique contribution to choice.

6.4.2 Chapter 4

One of the main limitations in the design of the study from Chapter 4 was that gain-only gamble trials were not included, which would have been necessary to estimate both risk and loss aversion parameters in the same model. However given the time constraints in the scanner, the longer duration of each trial due to the addition of the jitters, and the need for a substantial number of trials per emotion condition in order to allow the loss aversion parameter to vary with emotion, it was not possible to add those extra trials. A separate estimation of risk aversion, based on the sensitivity to the variance of each gamble as has been used previously (De Martino et al., 2010; Canessa et al., 2013), ensured risk aversion did not contribute to the observed effects on loss aversion. Despite this, future studies should try and overcome this limitation by adding both trial types to their design. One possibility could be to start with only two types of primes (e.g. fearful vs neutral faces, similar to Schulreich et al., 2016), in order to simplify the design and maximize the number of trials and sensitivity for modelling loss and risk aversion in each condition. Then if an effect is found, other primes could then be added to the design.

A second limitation associated with the findings of Chapter 4 comes from the fact that the result of emotional priming was not significant across the entire sample, only when analysed in relation to individual differences in trait anxiety. Since one of the aims of this study was to examine individual differences, this is not a problem in this perspective, but the absence of a main effect of emotion across all participants means that the results cannot be generalized to the simple claim that emotion increases loss aversion.

In addition, even though the analysis of the combined data of Chapters 4 and 5 (see section **6.2** above) suggests that the effect holds over both samples, the effect was not in itself replicated in Chapter 5. There is therefore a need to replicate this result in future studies. Interestingly, the results of the pilot studies (**Chapter 2**, section **2.5**), even though they have to be taken with caution because the protocol was still being developed, seem to corroborate the effect of trait anxiety on the emotional modulation of loss aversion. When examining the specific correlation between trait anxiety and the percentage change in loss aversion between emotional and non-emotional primes, however, this correlation was only significant for pilot study 1, which used subliminal emotional primes [$r(30)=-0.468$, $P=0.009$], but not for pilot study 2 [$r(32)=-0.114$, $P=0.54$].

Another possibility to address some of these issues could be to use more arousing pictures (instead of faces) as primes. Even though faces have the advantage of allowing manipulation of the emotional content while keeping everything else constant (e.g. the face from the same individual depicting fearful, happy or neutral expression), they are usually not perceived as very arousing by participants. For example, in the debriefing questionnaire, several participants reported finding the fearful faces "funny" but clearly not scary. In addition, most studies that have found an effect of incidental emotional primes, presented for a few seconds, on economic choice (Knutson et al., 2008; Kuhnen and Knutson, 2011; Cassotti et al., 2012) have used pictures of scenes rather than faces. A similar procedure could be used, by perhaps having subjects subjectively rate the pictures on arousal and different emotions (happiness, fear, disgust, sadness, etc) in a preliminary session; then specifically selecting those images that the subject finds particularly arousing and emotionally-provoking as primes for the decision-making task. Visual primes could also be combined with primes presented in another modality (e.g. sounds) for a stronger effect. Finally, it would be interesting to try to replicate the same findings using emotional priming and a more long-lasting mood induction procedure, although as mentioned in **Chapter 1** (section **1.3**), the mechanisms may be different and result in differential effects on behaviour. Nonetheless, both play a role in influencing decisions, probably on a different timescale, and little is known about the concurrent integration of both short-lasting emotions and long-lasting mood effects during choice; therefore this warrants further investigation.

6.4.3 Chapter 5

As summarised above, the main finding of Chapter 5 is the difference in risk aversion (but not in loss aversion) between anxious patients and controls, independent of the influence of incidental emotional cues. However, because the design used those cues on every trial, and was embedded in a working memory cover story with subjects having to perform a memory task concomitantly with the gambling task, there is a need for future studies to replicate the risk aversion effect in a simpler design, with the only purpose of examining risk and loss aversion. In addition, implementing such a design would have the advantage of removing the emotional cues and the memory task, thus saving a substantial amount of time and allowing more trials in the task to estimate the model parameters, which would afford a greater degree of precision. In particular, it would allow adding loss-only trials, in which participants have to choose between a sure small loss and a risky gamble with 50% chance of a high loss and 50% chance of not losing (similar to the choice task used in **Chapter 3**, **Figure 3-1C**), in order to separate risk aversion in the gain and loss domains.

In addition, an alternative explanation for the increased risk aversion in the anxious group could be explained by the fact that anxious patients may underestimate the probability of winning in the gain-only trials. Given the finding that positive affect induces an overestimation of gain probabilities (Schulreich et al., 2014), one hypothesis could be that anxious patients, in contrast, exhibit a general tendency to underestimate gain probabilities, which could result in the decreased propensity to take risks observed in anxious patients. In order to disentangle between these two hypotheses and determine whether anxiety is best characterized by increased risk aversion or decreased probability weighting, future experiments should parametrically vary the probabilities of winning and losing in their design, rather than focus on 50-50 gambles.

6.5 Conclusions and implications for the development of possible interventions

6.5.1 Beneficial and detrimental effects of emotions on decision-making

Very few accounts of the role of emotion in decision-making have discussed whether such an influence is ultimately beneficial or detrimental for the decision-maker. It is obviously difficult to answer such a question given the still limited understanding of the detailed mechanisms by which emotions and decisions interact. However, given the focus of this thesis, a few points and speculations can be made.

Traditionally, most decision-making researchers, particularly in economics, would view any kind of emotion as an interference in the rational, optimal process of calculating expected value and making decisions. By making people deviate from rationality, emotions were in that sense systematically considered detrimental to the decision-making process. However, the early theories of an integral influence of emotions on decisions started diverging from this view. The somatic marker hypothesis (Bechara et al., 1994, 1997, 1999; Bechara and Damasio, 2005) was one of the first to suggest that emotions are necessary, and therefore beneficial, for decisions. The theory makes the assumption that it is thanks to our emotional reactions that we learn to seek rewards and avoid losses, and to make advantageous long-term decisions. As a result, people who cannot experience or process such emotional reactions exhibit impaired decision-making. Although the task that was used to test this somatic marker hypothesis (the IGT) is far from perfect (as described in **Chapter 1**, section **1.2.1**), the theory remains nonetheless an interesting one and has helped transforming the view of emotions as pivotal and beneficial components of decisions. The risk as feeling hypothesis proposed later (Loewenstein et al., 2001; Lerner et al., 2015) offers a more integrated and nuanced view, in particular distinguishing the role of expected versus immediate emotions. Expected emotions are emotions expected to be induced by the potential decisions outcomes should they be experienced later; these expected emotions are likely to be driven by past experiences of similar outcomes and similar to the somatic marker hypothesis, the risk as feelings hypothesis suggests they will inform the decision-maker and be beneficial to their decision. In contrast, immediate emotions, which are induced by the decision at hand, for example by the level of risk, will often bias decision-maker away from the rational course of action, and can in that sense be detrimental.

Overall I argue that emotions are mostly beneficial to the decision-making process if one considers that a decision-maker behaves optimally, not by maximizing the expected value of their outcomes, but by maximizing their positive feelings and minimizing their negative feelings at any given moment in time. With this view, a decision is considered optimal when it maximizes how good the decision-maker feels, rather than how much money they will win. The outcome of the decision can therefore be viewed as one component that will generate emotions (positive if the outcome is good, negative if the outcome is bad); however, once combined with all the other emotional components of the decision (e.g. feelings induced by the level of risk, or the anticipation, etc), feelings will often be maximized in cases where the outcome may not be the best. Therefore, emotions may act as primary reinforcers and an optimal decision-maker will be someone who seek to maximize positive emotional experiences and minimize negative emotional experiences, possibly in a simple Pavlovian manner (Seymour and Dolan, 2008; Hart et al., 2014; Ly et al., 2014; Rutledge et al., 2015). With this view, integral emotions are largely beneficial to decision-making.

Another potentially important idea consistent with a beneficial role of emotions in decisions is the view that emotions help people decide quickly. Because in reality, a decision-maker rarely has much time to carefully consider and weigh up all possible decision options, especially when they are close in value, emotion can be key in speeding the decision-making process. In particular, simple heuristics, driven by the negative emotional impact of potential losses, help participants prune away some branches of the decision tree they face in a complex sequential decision-making task, thus reducing the number of possible decisions and the time needed to choose (Huys et al., 2012, 2015). Even though previous work indicates that emotions affect timing and the perception of time (see Droit-Volet and Meck, 2007 for a review), suggesting a possible mechanism by which emotions may reduce decision times, this question has, to my knowledge, never been directly examined. If such an effect of emotion in speeding decision processes exists, it can also be viewed as an adaptive role of emotion, especially when considered from an evolutionary perspective and applied to situations in which making quick decisions (e.g. avoiding danger) is necessary for survival and improves evolutionary fitness.

Nonetheless, there are cases where the influence of emotions can become detrimental. Those are cases where decisions fail to maximize positive feelings, and might instead induce more negative feelings, where the decision-maker fails to learn from these feelings to adapt their subsequent decisions, or where emotions may slow down the decision process instead of speeding it up. This will often occur in emotional disorders, such as anxiety and depression, and can be one of the main causes for the persistence of these negative feelings and biases.

6.5.2 Can emotion regulation strategies target and reduce detrimental influences of emotions on decisions?

When emotions have a detrimental influence on people's decisions, or even people's behaviour and mental health in general, some interventions exist to try and override this negative influence. Such interventions involve cognitive training to learn to reduce or regulate one's emotions. The two most common examples of emotion regulation strategies are emotion suppression, which simply involves controlling and reducing any negative emotion, and reappraisal, which involves reframing and reinterpreting in a positive ways the meaning of an event that generated a negative emotional response (for example, viewing losing a job as an opportunity to pursue a new exciting career path; Gross, 2002; Gross and John, 2003). Most studies comparing the effect of both strategies on a range of tasks, as well as in patients with affective disorders, have shown a clear advantage for reappraisal over suppression (Gross, 2002; Gross and John, 2003), mainly because in addition to reducing negative feelings, reappraisal reduces neural and physiological responses to negative events (Ochsner et al., 2002; Jamieson et al., 2012) and increases positive emotional experiences (Gross and John, 2003), whereas suppression fails to do so (Gross and Levenson, 1993; Gross, 2002). As yet, only a handful of studies have examined the influence of emotion regulation strategies on decision-making under risk, but all converge towards the finding that cognitive reappraisal of emotions increases risk taking behaviour (Sokol-Hessner et al., 2009; Heilman et al., 2010; Panno et al., 2013; Martin Braunstein et al., 2014). In particular, using a reappraisal technique that made participants focus on the global outcome of all their decisions, rather than on individual outcomes (more likely to induce incidental emotions carrying over to the next decisions) combined with a Prospect Theory model, Sokol-Hessner et al. (2009) found that the increased propensity to gamble under reappraisal was driven by reduced loss aversion rather than risk aversion, accompanied by reduced SCRs to loss outcomes. Panno et al. (2013) extended the effect of reappraisal as a within-subject manipulation to individual differences, showing that individuals who generally used more cognitive reappraisal in daily life situations took more risk in a gambling task and were less sensitive to losses.

The use of such emotion regulation techniques could be promising as clinical interventions for anxiety. As described in **Chapter 1** (section **1.4.1**), individuals with anxiety have difficulties regulating their emotions, both during emotional conflict tasks (Etkin et al., 2010; Etkin and Schatzberg, 2011) and in their daily life (Farmer and Kashdan, 2012). In addition, anxiety is characterized by the presence of negative attentional biases, such that anxious individuals primarily allocate their attention towards threat-related stimuli and have difficulty disengaging their attention from such stimuli (Bar-Haim et al., 2007). Attentional bias modification is an intervention that has been developed to try and counteract this threat-related bias. In most cases, this intervention uses a variant of the dot-probe task, in which instead of having the dot probe appearing randomly behind the neutral or threatening face, the contingencies are modified such that the dot mostly or always appear behind the neutral face (MacLeod et al., 2002). Through learning, patients can therefore learn to allocate their attention away from the threatening stimuli. This and similar tasks are effective in reducing attentional biases in clinical anxiety (see Browning et al., 2010 for a review) and significantly reduce anxiety symptoms (see Hakamata et al., 2010; Linetzky et al., 2015 for meta-analyses) with effects lasting at least several months (Schmidt et al., 2009). Interestingly a recent meta-analysis that included clinical trials using attentional bias modification, as well as other trials using cognitive bias modification (an intervention focusing on biases in interpreting information, rather than attentional biases) or other approaches such as concreteness training or alcohol approach and avoidance training, found no reliable effect on anxiety symptoms (Cristea et al., 2015). This suggests that attentional bias modification may be specifically well suited to anxiety, while other cognitive interventions are not.

Despite their efficacy, the mechanisms by which such interventions work, and in particular the role they play in the integration of emotions during decision-making, remain poorly understood. As yet, the potential link between interventions such as cognitive reappraisal (which seems to reduce risk/loss aversion) or attentional bias modification (which seems to improve anxiety symptoms) and risk-taking behaviour in anxiety has not been examined. In particular, two interesting questions for future research would be (i) to determine whether cognitive reappraisal may reduce risk aversion in clinical anxiety, and if so whether this mediates any clinical improvements in symptoms; and (ii) to investigate the possibility that reduced risk aversion may mediate the link between attentional bias modification and reduction in anxiety symptoms. Finally, intolerance to uncertainty has been defined as a pivotal feature of clinical anxiety (Dugas et al., 1998) and may also be a primary driver of the observed increased risk aversion. However, whether such aversion to uncertainty arises from similar or different mechanisms than threat-related attentional biases, and whether this plays a role in the mechanisms of attentional bias modification, are also unresolved questions. If attention to threat and intolerance to uncertainty are in fact two distinct processes, future interventions focusing on reducing intolerance to uncertainty may prove useful in anxiety.

6.5.3 Overall conclusions

Taken together, the findings of this thesis help provide a more complete understanding of the complex interactions between emotions, mood and decision-making. They indicate (i) that traditional models of economic choice, such as Prospect Theory, can be improved by accounting for the role played by subjective emotions, (ii) that loss aversion is best explained by an asymmetry in how people weigh their feelings about losses relative to gains, (iii) that an arousal account of loss aversion is probable, whereby the emotional modulation of loss aversion recruits amygdala-striatal interactions, and (iv) that anxiety is associated with enhanced risk aversion but no change in loss aversion, and possibly with difficulties in modulating one's decisions in response to emotionally-arousing cues.

Interventions based on the regulation or modification of emotional responses are promising; yet, they may greatly benefit from better mechanistic accounts of how emotions affect behaviour in the first place. This thesis attempted to provide such a mechanistic account of economic decision-making behaviour and to improve the understanding of the combined influence of integral feelings, incidental emotions, and clinical anxiety in this process, in the hope of paving the way for future avenues of research applied to economic decision-making, as well as other cognitive processes.

References

Adolphs R (2002) Neural systems for recognizing emotion. Curr Opin Neurobiol 12:169–177.

Allais M (1953) Le comportement de l’homme rationnel devant le risque: critique des postulats et axiomes de l'ecole americaine. Econometrica 21:503–546.

Andrade EB, Odean T, Lin S (2016) Bubbling with excitement: an experiment. Rev Financ:447–466.

Arnsten AFT (2009) Stress signalling pathways that impair prefrontal cortex structure and function. Nat Rev Neurosci 10:410–422.

Bar-Haim Y, Lamy D, Pergamin L (2007) Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. Psychol Bull 133:1–24.

Barrash J, Tranel D, Anderson SW (2000) Acquired personality disturbances associated with bilateral damage to the ventromedial prefrontal region. Dev Neuropsychol 18:355–381.

Bechara A, Damasio AR (2005) The somatic marker hypothesis: A neural theory of economic decision. Games Econ Behav 52:336–372.

Bechara A, Damasio AR, Damasio H, Anderson SW (1994) Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 50:7–15.

Bechara A, Damasio H, Damasio AR, Lee GP (1999) Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. J Neurosci 19:5473–5481.

Bechara A, Damasio H, Tranel D, Damasio AR (1997) Deciding advantageously before knowing the advantageous strategy. Science (80-) 275:1293–1295.

Bechara A, Tranel D, Damasio H (2000) Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. Brain 123:2189–2202.

Beck AT, Erbaugh J, Ward CH, Mock J, Mendelson M (1961) An inventory for measuring depression. Arch Gen Psychiatry 4:561–571.

Beck AT, Steer RA, Carbin MG (1988) Psychometric properties of the Beck Depression Inventory: Twenty-five years of evaluation. Clin Psychol Rev 8:77–100.

Beddington J, Cooper CL, Goswami U, Huppert FA, Jenkins R, Jones HS, Tom BL, Sahakian BJ, Thomas M (2008) The mental wealth of nations. Nature 455:1057–1059.

Benjamin DJ, Heffetz O, Kimball MS, Rees-jones A (2012) What do you think would make you happier? What do you think you would choose? Am Econ Rev 102:2083–2110.

Benjamin DJ, Heffetz O, Kimball MS, Rees-jones A (2014) Can marginal rates of substitution be inferred from happiness data? Evidence from residency shoices.

Am Econ Rev 104:3498–3528.

Bernoulli D (1954) Exposition of a new theory on the measurement of risk. Econometrica 22:23–36.

Bishop SJ (2007) Neurocognitive mechanisms of anxiety: an integrative account. Trends Cogn Sci 11:307–316.

Bishop SJ (2009) Trait anxiety and impoverished prefrontal control of attention. Nat Neurosci 12:92–98.

Bishop SJ, Forster S (2013) Trait anxiety, neuroticism, and the brain basis of vulnerability to affective disorder. In: The Cambridge Handbook of Human Affective Neuroscience (Armony J, Vuilleumier P, eds), pp 553–574. Cambridge University Press.

Blair K, Shaywitz J, Smith BW, Rhodes R, Geraci M, Jones M, McCaffrey D, Vythilingam M, Finger E, Mondillo K, Jacobs M, Charney DS, Blair RJ, Drevets WC, Pine DS (2008) Response to emotional expressions in generalized social phobia and generalized anxiety disorder: evidence for separate disorders. Am J Psychiatry 165:1193–1202.

Blanchette I, Richards A (2003) Anxiety and the interpretation of ambiguous information: Beyond the emotion-congruent effect. J Exp Psychol Gen 132:294–309.

Boubela RN, Kalcher K, Huf W, Seidel E-M, Derntl B, Pezawas L, Našel C, Moser E (2015) fMRI measurements of amygdala activation are confounded by stimulus correlated signal fluctuation in nearby veins draining distant brain regions. Sci Rep 5:10499.

Boyce CJ, Wood AM, Banks J, Clark AE, Brown GDA (2013) Money, well-being, and loss aversion: does an income loss have a greater effect on well-being than an equivalent income gain? Psychol Sci 24:2557–2562.

Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433–436.

Breiter HC, Aharon I, Kahneman D, Dale A, Shizgal P (2001) Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron 30:619–639.

Browning M, Behrens TE, Jocham G, Reilly JXO, Bishop SJ (2015) Anxious individuals have difficulty learning the causal statistics of aversive environments. Nat Neurosci 18:590–596.

Browning M, Holmes EA, Harmer CJ (2010) The modification of attentional bias to emotional information: a review of the techniques, mechanisms, and relevance to emotional disorders. Cogn Affect Behav Neurosci 10:8–20.

Buckert M, Schwieren C, Kudielka BM, Fiebach CJ (2014) Acute stress affects risk taking but not ambiguity aversion. Front Neurosci 8:82.

Butler G, Mathews A (1983) Cognitive processes in anxiety. Adv Behav Res Ther 5:51–62.

Camara E, Rodriguez-Fornells A, Münte TF (2008) Functional connectivity of reward processing in the brain. Front Hum Neurosci 2:19.

Camerer C (2005) Three Cheers - Psychological , Theoretical, Empirical - for Loss Aversion. J Mark Res 42:129–133.

Canessa N, Crespi C, Motterlini M, Baud-Bovy G, Chierchia G, Pantaleo G, Tettamanti M, Cappa SF (2013) The functional and structural neural basis of individual differences in loss aversion. J Neurosci 33:14307–14317.

Carter S, McBride M (2013) Experienced utility versus decision utility: Putting the “S” in satisfaction. J Socio-Econ 42:13–23.

Cassotti M, Habib M, Poirel N, Aïte A, Houdé O, Moutier S (2012) Positive emotional context eliminates the framing effect in decision-making. Emotion 12:926–931.

Chib VS, De Martino B, Shimojo S, O’Doherty JP (2012) Neural mechanisms underlying paradoxical performance for monetary incentives are driven by loss aversion. Neuron 74:582–594.

Chib VS, Rangel A, Shimojo S, O’Doherty JP (2009) Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. J Neurosci 29:12315–12320.

Chiu Y-C, Lin C-H (2007) Is deck C an advantageous deck in the Iowa Gambling Task? Behav brain Funct 3:37.

Christopoulos GI, Tobler PN, Bossaerts P, Dolan RJ, Schultz W (2009) Neural correlates of value, risk, and risk aversion contributing to decision making under risk. J Neurosci 29:12574–12583.

Cisler JM, Koster EHW (2010) Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. Clin Psychol Rev 30:203–216.

Clark L, Li R, Wright CM, Rome F, Fairchild G, Dunn BD, Aitken MRF (2012) Risk-avoidant decision making increased by threat of electric shock. Psychophysiology 49:1436–1443.

Cloninger CR (1990) Comorbidity of Anxiety and Depression. J Clin Psychopharmacol 10:43S – 46S.

Cohen JD (2005) The vulcanization of the human brain: a neural perspective on interactions between cognition and emotion. J Econ Perspect 19:3–24.

Cools R, Barker RA, Sahakian BJ, Robbins TW (2003) L-Dopa medication remediates cognitive inflexibility, but increases impulsivity in patients with Parkinson’s disease. Neuropsychologia 41:1431–1441.

Crawford J, Cayley C, Lovibond PF, Wilson PH, Hartley C (2011) Percentile norms and accompanying interval estimates from an australian general adult population sample for self-report mood scales (BAI, BDI, CRSD, CES-D, DASS, DASS-21, STAI-X, STAI-Y, SRDS, and SRAS). Aust Psychol 46:3–14.

Crişan LG, Pană S, Vulturar R, Heilman RM, Szekely R, Drugă B, Dragoş N, Miu AC (2009) Genetic contributions of the serotonin transporter to social learning of fear and economic decision making. Soc Cogn Affect Neurosci 4:399–408.

Cristea IA, Kok RN, Cuijpers P (2015) Efficacy of cognitive bias modification interventions in anxiety and depression: meta-analysis. Br J Psychiatry 206:7–16.

Dalgleish T (2004) The emotional brain. Nat Rev Neurosci 5:583–589.

Dalgleish T, Yiend J, Bramham J, Teasdale JD, Ogilvie AD, Malhi G, Howard R (2004) Neuropsychological processing associated with recovery from depression after stereotactic subcaudate tractotomy. Am J Psychiatry 161:1913–1916.

Davis M, Walker DL, Miles L, Grillon C (2010) Phasic vs sustained fear in rats and humans: role of the extended amygdala in fear vs anxiety. Neuropsychopharmacol Rev 35:105–135.

De Martino B, Camerer CF, Adolphs R (2010) Amygdala damage eliminates monetary loss aversion. Proc Natl Acad Sci U S A 107:3788–3792.

De Martino B, Kumaran D, Seymour B, Dolan RJ (2006) Frames, Biases, and Rational Decision-Making in the Human Brain. Science (80-) 313:684–687.

De Neve J-E, Ward G, De Keulenaer F, Van Landeghem B, Kavetsos G, Norton M (2015) Individual experience of positive and negative growth is asymmetric: global evidence using subjective well-being data. Cent Econ Perform Discuss Pap No 1304.

Delgado MR, Jou RL, Ledoux JE, Phelps EA (2009) Avoiding negative outcomes: tracking the mechanisms of avoidance learning in humans during fear conditioning. Front Behav Neurosci 3:33.

Derryberry D, Reed MA (2002) Anxiety-related attentional biases and their regulation by attentional control. J Abnorm Psychol 111:225–236.

Droit-Volet S, Meck WH (2007) How emotions colour our perception of time. Trends Cogn Sci 11:504–513.

Dugas MJ, Gagnon F, Ladouceur R, Freeston MH (1998) Generalized anxiety disorder: a preliminary test of a conceptual model. Behav Res Ther 36:215–226.

Dunn BD, Dalgleish T, Lawrence AD (2006) The somatic marker hypothesis: A critical evaluation. Neurosci Biobehav Rev 30:239–271.

Engelmann XJB, Meyer F, Fehr E, Ruff XCC (2015) Anticipatory anxiety disrupts neural valuation during risky choice. J Neurosci 35:3085–3099.

Ernst M, Plate RC, Carlisi CO, Gorodetsky E, Goldman D, Pine DS (2014) Loss aversion and 5HTT gene variants in adolescent anxiety. Dev Cogn Neurosci 8:77–85.

Etkin A, Klemenhagen KC, Dudman JT, Rogan MT, Hen R, Kandel ER, Hirsch J (2004) Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. Neuron 44:1043–1055.

Etkin A, Prater KE, Hoeft F, Menon V, Schatzberg AF (2010) Failure of anterior cingulate activation and connectivity with the amygdala during implicit regulation of emotional processing in generalized anxiety disorder. Am J Psychiatry 167:545–554.

Etkin A, Schatzberg AF (2011) Common abnormalities and disorder-specific compensation during implicit regulation of emotional processing in Generalized Anxiety and Major Depressive Disorders. Am J Psychiatry 168:968–978.

Everitt BJ, Robbins TW (1992) Amygdala-ventral striatal interactions and reward-related processes. In: The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction. (Aggleton JP, ed), pp 401–429. New York, NY, US: Wiley-Liss.

Eysenck MW, Santos R, Calvo MG (2007) Anxiety and cognitive performance: Attentional Control Theory. Emotion 7:336–353.

Farmer AS, Kashdan TB (2012) Social anxiety and emotion regulation in daily life: spillover effects on positive and negative social events. Cogn Behav Ther 41:152–162.

Faul F, Erdfelder E, Lang A, Buchner A (2007) A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods 39:175–191.

Fellows LK, Farah MJ (2005) Different underlying impairments in decision-making following ventromedial and dorsolateral frontal lobe damage in humans. Cereb Cortex 15:58–63.

Ferenczi EA, Zalocusky KA, Liston C, Grosenick L, Warden MR, Amatya D, Katovich K, Mehta H, Patenaude B, Ramakrishnan C, Kalanithi P, Etkin A, Knutson B, Glover GH, Deisseroth K (2016) Prefrontal cortical regulation of brainwide circuit dynamics and reward-related behavior. Science (80-) 351:aac9698.

Ferreira TL, Shammah-Lagnado SJ, Bueno OF a, Moreira KM, Fornari R V, Oliveira MGM (2008) The indirect amygdala-dorsal striatum pathway mediates conditioned freezing: insights on emotional memory networks. Neuroscience 153:84–94.

Fishburn PC, Kochenberger GA (1979) Two-piece Von Neumann-Morgenstern utility functions. Decis Sci 10:503–518.

Fox CR, Poldrack RA (2014) Prospect Theory and the brain. In: Handbook of Neuroeconomics (2nd edition). New York: Elsevier.

Fox E, Mathews A, Calder AJ, Yiend J (2007) Anxiety and sensitivity to gaze direction in emotionally expressive faces. Emotion 7:478–486.

Galván A, Peris TS (2014) Neural correlates of risky decision making in anxious youth and healthy controls. Depress Anxiety 14:488–501.

Gilbert DT, Pinel EC, Wilson TD, Blumberg SJ, Wheatley TP (1998) Immune neglect: a source of durability bias in affective forecasting. J Pers Soc Psychol 75:617–638.

Giorgetta C, Grecucci A, Zuanon S, Perini L, Balestrieri M, Bonini N, Sanfey AG, Brambilla P (2012) Reduced risk-taking behavior as a trait feature of anxiety. Emotion 12:1373–1383.

Glascher J, Adolphs R (2003) Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. J Neurosci 23:10274–10282.

Gottfried JA, O'Doherty J, Dolan RJ (2003) Value in human amygdala and orbitofrontal cortex. Science (80-) 301:1104–1107.

Grillon C (2008) Models and mechanisms of anxiety: evidence from startle studies. Psychopharmacology (Berl) 199:421–437.

Grillon C, Ameli R, Woods SW, Merikangas K, Davis M (1991) Fear-potentiated startle in humans: effects of anticipatory anxiety on the acoustic blink reflex. Psychophysiology 28:588–595.

Gross JJ (2002) Emotion regulation: affective, cognitive, and social consequences. Psychophysiology 39:281–291.

Gross JJ, John OP (2003) Individual differences in two emotion regulation processes: implications for affect, relationships, and well-being. J Pers Soc Psychol 85:348–362.

Gross JJ, Levenson RW (1993) Emotional suppression: physiology, self-report, and expressive behavior. J Pers Soc Psychol 64:970–986.

Hahn T, Dresler T, Plichta MM, Ehlis AC, Ernst LH, Markulin F, Polak T, Blaimer M, Deckert J, Lesch KP, Jakob PM, Fallgatter AJ (2010) Functional amygdala-hippocampus connectivity during anticipation of aversive events is associated with Gray’s trait “sensitivity to punishment.” Biol Psychiatry 68:459–464.

Hakamata Y, Lissek S, Bar-Haim Y, Britton JC, Fox NA, Leibenluft E, Ernst M, Pine DS (2010) Attention bias modification treatment: a meta-analysis toward the establishment of novel treatment for anxiety. Biol Psychiatry 68:982–990.

Han S, Lerner JS, Zeckhauser R (2012) The disgust-promotes-disposal effect. J Risk Uncertain 44:101–113.

Hardie BGS, Johnson EJ, Fader PS (1993) Modeling loss aversion and reference dependence effects on brand choice. Mark Sci 12:378–394.

Harinck F, Van Dijk E, Van Beest I, Mersmann P (2007) When gains loom larger than losses: reversed loss aversion for small amounts of money. Psychol Sci 18:1099–1105.

Hart AS, Rutledge RB, Glimcher PW, Phillips PEM (2014) Phasic dopamine release in the rat nucleus accumbens symmetrically encodes a reward prediction error term. J Neurosci 34:698–703.

Hartley CA, Phelps EA (2012) Anxiety and decision-making. Biol Psychiatry 72:113–118.

Heilman RM, Crişan LG, Houser D, Miclea M, Miu AC (2010) Emotion regulation and decision making under risk and uncertainty. Emotion 10:257–265.

Herrero AI, Sandi C, Venero C (2006) Individual differences in anxiety trait are related to spatial learning abilities and hippocampal expression of mineralocorticoid receptors. Neurobiol Learn Mem 86:150–159.

Hinson JM, Jameson TL, Whitney P (2002) Somatic markers, working memory, and decision making. Cogn Affect Behav Neurosci 2:341–353.

Hirschfeld RM (2001) The Comorbidity of Major Depression and Anxiety Disorders: Recognition and Management in Primary Care. Prim Care Companion J Clin Psychiatry 3:244–254.

Hochman G, Yechiam E (2011) Loss aversion in the eye and in the heart: the autonomic nervous system's responses to losses. J Behav Decis Mak 24:140–156.

Hsu M, Bhatt M, Adolphs R, Tranel D, Camerer CF (2005) Neural systems responding to degrees of uncertainty in human decision-making. Science (80-) 310:1680–1683.

Huber J, Payne JW, Puto C (1982) Adding asymmetrically dominated alternatives: violations of regularity and the similarity hypothesis. J Consum Res 9:90–98.

Huys QJM, Eshel N, O'Nions E, Sheridan L, Dayan P, Roiser JP (2012) Bonsai trees in your head: how the pavlovian system sculpts goal-directed choices by pruning decision trees. PLoS Comput Biol 8:e1002410.

Huys QJM, Lally N, Faulkner P, Eshel N, Seifritz E, Gershman SJ, Dayan P, Roiser JP (2015) Interplay of approximate planning strategies. Proc Natl Acad Sci U S A 112:3098–3103.

Isen AM, Nygren TE, Ashby FG (1988) Influence of positive affect on the subjective utility of gains and losses: it is just not worth the risk. J Pers Soc Psychol 55:710–717.

Jamieson JP, Nock MK, Mendes WB (2012) Mind over matter: reappraising arousal improves cardiovascular and cognitive responses to stress. J Exp Psychol Gen 141:417–422.

Jarosz AF, Wiley J (2014) What are the odds? A practical guide to computing and reporting Bayes Factors. J Probl Solving 7:2–9.

Jeffreys H (1961) Theory of probability, 3rd Ed. Oxford, UK: Oxford University Press.

Johnson EJ, Tversky A (1983) Affect, generalization, and the perception of risk. J Pers Soc Psychol 45:20–31.

Julian LJ (2011) Measures of anxiety: State-Trait Anxiety Inventory (STAI), Beck Anxiety Inventory (BAI), and Hospital Anxiety and Depression Scale-Anxiety (HADS-A). Arthritis Care Res 63:467–472.

Kable JW, Glimcher PW (2009) The neurobiology of decision: consensus and controversy. Neuron 63:733–745.

Kahn I, Yeshurun Y, Rotshtein P, Fried I, Ben-Bashat D, Hendler T (2002) The role of the amygdala in signaling prospective outcome of choice. Neuron 33:983–994.

Kahneman D (2011) Thinking, fast and slow. New York: Farrar, Straus and Giroux.

Kahneman D, Knetsch JL, Thaler RH (1990) Experimental Tests of the Endowment Effect and the Coase Theorem. J Polit Econ 98:1325–1348.

Kahneman D, Knetsch JL, Thaler RH (1991) Anomalies: the endowment effect, loss aversion, and status quo bias. J Econ Perspect 5:193–206.

Kahneman D, Tversky A (1979) Prospect theory: an analysis of decision under risk. Econometrica 47:263–292.

Kahneman D, Wakker PP, Sarin R (1997) Back to Bentham? Explorations of Experienced Utility. Q J Econ 112:375–405.

Kassam KS, Morewedge CK, Gilbert DT, Wilson TD (2011) Winners love winning and losers love money. Psychol Sci 22:602–606.

Kermer DA, Driver-Linn E, Wilson TD, Gilbert DT (2006) Loss aversion is an affective forecasting error. Psychol Sci 17:649–653.

Kirschbaum C, Pirke K-M, Hellhammer DH (1993) The “Trier Social Stress Test”- a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobiology 28:76–81.

Kleiner M, Brainard D, Pelli D (2007) What’s new in Psychtoolbox-3? In: Perception 36 ECVP Abstract Supplement.

Knetsch JL (1989) The endowment effect and evidence of nonreversible indifference curves. Am Econ Rev 79:1277–1284.

Knetsch JL, Sinden JA (1984) Willingness to pay and compensation demanded: Experimental evidence of an unexpected disparity in measures of value. Q J Econ 99:507–521.

Knight F (1921) Risk, Uncertainty, and Profit. Boston, MA: Houghton-Mifflin.

Knight RG, Waal-Manning HJ, Spears GF (1983) Some norms and reliability data for the State-Trait Anxiety Inventory and the Zung Self-Rating Depression scale. Br J Clin Psychol 22:245–249.

Knutson B, Wimmer GE, Kuhnen CM, Winkielman P (2008) Nucleus accumbens activation mediates the influence of reward cues on financial risk taking. Neuroreport 19:509–513.

Kuhnen CM, Knutson B (2005) The neural basis of financial risk taking. Neuron 47:763–770.

Kuhnen CM, Knutson B (2011) The influence of affect on beliefs, preferences, and financial decisions. J Financ Quant Anal 46:605–626.

Kvaal K, Ulstein I, Nordhus IH, Engedal K (2005) The Spielberger State-Trait Anxiety Inventory (STAI): The state scale in detecting mental disorders in geriatric patients. Int J Geriatr Psychiatry 20:629–634.

Kwong JYY, Wong KFE, Tang SKY (2013) Comparing predicted and actual affective responses to process versus outcome: and emotion-as-feedback perspective. Cognition 129:42–50.

Lak A, Stauffer WR, Schultz W (2014) Dopamine prediction error responses integrate subjective value from different reward dimensions. Proc Natl Acad Sci U S A 111:2343–2348.

Landgraf R, Wigger A (2002) High vs low anxiety-related behavior rats: an animal model of extremes in trait anxiety. Behav Genet 32:301–314.

Lang PJ, Bradley MM, Cuthbert B. (1997) International affective picture system (IAPS): technical manual and affective ratings. NIMH Cent Study Emot Atten:39–58.

Lasa L, Ayuso-Mateos JL, Vázquez-Barquero JL, Díez-Manrique FJ, Dowrick CF (2000) The use of the Beck Depression Inventory to screen for depression in the general population: a preliminary analysis. J Affect Disord 57:261–265.

LeDoux JE, Gorman JM (2001) A call to action: overcoming anxiety through active coping. Am J Psychiatry 158:1953–1955.

Lee CJ, Andrade EB (2014) Fear, excitement, and financial risk-taking. Cogn Emot:(in press).

Lerner JS, Keltner D (2000) Beyond valence: Toward a model of emotion-specific influences on judgement and choice. Cogn Emot 14:473–493.

Lerner JS, Keltner D (2001) Fear, anger, and risk. J Pers Soc Psychol 81:146–159.

Lerner JS, Li Y, Valdesolo P, Kassam KS (2015) Emotion and decision making. Annu Rev Psychol 66:799–823.

Lerner JS, Small D a, Loewenstein G (2004) Heart strings and purse strings: carryover effects of emotions on economic decisions. Psychol Sci 15:337–341.

Lesch K-P, Bengel D, Heils A, Sabol SZ, Greenberg BD, Petri S, Benjamin J, Muller CR, Hamer DH, Murphy DL (1996) Association of anxiety-related traits with a polymorphism in the serotonin transporter gene regulatory region. Science (80-) 274:1527–1531.

Levine LJ, Lench HC, Kaplan RL, Safer MA (2013) Like Schrodinger's cat, the impact bias is both dead and alive: reply to Wilson and Gilbert (2013). J Pers Soc Psychol 105:749–756.

Lighthall NR, Mather M, Gorlick MA (2009) Acute stress increases sex differences in risk seeking in the Balloon Analogue Risk Task. PLoS One 4:e6002.

Lighthall NR, Sakaki M, Vasunilashorn S, Nga L, Somayajula S, Chen EY, Samii N, Mather M (2012) Gender differences in reward-related decision processing under stress. Soc Cogn Affect Neurosci 7:476–484.

Lin C-H, Chiu Y-C, Lee P-L, Hsieh J-C (2007) Is deck B a disadvantageous deck in the Iowa Gambling Task? Behav brain Funct 3:16.

Lindquist K a, Barrett LF (2008) Constructing emotion: the experience of fear as a conceptual act. Psychol Sci 19:898–903.

Linetzky M, Pergamin-Hight L, Pine DS, Bar-Haim Y (2015) Quantitative evaluation of the clinical efficacy of attention bias modification treatment for anxiety disorders. Depress Anxiety 32:383–391.

Loewenstein GF, Weber EU, Hsee CK, Welch N (2001) Risk as feelings. Psychol Bull 127:267–286.

Lorian CN, Grisham JR (2010) The safety bias: risk-avoidance and social anxiety pathology. Behav Chang 27:29–41.

Love J, Selker R, Marsman M, Jamil T, Dropmann D, Verhagen AJ, Ly A, Gronau QF, Smira M, Epskamp S, Matzke D, Wild A, Knight P, Rouder JN, Morey RD, Wagenmakers E-J (2015) JASP (Version 0.7.1) [Computer Software].

Ly V, Huys QJM, Stins JF, Roelofs K, Cools R (2014) Individual differences in bodily freezing predict emotional biases in decision making. Front Behav Neurosci

8:237.

MacLeod C, Mathews A (1988) Anxiety and the allocation of attention to threat. Q J Exp Psychol Sect A Hum Exp Psychol 40:653–670.

MacLeod C, Mathews A (2012) Cognitive Bias Modification Approaches to Anxiety. Annu Rev Clin Psychol 8:189–217.

MacLeod C, Rutherford E, Campbell L, Ebsworthy G, Holker L (2002) Selective attention and emotional vulnerability: assessing the causal basis of their association through the experimental manipulation of attentional bias. J Abnorm Psychol 111:107–123.

MacLeod CM, Mathews A, Tata P (1986) Attentional bias in emotional disorders. J Abnorm Psychol 95:15–20.

Maia T V., McClelland JL (2004) A reexamination of the evidence for the somatic marker hypothesis: What participants really know in the Iowa gambling task. Proc Natl Acad Sci U S A 101:16075–16080.

Maia T V., McClelland JL (2005) The somatic marker hypothesis: still many questions but no answers. Trends Cogn Sci 9:162–164.

Maner JK, Richey JA, Cromer K, Mallott M, Lejuez CW, Joiner TE, Schmidt NB (2007) Dispositional anxiety and risk-avoidant decision-making. Pers Individ Dif 42:665–675.

Maner JK, Schmidt NB (2006) The role of risk avoidance in anxiety. Behav Ther 37:181–189.

Martin Braunstein L, Herrera SJ, Delgado MR (2014) Reappraisal and expected value modulate risk taking. Cogn Emot 28:172–181.

Mather M, Gorlick MA, Lighthall NR (2009) To brake or accelerate when the light turns yellow? Stress reduces older adults' risk taking in a driving game. Psychol Sci 20:174–176.

Mathews A, Mackintosh B (1998) A cognitive model of selective processing in anxiety. Cogn Ther Res 22:539–560.

Mathews A, MacLeod C (1986) Discrimination of threat cues without awareness in anxiety states. J Abnorm Psychol 95:131–138.

McEwen BS (2007) Physiology and neurobiology of stress and adaptation: central role of the brain. Physiol Rev 87:873–904.

McGraw AP, Larsen JT, Kahneman D, Schkade D (2010) Comparing gains and losses. Psychol Sci 8:423–429.

Mellers BA, Schwartz A, Ho K, Ritov I (1997) Decision affect theory: emotional reactions to the outcomes of risky options. Psychol Sci 8:423–429.

Menard S (2004) Six approaches to calculating standardized logistic regression coefficients. Am Stat 58:218–223.

Miu AC, Heilman RM, Houser D (2008) Anxiety impairs decision-making: psychophysiological evidence from an Iowa Gambling Task. Biol Psychol

77:353–358.

Mobbs D, Marchant JL, Hassabis D, Seymour B, Tan G, Gray M, Petrovic P, Dolan RJ, Frith CD (2009) From threat to fear: the neural organization of defensive fear systems in humans. J Neurosci 29:12236–12243.

Mobbs D, Petrovic P, Marchant JL, Hassabis D, Weiskopf N, Seymour B, Dolan RJ, Frith CD (2007) When fear is near: threat imminence elicits prefrontal-periaqueductal gray shifts in humans. Science (80-) 317:1079–1083.

Mobbs D, Weiskopf N, Lau HC, Featherstone E, Dolan RJ, Frith CD (2006) The Kuleshov Effect: the influence of contextual framing on emotional attributions. Soc Cogn Affect Neurosci 1:95–106.

Mogg K, Bradley BP (2005) Attentional bias in generalized anxiety disorder versus depressive disorder. Cognit Ther Res 29:29–45.

Monk CS, Telzer EH, Mogg K, Bradley BP, Mai X, Louro HMC, Chen G, McClure-Tone EB, Ernst M, Pine DS (2006) Amygdala and ventrolateral prefrontal cortex activation to masked angry faces in children and adolescents with generalized anxiety disorder. Am J Psychiatry 163:1091–1097.

Morewedge CK, Buechel EC (2013) Motivated underpinning of the impact bias in affective forecasts. Emotion 13:1023–1029.

Morey RD, Rouder JN (2015) BayesFactor (Version 0.9.11-3) [Computer Software].

Morris JS, Ohman A, Dolan RJ (1999) A subcortical pathway to the right amygdala mediating “unseen” fear. Proc Natl Acad Sci U S A 96:1680–1685.

Morrison SE, Salzman CD (2010) Re-valuing the amygdala. Curr Opin Neurobiol 20:221–230.

Mueller EM, Nguyen J, Ray WJ, Borkovec TD (2010) Future-oriented decision-making in Generalized Anxiety Disorder is evident across different versions of the Iowa Gambling Task. J Behav Ther Exp Psychiatry 41:165–171.

Murphy ST, Zajonc RB (1993) Affect, cognition, and awareness: affective priming with optimal and suboptimal stimulus exposures. J Pers Soc Psychol 64:723–739.

Myung IJ (2003) Tutorial on maximum likelihood estimation. J Math Psychol 47:90–100.

Niedenthal PM (1990) Implicit perception of affective information. J Exp Soc Psychol 26:505–527.

Noguchi T, Stewart N (2014) In the attraction, compromise, and similarity effects, alternatives are repeatedly compared in pairs on single dimensions. Cognition 132:44–56.

O’Neill M, Schultz W (2010) Coding of reward risk by orbitofrontal neurons is mostly distinct from coding of reward value. Neuron 68:789–800.

Ochsner KN, Bunge SA, Gross JJ, Gabrieli JDE (2002) Rethinking feelings: an fMRI study of the cognitive regulation of emotion. J Cogn Neurosci 14:1215–1229.

Orne MT (2009) Demand characteristics and the concept of quasi-controls. In: Artifact in Behavioral Research (Rosnow RRRL, ed), pp 110–137. New York: Oxford University Press.

Ousdal OT, Reckless GE, Server A, Andreassen OA, Jensen J (2012) Effect of relevance on amygdala activation and association with the ventral striatum. Neuroimage 62:95–101.

Pabst S, Brand M, Wolf OT (2013) Stress effects on framed decisions: there are differences for gains and losses. Front Behav Neurosci 7:142.

Panno A, Lauriola M, Figner B (2013) Emotion regulation and risk taking: predicting risky choice in deliberative decision making. Cogn Emot 27:326–334.

Paulus MP, Yu AJ (2012) Emotion and decision-making: affect-driven belief systems in anxiety and depression. Trends Cogn Sci 16:476–483.

Paz R, Pare D (2013) Physiological basis for emotional modulation of memory circuits by the amygdala. Curr Opin Neurobiol 23:381–386.

Pessoa L, Adolphs R (2010) Emotion processing and the amygdala: from a “low road” to “many roads” of evaluating biological significance. Nat Rev Neurosci 11:773–782.

Phelps EA (2006) Emotion and cognition: insights from studies of the human amygdala. Annu Rev Psychol 57:27–53.

Phelps EA, Lempert KM, Sokol-Hessner P (2014) Emotion and decision making: multiple modulatory neural circuits. Annu Rev Neurosci 37:263–289.

Phelps EA, O’Connor KJ, Gatenby JC, Gore JC, Grillon C, Davis M (2001) Activation of the left amygdala to a cognitive representation of fear. Nat Neurosci 4:437–441.

Plassmann H, O’Doherty J, Rangel A (2007) Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. J Neurosci 27:9984–9988.

Porcelli AJ, Delgado MR (2009) Acute stress modulates risk taking in financial decision making. Psychol Sci 20:278–283.

Preuschoff K, Bossaerts P, Quartz SR (2006) Neural differentiation of expected reward and risk in human subcortical structures. Neuron 51:381–390.

Price JL (2003) Comparative aspects of amygdala connectivity. Ann N Y Acad Sci 985:50–58.

Putman P, Antypa N, Crysovergi P, van der Does WAJ (2010) Exogenous cortisol acutely influences motivated decision making in healthy young men. Psychopharmacology (Berl) 208:257–263.

Raghunathan R, Pham MT (1999) All negative moods are not equal: motivational influences of anxiety and sadness on decision making. Organ Behav Hum Decis Process 79:56–77.

Rigoli F, Rutledge RB, Chew B, Ousdal OT, Dayan P, Dolan RJ (2016) Dopamine increases a value-independent gambling propensity. Neuropsychopharmacology:in press.

Robinson OJ, Bond RL, Roiser JP (2015a) The impact of stress on financial decision-making varies as a function of depression and anxiety symptoms. PeerJ 3:e770.

Robinson OJ, Bond RL, Roiser JP (2015b) The impact of threat of shock on the framing effect and temporal discounting: executive functions unperturbed by acute stress? Front Psychol 6:1315.

Robinson OJ, Charney DR, Overstreet C, Vytal K, Grillon C (2012) The adaptive threat bias in anxiety: amygdala-dorsomedial prefrontal cortex coupling and aversive amplification. Neuroimage 60:523–529.

Robinson OJ, Krimsky M, Lieberman L, Allen P, Vytal K, Grillon C (2014) The dorsal medial prefrontal (anterior cingulate) cortex-amygdala aversive amplification circuit in unmedicated generalised and social anxiety disorders: an observational study. Lancet Psychiatry 1:294–302.

Robinson OJ, Vytal K, Cornwell BR, Grillon C (2013) The impact of anxiety upon cognition: perspectives from human threat of shock studies. Front Hum Neurosci 7:203.

Roe RM, Busemeyer JR, Townsend JT (2001) Multialternative Decision Field Theory: a dymanic connectionist model of decision making. Psychol Rev 108:370–392.

Roiser JP, de Martino B, Tan GCY, Kumaran D, Seymour B, Wood NW, Dolan RJ (2009) A genetically mediated bias in decision making driven by failure of amygdala control. J Neurosci 29:5985–5991.

Roozendaal B, McEwen BS, Chattarji S (2009) Stress, memory and the amygdala. Nat Rev Neurosci 10:423–433.

Roy AK, Shehzad Z, Margulies DS, Kelly a MC, Uddin LQ, Gotimer K, Biswal BB, Castellanos FX, Milham MP (2009) Functional connectivity of the human amygdala using resting state fMRI. Neuroimage 45:614–626.

Roy AK, Vasa RA, Bruck M, Mogg K, Bradley BP, Sweeney M, Bergman RL, McClure-Tone EB, Pine DS (2008) Attention bias toward threat in pediatric anxiety disorders. J Am Acad Child Adolesc Psychiatry 47:1189–1196.

Rutledge RB, Skandali N, Dayan P, Dolan RJ (2014) A computational and neural model of momentary subjective well-being. Proc Natl Acad Sci U S A 111:12252–12257.

Rutledge RB, Skandali N, Dayan P, Dolan RJ (2015) Dopaminergic modulation of decision making and subjective well-being. J Neurosci 35:9811–9822.

Sabatinelli D, Fortune EE, Li Q, Siddiqui A, Krafft C, Oliver WT, Beck S, Jeffries J (2011) Emotional perception: meta-analyses of face and natural scene processing. Neuroimage 54:2524–2533.

Samuelson W, Zeckhauser R (1988) Status quo bias in decision making. J Risk Uncertain 1:7–59.

Sandi C, Richter-Levin G (2009) From high anxiety trait to depression: a neurocognitive hypothesis. Trends Neurosci 32:312–320.

Sanfey AG, Hastie R, Colvin MK, Grafman J (2003) Phineas gauged: decision-making and the human prefrontal cortex. Neuropsychologia 41:1218–1229.

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113.

Schmidt NB, Richey JA, Buckner JD, Timpano KR (2009) Attention Training for Generalized Social Anxiety Disorder. J Abnorm Psychol 118:5–14.

Schmitz A, Grillon C (2012) Assessing fear and anxiety in humans using the threat of predictable and unpredictable aversive events (the NPU-threat test). Nat Protoc 7:527–532.

Schulreich S, Gerhardt H, Heekeren HR (2016) Incidental fear cues increase monetary loss aversion. Emotion 16:402–412.

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

Schwartz G (1978) Estimating the dimension of a model. Ann Stat 5:461–464.

Seara-Cardoso A, Sebastian CL, Viding E, Roiser JP (2016) Affective resonance in response to others' emotional faces varies with affective ratings and psychopathic traits in amygdala and anterior insula. Soc Neurosci 11:140–152.

Sehlmeyer C, Dannlowski U, Schöning S, Kugel H, Pyka M, Pfleiderer B, Zwitserlood P, Schiffbauer H, Heindel W, Arolt V, Konrad C (2011) Neural correlates of trait anxiety in fear extinction. Psychol Med 41:789–798.

Seymour B, Dolan R (2008) Emotion, Decision Making, and the Amygdala. Neuron 58:662–671.

Sheehan D V, Lecrubier Y, Sheehan KH, Amorim P, Janavs J, Weiller E, Hergueta T, Baker R, Dunbar GC (1998) The Mini-International Neuropsychiatric Interview (M.I.N.I.): the development and validation of a structured diagnostic psychiatric interview for DSM-IV and ICD-10. J Clin Psychiatry 59 Suppl 2:22–33;quiz 34–57.

Sifneos PE (1973) The prevalence of "alexithymic" characteristics in psychosomatic patients. Psychother Psychosom 22:255–262.

Simonson I (1989) Choice based on reasons: the case of attraction and compromise effects. J Consum Res 16:158.

Sip KE, Smith D V, Porcelli AJ, Kar K, Delgado MR (2015) Social closeness and feedback modulate susceptibility to the framing effect. Soc Neurosci 10:35–45.

Sokol-Hessner P, Camerer CF, Phelps EA (2013) Emotion regulation reduces loss aversion and decreases amygdala responses to losses. Soc Cogn Affect Neurosci 8:341–350.

Sokol-Hessner P, Hartley CA, Hamilton JR, Phelps EA (2015a) Interoceptive ability predicts aversion to losses. Cogn Emot 29:695–701.

Sokol-Hessner P, Hsu M, Curley NG, Delgado MR, Camerer CF, Phelps EA (2009) Thinking like a trader selectively reduces individuals' loss aversion. Proc Natl Acad Sci U S A 106:5035–5040.

Sokol-Hessner P, Lackovic SF, Tobe RH, Camerer CF, Leventhal BL, Phelps EA

(2015b) Determinants of propanolol’s selective effect on loss aversion. Psychol Sci 26:1123–1130.

Sokol-Hessner P, Phelps EA (2016) Affect, decision-making, and value: neural and psychological mechanisms. In: Handbook of Value: Perspectives from Economics, Neuroscience, Philosophy, Psychology and Sociology (Brosch T, Sander D, eds). Oxford University Press.

Spielberger CD, Gorsuch RL, Lushene PR, Vagg PR, Jacobs AG (1983) Manual for the State-Trait Anxiety Inventory. Palo Alto, CA: Consulting Psychologists Press.

Sprinkle SD, Lurie D, Insko SL, Atkinson G, Jones GL, Logan AR, Bissada NN (2002) Criterion validity, severity cut scores, and test-retest reliability of the Beck Depression Inventory-II in a university counseling center sample. J Couns Psychol 49:381–385.

St. Onge JR, Floresco SB (2009) Dopaminergic modulation of risk-based decision making. Neuropsychopharmacology 34:681–697.

Stauffer WR, Lak A, Schultz W (2014) Dopamine reward prediction error responses reflect marginal utility. Curr Biol 24:2491–2500.

Stein MB, Simmons AN, Feinstein JS, Paulus MP (2007) Increased amygdala and insula activation during emotion processing in anxiety-prone subjects. Am J Psychiatry 164:318–327.

Stopper CM, Tse MTL, Montes DR, Wiedman CR, Floresco SB (2014) Overriding phasic dopamine signals redirects action selection during risk/reward decision making. Neuron 84:177–189.

Taylor GJ, Bagby RM, Parker JDA (1999) Disorders of affect regulation: Alexithymia in medical and psychiatric illness. New York: Cambridge University Press.

Telzer EH, Mogg K, Bradley BP, Mai X, Ernst M, Pine DS, Monk CS (2008) Relationship between trait anxiety, prefrontal cortex, and attention bias to angry faces in children and adolescents. Biol Psychol 79:216–222.

Thaler R (1980) Toward a positive theory of consumer choice. J Econ Behav Organ 1:39–60.

Tobler PN, Christopoulos GI, O’Doherty JP, Dolan RJ, Schultz W (2009) Risk-dependent reward value signal in human prefrontal cortex. Proc Natl Acad Sci U S A 106:7185–7190.

Tom SM, Fox CR, Trepel C, Poldrack RA (2007) The neural basis of loss aversion in decision-making under risk. Science (80-) 315:515–518.

Tsai H-C, Zhang F, Adamantidis A, Stuber GD, Bonci A, de Lecea L, Deisseroth K (2009) Phasic firing in dopaminergic neurons is sufficient for behavioral conditioning. Science (80-) 324:1080–1084.

Tversky A (1972) Elimination by aspects: a theory of choice. Psychol Rev 79:281–299.

Tversky A, Kahneman D (1981) The framing of decisions and the psychology of choice. Science (80-) 211:453–458.

Tversky A, Kahneman D (1986) Rational choice and the framing of decisions. J Bus 59:S251–S278.

Tversky A, Kahneman D (1991) Loss Aversion in Riskless Choice: A Reference-Dependent Model. Q J Econ 106:1039–1061.

Tversky A, Kahneman D (1992) Advances in Prospect Theory: cumulative representation of uncertainty. J Risk Uncertain 5:297–323.

Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15:273–289.

Usher M, McClelland JL (2001) The time course of perceptual choice: the leaky, competing accumulator model. Psychol Rev 108:550–592.

Von Neumann J, Morgenstern O (1947) Theory of Games and Economic Behavior, 2nd ed. Princeton, NJ: Princeton University Press.

Wang S, Tudusciuc O, Mamelak AN, Ross IB, Adolphs R, Rutishauser U (2014) Neurons in the human amygdala selective for perceived emotion. Proc Natl Acad Sci U S A 111:E3110–E3119.

Weber EU, Blais A-R, N. B (2002) A domain-specific risk-attitude scale: Measuring risk perception and risk behaviors. J Behav Decis Mak 15:263–290.

Wechsler D (2001) Wechsler Test of Adult Reading (WTAR). San Antonio, TX: The Psychological Corporation.

Whalen PJ (1998) Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. Curr Dir Psychol Sci 7:177–188.

Wilson TD, Gilbert DT (2013) The impact bias is alive and well. J Pers Soc Psychol 105:740–748.

Winecoff A, Clithero JA, Carter RM, Bergman SR, Wang L, Huettel SA (2013) Ventromedial prefrontal cortex encodes emotional value. J Neurosci 33:11032–11039.

Winkielman P, Berridge KC, Wilbarger JL (2005) Unconscious affective reactions to masked happy versus angry faces influence consumption behavior and judgments of value. Pers Soc Psychol Bull 31:121–135.

Witten IB, Steinberg EE, Lee SY, Davidson TJ, Zalocusky KA, Brodsky M, Yizhar O, Cho SL, Gong S, Ramakrishnan C, Stuber GD, Tye KM, Janak PH, Deisseroth K (2011) Recombinase-driver rat lines: Tools, techniques, and optogenetic application to dopamine-mediated reinforcement. Neuron 72:721–733.

Xu P, Gu R, Broster LS, Wu R, Van Dam NT, Jiang Y, Fan J, Luo Y (2013) Neural basis of emotional decision making in trait anxiety. J Neurosci 33:18641–18653.

Yechiam E, Hochman G (2013) Losses as modulators of attention: review and analysis of the unique effects of losses over gains. Psychol Bull 139:497–518.

Yechiam E, Telpaz A, Hochman G (2014) The complaint bias in subjective evaluations of incentives. Decision 1:147–160.

Yen HR, Chuang S-C (2008) The effect of incidental affect on preference for the status quo. J Acad Mark Sci 36:522–537.

Zalocusky KA, Ramakrishnan C, Lerner TN, Davidson TJ, Knutson B, Deisseroth K (2016) Nucleus accumbens D2R cells signal prior outcomes and control risky decision-making. Nature 531:642–646.

Zemack-Rugar Y, Bettman JR, Fitzsimons GJ (2007) The effects of nonconsciously priming emotion concepts on behavior. J Pers Soc Psychol 93:927–939.

Zorrilla EP, Koob GF (2013) Amygdalostriatal projections in the neurocircuitry for motivation: a neuroanatomical thread through the career of Ann Kelley. Neurosci Biobehav Rev 37:1932–1945.